Biodiversity of shipwrecks from the Southern Bight of the North Sea

VINCENT ZINTZEN

FÉVRIER 2007

Thèse présentée en vue de l'obtention
du grade de docteur en sciences

Faculté des sciences
École doctorale en biologie

Université catholique de Louvain

To all these people who believe that exploration makes them live in a world
of miracles and endless surprises.

N'étaient les 'si' et les 'mais', nous serions tous parfaits
Proverbe d'ici et d'ailleurs

A dissertation presented in Candidacy for the Degree of Doctor of Philosophy

UNIVERSITE CATHOLIQUE DE LOUVAIN
UNIVERSITY OF LOUVAIN
Faculté des Sciences
Laboratoire de Biologie Marine
Bâtiment Kellner, place Croix du Sud 3, B-1348 Louvain-la-Neuve, Belgique.

INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE
ROYAL BELGIAN INSTITUTE OF NATURAL SCIENCES
Département de Malacologie
Rue Vautier 29, B-1000 Bruxelles, Belgique

Academic year 2006-2007

Promotors
Prof. Dr. Jérôme Mallefet (UCL)
Dr. Claude Massin (IRSNB)

The research presented in this PhD was made feasible thanks to the implication of the following partners:

Funding agencies
The following PhD was funded by an 'Action II' grant from the Belgian Science Policy (contract N° WI/36/C04)
Malacology Department, Royal Belgian Institute of natural Sciences
Fond National de Recherche Scientifique (FNRS), Belgique
Biodiversity Research Center (BDIV), University of Louvain, Belgium

Non funding agencies
Management Unit of the North Sea Mathematical Models, Belgium
Ghent University, Biology Department, Marine Biology Section, Belgium
Flanders marine Institute, Belgium
Station Marine de Wimereux, France

The research presented in this study was partly carried out in the framework of the project 'Belgian shipwrecks: hotspot for marine biodiversity' from the Scientific Support Plan for a Sustainable Development Policy (SPSDII).

Biodiversity of shipwrecks from the Southern Bight of the North Sea

Preface

Il y a toujours un commencement à tout, mais il s'avère souvent bien compliqué, avec le recul, de mettre le doigt sur ce qui a réellement déclenché cet événement. Peut-être simplement parce qu'un doigt ne suffit pas et que c'est bien de toute une paume de main, voire d'un bras, d'un corps ou encore d'une armée de têtes bien faites dont on aurait besoin pour comprendre le phénomène. Il y a bien entendu les commencements qui sont plus faciles à cerner, car on les a vécus de toute notre chaire.

Je me souviens fort bien de ces images de l'équipe de la Calypso qui me fascinèrent tellement. Des extraterrestres aux combinaisons étranges et argentées, capables d'activité sous-marine et qui de plus, étaient à même de discerner l'animal nuisible du bon grain. En l'occurrence, le nuisible répondait au terrible nom de requin et il est clair qu'au vu de la taille de ses dents acérées, il ne pouvait séjourner que du mauvais côté de la barrière. L'équipe de la Calypso leur firent comprendre de façon très claire qu'ils n'étaient pas désirables et j'approuvai à mon tour leur action. Un massacre. Il faut croire que quelque chose a dû se passer depuis lors, car je n'ai plus jamais vu d'émission de sensibilisation au milieu marin qui favorise l'extermination de prédateurs. Peut-être le commencement d'une prise de conscience qu'une force plus illuminée que la nôtre a forgé un monde dont la complexité nous dépasse et nous intrigue. Même le détestable requin y aurait un rôle à jouer, peut-être même aussi cette bactérie que je ne vois pas ou cette fougère que personne ne décrira jamais… N'empêche que ces images de paysages subaquatiques me fascinèrent et furent certainement à l'origine de mon intérêt pour le monde du grand bleu. Car c'est d'abord cela, loin de vouloir cataloguer, étudier, comprendre, c'est l'attirance et la fascination d'un autre monde qui primera au commencement. Et comment se passionner pour quelque chose sans pouvoir le regarder? La plongée fut une fabuleuse porte vers la réalité du vivant, peut-être bien plus que les *syllabi* qui ont croupis sur mon bureau à la même époque. Voici un commencement facile à cerner.

Il deviendra néanmoins complexe et multiple par la suite, le présent manuscrit en étant une preuve en substance. Le commencement d'une autre réalité. Car il faut maintenant s'atteler à comprendre ce monde qui nous entoure et aussi comprendre que le lot du scientifique est de perpétuellement commencer par remettre en doute ses certitudes, hormis celle qui l'a poussé dans cette voie.

Bruxelles, janvier 2007.

TABLE OF CONTENT

Chapter I - Introduction

Clump of *Mytilus edulis* on a fishing net lost on the Kilmore shipwreck.

1. CONTEXT

The title of this thesis includes the term biodiversity. Citing Tilman (2000), one of the most striking feature of Earth is the existence of life, and the most striking feature of life, is its diversity. Biodiversity is the popular contraction of "biological diversity" and was introduced to the public in 1988 through the proceedings of a conference on biological diversity (Wilson, 1988). In the literature, most authors are using both terms interchangeably. The United Nations Environment Programme (UNEP) provides a widely accepted definition of biodiversity (Heywood, 1995):

> "Biodiversity means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems."

Another definition that will be closer to the subject of this thesis and that we will use in this text is given by Hubbell (2001): he defines biodiversity as "the species richness and their relative abundance in space and time". According to this definition, biodiversity includes two ideas: the first one matters with the number of species per unit area and the second with their abundances. Abundances of species is an essential question because the importance of a species is often related to its relative abundance (Magurran, 2004).

The term biodiversity has been extensively used during the last two decades, first because it was a source of wonderment and scientific curiosity and then mostly because a decline of biological diversity has been globally observed both on terrestrial and aquatic ecosystems (Tilman, 2000; Gaston, 2000). One of the most pragmatic question regarding this threat to biodiversity is the extent to which this loss of biodiversity matters. Several scientists asked if productivity, stability or other functionality of ecosystems rely on biodiversity. Although still debated (Loreau *et al.*, 2001), there are evidences supporting that ecosystem functioning is impacted by biodiversity. For example, on grassland communities, it has been shown that, on average, greater diversity leads to greater productivity and improves several variables of the community like resource use (space, light, nitrogen) and decomposition (Tilman *et al.*, 1996; Tilman *et al.*, 1997; Vitousek *et al.*, 1997; Hector *et al.*, 1999; Spehn *et al.*, 2005). So well, it seems that biodiversity matters.

On marine ecosystems, current results (reviewed in Covich *et al.*, 2004) indicate that, on average, a reduction of biodiversity is likely to impair the short-term provision and long-term sustainability of ecosystems processes.

On a recent paper, Worm *et al.* (2006) analyzed local experiments, long-term regional time series, and global fisheries data to test how biodiversity affects marine ecosystem services to human populations across temporal and spatial scales. Overall, the results indicated that the rates of resource collapses increased and recovery potential, stability and water quality decreased exponentially with declining biodiversity. The conclusions were that marine biodiversity loss is increasingly impairing the ocean's capacity to provide food, maintain water quality and recover from perturbations.

Most of the coastal habitats around the globe have been impacted by pollutions, fishing practices, overfishing and habitat loss (UNEP, 2006). Soft sedimented and hard bottom habitats severely suffer from fishing practices like bottom trawling (Bergman & Hup, 1992; Engel & Kvitek, 1998; Schratzberger *et al.*, 2002; Freese *et al.*, 2005) and dreding (Boyd *et al.*, 2003; Boyd & Rees, 2003). In the North Sea, each square meter is trawled at least once a year (ICES data) and there are clues that these practices cause shift towards communities dominated by opportunistic species and species adapted to frequent perturbation (Engel & Kvitek, 1998; Freese *et al.*, 1999).

At the same time, there has been an increase in hard bottoms or "reef" habitats in the marine environment during the last two centuries (Steimle & Zetlin, 2000). Shipwrecks, lost cargos, disposed solid materials, offshore platforms, shore-line jetties, groins, artificial reefs and all other similar objects providing hard substrates to the structure of the seabed were frequently added to the marine habitat. All these objects are the results of human actions and probably have an effect on marine species distribution and fisheries. Here, at least when the addition of hard substrates was not realized at the cost of other natural habitats (like in coastal management), the addition of hard substrate tends to increase the structural complexity of the seabed, hence potentially increasing locally the biodiversity.

Shipwrecks in the Southern Bight of the North Sea are a common feature of the seabed, as it will be shown in the following text. The addition of these unplanned artificial reefs goes in the opposite direction of the general observed trend in biodiversity loss. They will tend to a local and patchy increase of biodiversity by providing new surfaces for the colonization of the epibenthos. The addition of artificial structures is a hot topic in a context of growing manipulation of the marine environment, like for example the future implantation of large windmills projects on Belgian waters. Indeed, the implications for ecosystem functioning of such additions are barely known and even if biodiversity will increase, its intrinsic value still needs to be evaluated. Besides new species, shipwrecks and other artificial structures could also act as stepping stones for the dissemination of harmful species, change the rate of genetic transfer between populations, redistribute fisheries resource or more basically be a source of heavy metals that could accumulate in the food chain.

For all these reasons, we believe that characterizing the biodiversity of shipwrecks from the Southern Bight of the North Sea was an important question to be tackled. The present thesis is an attempt to answer this question.

2. BIRTH AND DEVELOPMENTS OF ARTIFICIAL REEFS AND HABITATS

2.1 The birth of artificial reefs

A number of observations from the Neolithic attest that man already tried at that time to foster a greater harvest of organisms from the sea or freshwater bodies (Seaman & Sprague, 1991). There are clues that different shorelines in the world were the centre of deployment for a variety of structures. Our ancestors probably observed that fish were more abundant in the proximity of floating debris or lost material in water leading to an improved harvest of food. At first, artificial habitats were used to sustain traditional fisheries in which the population of a village might subsist on the harvest from nearby habitats (Seaman & Sprague, 1991). The broad goal is production of food to maintain the diet and sometimes, at least partly, the economy of individuals, families and communities in local coastal areas (Seaman & Jensen, 2000). Such practice still exists in about 40 countries, including India where indigenous technology to deploy natural materials such as weighted trees has existed for 18 centuries (Sanjeeva Raj, 1996). Artisanal efforts are particularly prominent in the Philippines, Thailand, Indonesia, Malaysia, Maldive Islands, India, and islands of the South Pacific Ocean. In the Philippines for example, approximately 16,000 pyramid bamboo modules in clusters of 50 have been set along 40 km of coast (Polovina, 1991).

2.2 Towards the present definition of artificial reefs

In the 1930s, the Japanese government invested in a large scale artificial reefs project to improve commercial fishing (Stone *et al.*, 1991). This is the first large project of artificial reefs, but it rapidly comes up that sound science is needed to solve the questions raised, especially for fisheries applications. The first Conference on Artificial Reefs and Habitats (CARAH) was set up to initiate a "...forum for the exchange of information, experiences and thoughts..." (Clark *et al.*, 1974). Since this first conference, seven other CARAH have been organized regularly, the last one in 2005 (Biloxi, Mississippi, USA). The first three CARAH mainly asked and answered questions about the improvement of fisheries around the world (Grove & Wilson, 1994). During the fourth conference in 1987, additional types of materials for fisheries improvement were studied (grass beds, marsh, gravel beds,...). It is only during the call for the fifth CARAH (1991) that the question of the precise definition of what is an artificial reef was raised and whether its purpose is only for fisheries management (Grove & Wilson, 1994). Undoubtedly, scientists had broaden their research questions since sessions devoted to function and ecology, mitigation and restoration, monitoring and assessment, offshore structure and artificial reefs in urban environment were organized. This last theme has to be highlighted because it emphasizes the fact that artificial reefs are not only planned by scientists or managers but can also be the result of the multiple action of man at sea (e.g. maritime traffic, offshore oil and gas extraction, harbour constructions,...) (Steimle & Zetlin, 2000).

This leads to a broader definition of what an artificial can be. However, the usual definition of an artificial reef is: "a submerged structure placed on the substratum (seabed) deliberately, to mimic some characteristics of natural reef and to influence physical, biological and socio-economic processes related to living marine resources" (Jensen, 1998; Seaman, 2000). Bohnsack *et al.* (1991) already made a further distinction between 'artificial reefs' which are benthic structures created accidentally or deliberately by human activities and the more general term 'artificial habitat' which refers to structures deployed either on or above the sea floor, including floating or midwater fish aggregating devices (FADs).

2.3 A global definition of artificial reefs

Artificial reefs have long been defined by the use or benefit that people wanted to make of them. Since the first purpose of artificial reefs was to improve local fisheries, they were defined as any structure dumped at sea to attract and enhance fish harvesting. However, artificial reefs occur with or without the directed action of man. A jetty, a groin, or lost cargos are as susceptible as a designed reef to attract fish. The main difference lies in the fact that part of the process is controlled for the conception of some reefs while it is not the case for others. As a consequence, artificial reefs should not be defined only by the intended use we want to make of it, but also by the consequences of its presence at sea. Then, I will deem that every structure resulting from the action of man and pushed at sea can be considered as an artificial reef. This includes of course planned reefs but also all coastal management which took place all around the world, the results of the presence of man working and exploiting the sea (buoys, lighthouses, oil platforms, dumping sites, wind farms base protections, ...) and all the material unintentionally lost at sea like shipwrecks and lost cargos. This broader definition than what is usually seen on scientific publications implies that artificial reefs have certainly more effect on the marine environment than the admitted concept of planned structure. In the next sections, when referring to artificial reefs, we will make a distinction between planned and unplanned structures.

3. FUNCTIONS OF ARTIFICIAL REEFS

Most of the artificial reefs have been deployed all around the world with different purposes in mind. In the next paragraphs, we will discern between the functions of planned artificial reefs whose life at sea is the result of a thoughtful decision and those which can be categorized as unplanned.

3.1 Planned artificial reefs

Recently, the use of artificial reefs extended from a purely fisheries management based to a more diversified range of uses. Interest in artificial reefs has gone beyond benthic artificial reefs to include structures deployed at varying depths (Seaman *et al.*, 1989a). The following reasons why artificial reefs are deployed at sea are found in the literature. For the moment, not all of these goals seem to have been reached by the deployment of artificial reefs (Bohnsack & Sutherland, 1985; Jensen *et al.*, 2000a; Bohnsack, 2005).

3.1.1 Fisheries management

Fisheries production is the oldest and more ubiquitous motivation for artificial reef construction (Miller, 2002). Artificial reefs have often been developed because they could enhance fisheries outcome. However, there is still some debate on the possible reasons of this improved outcome. Artificial reefs could either just attract fish or could increase biomass production (see page 49 for discussion).

Multiple elements can lead to the enhancement of local harvesting of fishery resources. The majority of the papers dealing with artificial reefs describe the colonization, abundance, biomass and behaviour of fish. Depending on local resources, other taxa than fish are sometimes targeted. Crabs (Jara & Cespedes, 1994), lobsters (Lozano-Alvarez *et al.*, 1994; Jensen *et al.*, 2000c), sea cucumbers (Chen, 2003), bivalves (mussels and oysters) (Sauriau *et al.*, 1997) or sea urchins are also commercially important species. In most cases artificial reefs are 3-dimensional and made of varying materials which provide a direct habitat for species.

Artificial reefs can also be designed to increase nutrient availability in coastal waters by creating an upwelling of rich waters (Liu *et al.*, 1999; Berntsen *et al.*, 2002; Kirke, 2003; Maruyama *et al.*, 2004) and as collectors to estimate recruitment of commercially interesting species (Blau & Byersdorfer, 1994).

The largest programme of fisheries development was ongoing in Japan, at that time the technologically most advanced country for reef building (Seaman *et al.*, 1989a). The aim was to establish domestic fisheries as the primary source of seafood for the country, ending its dependency on foreign countries (Grove *et al.*, 1994). On a long-term basis, the programme had to reorient towards the achievement of ecological enhancement of the environment. Recent scientific publications are missing to estimate the actual results of this large programme. Fisheries management implies also the sustainability of artisanal fishing practice which is in strong competition with industrial trawling. Artificial reefs have been implemented to avoid illegal trawling and allow traditional fishermen to have an acceptable access to resources (Bombace *et al.*, 2000; Barnabé *et al.*, 2000; Revenga *et al.*, 2000; Relini, 2000b; Watanuki & Gonzales, 2006).

3.1.2 Restoration

Restoring, i.e. returning to a pre-disturbance condition allows to recover at least part of the ecological structure and function of a habitat (Pratt, 1994). Many habitats are degraded worldwide and the selection of an appropriate restoration approach is never straightforward nor easy to implement (Abelson, 2006). For example in the Maldives, a restoration programme on reef flats degraded by coral mining, used artificial reefs to avoid erosion and inundation (Clark & Edwards, 1999). However, the restoration of degraded reefs is still at an experimental stage because of our incomplete understanding of their ecological dynamics (Abelson, 2006).

Artificial reefs may also help restoring the water quality in an impacted area through the development of large suspension feeding colonies (Relini & Relini, 1989; Antsulevich, 1994; Relini, 2000b). Some of the taxa (e.g. sponges) growing on these structures may even allow for the removal of heavy metals pollutants (Miller, 2002). The filtering effectiveness of suspension feeders is well documented on some natural habitats (e.g. above mussel beds (Dolmer, 2000) or above coral reefs (Ayukai, 1995)). However, the release of large quantities of dissolved organic compounds (N and P) could hamper the advantage of filter feeding by promoting algal blooms (Miller, 2002).

3.1.3 Mitigation

Artificial reefs are used as a mitigation tool, i.e. a tool to reduce the adverse impacts of a development project and compensate for unavoidable impacts in a variety of situations (Ambrose, 1994). The appropriateness of artificial reefs as a mitigation tool is now under greater scrutiny since replacing a habitat (e.g. soft sediment) by another to compensate for a loss (which could also be soft sediment) is not always appropriate (Ambrose, 1994). Replacement with the same type of habitat (in-kind mitigation as opposed to out-kind mitigation) is usually preferred (Cheney *et al.*, 1994). The largest mitigation design on its way aims at restoring 61 ha of the giant kelp (*Macrocystis pyrifera* C. Agardh) in the Southern California for the loss due to implantation of a nuclear generating station (Deysher *et al.*, 2002; Reed *et al.*, 2006). In the Mediterranean, the transplantation of the algae genus *Cystoseira* on artificial reefs is investigated to improve habitat enhancement procedures (Falace *et al.*, 2006). The same kind of research focuses on a seagrass, *Phyllospadix torreyi* S. Watson on the West coast of North America (Holbrook *et al.*, 2002) and on *Zostera marina* in California, USA (Pondella *et al.*, 2006).

Fish farming may have a strong impact on their surrounding environment and the installation of artificial reefs close to them has been proposed as a mitigation tool against nutrient loading and organic matter accumulation (Antsulevich, 1994; Antsulevich *et al.*, 2000; Angel & Spanier, 2002; Tsemel *et al.*, 2006). The criteria for estimating what amount of out-of-kind reef (different type of habitat than the pristine situation) has to be used to replace a certain area of lost habitat are always very subjective. Some studies used the secondary production as an estimate of ecological benefit (Burton *et al.*, 2002), arguing that secondary production is a valuable tool to compare habitats inhabited by a variety of species with different life histories and growth rates.

The efficiency of artificial reef in replacing non-reef habitats to address local and global needs is still poorly documented (Foster *et al.*, 1994). The potential of artificial reefs to mitigate impacts of man at sea needs further work since the area concerned by this situation is increasing on a daily basis (Relini *et al.*, 1994). In any case, research on mitigation has to consider the ecological implications of the new habitats in the light of the natural habitat to be replaced (Thanner *et al.*, 2006).

3.1.4 Protection and conservation

Artificial reefs have the potential to protect some habitats by their unique presence. Illegal trawling is a recurrent problem for the protection of habitats of special interest, for example essential nursery and feeding habitats (Kaiser *et al.*, 2000; Relini, 2000b; Watling & Norse, 1998). In the Mediterranean, *Posidonia oceanica* (L.) meadows are significantly protected from trawling by installing specially designed modules (Guillen *et al.*, 1994) or at least deployed to achieve this goal (Relini & Relini, 1989; Moreno *et al.*, 1994;

Bayle-Sempere *et al.*, 1994; Bombace *et al.*, 2000; Revenga *et al.*, 2000; Ramos-Espla *et al.*, 2000; Moreno, 2000; Relini, 2000b; Sanchez-Jerez *et al.*, 2002; Lok *et al.*, 2002). In a context of highly dispersed fishery, population heavily dependent on coastal resources and great difficulties to enforce fishery regulations, artificial reefs may prove useful to manage and protect fisheries resources (Campos & Gamboa, 1989). Physical protection of the seabed and coast by artificial reefs is also an option to reduce wave energy reaching the shore (Hamer *et al.*, 2000).

Indirectly, artificial reefs can be used as a conservation tool. They can potentially divert pressure from human activities that receive natural sites. Vessels were purposely sunk to attract divers with the resulting effect of decreasing human pressure on natural reefs (Leeworthy *et al.*, 2006; Perkol-Finkel & Benayahu, 2004). In some cases, one of the multiple goals of artificial reefs is to allow the settlement and enhance the status of some endangered species. Colonies of the red coral (*Corallium rubrum* (L.)) has been transplanted and monitored in the Principality of Monaco area (Allemand *et al.*, 2000).

3.1.5 Commercial activities (other than fisheries)

The main purpose of some artificial reefs is the practice of commercial activities other than professional fisheries. Most of these activities concern anglers and divers. In Australia for example, most of the reef structures are devoted to these activities (Branden *et al.*, 1994). Anglers or sport fishermen are keen on targeting artificial reefs because it concentrates potential catches in their vicinity (Milon, 1989). In Louisiana (Gulf of Mexico, USA), it has been estimated that 70% of all recreational angling trips in the Exclusive Economic Zone took place around oil and gas platforms (Stanley & Wilson, 1989). Another use of artificial reefs is by divers who are preferably attracted by large structures like shipwrecks and decommissioned oil platforms rather than sites made of by-products or purpose built (Ditton *et al.*, 2002; Ramos *et al.*, 2006b). However, it should be noted that, most of the time, these structures were not added to the seabed with this purpose in mind (see page 13). Scuba and angling are often in conflict because lines represent a danger for the divers. As a consequence, the presence of divers allows the artificial reef to receive less pressure from fishing activities (Brock, 1994).

3.1.6 Scientific research

Many artificial reefs have been deployed for hypothesis testing by scientists (Bortone, 2006) or at least to create an environment where research could be conducted (DeBernardi, 1989). For example in the Gulf of Mexico, an artificial reef was set up to study the 'resource mosaic hypothesis' (Frazer & Lindberg, 1994). It postulates that species which need a refuge but feed on the surrounding soft-sediment will see their abundance and/or biomass affected by the spatial configuration of the refuge. This can be tested by changing the distance between reef patches without altering other variables. In the Adriatic coast of Italy, artificial reefs were built to compare the fishing yields of the reef with the surrounding soft sedimented seabed (Fabi & Fiorentini, 1994). Other structures were used to study the colonization and succession of hard substrate benthic communities under varying environmental conditions (D'Anna *et al.*, 2000). Different artificial reef designs were also assessed for the mitigation power to habitat losses (Reed *et al.*, 2006).

3.2 Unplanned artificial reefs

Besides all the material constituting designed artificial reefs, a large amount of structures were added to the sea without any purpose in mind because there was no clear *a priori* defined goal or simply because it was at first not considered as an artificial reef. As a consequence, all these reefs have no proper expected ecological functions and lost one of the stronger key in designing meaningful artificial reefs: their structure management and location of establishment. However, some of these structures are currently under study to investigate their impact at sea. Oil and gas platforms receive currently most of the attention because many fields will be soon depleted and their decommission has to be decided (Scarborough Bull & Kendall, 1994; Picken *et al.*, 2000; Schroeder & Love, 2004). Their function is mostly seen in the context of the attraction-production of fish (Stanley & Wilson, 1989; Seaman *et al.*, 1989b; Render & Wilson, 1994; Stanley & Wilson, 1996; Love *et al.*, 1999; Stanley & Wilson, 2000; Caselle *et al.*, 2002; Helvey, 2002; Frumkes, 2002; Soldal *et al.*, 2002; Jorgensen *et al.*, 2002; Lokkeborg *et al.*, 2002; Fabi *et al.*, 2002; Fabi *et al.*, 2004; Love *et al.*, 2005; Love & York, 2005), crab species (Page *et al.*, 1999) or recreational activities (Stanley & Wilson, 1989; Ditton *et al.*, 2002; Frumkes, 2002; Cripps & Aabel, 2002; Ramos *et al.*, 2006b).

The construction of wind farms, mainly in Northern Europe is also a source of hard substrate in the marine environment. Around the wind turbine foundations which are mono-piles, a gravel/pebble mattress or scour protection is added to minimize erosion. The colonization by epifauna and fish species is followed in the context of monitoring programmes (Leonhard *et al.*, 2005).

Shipwrecks could act as a protection tool for soft sediment communities because they protect them from some fisheries impacts (Hall *et al.*, 1993). They are also known to attract fish (Lindquist & Pietrafesa, 1989; Stephan & Lindquist, 1989; Leewis *et al.*, 2000; Leewis & Hallie, 2000) and could enhance their production.

If the physical function of urban construction is evident, their ecological implications and functions have been barely addressed (Connell & Glasby, 1999; Lin & Shao, 2002; Pinn *et al.*, 2005). It is emphasized that the added hard substrate could provide an entirely new habitat compared to the natural grounds that they are replacing at a fast speed (Carr & Hixon, 1997; Glasby, 2001; Smith & Rule, 2002; Badalamenti *et al.*, 2002; Knott *et al.*, 2004).

4. DISTRIBUTION AND EXTENSION OF ARTIFICIAL REEFS

Large planned artificial reef projects have limited their extension to industrialized countries. The following paragraphs introduce the reader to the distribution and extension of artificial reefs in these areas. However, even for artificial reefs programmes under the supervision of scientists, the details of the reef structure and extension are not always available. Programmes are also initiated in the so-called developing countries (Philippines, Senegal) but are always small scale projects (Watanuki & Gonzales, 2006). A notable exception are the Philippines (Polovina, 1991). The last paragraph will be devoted to the case of unplanned reefs.

4.1 General characteristics of planned artificial reefs locations

Since the first goal of artificial reefs is to improve fisheries, most of them have been placed in areas of low or depleted value to fisheries in order to enhance this situation. Major area of developments includes the basins of the Caribbean and Mediterranean Seas, South-East Asia, Japan, Australia, North America and some Pacific Ocean islands. Lesser levels of activity are reported for Central America, Northern and Central Europe, and limited areas of Africa and South America (Seaman & Sprague, 1991). However, the information described here under is based on available literature and could not be representative of the actual situation.

4.1.1 Asia

Taiwan has an artificial reef program running since 1973 (Lin & Su, 1994).

In South Korea, artificial reefs have been installed since the 1970s in many coastal areas for the enhancement of coastal fisheries productivity. In 1999, the total installation volume was 7 millions m^3 (Kim, 2001) and large budgets (2 billions US$) were to be invested until 2005 for the deployment of new structures.

Japan designed massive structures in pursuit of national goals for commercial seafood production in national waters (Seaman *et al.*, 1989a). Artificial reefs construction started in 1976 and in 1987 a total of 17 million m^3 were at sea (Grove *et al.*, 1989). The plans for the next 6 years following 1987 were to increase the volume of artificial reefs by 14 million m^3. Information on the evolution of this programme was not yet mentioned in the literature.

In 1995, Hong-Kong initiated a large artificial reef programme deployed for nursery and spawning ground protection, habitat enhancement and habitat protection (Wilson *et al.*, 2002). An amount of 28,000 m^3 of vessels, tyres, quarry rocks and concrete units were placed in marine parks.

4.1.2 United States of America

Since the 1970's , more than 500 reefs have been deployed in the US coastal waters (Grossman *et al.*, 1997; Lukens & Christian, 2000). Almost half of them are located in Florida state. Reefs are popular in this region simply because anglers visiting them experience high catch rates (Grossman *et al.*, 1997). In 1998, 7.5 millions Americans participated in 81 millions saltwater recreational fishing trips resulting in the harvest of 312 millions fish (106,000 T) (Lukens & Christian, 2000). In California, mitigation programme for the eelgrass *Zostera marina* is ongoing (Pondella *et al.*, 2006). In Delaware Bay (North Carolina) and Puget Sound (Washington) artificial reefs were constructed for the mitigation of habitat loss in estuaries and coastal areas.

4.1.3 Australia

Artificial reefs in Australia exist since 1965 (Branden *et al.*, 1994). But it is only since the mid 1980's that the amount of artificial reefs became consequent. They have been deployed with the primary objectives of recreational activities development such as angling and diving. They are made of tyres (28 tyres for one module) and sunken vessels. Until 1994, 7000 modules were deployed on 10 sites. The number of sunken vessels is unavailable.

4.1.4 The European area

Artificial reef programmes in the European area have been initiated in 12 countries, including countries surrounding the Mediterranean (Table 1). In addition to these countries, Ireland and Denmark have indicated their interests in artificial reefs (Jensen, 2002a). Norway is also studying the concept of rig-to-reefs (Cripps & Aabel, 2002) and has implemented some experimental structures. Projects range from very local and limited in space to large coastal management, like for example in Portugal, Italy or also in the United Kingdom (Loch Linne). Estimation of the total amount of artificial reefs in European waters is not straightforward because part of the data on the amount and structure of material dumped at sea is unavailable. Very often, only the entire area where the material is spread is given. Gross estimation can however be calculated with the information included here under (Table 1). Using the available ratio on real surface against spread area covered by artificial reefs and usual surfaces of modules to complete gaps, we can estimate that the total projected area covered by artificial reefs for European area lies between 10 and 20 ha. It represents an amount of 100,000 to 200,000 T of materials.

4.2 General characteristics of unplanned artificial reefs locations

Quantifying the amount of structures other than planned found at sea is a difficult task. Coastal management took place almost everywhere and the extension of hard substrate added to the sea could only be calculated by gathering management plans of all the concerned localities. Lost cargos, disposed solid materials, shoreline jetties, groins, breakwaters walls, submerged pipelines and cables, all substantially contribute to the amount of hard substrate at sea (Steimle & Zetlin, 2000). It has also been demonstrated that accumulation of large debris along continental shelves occurs in some places due to the influence of geomorphological factors, local human activities and river input (Galgani *et al.*, 2000).

Information on some structures like shipwrecks and oil/gas platforms is more readily available. In the Middle Atlantic Bight, the bulk of artificial reef has been attributed to shipwrecks, planned artificial reefs being only marginally represented (Steimle & Zetlin, 2000). In this area, the dominant sediment type is the sand with varying amount of silt and clay. Rocky outcrops are scarce. In the Southern Bight of the North Sea, shipwrecks represent also an important source of the available subtidal hard substrate in the same kind of sedimentary environment (see on page 13).

Several oil fields have been studied for their importance as artificial reefs around the world. Usually, platforms are removed from water when exploitation ceased, but an alternative is to keep them offshore and use them as artificial reefs. The surface available for colonization of a typical platform standing in 50 m of water has been estimated ranging between 1.2 and 1.6 ha (Picken *et al.*, 2000). 6500 platforms are in use worldwide with 4000 of them located in the Gulf of Mexico (Picken *et al.*, 2000). It has been estimated that the 4000 platforms provide 1800 ha of hard substrate (28% of the known hard substrate habitat in the Gulf of Mexico) (Reggio *et al.*, 1986). Off the Louisiana state, they represent 90% of coastal hard bottom habitat (Stanley & Wilson, 1989). 115 of these platforms have already been decommissioned into artificial reefs (Kaiser & Pulsipher, 2005). In the North Sea, the Ekofisk field is approaching its end of exploitation and 14 out of the 29 platforms will have to be decommissioned (Lokkeborg *et al.*, 2002). In the Northern Adriatic Sea, the fate of 80 platforms has not been decided yet (Fabi *et al.*, 2002).

4.3 Shipwrecks in the Southern Bight of the North Sea

The Dover Strait represents a transition zone between the Atlantic waters and the North Sea. The coastal geomorphology of this zone creates an increase of the tidal amplitude and strength of the currents. As a result, gravels and pebbles with rare rocky outcrops characterize the offshore zone of the Dover Strait (Cabioch, 1997). Current strength above 2.5 knots are a prerequisite for preventing sand to sediment (Castric-Fey *et al.*, 1997). After the Dove Strait, the currents strength decrease and allow for the sedimentation of finer sediments. The Southern Bight of the North Sea is characterized by sandy-muddy seabed. Some residuals gravels beds have been identified in the gullies between sandbanks on the Belgian waters (Kerckhof & Houziaux, 2003) and in other places along the French and UK waters (Figure 1). These beds are rarely bedrocks or boulder field but are a mix of sand and gravel/pebble (Doody *et al.*, 1993). Another source of available hard substrate for the epifauna has an anthropogenic origin: shipwrecks. These 3-dimensional structures represent a very special habitat especially when they are widely distributed in flat and soft sediment dominated area (Steimle & Zetlin, 2000) as it is the case in the Southern Bight of the North Sea (Houbolt, 1968).

This region of the North Sea in general and the Belgian Part of the North Sea (BPNS) in particular is one of the most heavily navigated areas in the world (Maes *et al.*, 2000) and combined with the consequences of World War I & II, the number of obstructions, most of them being shipwrecks is not anecdotic. The Belgian waters harbour an official total number of 231 obstructions for navigation or fisheries (Administration for Navigation and Coast, pers. com). Along the coast of The Netherlands, Leewis *et al.* (2000) state that more than 10,000 vessels may be present on the seabed while the official figures lies around 2000 (Wrakkenregister Nederlands Continentaal Plat en Westerschelde, Koninkelijke Marine, Dienst der Hydrografie, 2002), which is close to the density of the Belgian waters. The English register of shipwrecks is not readily available at low cost.

Table 1. Main recent artificial reefs programme in European area (including countries around the Mediterranean).

Location	Year	Units	Volume	Covered area	Objectives	References
FRANCE						
Mediterranean coast	1980	13 sites	59,000 m^3		Enforcing anti-trawling legislation Protection of *Posidonia oceanica* beds Fisheries management	Barnabé *et al.*, 2000
Atlantic coast	1970-80	3 sites, lost now			Test on waste material	Barnabé *et al.*, 2000
GERMANY	1992	Small experiment			Material test experiment	Jensen, 1998
GULF OF FINLAND	1992	Panels		1x1.5 m.panel^{-1}	Mitigation of eutrophication	Antsulevich, 1994; Antsulevich *et al.*, 2000
ISRAEL	1982	2 sites, small size			Research	Spanier, 2000
Haifa						
ITALY						
Loano	1986	500 units of 1.2x1.2x1.2 or 2x2x2 m	1845 m^3	Spread over 350 ha	Fisheries management Protection of *Posidonia oceanica* beds Enforcing anti-trawling legislation	Relini *et al.*, 1994; Relini, 2000b; Relini *et al.*, 2002a
Fregene	1981	280 units of 2x2x2 m		Spread over 6 ha. Real projected surface: 0.11 ha	Fisheries management Protection of *Posidonia oceanica* beds Enforcing anti-trawling	Ardizzone *et al.*, 1989; Ardizzone *et al.*, 2000

Table 1 continued

Location	Year	Units	Volume	Covered area	Objectives	References
					legislation	
north-west Sicily	1982	174 units of 2x2x2 m		Projected surface: 0.06 ha	Fisheries management Protection of *Posidonia oceanica* beds Enforcing anti-trawling legislation	Riggio *et al.*, 2000; D'Anna *et al.*, 2000
Adriatic coast	1980-90	592 units	46,500 m^3	Spread over 8.3 ha	Fisheries management Protection of *Posidonia oceanica* beds Enforcing anti-trawling legislation Mitigation of eutrophication	Bombace, 1989; Bombace *et al.*, 1994; Bombace *et al.*, 2000
MONACO	1979-90	31 units	112 T	101 m^2	Protection of *Posidonia oceanica* beds Conservation of *Corallium rubrum*	Allemand *et al.*, 2000
POLAND						
Pomerianan Bay	1990	12 units		Spread on 23,000 m^2	Mitigation of eutrophication	Chojnacki, 2000
PORTUGAL						
Madeira	1983	Cars, boat, tyres			Fisheries management	Jensen, 2002a

Table 1 continued.

Location	Year	Units	Volume	Covered area	Objectives	References
Algarve	1997	4 modules in two sites	5053 m^3	Spread on 60 ha	Research on fisheries management	Santos & Monteiro, 1997; Santos & Monteiro, 1998; Monteiro & Santos, 2000; Santos *et al.*, 2002; Jensen, 2002b
	2002	4 sites, 19,000 modules	66,690 T	Spread on 39 km^2	Fisheries management	
SPAIN						
Cataluna	90's	6 sites				Revenga *et al.*, 2000
Murcia	90's	1 site				Revenga *et al.*, 2000
Alicante	1992	5 sites, 796 units	7.9-8.4 T.unit^{-1}	Spread over 2417 ha. Real projected surface: 0.65 ha	Protection of *Posidonia oceanica* beds Protection of artisanal fisheries	Guillen *et al.*, 1994; Bayle-Sempere *et al.*, 1994; Ramos-Espla *et al.*, 2000; Sanchez-Jerez *et al.*, 2002; Ramos *et al.*, 2006a; Ramos *et al.*, 2006b
Balearic islands	1989	17 sites, 850 units		Spread over 4 ha on each site	Enforcing anti-trawling legislation Fisheries management	Moreno *et al.*, 1994; Moreno, 2000; Moreno, 2002
Valencia	90's	18 sites				Revenga *et al.*, 2000
Andalucia	90's	5 sites				Revenga *et al.*, 2000
Canary Islands	1991	4 sites, 205 units	0.8-6.2 T.unit^{-1}	Spread over 58,600 m^2 Real projected surface: $\approx$0,1 ha	Enforcing anti-trawling legislation Fisheries management	Haroun *et al.*, 1994; Gomez-Buckley & Haroun, 1994; Haroun & Herrera, 2000; Herrera *et al.*, 2002

Table 1 continued

Location	Year	Units	Volume	Covered area	Objectives	References
Asturias	1988-93	6 sites with 883 units	3.5-5.5 T.unit^{-1}	Spread over 170 km^2.	Enforcing anti-trawling legislation Fisheries management	Revenga *et al.*, 2000
THE NETHERLANDS						
Noordwik	1992-96	4 modules	500 T	12 m ø.module^{-1}	Biological colonization	Leewis & Hallie, 2000
TURKEY Mediterranean coast	1989-03	12 sites, 1300 units	2,560 m^3 - 1716 T		Research on *Posidonia oceanica* beds Fisheries management	Lok *et al.*, 2002; Duzbastilar *et al.*, 2006
UK						
Poole Bay	1989	8 units at 10 m from each other	50 T	4 m ø.units-1	Material test experiment Biological follow-up Fishery potential	Jensen *et al.*, 1994; Collins *et al.*, 1994a; Collins *et al.*, 1994b; Jensen & Collins, 1995; Hatcher, 1997; Hatcher, 1998; Mallinson *et al.*, 1999; Jensen *et al.*, 2000b; Jensen *et al.*, 2000c; Smith *et al.*, 2001; Collins *et al.*, 2001a; Collins *et al.*, 2001b; Collins *et al.*, 2002a; Collins *et al.*, 2002b
Torness	1984				Biological colonization	Todd *et al.*, 1992
Salcombe	2000				Restoration programme	Jensen, 2002a
Loch Linne	2001-06	25-46 reef modules	25,000-42,000 T	30-70 m ø. module^{-1}	Study of interaction between reefs and animals/plants	Sayer & Wilding, 2002; Wilding & Sayer, 2002a; Wilding & Sayer, 2002b

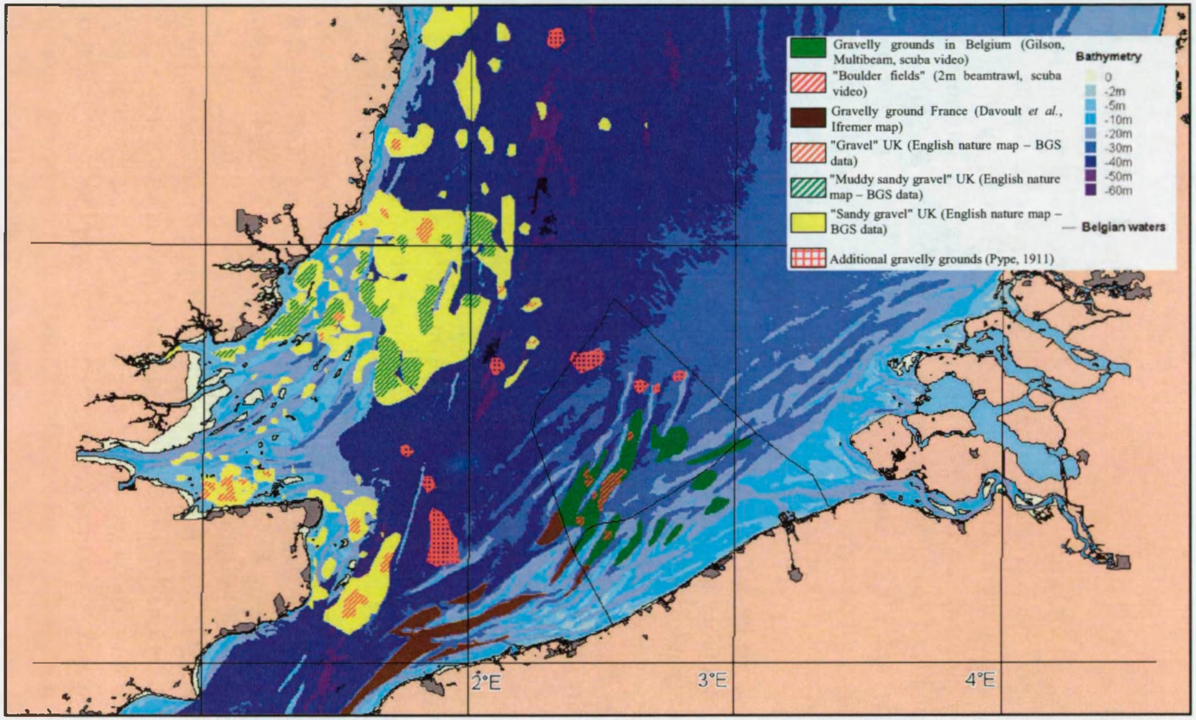


Figure 1. Suggestion of "gravel" distribution in the Southern Bight of the North Sea. Compilation of available geo-referenced data. Data sources: Jones *et al.*, 2004 (BGS 1:250,000 seabed sediment map, British Geological Survey, ©NERC (IPR/37-32c)); Pype, 1911; personal communications from MINECO (M. Roche), RCMG (S. Deleu, V. Van Lancker) and "Bewremabi" project; Gilson data; Augris *et al.*, 1995; Davoult *et al.*, 1988. Map compiled by J.S. Houziaux.

5. PHYSICO-BIOLOGICAL CHARACTERISTICS OF ARTIFICIAL REEFS

5.1 Materials

Different kind of materials are used for the construction of artificial reefs. Rocky structures have been erected (groins, breakwall, jetties,...) or are used for artificial reef deployment (Demartini *et al.*, 1989; Hueckel *et al.*, 1989; West *et al.*, 1994; Johnson *et al.*, 1994; Palmer-Zwahlen & Aseltine, 1994; Pondella & Stephens, 1994; Pondella *et al.*, 2002; Abelson & Shlesinger, 2002; Guidetti *et al.*, 2005; Thanner *et al.*, 2006). However, the most ubiquitous material is concrete. It has been extensively used for planned reefs and constructions at sea but since a major factor driving the economic viability of an artificial reef programme is the cost of the construction material, other sources have been tested (Wilding & Sayer, 2002b).

Scrap tyres are available at low cost and largely exploited in the marine environment worldwide (Collins *et al.*, 2002a). Their environmental impact is not yet fully acknowledged. Leaching of Zn^{++} and its bioaccumulation in the colonizing epifauna has been demonstrated in the first year after immersion (Collins *et al.*, 2002a), but long-term studies are missing.

Other by-products like cement-stabilized recycled waste material are tested as alternative source of reef material with promising results. A major source of material suitable for the stabilization of cement is ash from coal-power stations (Collins *et al.*, 1994a; Collins *et al.*, 1994b; Relini, 2000a; Kress *et al.*, 2002), oil (Metz & Trefy, 1988), granite quarrying (Wilding & Sayer, 2002b) and incinerators (Breslin *et al.*, 1988). Tests on granite quarrying and coal ash by-products showed that they were stable in time when immersed and that leaching and bioaccumulation of heavy metals in epifauna was low or unsignificant (Sampaolo & Relini, 1994; Collins *et al.*, 1994b; Relini, 2000a; Kress *et al.*, 2002; Wilding & Sayer, 2002b).

Wood is mainly present at sea in pontoons and harbour constructions. In the past, wood was intentionally (or not) added to the sea as material for reef creation mainly because of its use in the construction of vessels (Steimle & Zetlin, 2000). However, wood proved to be very susceptible to degradation in sea water and most of the wood vessels disappeared, fungi being certainly an important recycling agent of these organic compounds (Hyde *et al.*, 1998).

Steel is found as building component in shipwrecks, oil and gas platforms, cars, in the anchors and chains of buoys, lost fishing gears and dumping of industrial waste materials (Chou *et al.*, 2002). Most metals are thermodynamically unstable in the natural environment and have a tendency to revert to their natural ore. This instability is the driven force for corrosion (Gardiner & Melchers, 2003).

The stability of metals is under the recognized influence of the type of steel, the physico-chemical properties of the seawater, the current velocity of surrounding waters and the type and amount of biofouling (including the biofilm) developing on it (Videla, 1994). Biofouling has a positive impact on steel longevity by decreasing water velocity at the interface layer (Melchers & Jeffrey, 2004), but has a negative impact by causing a noble shift (a change in redox potential) in the open circuit potential of the stainless steel (leading to a increased speed of corrosion) (Compere *et al.*, 2001; Acuna *et al.*, 2006). Surface heterogeneities within fouling communities and the resulting increased variability of the chemical environment from point to point along the material surface encourage localized corrosion (Shifler, 2005). Barnacles have a recognized impact on corrosion rates (Eashwar *et al.*, 1992; Koryakova *et al.*, 1995). The anaerobic conditions under their basal plates could be responsible for increased local corrosion rate (Koryakova *et al.*, 1995). On some instances, fouling organisms have been shown to locally increase corrosion rate but reduce to great extend the general corrosion (Sun *et al.*, 2003). The longevity of a structure like a shipwreck cannot be inferred because too many parameters are controlling its degradation. Industrial production of steel and the construction of steel-vessel started in 1855. The life-span of these structures can potentially be long, certainly several centuries. For example, the military steel ship USS Huron which sank in 1877 in the Atlantic waters of North Carolina (USA) is still in very good shape. The Kilmore sank in 1906 in the Belgian waters and still holds clearly recognizable structures.

5.2 Structure

Reef design is an essential part of artificial reef construction. Size and complexity of a reef are two parameters which will affect its function.

Reef size influences total number of species, abundance and biomass. Smaller units have greater fish density while larger reefs have higher biomass from larger, but fewer, individuals (Bohnsack *et al.*, 1994). The volume of a reef will have an effect on its range of influence. For a reef with an average bulk volume of about 3,000 m^3, the effective range of its influence was about 200 m from its edge, this value extending to 900 m for typical bottom-dwelling species like sole, dab or flounder (Japan Coastal Fisheries Promotion Association, 1986 *in* Grove *et al.*, 1991).

Reef structures tend to attract different fish assemblages with some fish showing a positive attraction to a particular structure and others having no distinctive preferences (Kim *et al.*, 1994). The effect of increased habitat complexity on fish assemblages has been clearly highlighted. Fish metrics (diversity and abundance) are positively correlated with an increased habitat complexity (Gorham & Alevizon, 1989; Charbonnel *et al.*, 2002). Concrete allows the development of endless forms of structures but few studies concentrated on optimum complexity needed to achieve their ecological function. A Japanese fish-aggregation study also revealed that fish aggregation, expressed in fish volume in kilograms per unit reef bulk volume (m^3), was bout 5.0 for reefs consisting of concrete cylinders and hollow cubes, about 0.6 for large modular reefs, and as low as 0.03 for natural reefs (Japan Coastal Fisheries Promotion Association, 1986 *in* Grove *et al.*, 1991). The dispersion in space of the different modules can also affect species distribution and abundances. For example, Lindberg *et al.* (1990) noted for a crab species that as refuge spacing (i.e. reef distance) decreases, so does access to prey on soft sediments that surround reef.

Oil and gas platforms offer a structure which extends throughout the whole water column with usual surface at base of 50x50 m and a height of 30-100 m, providing benthic, mid-water and surface habitats (Stanley & Wilson, 2000; Picken *et al.*, 2000; Jorgensen *et al.*, 2002; Fabi *et al.*, 2002; Fabi *et al.*, 2004). They provide reference point, structural openness, large surface area and complex physical design (Picken *et al.*, 2000).

Shipwrecks usually do not extend over the whole water column and their structure evolves during their immersion time. The initial structure of shipwrecks is less complex than what is offered by concrete units or platforms. The desegregation of shipwrecks caused by steel corrosion will lead to an increase in the complexity of the structure accompanied by a general decrease in the available surface for epifauna. However, this evolution has never been studied so far. Only one attempt was made to compare an old and new shipwreck as an aggregation device in North Carolina (Stephan & Lindquist, 1989). The old site was at sea since approximately 50 years and only remains were left. If the species richness observed was higher on the oldest site, it was however impossible to consider whether this effect was due to physical structural complexity of the wreck itself or a result of the maturation process of the epifauna.

5.3 Biological colonization

5.3.1 Fish populations

The colonization of artificial reefs by fish and the description of fish population (qualitative and/or quantitative) around them have been extensively described in literature. Some papers also tried to explain fish behaviour in relation to reef use.

5.3.1.1 Initial colonization and community structure equilibrium

The colonization of artificial reefs by fish population is a very rapid phenomenon (Russel, 1975; Bohnsack & Talbot, 1980). Fish may appear within hours after the deployment of the reef, regardless of the size of the reef (Molles, 1978). Fish populations often reach their maximum population size after a few months of reef placement (Bohnsack & Talbot, 1980; Fabi *et al.*, 2002; Thanner *et al.*, 2006). Equilibrium community structure is achieved within one year to a maximum of five years but seasonal variation in the equilibrium can have more profound influence on fish species succession than age of structure (Molles, 1978; Talbot *et al.*, 1978; Bohnsack & Talbot, 1980; Herrera *et al.*, 2002). However, in another study, fish community structure seems not being stabilized even after a 10 years census on an artificial reef in the Adriatic Sea (Italy). After 10 years, new species typically associated to hard substratum still arrive on the reef and find space to thrive (Relini *et al.*, 2002b).

5.3.1.2 Fish behaviour around artificial reefs

The use of artificial reef by fish and behavioural patterns of fish attraction can be classified into three categories (Bohnsack & Sutherland, 1985):

1. Surface and mid-water fish that show a swarming response to a reef and generally remain at some distance from the reef.
2. Fish that swim along the bottom and take a stationary position near the reef but usually do not remain on it permanently.
3. Bottom and other fish that take a stationary position inside a reef or on the bottom in its vicinity.

A variety of environmental factors and senses play a role in the attraction of fish by reefs. These include current pattern, shadow, species interactions, visual cues of size, shape, colour, light, sound, touch and pressure (reviewed by Bohnsack & Sutherland, 1985). Rostad *et al.* (2006) also showed that the fish abundance under research vessels increased by an order of magnitude in less than an hour. They suggested that noise could explain this pattern of aggregation. However, the basic question of what is specifically attracting the fish remains mostly unanswered (Bohnsack & Sutherland, 1985).

Gut content studies indicated that some fish species feed mainly on reef-associated species, while others do not use the reef as a food source or use a mixture of soft sediment and reef-associated species (Lindquist *et al.*, 1994; Johnson *et al.*, 1994; Relini *et al.*, 2002a; Fabi *et al.*, 2006). Bohnsack (1985) states that most fish biomass around oil and gas platforms is represented by species which are trophically independent from the platforms while an artificial reef in Southern California was said to produce 70% of the diet of the reef associated species (Johnson *et al.*, 1994). Clearly, some species are not attracted by reef for food search. Interestingly, an experiment with identical reefs with or without epibenthic organisms (treated or not with an anti-fouling paint) showed that species diversity and evenness was significantly greater at the site with the fouling species, pointing that the epifauna has to be of any use for the fish population (Sutterer & Szedlmayer, 2005).

Several studies investigated the site fidelity of a set of species, mainly around oil and gas platforms. About 50% of the tagged cod (*Gadus morhua* L.) around a North Sea oil platform were still at the platform after a four month period. It dropped to 14% after a year but another 16% of the specimens were caught in the meantime at the platforms (3%), in another platform in the vicinity (7%) or at 9 km (3%) and 150 km (3%) from release (Jorgensen *et al.*, 2002). In the Gulf of Mexico, red snappers (*Lutjanus campechanus* (Poey)) around platforms had a median residence time of 373 days and for most of their time (99%) stayed within a 200 m radius from the site (Schroepfer & Szedlmayer, 2006).

5.3.1.3 Abundance and biomass of fish around artificial reefs

Attraction of fish by artificial reef is stated on almost all the papers whose focus was on fish and artificial reefs. The area of fish concentration is known to lie between 200 and 300 m from the reef for mid-water and surface fish (Bohnsack & Sutherland, 1985; Lokkeborg *et al.*, 2002). The abundance and biomass of resident fish population have been compared with natural reefs occurring in the vicinity and/or control sites (here control sites are considered sites out of the reef and representative of the surrounding environment). Fish abundance and biomass generally exceed that found on natural hard substrate grounds even thought general composition is often very similar (Fabi & Fiorentini, 1994; Danner *et al.*, 1994; Johnson *et al.*, 1994; Love *et al.*, 1994; Pondella *et al.*, 2002; Charbonnel *et al.*, 2002;

Soldal *et al.*, 2002). This is particularly true when the artificial reefs are located far from other natural hard substrate sites and for a set of benthic and nekto-pelagic species (Bombace *et al.*, 1994). Nevertheless, the global ratio of estimated fishing yields on artificial reefs to surrounding habitats are rarely mentioned. Exceptions are Fabi & Fiorentini (1994) who estimated a ratio of 1.3 and Johnson *et al.* (1994) a ration of 8.9. Hydroacoustic estimation of fish density and biomass in the vicinity of oil platform in the North Sea did not give concluding results due to the sampling strategy but the authors stated that cod (the most abundant species in gillnet catch) was closely associated with the steel jacket (Soldal *et al.*, 2002). In the Adriatic Sea, abundances and biomass of fish taken by trammel net in the close vicinity of one platform located close to the shore and on control site did not show any significant difference, even if species diversity was higher on the platform site (Fabi *et al.*, 2002; Fabi *et al.*, 2004). However, the same study with a site located further offshore did show significant differences in biomass and abundance (Fabi *et al.*, 2004). In the Gulf of Mexico, visibility conditions hampered the chosen protocol to quantitatively estimate fish density and biomass around oil platform (Scarborough Bull & Kendall, 1994). In Californian waters, higher densities are recorded on platforms than on natural rocky habitats surrounding them but opposite results were observed for species richness and diversity (Love *et al.*, 1994). Most of the other studies concentrated on a single commercially important species, the red snapper (*Lutjanus campechanus*) (cfr last international conference on artificial reefs and habitats, Biloxi, USA, April 2005).

5.3.2 Epifauna

The epifauna are the organisms living on or otherwise associated with the surface of the bottom as opposed to the infauna that are organisms living within the substrate (Nybakken, 1997).

The epifauna can be further divided into the sessile epifauna which is attached to the substrate, the slow moving epifauna which is strongly dependant on the substrate, and the vagile epifauna which is able to move freely on the substrate. Biofouling is a commonly used term to distinguish the assemblages living on artificial structures from these on natural outcrops (Hughes *et al.*, 2005).

5.3.2.1 Colonization and maturation

Initial colonization of invertebrates on artificial reef occurs very rapidly, within a few weeks. Barnacles are systematically noted among the pioneer species in association with hydrozoans and bryozoans (Otsuka & Dauer, 1982; Relini *et al.*, 1994; Palmer-Zwahlen & Aseltine, 1994; Nelson *et al.*, 1994). Mussels will finally dominate some shallow water communities (Picken, 1986; Ardizzone *et al.*, 1989) but it is not the general rule (Forteath *et al.*, 1982; Relini *et al.*, 1994). The domination by mussels can already be observed one year after submersion (Picken, 1986). Under the mussel layer, a base layer of calcareous species (Barnacles or calcareous annelids like *Pomatoceros* sp.) is overgrown by hydrozoans and bryozoans.

5.3.2.2 Biomass

In Delaware (Atlantic US coast), the wet biomass raised to 24,580 $g.m^{-2}$ when mussels dominated the community and dropped to a mean value of 596 $g.m^{-2}$ afterwards. It represents 147 to 895 times the mean biomass of the surrounding sediments (Foster *et al.*, 1994).

On the Dutch shipwrecks, the highest biomass values were obtained on a community dominated by *Metridium senile* (L.). They peaked at 1,954 g AFDW m^{-2}. The mean biomass was 642 $g.m^{-2}$, 209-364 times the mean biomass of the surrounding sediments (Leewis *et al.*, 2000).

In the North Sea wind farms of Denmark, mean biomass (wet weight) was 3,364 $g.m^{-2}$ on mono-piles and 236 $g.m^{-2}$ on the scouring protections (Leonhard *et al.*, 2005) two years after immersion. The high mono-pile values are due to *Mytilus edulis*.

In the Northern Adriatic Sea, the biomass of two outcrops was compared with the biomass of two artificial reefs (one shipwreck and one barrier of concrete blocks) (Gabriele *et al.*, 1999). Artificial reefs (391 g $AFDW.m^{-2}$) had a significant larger value of biomass than natural outcrops (135 g $AFDW.m^{-2}$). However, the reefs were also located in more turbid waters which could potentially lead to increased biomass through the promotion of some species from the epifauna.

Other studies failed to mention clearly the mean biomass values observed on artificial reefs (Wendt *et al.*, 1989; Relini *et al.*, 1994; Hatcher, 1997).

5.3.2.3 Epifauna diversity in temperate waters

Delaware artificial reef (Foster et al., 1994)

In Delaware (USA), the blue mussel (*Mytilus edulis*) covered in May most of the upper part of the reef (9-13 m depth) two years after immersion. Accompanying species were *Tubularia* sp., *Sabellaria* sp., *Bugula* sp. and *Asterias* sp. associated with the seabed. Epifaunal samples contained a total of 50 species including sponges, *Balanus* sp. and *Metridium* sp., *Stenothoe minuta* Holmes and P*olydora* sp. In August, the samples were numerically dominated by *Metridium* sp. and the remaining mussels associated with some amphipods (*Stenothoe minuta* and *Caprella* sp.). Similar observations were made on submerged bricks in the New-York Bight (Woodhead & Jacobson, 1985).

Poole Bay artificial reef (Jensen et al., 1994; Collins et al., 1994b; Jensen & Collins, 1995; Hatcher, 1997; Hatcher, 1998; Mallinson et al., 1999)

In the Poole Bay Artificial reef (UK, depth: 10 m), the cover was virtually of 100% after nine months of deployment. The first colonizers were calcareous tubeworms (*Pomatoceros triqueter* (L.)) and ascidians (*Ascidia mentula* (Müller), *Botryllus schlosseri* (Pallas) and didemnids). The upper parts of the reef were soon dominated by red algae in association with a turf composed of bryozoans and hydrozoans in development. The colonization pattern of the reef blocks appears to be following two cycles: a seasonal fluctuation which overlies the natural succession from primary opportunistic species to those that recruited later in the reef's history and have successfully competed for space. A difference could also be seen between horizontal and vertical surfaces, the former, receiving more illumination, being dominated by algae and the latter dominated by faunal species. Seasonal variation was clearly highlighted by algae and some hydrozoan and bryozoan species (*Aglaophenia* sp., *Plumularia setacea* L., *Bugula plumosa* (Pallas), *Bicellariella ciliata* (L.)). Later, species typical of more mature assemblages like sponges (*Sycon ciliatum* (Fabricius), *Dysidea fragilis* (Montagu) and *Esperiopsis fucorum* (Esper)) appeared. As the reef matured, convergence with natural rocky habitat of the region became more apparent: algae development increased, *Lithothamnion* spp., sponges and anthozoans (*Actinothoe sphyrodeta* (Gosse), *Anemonia viridis* (Forskål), *Cereus pedunculatus* (Pennant), *Halcampa chrysanthellum* (Peach *in* Johnston), *Sagartia* sp., *Urticina felina* (L.)) started to develop. An exhaustive list of the species recorded on the Poole Bay reef is available and includes 189 species of the macrofauna and 64 algae species (Hatcher, 1998).

Horns Rev Offshore Wind Farm (Leonhard et al., 2004; Leonhard et al., 2005)

Horns Rev is situated 14-20 km off Blåvands Huk, Denmark's most western point. The Horns Rey Wind Farm was constructed in 2002 and its introduced hard substrate (central mono-pile and anti-erosion protection gravels/pebbles) was monitored in 2003 and 2004.

A total of 70 taxa of invertebrates were registered. Great spatial and temporal variations in assemblages were found between the two surveyed years. *Jassa marmorata* was the most frequently species found on the mono-piles (mean value for piles: 259,200 ind.m^{-2}; for foundations: 66,400 ind.m^{-2}). *Caprella linearis* was also very common (mean value for piles: 22,100 ind.m^{-2}; for foundations: 1,200 ind.m^{-2}). Dense aggregations of either spat or larger individuals of *Mytilus edulis* were found in the sublittoral just beneath the sea surface at the mono-piles. Changes in population structure between 2003 and 2004 clearly demonstrated growth of the common mussels. Discrepancies in the distribution and abundance between *M. edulis*, *Balanus crenatus* and *Asterias rubens* indicated that the starfish was the main keystone predator controlling the vertical and horizontal distribution of its prey species. Larger starfish eat mainly larger mussels whereas smaller starfish eat both smaller mussels and barnacles. In the lower zone at the mono-piles, *Pomatoceros triqueter*, was more abundant than in the upper zones. Another primary colonizer, *Tubularia indivisa*, was also present.

The growth of *Cancer pagurus* was demonstrated from September 2003 to March 2004 and visualization of both juveniles of other crabs and egg masses of bristle worms and sea slugs indicated that the turbine foundations were used as hatchery and nursery grounds.

Metridium senile, *Sargartia elegans* and *Sargartiogeton lacerates* were the commonest sea anemones species observed by divers and constituted 5% of the total biomass on the mono-pile and 46% on foundations.

Other species typically associated with the mono-pile included *Hydractinia echinata*, *Alcyonium digitatum*, *Harmothoe imbricata*, *Flabellina* (*Coryphella*) *lineata*, *Modiolarca tumida*, *Ostrea edulis*, *Hiatella arctica*, *Buccinum undatum*, *Hinia pygmaea* and *Carcinus maenas*.

Moray Firth (oil/gas platform Beatrice) (Picken, 1986)

The Beatrice extraction platform (UK waters, 58°06'55"N 03°05'10"W) and some other surrounding artificial structures (jetties and buoys) closer to the coast have been examined in the course of annual engineering inspection during four years after immersion. The platform is 20 km off the coast and lies in a depth of 45 m. Within one year of placement, all the structure was covered by solitary tubeworms (*Hydroides norvegicus* Gunnerus and *Pomatoceros triqueter*) and barnacles (*Balanus crenatus* Bruguiére, *Balanus balanoides* (L.) and *Balanus balanus* (L.)). Three years after placement, tubeworms and barnacles were overgrown to various extents by other foulers, and by year four, the greatest extent of exposed tubeworm growth was found in the depth range 26-45 m. Mussels (*Mytilus edulis*) dominated the zone exposed to the tides and the first 4 m. They were covered to some extent by seaweeds (*Enteromorpha* sp., *Polysiphonia* sp., *Ulva lactuca* L., *Ceramium rubrum* C. Agardh, *Lomentaria clavellosa* Gaillon, *Palmaria palmata* Kuntze, *Porphyra* sp. and *Spongomorpha* sp.). Their maximum cover was observed in the first 4 m. Hydroids were found throughout the depth range of the structure after year one and remained an important component of the growth in the following years. Under the mussel layer, the cover of hydroids was up to 70% at a number of locations. The principal species were *Bougainvillia ramosa* (van Beneden) and *Tubularia larynx* Ellis & Solander, but *Garvia mutans* Wright, *Obelia dichotoma* (L.) and *Sarsia eximia* (Allman) were also found. The bryozan *Electra pilosa* (L.) was told prominent in this assemblage. The soft coral *Alcyonium digitatum* L. developed on year three and became ubiquitous on year four. Its greatest densities and sizes were observed on the undersides of a large horizontal surface at a depth of 26 m, protected from the settlement of silt. Ascidians (*Ascidiella aspersa* (Müller) and *Ciona intestinalis* (L.)) became significant foulers on year four especially in deep waters (under -36 m) and in area protected from silting.

On the structures closer to the coast again a layer of mussels and occasionally barnacles dominated the first meter in association with algae and the deeper surfaces were dominated by an unidentified hydroid, the sponge *Halichondria* sp., and the cnidarians *Alcyonium digitatum* and *Metridium senile*.

Montrose (oil/gas platform Montrose Alpha) (Forteath et al., 1982)

The Montrose oil field is located 175 km off the coast of Scotland in the North Sea (57°27'N 01°23'E). The Montrose Alpha jacket lies in 91 m of waters and was inspected during five years after its immersion. The first 10 m of the structure receiving light were dominated by seaweeds with scattered individuals of mussels (*Mytilus edulis*) and hydroids (*Obelia dichotoma* and *Bougainvillia ramosa*). Where light was insufficient, hydroids dominated. Below -10 m and to -30 m, algae gave way to hydroids and bryozoans. *Obelia dichotoma*, *Laomedea flexuosa* Alder and *Bougainvillea ramosa* were the most common hydroid species. *Tubularia larynx* dominated horizontal and oblique structures on year two but was finally overgrown by other hydroids on year four. The most common bryozoan was a bush-like form of *Electra pilosa*, covering 90-95% of the surface. *Bicellariella ciliata* and *Bugula avicularia* (L.) were also found among the hydroids. Below -30 m, arborescent bryozoans were steadily replaced by calcareous bryozoans (*Tubulipora liliacea* (Pallas) and *Omalosecosa ramulosa* (L.)), covering up to 80% of the surface. Hydroids continued to be present but more scattered. Below -50 m, calcareous bryozoans were replaced by encrusting bryozoan species (mainly *Alcyonidium hirsutum* (Flemming)). Deeper, the tubeworm *Filograna implexa* Berkeley became more and more common as was the deep barnacle *Balanus hameri* (Ascanius). Other sessile species were recorded, scattered on the jacket: *Pomatoceros triqueter*, *Hydroides norvegica*, *Metridium senile* and *Alcyonium digitatum*. Motile species in the samples recurrently included *Jassa falcata* (Montagu), *Dendronotus frondosus* (Ascanius), *Asterias rubens* L. and *Nereis pelagica* L.

Gas platforms off Ravenna (Northern Adriatic, Italy) (Relini et al., 1998)

The two platforms off Ravenna (7.5 and 10 km from the coast) lie on a sand-muddy bottom at a depth of 12-14 m in eutrophic and stratified waters with the presence of freshwater in the surface layer. They were sampled 20 years after immersion. Both platforms were strongly dominated by *Mytilus galloprovinciallis* Lamarck which was present from the surface to 2 m from the bottom. In the bottom layer, scientists found empty shells of *Crassostrea gigas* (Thundberg), largely covered by zoantharians associated with barnacles, serpulids and hydrozoans. The mussel community was characterized by a relatively low number of species (32 sp.) but a high biomass value (up to 1,561 g wet weight.dm^{-2}).

The Pinta shipwreck (Middle Atlantic Bight: Cape Cod to Cape Hatteras, USA) (Bulloch, 1965)

This shipwreck (depth: 25 m) was surveyed from nine months until two years after submersion. The first conspicuous colonizers were the hydroid *Tubularia crocea* Agassiz and *Sertularella gayi* (Lamoureux). Mussels and *Asterias* sp. were also present and in expansion. Scraped samples showed nemertines and caprellid amphipods. *Metridium senile* was abundant in the hull and in occasional openings in the hydroid growth. The authors conclude that the community is not fully mature compared to the surrounding shipwrecks. Species like *Bugula* sp. and Bicellaridae are still missing. However, the description of these mature sites is not given.

The M.V. Robert shipwreck (Lundy, UK) (Hiscock, 1980)

This shipwreck (depth: 19 m) was investigated for several years, starting four years after its submersion. Horizontal surfaces are patchily covered by a mat of hydroids, erect bryozoans and scattered algae. However, an almost continuous crust of *Sabellaria spinulosa* Leuckart was found beneath the turf. A variety of small worms, crustaceans and molluscs were living in the turf. *Metridium senile* dominated the edge of horizontal surfaces and were scattered over the port side. Vertical surfaces had a sparser community with *Pomatoceros triqueter* being a conspicuous element. Inside the hold, *M. senile* were abundant with patches of *Ascidia mentula*. A less extensive habitat were spars and rails which were dominated by *M. senile*, *Tubularia larynx* and *Tubularia indivisa* L. associated with tube building amphipods (probably *Jassa falcata*). A total of 187 species were recorded from a 1.4 m^2 of horizontal area of hull, and together with species recording during *in-situ* surveys, a total of 222 algae and animal taxa have been identified.

Shipwreck and concrete structure in the Northern Adriatic Sea (Italy) (Gabriele et al., 1999)

Samples were taken from natural outcrops and artificial structures (one shipwreck and one concrete structure, depth: 17-22 m). Typical species for the shipwreck in order of importance were *Ostrea edulis* L., *Arca noae* L., *Pomatoceros triqueter*, *Ophiothrix* sp., *Balanus* sp. and *Dysidea fragilis*. On concrete, they were *Aplidium elegans* (Giard), *Ostrea edulis*, *Balanus* sp., *Eunice aphroditois*, *Pomatoceros triqueter* and *Nassarius incrassatus* (Ström). Total species number for the shipwreck is 50 (15 replicates) and 62 for the concrete structure (15 replicates). The biomass was dominated on both habitats by bivalves followed by ascidians.

Shipwrecks on South California and Georgia waters (USA) (Wendt et al., 1989)

Five shipwrecks of different age (3.5 to 10 years, depth: 22-31 m) were sampled and it appeared that there was no consistent trend in biomass, percent cover or number of sessile species with increasing age of artificial reef. However, all three variables were significantly greater on vertical than on horizontal surfaces, suggesting a heavier sedimentation and/or greater predation rate on horizontal surfaces. The cover was dominated by hydrozoans and bryozoans on all sites. The absence of large sponges and corals which are frequent on natural outcrops in the region suggest either that the substrate of shipwrecks is intrinsically different from the one offered by natural substrata or that these particular organisms are late colonizers or slow to mature.

Shipwrecks in the Nord-pas de Calais (France) (Müller, 1994; Müller, 1999; Müller, 2004)

Seven shipwrecks (depth: 12-40 m) were briefly described by a limited number of samples taken on the different sites. The most conspicuous species were hydrozoans: *Tubularia indivisa* and *Tubularia larynx*, *Diadumene cincta* Stephenson, and *Metridium senile*. Other species were abundant such as *Mytilus edulis*, *Pisidia longicornis* (L.), *Jassa* sp., Caprellidae, *Ophiothrix fragilis* (Abildgaard) and patches of *Hydractinia echinata* (Flemming). Sponges were also present (*Halichondria* sp., *Leucosolenia* sp., *Haliclona* sp. and *Sycon ciliatum*). Their communities were split between a coastal zone and an offshore zone which is deeper and faces stronger currents.

Shipwrecks in The Netherlands (Waardenburg, 1987; van Moorsel et al., 1988; van Moorsel & Waardenburg, 1990; van Moorsel et al., 1991; Leewis, 1991; Leewis & Waardenburg, 1991; Leewis et al., 2000)

A total of 21 shipwrecks (depth: 14-34 m) in the Netherlands waters were visited during the summer months. From video images, the cover of the major communities was estimated:

- *Metridium senile* community (37%)
  This species excluded nearly all other species and was particularly obvious on horizontal surfaces, but not exclusively.

- Tube dwelling amphipod community (32%)
  This community was dominated by *Jassa* spp. but *Corophium* spp. were also involved. These species build tubes made of silt and detritus. The thickness of the tube layer ranged from 1 mm to 10 cm. On horizontal surfaces, the sea anemone *Sagartia troglotydes* (Price *in* Johnston) was thriving between the tubes.

- *Halicondria panicea* (Pallas) community (11%)
  It was predominantly found on vertical surfaces. The sea anemones *Diadumene cincta* and *Sagartia troglodytes*, caprellidae and *Ophiothrix fragilis* were associated with this sponge.

- Another 10% was dominated by *Hydractinia echinata*, *Diadumene cincta*, *Tubularia larynx* and *Tubularia indivisa*
  The athecata *Hydractinia echinata* sometimes covered large surface (up to several m^2) on protruding structures. This species excluded all others except the nudribranch *Cuthona nana* (Alder & Hancock) which feeds on it.
  Tubularia sp. were mainly early colonizers and found occasionally on matured sites.

- A final 21 species made up nearly 5% of the remaining cover and the final 5% were uncovered surfaces.

Spatial analysis of the sites distinguished a group of shipwrecks located in coastal waters (characterizing species: *Halichondria panicea* and *Hyas araneus* (L.)) and a group of offshore sites (*Sagartia elegans* (Dalyell), *Urticina felina*, *Alcyonium digitatum*, *Psammechinus miliaris* (Gmelin) and *Pomatoceros triqueter*). A further gradient running from south to north was observed: in the southern group, *Sagartiogeton undatum* (Müller), *Gadus morhua* and *Hyas araneus* were absent while the northern group missed *Ophiothrix fragilis*, *Haliclona oculata* (Pallas) and *Hyas coarctatus*. Temporal variation in species presence and abundance was linked to particularly cold winters. *Sagartia elegans*, *Pomatoceros triqueter*, *Pisidia longicornis*, *Galathea squamifera* Leach, *Diplosoma listerianum* (Milne-Edwards), *Aplidium glabrum* (Verrill), *Liocarcinus puber* (L.) and *Ophiothrix fragilis* showed marked decrease in abundance after cold winter.

Summary on temperate epifaunal communities

All structures at sea, being purposely deployed or not, will rapidly develop a fouling community. Stable communities are unlikely to develop where scours by sand will be a recurrent action (close to the seabed where wave action and/or currents are prevailing). Marine growth will start with fast colonizing species producing a large number of planktonic larvae that are fast growing when settled even if this last point is not always evident. They are typically represented by algae, barnacles and mussels in the intertidal and shallow sublittoral. In deeper water, the keeled tubeworm *Pomatoceros triqueter*, encrusting seamats and barnacles are generally the first settlers. Where sand scour occurs, the community could be characterized by the ross worm *Sabellaria spinulosa*. In the following year, the first settler will be overgrown by a set of new species. The algae of the euphotic zone will diversify and mussels will often expand. In the aphotic zone, a set of hydrozoans (*Tubularia* spp., *Obelia* spp.), anthozoans (*Metridium senile*, *Alcyonium digitatum*, and also *Sagartia* spp.), tunicates (*Ciona intestinalis*, *Botryllus schlosseri*) and bryozoans (*Electra pilosa*) will develop. These key species (i.e. cnidarians and bryozoans) will allow the settlement of many other sessile and slow moving epifauna like annelids and amphipods (tube building of the genus *Jassa* and caprellids species). Species specific colonization will depend mainly on depth to the seabed, degree of scour and geographical location. Close to the coast, *Metridium senile* is often found dominating while its distribution further offshore is patchier. The community will mature with the development of long-lived species like sponges. The time required to reach a fully mature community is not known with precision since most of the studies either worked on the first years (maximum five) after deployment or on very old structures (shipwrecks). However, there is a general agreement to suggest that, after a time of five to ten years, no more profound changes in the constituted community will be observed.

Synopsis of sessile and slow moving taxa typical of temperate fouling assemblages

In the North Atlantic waters (Europe and USA) and in the Mediterranean Sea, a set of sessile and slow moving taxa are recurrently associated with artificial habitats. We screened the major papers dealing with these assemblages on temperate waters and extracted the set of taxa which were found in several locations (Table 2). Picken (1986) states that by comparing the fouling of artificial structures in the North Sea, it seems that key species are common to many sites and may have a wide geographic and bathymetric range. This seems to be true even at larger scale than the North Sea. If the association is made at the genus level for many taxa, there are also species which are recurrently associated with artificial habitats like the hydrozoans *Bougainvillia ramosa*, *Clytia hemisphaerica* and *Obelia dichotoma*, the tube worms *Pomatoceros triqueter*, and the bivalves *Anomia ephippium*, *Mytilus edulis* and *Ostrea edulis*. The ability of these species to colonize artificial habitats is dependent on several characteristics: a free swimming larval phase, a sedentary adult form that can firmly adhere to substratum and an ability to extract organic material from the water column (Richmond & Seed, 1991). In addition, many non-sessile organisms are able to colonize artificial habitats and typically reside within the sessile biofouling community (Hughes *et al.*, 2005). Examples of these organisms are echinoderms, isopods, amphipods, errant polychaetes, crabs, shrimps and pycnogonids (Hughes *et al.*, 2005).

Their commonness resides certainly partly in their fast dispersal capabilities. However, all of these taxa do not have a planktonic dispersal capability. For example, the genus *Tubularia* produce a planula larvae which does not seem to possess large dispersal ability (Hughes, 1983). The genus *Jassa* and *Corophium* and the caprellids, like other amphipods, have a direct development. They must have used dispersal capability at another stage than during the larval phase.

Table 2. Sessile taxa associated with artificial hard habitats in temperate waters. The list originates from the review of the major part of the literature where taxa are mentioned on temperate artificial hard structures.

Taxa		Region
PORIFERA		
Clathrina sp.		Bal[5], Irl[40], Tyr[13]
Dysidea fragilis (Montagu, 1818)	●	Adr[29], Irl[40], UK[22,24]
Halichondria spp.	●	Adr[37,39], Den[31], Fra[30], Irl[40], Net[9], Pom[10], UK[7,24,26], USA[14,42]
Leucosolenia spp.		Irl[40], Tyr[12,23], UK[18,24], USA[42]
Sycon sp.	●	Adr[15,37,39], Bal[5], Fra[30], Irl[40], Tyr[12,13,19,23], UK[7,20,22,24], USA[42]
CNIDARIA		
Bougainvillia ramosa (van Beneden, 1844)		Adr[2], Irl[40],NS[27], Tyr[4,12,13], UK[26], USA[38]
Clytia hemisphaerica (Linnaeus, 1767)	●	Adr[2], Bal[5], Tyr[12,23], UK[24], USA[20]
Eudendrium sp.		Adr[29], Bal[5], Tur[1], Tyr[12,13,23], UK[24], USA[42]
Halecium halecinum (Linnaeus, 1767)	●	Irl[40], UK[7,18,24], USA[20]
Hydractinia echinata (Flemming, 1828)	●	Fra[30], Net[9]
Laomedea sp.		NS[27], Tyr[23], UK[18,24]
Obelia dichotoma (Linnaeus, 1758)	●	Adr[37], Bal[5], Can[36], NS[27], Tyr[4,12,13,23], UK[24,26], USA[20]
Sertularella sp.		Bal[5], Tyr[12], UK[18,22,24]
Tubularia spp.	●	Can[36], Fra[30], Net[8,9], NS[27], UK[7,24], USA[21,42]
Tubularia crocea Agassiz 1862		Adr[37,39], Tyr[12,13,23], USA[20,25,28,34,35,38]
Tubularia indivisa Linnaeus, 1758	●	Den[31],Fra[30], Irl[40], Net[8], UK[18,24]
Alcyonium digitatum Linnaeus, 1758	●	Net[8,9], NS[27], UK[24,26]
Metridium senile (Linnaeus, 1767)	●	Can[36], Den[31], Fra[30], Irl[40], Net[8,9], NS[27], UK[26], USA[17,20,21,25,28,42]

Table 2 continued

Taxa		Region
ANNELIDA		
Autolytus sp.	•	Adr[15], Tyr[19]
Filograna spp.		Bal[5], NS[27], Tyr[12,23], UK[22]
Harmothoe spp.	•	Adr[15], Can[36], Den[31], Tyr[4,19], USA[17,20]
Hydroides spp.		Adr[15,29,37], Tur[1], Tyr [4,12,13,19,23], UK[26,41], USA[14,34,42]
Nereis spp.	•	Adr[29], Can[36], NS[27], Pom[10], Tur[1], Tyr[12,19], USA[17,38]
Polydora ciliata Johnston, 1838		Adr[15], Tyr[4,19]
Polydora sp.		USA[21]
Pomatoceros triqueter (Linnaeus, 1767)	•	Adr[2,15,29,37], Bal[5], Den[31], Irl[40], Net[9],NS[27], Sic[3], Tur[1], Tyr[4,12,13,19,23], UK[18,22,24,26,41]
Sabellaria spinulosa Leuckaert, 1849	•	Den[31], Net[8], Tyr[4,19], UK[18,24]
Sabellaria vulgaris		USA[20,21,35,42]
Serpula spp.		Adr[15], Bal[5], Tyr[4,12,13,19,23]
CRUSTACEA		
Balanus spp.	•	Adr[2,29,37,39], Bal[5], Den[31], Fin[11], NS[27], Pom[10], Por[6], Tur[1], Tyr[4,12,13,15,19,23], UK[24,26,41], USA[14,17,20,34,42]
Caprellidae	•	Adr[39], Can[36], Den[31], Net[9], Pom[10], Tyr[12,13,23], UK[24], USA[20,21,28,35,38]
Corophium spp.	•	Adr[15,39], Gre[32], Net[9], Pom[10], Tyr[4,16], UK[24,33], USA[14,38]
Jassa spp.	•	Adr[39], Den[31], Fra[30], Gre[32], Net[9], NS[27], Tyr[16], UK[24,33]
Macropodia spp.	•	Tyr[19], UK[24]
Phtisica marina Slabber, 1769	•	Tyr[16], UK[24]
Pilumnus hirtellus (Linnaeus, 1761)	•	Adr[15], Tyr[16,19], UK[24]
Pisidia longicornis (Linnaeus, 1767)	•	Den[31], Fra[30], Net[9], UK[24]
Pisidia longimana (Risso, 1816)		Adr[15], Tyr[19]
Stenothoe spp.	•	Adr[39], Gre[32], Tyr[4,16], UK[33], USA[21,34,35,38]

Table 2 continued

Taxa		Region
PYCNOGONIDA		
Achelia echinata (Costa, 1861)	•	Tyr[19], UK[24]
MOLLUSCA		
Anomia ephippium (Linnaeus, 1758)	•	Adr[15],Bal[5], Fin[11], Irl[40], Pom[10], Por[6], Tur[1], Tyr[4,12,13,19,23,]
Chlamys varia		Adr[12,29], Tyr[12,19], UK[24]
Crassostea gigas (Thunberg, 1793)		Adr[2,37], Sic[3]
Mytilus edulis Linnaeus, 1758	•	Can[36], Den[31], Fin[11], Fra[30], Irl[40], Net[9], NS[27], Pom[10], UK[26], USA[14,17,20,21,28,34]
Mytilus galloprovincialis (Lamarck, 1819)		Adr[2,15,37,39], Tur[1], Tyr[4,12,13,19,23]
Ostrea edulis (Linnaeus, 1758)		Adr[2,29,37], Bal[5], Den[31], Sic[3], Tur[1] , Tyr[4,12,13,19,23], UK[24]
Nassarius reticulus (Linnaeus, 1758)	•	Adr[29], Bal[5], UK[24]
Nassarius incrassatus (Ström, 1768)	•	Adr[2,29], Tyr[4,19], UK[24]
BRYOZOA		
Bicellariella sp.	•	Irl[40], NS[27], UK[7,18,20,22,24]
Bowerbankia gracilis (Leidy, 1855)		Adr[37], Net[8], Tyr[12,23], USA[20,42]
Bugula spp.		Adr[2,37,39], Bal[5], Irl[40], NS[27], Sic[3], Tyr[12,23], UK[7,18,20,24], USA[20,21,42]
Electra pilosa (Linnaeus, 1767)	•	Irl[40], Net[8], NS[27], UK[24,26], USA[20]
Schizoporella spp.		Adr[2,29], Irl[40], Tur[1], Tyr[4,12,13,23], USA[20,42]
Scrupocellaria spp.	•	Adr[37], Bal[5], Irl[40], Tyr[4,12], UK[18,24]
ECHINODERMATA		
Amphipholis squamata (Delle Chiaje, 1829)	•	Adr[15], Can[36], UK[24]
ASCIDIACEA		
Aplidium spp.		Adr[29], Bal[5], UK[22,24]
Ascidia mentula (Müller, 1776)		Tur[1], UK[7,22,24]
Ascidiella aspersa (Müller, 1776)		Adr[29], Tyr[12,23], UK[18,24,26,41]
Botryllus schlosseri (Pallas, 1776)		Adr[37], Irl[40], Tyr[12,23], UK[22,24], USA[14,42]

Table 2 continued

Taxa		Region
Ciona intestinalis (Linnaeus, 1767)		Tyr[12,23], UK[24,26,41], USA[42]
Didemnum spp.		Adr[29], Bal[5], Irl[40], Tur[1], Tyr[12,13,23], UK[18,24], , USA[42]
Diplosoma spp.	●	Adr[29], Bal[5], Tyr[12,13,19], UK[24],
Molgula spp.	●	Adr[29,37,39], Tyr[23], UK[18,24], USA[14,20,34,42]

●: indicates that the taxa has been found in the present study.

Adr: Adriatic Sea (Italy), **Bal**: Balearic islands (Spain), **Can**: Atlantic coast of Canada, **Den**: Denmark, **Fra**: Atlantic coast of France, **Gre**: Greece Aegen Sea, **Irl**: South coast of Ireland, **Net**: The Netherlands, **NS**: North Sea, **Pom**: Pomerianan Bay (South Baltic), **Por**: Portugal, **Sic**: Sicily (Italy), **Tur**: Mediterranean coast of Turkey, **Tyr**: Tyrrhenian Sea (Italy), **UK**: United Kingdom, **USA**: Atlantic coast of United State of America.

[1] Lok & Tokac, 2000; [2] Bombace *et al.*, 2000; [3] D'Anna *et al.*, 2000; [4] Ardizzone *et al.*, 2000; [5] Moreno, 2000; [6] Monteiro & Santos, 2000; [7] Jensen *et al.*, 2000b; [8] Leewis & Hallie, 2000; [9] Leewis *et al.*, 2000; [10] Chojnacki, 2000; [11] Antsulevich *et al.*, 2000; [12] Relini, 2000a; [13] Relini, 2000b; [14] Otsuka & Dauer, 1982; [15] Ponti *et al.*, 2002; [16] Relini *et al.*, 2002a; [17] Steimle *et al.*, 2002; [18] Collins *et al.*, 2002a; [19] Ardizzone *et al.*, 1989; [20] Woodhead & Jacobson, 1985; [21] Foster *et al.*, 1994; [22] Jensen *et al.*, 1994; [23] Sampaolo & Relini, 1994; [24] Mallinson *et al.*, 1999; [25] Steimle & Zetlin, 2000; [26] Picken, 1986; [27] Forteath *et al.*, 1982; [28] Bulloch, 1965; [29] Gabriele *et al.*, 1999; [30] Müller, 2004; [31] Leonhard *et al.*, 2005; [32] Baxevanis & Chintiroglou, 2000; [33] Myers & Southgate, 1980; [34] Dean, 1981; [35] Hidu, 1978; [36] Claereboudt *et al.*, 1994; [37] Sconfietti & Marino, 1989; [38] Caine, 1987; [39] Sconfietti, 1983; [40] Watson & Barnes, 2004; [41] Brown, 2005; [42] Osman, 1977.

5.3.2.4 Comparison with natural reefs

It is essential to compare the communities (being focussed on fish or epifauna) which develop on artificial reefs with those from natural habitats. Most of the time, reefs have been deployed purposely and their performance has to be evaluated. For example, to determine how well artificial reefs mitigate for the losses due to human activities on natural reefs, their performance should be evaluated using contemporaneous comparisons with relatively undisturbed natural reef (Carr & Hixon, 1997).

Several studies compared epifauna from natural and artificial substrata (Myers & Southgate, 1980; Wendt *et al.*, 1989; Edgar, 1991; Aseltine-Neilson *et al.*, 1999; Gabriele *et al.*, 1999; Smith & Rule, 2002; Badalamenti *et al.*, 2002; Perkol-Finkel & Benayahu, 2004; Perkol-Finkel *et al.*, 2005). They all showed that natural and artificial reef epifauna were not similar, sometimes only because of species cover/dominance differences and not variations in species presence/absence (Myers & Southgate, 1980; Edgar, 1991). However, the age, size, environmental parameters and structure of both habitats were not always comparable (Gabriele *et al.*, 1999; Badalamenti *et al.*, 2002) leading to non interpretable results. It was also evident that the time of immersion was sometimes too short to allow a meaningful comparison of artificial and natural habitat (see the paper of Smith & Rule, 2002). An old shipwreck (119 years) in the Red Sea was compared with a natural reef and the results support that both habitats resemble only if both possess similar structural features. Wendt *et al.* (1989) studied the effect of age on the community structure of artificial reefs, but was unable to discern a pattern, maybe because the distance between these artificial reefs and natural reefs was not standardized. Some reefs were very close to natural hard substrates while other located a great distances. A general feeling more than a scientific proof exists that artificial reefs resemble more and more to natural communities with time (Aseltine-Neilson *et al.*, 1999; Svane & Petersen, 2001).

An interesting series of experimental work has been realized in Australia, on urban structures at sea. The communities of artificial substrata (pier pilings and pontoons) in a variety of marinas were compared to vertical natural rocky zones in the vicinity (Glasby, 1999a; Connell, 2000). It was found that these communities were dominated by very different species, suggesting that artificial substrata create a different habitat from the primary natural hard substrata. These differences were consistent with varying composition of

pier pilings, an indication that the substratum only was not responsible for the observed differences (Glasby, 1999a). The effect of substratum was afterwards formerly tested by providing substrata of two types (natural rock and concrete) in both habitats (natural rocky reef and pontoons) (Connell, 2000; Connell, 2001). The results indicated that the epibiotic assemblages were unaffected by the type of substratum but strongly affected by the type of habitat (i.e. natural *versus* artificial). Invocated reasons are the degrees of shading which is different on the two habitats and the position relative to the shore; samples were taken at the same depth but on pilling, it was well above the seafloor while close to it on natural rock (Glasby, 1999b).
It also appears that parameters such as orientation (vertical versus horizontal) have greater influence on biological diversity of epibiota on subtidal reefs than origin of reefs (natural versus artificial) (Connell, 1999; Knott *et al.*, 2004). Size and shape were also noted to be totally different on the two habitats. Urban structure may finally increase local biodiversity of subtidal epibiota in the shallow area, but are not a surrogate for natural substrata (Connell & Glasby, 1999).

Species assemblage on artificial reef will also be influenced by the regional species pool. This regional species pool is dependent on the range of habitats in the region, their extent and repartition. In area dominated by soft sediments and with few natural hard substrates, only the species with a high dispersal capacity will be able to easily colonize newly added hard substrates because they have to travel long distances before finding a suitable habitat to settle. Most of the species will have to recruit via the plankton while migration by adults will be an improbable event. It may limit the number of species which can be found in an artificial reef, at least in the period just after its submersion (Carter *et al.*, 1985). This is particularly true for algae species whose spore life span is very short (a few hours). In this case, the formal comparison with natural hard substrates is also problematic due to the lack of suitable habitat.

6. CONSEQUENCES OF THE PRESENCE OF ARTIFICIAL REEFS

The implantation of artificial reefs, being planned or unplanned, will have consequences on the chemical, physical and biological environment of the seabed. These effects are due to the sole structural presence of the reef and to its consequent biotic colonization. The socio-economic aspects of artificial reefs are beyond the scope of this review and will just be briefly mentioned.

6.1 Chemical interactions with the environment

A lot of different materials have been used as artificial reefs, all trying to maximize the following constrains: durability, safety, functionality and economy (Grove *et al.*, 1991). The chemical monitoring of these materials has been rarely followed. Recently, the construction of the Poole Bay artificial reef (UK) was made with cement-stabilized pulverized fuel ash (PFA) and flue gas desulphurization (FGD) gypsum derived from power stations (Jensen *et al.*, 1994; Collins *et al.*, 1994b; Jensen & Collins, 1995). The heavy metals are concentrated by the combustion process and may leach out. These studies followed the chemical composition and evolution (heavy metals: Cd, Cr, Cu, Pb, Mn, Ni, Zn) in both materials and in the epifauna. There have been no significant changes in heavy metal concentration in the blocks, except for cadmium which redistributed internally and leached out in small amount (<5% of total Cd). A surface enrichment of manganese and chromium is noted. Replacement of calcium by magnesium is evident in the first 2-4 cm of the blocks. No sign of bioaccumulation was suggested by the chemical analysis of the epifauna, compared to a nearby reference population growing on concrete. The same results were obtained with coal fly ash in concrete during two studies in the Mediterranean (Sampaolo & Relini, 1994; Kress *et al.*, 2002) and one in the West-Atlantic (Shieh & Duedall, 1994; Nelson *et al.*, 1994). Unfortunately, levels of Aluminium were not measured in the Poole Bay project. Kress *et al.* (2002) did measure Al concentrations on epifauna developing on coal-ash concrete but did not compare it to concentration in unexposed specimens and consequently did not allow for any conclusions to be drawn.

Similar experiments were carried out with scrap tyres in Poole Bay (Collins *et al.*, 2001a; Collins *et al.*, 2002a). One year after immersion, there was no indication of bioaccumulation of heavy metals in the epifauna.

6.2 Small-scale physical consequences on the environment

6.2.1 Local upwelling and pattern of water flows

The vertical water motion in coastal waters is generally negligible when compared to the horizontal movement. However, the presence of a reef in the flow can create a locally significant zone of upwelling. This can lead to the transport of sediment and nutrients from the bottom water column to the surface water (Sheng, 2000).

The presence of substrata such as reefs modifies the pattern of moving waters. In shallow waters, the interaction of a reef with a prevailing current usually results in the formation of a wake zone and eddies downstream of the reef (Sheng, 2000). This can alter the selection of the faunal feeding type (Baynes & Szmant, 1989; Leichter & Witman, 1997) and some species can be attracted either by relative calm or turbulent waters (Lindquist & Pietrafesa, 1989; Sheng, 2000). Vortices create low frequency vibrations which may act as stimuli for the attraction of pelagic fish (Ogawa & Kuroki, 1982 cited by Lindquist & Pietrafesa, 1989). Currents acceleration at the peaks/tops of varying obstacles ranging from hydroids to seamounts can induce increased secondary productivity due to current acceleration (Hughes, 1975; Genin *et al.*, 1986; Leichter & Witman, 1997).

6.2.2 Sediment resuspension/scouring

The presence of large reef structures in a coastal area with significant currents may create a downward flow adjacent to the upstream side of the reef structure. As the downstream current approaches the bottom, a horseshoe vortex is formed and may cause resuspension or scouring of sediment around the reef bottom (Sheng, 2000).

6.3 Ecological effects

6.3.1 Effects on existing habitats and species (excluding fish)

The placement of an artificial reef can damage the fauna by physical disturbance during operations and as a result of the existence of the reef (Hiscock *et al.*, 2002).

Artificial reefs will change the hydrodynamic regime in the sediment surrounding it. As a consequence, they can potentially alter species abundance and distribution through changes in current intensity and direction, erosion and sedimentation rates, grain-size distributions, organic content of sediments, and attraction of predators (Ambrose & Anderson, 1990; Hiscock *et al.*, 2002). Unfortunately, extensive multi-disciplinary research is most of the time only conducted post reef-deployment so that the baseline is missing (Wilding & Sayer, 2002a). Comparisons of sedimentology and benthic communities can always be achieved close to the reef and along a transect running from it to discern the effect of the reef. This effect can be limited in space (<20 m) (Ambrose & Anderson, 1990) or more dispersed (200 m) (Davis *et al.*, 1982) depending on the size and structure of the reef. The densities of the infauna species can be enhanced or depleted in their vicinity (Ambrose & Anderson, 1990). This may either be due to a change in sedimentology or to foraging of reef associated predators (Davis *et al.*, 1982; Ambrose & Anderson, 1990). These authors also note that the density of a tube-building annelid (*Diopatra* sp.) was by far enhanced by the presence of the reef and that the structure created by these tubes stabilizes the substratum, increasing local densities of benthos. Hiscock *et al.* (2002) note that another tube building annelid, *Sabella pavonina* Savigny, is often found associated with the coarse sediments present on contact with reefs. Jensen *et al.* (1994) did not find any evidence that the presence of the reef will create a 'feeding zone' of low abundance and diversity by grazing pressure of the infauna just around the reef (Poole Bay artificial reef (UK)). They rather observed that the most abundant fish species (pouting) feeds on *Crangon crangon* (L.) (a surface dwelling shrimp) and small crustaceans, an activity that is not susceptible to alter the infaunal population.

One study worked on the meiofauna around two reefs in the Adriatic and Tyrrhenian Sea (Italy) (Danovaro *et al.*, 2002). Environmental parameters and spatial distribution of the meiofauna were affected by the presence of the reef. Total densities inside the reef were significantly lower than on the control site 50 m from the reef. The highest densities were observed at intermediate sites (2 and 20 m from the reef). Nematodes dominated the samples. Although poorly detailed, the authors affirm that the meiofaunal composition was also affected by the reef, with potentially important implications for their secondary production and energy transfer to higher trophic levels.

The attraction of predators may have an impact on the fauna living around the reef. Davis *et al.* (1982) found that reef associated fish produced profound alteration of the epifaunal population around the reef. However, Ambrose & Anderson (1990) found no evidence that foraging by reef-associated predators caused a widespread reduction in infaunal densities. In fact, the most common taxa (*Spiophanes* spp.) had higher densities near the reef. A study around wind farms in Denmark showed than on average, the biomass of the infauna at the wind farm site was 60 times bigger than on the surrounding sediments (Leonhard *et al.*, 2005; Bech *et al.*, 2005). They concluded that this biomass could enhance fish production but without any substantial proof of it.

Caine (1987) argued that the implantation of floating docks and consequent fouling colonization on a South Carolina estuary could have a profound effect on the entire ecosystems because they are attracting a set of unusual species for the habitat (which is soft-sedimented). He estimated that the sessile species themselves were not susceptible to impact the habitat but that the attraction of motile species could: (1) increase the selective recruitment of motile species, (2) allow for the emigration of juveniles which preferentially settled on sessile species and (3) provide a food source for the nekton.

6.3.2 Addition of new habitat

The presence of an artificial reef will locally increase species richness by providing new settling hard surfaces. This effect will be even more pronounced if the reef lies on a soft sediment dominated area (Steimle & Zetlin, 2000). However, a concept linked to this increased biodiversity is naturalness. Its definition is still very ambiguous since it remains always arbitrary to decide where the action of man can be placed outside the range of what we call 'natural processes' (see Haydon (1997) for a thorough discussion). The species assemblages present on artificial reefs can be seen as exotic or non-native. This is especially true when hard structures are added to benthic communities mainly composed of soft sediments, but most of the time it is also the case when communities of artificial reefs can be compared to natural hard substrate. Generally, epifaunal communities have been found to be different on these two kinds of substrates (Aseltine-Neilson *et al.*, 1999; Badalamenti *et al.*, 2002; Edgar, 1991; Gabriele *et al.*, 1999; Myers & Southgate, 1980; Perkol-Finkel *et al.*, 2005; Perkol-Finkel & Benayahu, 2004; Smith & Rule, 2002; Wendt *et al.*, 1989). The question of protecting and promoting such kind of habitat must be carefully addressed in the light of the initial objectives. For example, the protection of shipwrecks from Belgian waters which lie in a sand dominated continental shelf is still being discussed. If a protection status is given only because it increases locally the biodiversity, the question of the naturalness of these communities (and so the local significance of the species which are present) needs to be put forward. However, a special status for these reefs could be decided for other reasons, for example because they have an impact on regional halieutic resources.

6.3.3 Attraction of fish

The popularity of artificial reef is firstly due to the fact that fish aggregate around them, making their capture easier. This established fact has long been granted for a sufficient proof that artificial reefs 'produce' fish (Lindberg, 1997). However, some scientists challenged that assumption by asking if artificial reefs actually produce more fish or simply aggregate them at specific sites (Bohnsack & Sutherland, 1985; Polovina, 1991). In this latter case, artificial reefs could have a negative impact on fish stocks by attracting and concentrating species that are already depleted by overfishing (Bohnsack, 1989). The construction of artificial reef will so merely cause a redistribution of existing biomass. The basic for challenging the production hypothesis is based on the following hypothesis (From Lindberg, 1997):

"Before reef fish were heavily exploited, the existing natural habitat supported an abundance of reef fish, presumably at or near carrying capacity. Fishing mortality then reduced stocks to some lower levels, yet the amount of natural habitat remained the same – still capable of supporting higher numbers. With fish stocks substantially below carrying capacity, the amount of hard bottom habitat could not be the factor limiting population size, in which case, the addition of artificial reefs would not benefit fish stocks by alleviating a limitation to produce more fish."

This issue became known as the attraction-production debate. Answering this question is not simple because of the high mobility of most fish and the large scale at which most fish population are distributed (Grossman *et al.*, 1997). To date, the most valuable paper dealing with this issue concluded that the huge artificial reef program in Japan increased the exploitable biomass and production only for octopus but not for flatfish (Polovina & Sakai, 1989; Polovina, 1991). Thus, if a species is limited by refuge availability, deployment of a reef with the appropriate refuge may result in increased regional production (Grossman *et al.*, 1997). This hypothesis has also been demonstrated on juvenile spiny lobsters in habitat limited environment (Briones-Fourzan & Lozano-Alvarez, 2001).

Actually, the attraction-production hypotheses are not mutually excluding and attraction-production probably interact via density-dependence in driving fish population dynamic (Osenberg *et al.*, 2002). The immediate effect of attraction is the reduction of fish densities (settlers, or juveniles, or adults) on natural reefs. Reduced density could easily lead to greater settlement or greater rates of production (via increased growth, survival or

reproduction) (Osenberg *et al.*, 2002). The two scenarios of either only-attraction or only-production are two extremes, with most real systems probably lying in between (Osenberg *et al.*, 2002).
From a biological perspective, artificial habitats may function in one or several of the following ways (Polovina, 1991):

1. It redistributes exploitable biomass
2. It increases exploitable biomass by aggregating previously unexploited biomass
3. It improves aspects of survival and growth, thereby providing new production

6.3.4 Summary of the ecological effects on living organisms

Even if unanswered questions regarding the implications of artificial reefs in the behaviour of fish remain, halieutic resources have been in the centre of the many research programmes around the world. Advances in the use of reef by fish have been achieved, but very often the question of fish production cannot be easily tackled.
The infauna of the surrounding sediments is affected by the presence of the reef itself, but the effect of the predators attracted by the reef on these sediments deserve further attention.
The epifauna of artificial reefs has been described in several papers. However, the role of these structures in the dissemination, repartition and genetic diversity of typically hard substrate species has never been addressed.

6.4 Social and economic effects

Unless the purpose of an artificial reef is for research or to mitigate environmental damages, most decision makers will judge the value or performance of a reef on its contribution to human satisfaction (Milon *et al.*, 2000). They primarily serve social functions by providing services or resources to different user groups. A set of methods exist to evaluate the social and economical effect of artificial reefs (Milon, 1991). These evaluations allow project administrators to judge the extent of social and economic change caused by a project and take decisions for future investments or legislation. Milon (1991) note that we have now some insights about the role of social evaluation methods in artificial habitats, but that it is also apparent that more evaluations are necessary and that their quality should be improved. Artificial habitats are susceptible to have a significant impact on professional and recreational fisheries as well as on commercial diving activities.

7. SHIPWRECKS AS ISOLATED ISLANDS

7.1 The theory of island biogeography

The theory of island biogeography (Mac Arthur & Wilson, 1967) was one of the most influential ideas regarding species diversity. It is known since the large prospectings of Darwin, Walace, Sclater and von Humboldt, that the number of species on islands is lower than on mainland with an equivalent area. The fundamental idea of this model is that the number of species on islands balances regional processes governing immigration/colonization against local processes governing extinction. Indeed, the further away an island is from the mainland, the less species will be able to colonize the island. The immigration rate depends on the dispersal capacity of taxa, the distance between the mainland and the island, and the dimension of the island. However, the colonization rate will be a function of other factors like the resources of the islands, its habitat diversity, and its resistance (competition and/or predation) to invasion. The model predicts also that the rate of colonization of new species will decrease as the number of species on the island increases and that the extinction rate will increase with this number. At the given period of its history, the number of species on an island will be at the equilibrium: the rate of colonization will be equal to the rate of extinction. This number is always under of the maximal richness that would be attained if all the mainland species succeeded in colonizing the island. The variables of the model are the size of the island and the distance from the source population. For a fixed degree of isolation, a large island will have a lower extinction rate than a small island (larger populations and more diversified habitats); for a fixed area and diversity of habitats, the immigration rate will be higher on a close island than for a remote place because the flux of propagules decreases with distance.

This model has been tested for a variety of taxa like birds, arthropods, mammals and was further used to describe and predict the consequences of the fragmentation of habitats on communities (see Blondel (1995) for a list of references). However, one of the central piece of this model, the renewal of species through colonization/extinction, has never been neither fully validated or invalidated (Blondel, 1995). What most ecologists have predicted, is that island size and distance to mainland may not be the only factors that influence species diversity patterns on islands (Ricklefs & Miller, 2000). Habitat structure and local populations influence colonization and extinction rate on islands as well.

The concept of islands is not only valid for oceanic islands but can be extended to any habitat isolated from the others by barriers which are difficult to get over. Examples are mountains summits, altitude lakes or even the body of human to be colonized by pathogens. Seamounts are another example isolated structure and the general featureless oceanic seabed. However, their isolation has been questioned since they were found to harbour a diversity which was not inferior to the nearest mainland (Gutt *et al.*, 2006). On seabeds dominated by soft sediments, shipwrecks could also be considered as isolated islands of hard substrates. The mainland is here the closer sources of hard bottoms, or the other shipwrecks if they can be considered as a source. The shipwrecks have a large variation in the two parameters of the island theory: they have different sizes and are located at varying distances from the source population. Consequently, they offer an opportunity to test for this model in the marine environment.

7.2 The paradox of Rockall

Rockall is a small and isolated island located in the North-East Atlantic, at 400 km from the Outer Hebrides, the nearest land in the area. Its littoral zone is exclusively composed of benthic species which lack a planktonic larva (Moore, 1977). This may look like a paradox, but Johannesson (1988) did provide supporting evidences that this was not such a surprising situation. The dispersal of planktotrophic larvae is generally considered as a more effective way of dispersal than direct development for benthic invertebrates. This is certainly true in the range of tens of kilometres. However, turbulent mixing and mortality during transportation will decrease the concentrations of propagules which will be able to settle in remote places. Consequently, the resulting density of settlers may be too low to sustain a viable population. Besides plankton transportation, adults, juveniles and eggs masses can drift over long distances and colonize new habitats (Johannesson, 1988; Thiel, 2003). Both species with direct and planktonic developments could use this dispersal behaviour, but if the founder species has a direct development or produce larvae with very short life-span, the low mobility of all life stages will maintain a population within a restricted area: the settlers will recruit in the same area than their parents and will not be lost by currents. This is less evident for founders with long planktonic stages. To illustrate its hypothesis, Johannesson (1988) took the example of two littoral gastropods (*Littorina saxatilis* and *L. littorea*) with similar niches in the shore and geographical distributions. *L. saxatilis* has a direct development and *L. litorea* a planktonic life of about four weeks. The first species is found on the mainland of North-East Atlantic, and also on many isolated islands in the area. However, *L. littorea* is absent from most of these islands. Another example is from breakwaters along the sandy Belgian coast which are the only available hard substrates in the area. *L. saxatilis* was able to colonize these substrates while *L. littorea* was not (Johannesson & Warmoes, 1990).

If shipwrecks can be considered as isolated spots of hard substrates, at least in some area, they could offer a nice opportunity for investigating the potential of different larval development for dispersal.

REFERENCES

Abelson, A. 2006. Artificial reefs vs coral transplantation as restoration tools for mitigating coral reef deterioration: Benefits, concerns, and proposed guidelines. *Bulletin of Marine Science*, **78**: 151-159.

Abelson, A. & Shlesinger, Y. 2002. Comparison of the development of coral and fish communities on rock-aggregated artificial reefs in Eilat, Red Sea. *ICES Journal of Marine Science*, **59**: S122-S126.

Acuna, N., Ortega-Morales, B.O. & Valadez-Gonzalez, A. 2006. Biofilm colonization dynamics and its influence on the corrosion resistance of austenitic UNSS31603 stainless steel exposed to Gulf of Mexico seawater. *Marine Biotechnology*, **8**: 62-70.

Allemand, D., DeBernardi, E. & Seaman, W. 2000. Artificial reefs in the Principality of Monaco: protection and enhancement of coastal zone. pp 151-166. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Ambrose, R.F. 1994. Mitigating the effects of a coastal power-plant on a kelp forest community - rationale and requirements for an artificial reef. *Bulletin of Marine Science*, **55**: 694-708.

Ambrose, R. F. & Anderson, T. W. 1990. The influence of an artificial reef on the surrounding infaunal community. *Marine Biology*, **107**: 41-52.

Angel, D.L. & Spanier, E. 2002. An application of artificial reefs to reduce organic enrichment caused by net-cage fish farming: preliminary results. *ICES Journal of Marine Science*, **59**: S324-S329.

Antsulevich, A.E. 1994. Artificial reefs project for improvement of water-quality and environmental enhancement of Neva Bay (St-Petersburg County Region). *Bulletin of Marine Science*, **55**: 1189-1192.

Antsulevich, A. E., Laihonen, P. & Vuorinen, I. 2000. Employment of artificial reefs for environmental maintenance in the Gulf of Finland. pp 319-329. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Ardizzone, G. D., Gravina, M. F. & Belluscio, A. 1989. Temporal development of epibenthic communities on artificial reefs in the central Mediterranean Sea. *Bulletin of Marine Science*, **44**: 592-608.

Ardizzone, G. D., Somaschini, A. & Belluscio, A. 2000. Prediction of benthic and fish colonization on the Fregene and other Mediterranean artificial reefs. pp 113-128. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Aseltine-Neilson, D.A., Bernstein, B.B., Palmer-Zwahlen, M.L., Riege, L.E. & Smith, R.W. 1999. Comparisons of turf communities from Pendleton Artificial Reef, Torrey Pines Artificial Reef, and a natural reef using multivariate techniques. *Bulletin of Marine Science*, **65**: 37-57.

Augris, C., Clabaut, P., Tessier, B., and Carré, D. 1995. The coastal area of Nord-Pas de Calais (France), superficial geology map. Editions IFREMER, région Nord - Pas de Calais.

Ayukai, T. 1995. Retention of phytoplankton and planktonic microbes on coral reefs within the Great Barrier Reef, Australia. *Coral Reefs*, **14**: 141-147.

Badalamenti, F., Chemello, R., D'Anna, G., Ramos, P.H. & Riggio, S. 2002. Are artificial reefs comparable to neighbouring natural rocky areas? A mollusc case study in the Gulf of Castellammare (NW Sicily). *ICES Journal of Marine Science*, **59**: S127-S131.

Barnabé, G., Charbonnel, E., Marinaro, J.-Y., Ody, D. & Francour, P. 2000. Artificial reefs in France: analysis, assessments and prospects. pp 167-184. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Baxevanis, A. & Chintiroglou, C. 2000. Peracarida crustacean populations of the artificial hard - substratum in N. Michaniona (N. Aegean). *Belgian Journal of Zoology*, **130 (Sup.)**: 11-16.

Bayle-Sempere, J.T., Ramos-Espla, A.A. & Charton, J.A.G. 1994. Intra-annual variability of an artificial reef fish assemblage in the marine reserve of Tabarca (Alicante, Spain, Sw Mediterranean). *Bulletin of Marine Science*, **55**: 824-835.

Baynes, T. W. & Szmant, A. M. 1989. Effects of current on the sessile benthic community structure of an artificial reef. *Bulletin of Marine Science*, **44**: 545-566.

Bech, M., Frederiksen, R., Pedersen, J. & Leonhard, S. B. 2005. Infauna Monitoring Horns Rev Offshore Wind Farm. Annual status report 2004. Bio/consult as, Copenhague, Denmark, 64p.

Bergman, M. J. N. & Hup, M. 1992. Direct effects of beamtrawling on macrofauna in a sandy sediment in the southern North Sea. *ICES Journal of Marine Research*, **49**: 5-11.

Berntsen, J., Aksnes, D.L. & Foldvik, A. 2002. Production enhancement by artificial upwelling: a simulation study. *Hydrobiologia*, **484**: 177-190.

Blau, S.F. & Byersdorfer, S.C. 1994. Sausage-Shaped Artificial Collector Developed in Alaska to Study Young-Of-Year Red King Crabs. *Bulletin of Marine Science*, **55**: 878-886.

Blondel, J. 1995. Biogéographie. Approche écologique et évolutive. Collection d'écologie N°27, Masson, Paris, 297 pp.

Bohnsack, J.A. 1989. Are high-densities of fishes at artificial reefs the result of habitat limitation or behavioral preference. *Bulletin of Marine Science*, **44**: 631-645.

Bohnsack, J. A. 2005. Artificial reefs: paradise found or lost. Proceedings of the 8th International Conference on Artificial Reefs and Habitats, Biloxi, USA2-.

Bohnsack, J.A., Harper, D.E., Mcclellan, D.B. & Hulsbeck, M. 1994. Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, USA. *Bulletin of Marine Science*, **55**: 796-823.

Bohnsack, J. A., Johnson, D. L. & Ambrose, R. F. 1991. Ecology of artificial reef habitats and fishes. pp 61-107. *In* Seaman, W. and Sprague, L. M. (eds), Artificial habitats for marine and freshwater fisheries, Academic Press, Inc., San-Diego, California.

Bohnsack, J. A. & Sutherland, J. P. 1985. Artificial reef research: a review with recommendations for future priorities. *Bulletin of Marine Science*, **37**: 11-39.

Bohnsack, J. A. & Talbot, F. H. 1980. Species-packing by reef fishes of Australian and Caribbean reefs: an experimental approach. *Bulletin of Marine Science*, **30**: 723-

Bombace, G. 1989. Artificial reefs in the Mediterranean-Sea. *Bulletin of Marine Science*, **44**: 1023-1032.

Bombace, G., Fabi, G. & Fiorentini, L. 2000. Artificial reefs in the Adriatic Sea. pp 31-63. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Bombace, G., Fabi, G., Fiorentini, L. & Speranza, S. 1994. Analysis of the efficacy of artificial reefs located in 5 different areas of the Adriatic Sea. *Bulletin of Marine Science*, **55**: 559-580.

Bortone, S.A. 2006. A perspective of artificial reef research: The past, present, and future. *Bulletin of Marine Science*, **78**: 1-8.

Boyd, S. E., Limpenny, D. S., Rees, H. L., Cooper, K. M. & Campbell, S. 2003. Preliminary observations of the effects of dredging intensity on the re-colonisation of dredged sediments off the southeast coast of England. *Estuarine, Coastal and Shelf Science*, **57**: 209-223.

Boyd, S. E. & Rees, H. L. 2003. An examination of the spatial scale of impact on the marine benthos arising from marine aggregate extraction in the central English Channel. *Estuarine, Coastal and Shelf Science*, **57**: 1-16.

Branden, K. L., Pollard, D. A. & Reimers, H. A. 1994. A review of recent artificial reef developments in Australia. *Bulletin of Marine Science*, **55**: 982-994.

Breslin, V. T., Roethel, F. J. & Schaeperkoetter, V. P. 1988. Physical and chemical interactions of stabilized incineration residue with the marine environment. *Marine Pollution Bulletin*, **19(11B)**: 628-632.

Briones-Fourzan, P. & Lozano-Alvarez, E. 2001. Effects of artificial shelters (Casitas) on the abundance and biomass of juvenile spiny lobsters *Panulirus argus* in a habitat-limited tropical reef lagoon. *Marine Ecology-Progress Series*, **221**: 221-232.

Brock, R.E. 1994. Beyond Fisheries Enhancement - Artificial Reefs and Ecotourism. *Bulletin of Marine Science*, **55**: 1181-1188.

Brown, C.J. 2005. Epifaunal colonization of the Loch Linnhe artificial reef: Influence of substratum on epifaunal assemblage structure. *Biofouling*, **21**: 73-85.

Bulloch, D. K. 1965. The development of the wreck *Pinta* as a marine habitat. *Underwater Naturalist.Bulletin of the American Littoral Society*, **31**: 17-32.

Burton, W.H., Farrar, J.S., Steimle, F. & Conlin, B. 2002. Assessment of out-of-kind mitigation success of an artificial reef deployed in Delaware Bay, USA. *ICES Journal of Marine Science*, **59**: S106-S110.

Cabioch, L. 1997. Les biocénoses subtidales macrobenthiques de la Manche, conditions écologiques et structure générale. pp 68-78. *In* Dauvin, J.-C. (ed), Les biocénoses marines et littorales françaises des côtes Atlantique, Manche et Mer du Nord, synthèse, menaces et perspectives, Collections Patrimoines Naturels, Vol 18, MNHN, Paris.

Caine, E.A. 1987. Potential effect of floating dock communities on a South Carolina estuary. *Journal of Experimental Marine Biology and Ecology*, **108**: 83-91.

Campos, J.A. & Gamboa, C. 1989. An artificial tire-reef in a tropical marine system - a management tool. *Bulletin of Marine Science*, **44**: 757-766.

Carr, M.H. & Hixon, M.A. 1997. Artificial reefs: the importance of comparisons with natural reefs. *Fisheries*, **22**: 28-33.

Carter, J. W., Carpenter, A. L., Foster, M. S. & Jessee, W. N. 1985. Benthic succession on an artifiacila reef designed to support a kelp-reef community. *Bulletin of Marine Science*, **37**: 86-113.

Caselle, J.E., Love, M.S., Fusaro, C. & Schroeder, D. 2002. Trash or habitat? Fish assemblages on offshore oilfield seafloor debris in the Santa Barbara Channel, California. *ICES Journal of Marine Science*, **59**: S258-S265.

Castric-Fey, A., Girard-Descatoire, A., Gentil, F., Davoult, D. & Dewarumez, J. M. 1997. Macrobenthos des substrats durs intertidaux et subtidaux. pp 83-95. *In* Dauvin, J.-C. (ed), Les biocénoses marines et littorales françaiss des côtes Atlantique, Manche et Mer du Nord, synthèse, menaces et perspectives, MNHN, Paris.

Charbonnel, E., Serre, C., Ruitton, S., Harmelin, J.G. & Jensen, A. 2002. Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). *ICES Journal of Marine Science*, **59**: S208-S213.

Chen, J. 2003. Aperçu des méthodes d'aquaculture et de mariculture d'holoturies en Chine. *La Bêche-de-mer*, **18**: 18-23.

Cheney, D., Oestman, R., Volkhardt, G. & Getz, J. 1994. Creation of rocky intertidal and shallow subtidal habitats to mitigate for the construction of a large marina in Puget-Sound, Washington. *Bulletin of Marine Science*, **55**: 772-782.

Chojnacki, J. C. 2000. Environmental effects of artificial reefs in the Southern Baltic (Pomeranian Bay). pp 307-317. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Chou, W.R., Tew, K.S. & Fang, L.S. 2002. Long-term monitoring of the demersal fish community in a steel-slag disposal area in the coastal waters of Kaohsiung, Taiwan. *ICES Journal of Marine Science*, **59**: S238-S242.

Claereboudt, M.R., Bureau, D., Cote, J. & Himmelman, J.H. 1994. Fouling development and its effect on the growth of juvenile giant scallops

(*Placopecten magellanicus*) in suspended culture. *Aquaculture*, **121**: 327-342.

Clark, S. & Edwards, A.J. 1999. An evaluation of artificial reef structures as tools for marine habitat rehabilitation in the Maldives. *Aquatic Conservation - Marine and Freshwater Ecosystems*, **9**: 5-21.

Clark, W., Mosely, J. & Stone, R. B. 1974. Foreword. *In* Colunga, L. and Stone, R. B. (eds), 1st International Conference on Artificial Reefs and Habitats, pp 3, Texas A & M Sea Grant College, USA.

Collins, K.J., Jensen, A.C., Lockwood, A.P.M. & Lockwood, S.J. 1994a. Coastal structures, waste materials and fishery enhancement. *Bulletin of Marine Science*, **55**: 1240-1250.

Collins, K.J., Jensen, A.C., Lockwood, A.P.M. & Turnpenny, A.W.H. 1994b. Evaluation of stabilized coal-fired power-station waste for artificial reef construction. *Bulletin of Marine Science*, **55**: 1251-1262.

Collins, K. J., Jensen, A. C., Mallinson, J. J., Mudge, S. M., Russel, A. & Smith, I. P. 2001a. Scrap tyres for marine construction: environmental impact. pp 149-162. *In* Dhir, R. K., Limbachiyya, M. C., and Paine, K. A. (eds), Recycling and reuse of used tyres, Thomas Telford Publisher, London.

Collins, K.J., Jensen, A.C., Mallinson, J.J., Roenelle, V. & Smith, I.P. 2002a. Environmental impact assessment of a scrap tyre artificial reef. *ICES Journal of Marine Science*, **59**: S243-S249.

Collins, K.J., Jensen, A.C. & Smith, I.P. 2002b. Oxygen fluxes of enclosed reef epibiota communities. *ICES Journal of Marine Science*, **59**: S94-S99.

Collins, K.J., Smith, I.P., Jensen, A.C., Addison, J.T. & Bannister, R.C.A. 2001b. Measuring lobster (*Homarus gammarus* (L.)) catchability using electromagnetic telemetry. 185-192.

Compere, C., Bellon-Fontaine, M.N., Bertrand, P., Costa, D., Marcus, P., Poleunis, C., Pradier, C.M., Rondot, B. & Walls, M.G. 2001. Kinetics of conditioning layer formation on stainless steel immersed in seawater. *Biofouling*, **17**: 129-145.

Connell, S.D. 1999. Effects of surface orientation on the cover of epibiota. *Biofouling*, **14**: 219-226.

Connell, S.D. 2000. Floating pontoons create novel habitats for subtidal epibiota. *Journal of Experimental Marine Biology and Ecology*, **247**: 183-194.

Connell, S.D. 2001. Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. *Marine Environmental Research*, **52**: 115-125.

Connell, S.D. & Glasby, T.M. 1999. Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Marine Environmental Research*, **47**: 373-388.

Covich, A.P., Austen, M.C., Barlocher, F., Chauvet, E., Cardinale, B.J., Biles, C.L., Inchausti, P., Dangles, O., Solan, M., Gessner, M.O., Statzner, B. & Moss, B.

2004. The role of Biodiversity in the functioning of freshwater and marine benthic ecosystems. *Bioscience*, **54**: 767-775.

Cripps, S.J. & Aabel, J.P. 2002. Environmental and socio-economic impact assessment of Ekoreef, a multiple platform rigs-to-reefs development. *ICES Journal of Marine Science*, **59**: S300-S308.

D'Anna, G., Badalamenti, F. & Riggio, S. 2000. Artificial reefs in North West Sicily: comparisons and conclusions. pp 97-112. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Danner, E. M., Wilson, T. C. & Schlotterbeck, R. E. 1994. Comparison of rockfish recruitment of neashore artificial and natural reefs off the coast of central California. *Bulletin of Marine Science*, **55**: 333-343.

Danovaro, R., Gambi, C., Mazzola, A. & Mirto, S. 2002. Influence of artificial reefs on the surrounding infauna: analysis of meiofauna. *ICES Journal of Marine Science*, **59**: S356-S362.

Davis, N., VanBlaricom, G. R. & Dayton, P. K. 1982. Man-made structures on marine sediments: effects on adjacent benthic communities. *Marine Biology*, **70**: 295-303.

Davoult, D., Dewarumez, J. M., Prygiel, J. & Richard, A. 1988. Carte des peuplements benthiques de la partie française de la Mer du Nord. *Comptes Rendus de l'Académie des Sciences, Série III*, **306**: 5-10.

Dean, T. A. 1981. Structural aspect of sessile invertebrates as organizing forces in an estuarine fouling community. *Journal of Experimental Marine Biology and Ecology*, **53**: 163-180.

DeBernardi, E. 1989. The Monaco underwater reserve-design and construction of artificial reefs (*Abstract*). *Bulletin of Marine Science*, **44**: 1066-1066.

Demartini, E.E., Roberts, D.A. & Anderson, T.W. 1989. Contrasting patterns of fish density and abundance at an artificial rock reef and a cobble bottom kelp forest. *Bulletin of Marine Science*, **44**: 881-892.

Deysher, L.E., Dean, T.A., Grove, R.S. & Jahn, A. 2002. Design considerations for an artificial reef to grow giant kelp (*Macrocystis pyrifera*) in Southern California. *ICES Journal of Marine Science*, **59**: S201-S207.

Ditton, R.B., Osburn, H.R., Baker, T.L. & Thailing, C.E. 2002. Demographics, attitudes, and reef management preferences of sport divers in offshore Texas waters. *ICES Journal of Marine Science*, **59**: S186-S191.

Dolmer, P. 2000. Algal concentration profiles above mussel beds. *Journal of Sea Research*, **43**: 113-119.

Doody, J. P., Johnston, C. & Smith, B. 1993. Directory of the North Sea coastal margin. Joint Nature Conservation Committee, Peterborough, UK, 262 pp.

Duzbastilar, F.O., Lok, A., Ulas, A. & Metin, C. 2006. Recent developments on artificial reef applications in Turkey: Hydraulic experiments. *Bulletin of Marine Science*, **78**: 195-202.

Eashwar, M., Subramanian, G., Chandrasekaran, P. & Balakrishnan, K. 1992. Mechanism for barnacle-induced crevice corrosion in stainless-steel. *Corrosion*, **48**: 608-612.

Edgar, G. J. 1991. Artificial algae as habitats for mobile epifauna: factors affecting the colonization in a Japanese *Sargassum* bed. *Hydrobiologia*, **226**: 111-118.

Engel, J. & Kvitek, R. 1998. Effects of otter trawling on a benthic community in monterey bay national marine sanctuary. *Conservation Biology*, **12**: 1204-1214.

Fabi, G. & Fiorentini, L. 1994. Comparison between an artificial reef and a control site in the Adriatic Sea - Analysis of 4 years of monitoring. *Bulletin of Marine Science*, **55**: 538-558.

Fabi, G., Grati, F., Lucchetti, A. & Trovarelli, L. 2002. Evolution of the fish assemblage around a gas platform in the northern Adriatic Sea. *ICES Journal of Marine Science*, **59**: S309-S315.

Fabi, G., Grati, F., Puletti, M. & Scarcella, G. 2004. Effects on fish community induced by installation of two gas platforms in the Adriatic Sea. *Marine Ecology-Progress Series*, **273**: 187-197.

Fabi, G., Manoukian, S. & Spagnolo, A. 2006. Feeding behavior of three common fishes at an artificial reef in the northern Adriatic Sea. *Bulletin of Marine Science*, **78**: 39-56.

Falace, A., Zanelli, E. & Bressan, G. 2006. Algal transplantation as a potential tool for artificial reef management and environmental mitigation. *Bulletin of Marine Science*, **78**: 161-166.

Forteath, G. N. R., Picken, G. B., Ralph, R. & Williams, J. 1982. Marine growth studies on the North Sea oil platform Montrose Alpha. *Marine Ecology-Progress Series*, **8**: 61-68.

Foster, K.L., Steimle, F.W., Muir, W.C., Kropp, R.K. & Conlin, B.E. 1994. Mitigation potential of habitat replacement - concrete artificial reef in Delaware Bay - preliminary results. *Bulletin of Marine Science*, **55**: 783-795.

Frazer, T.K. & Lindberg, W.J. 1994. Refuge spacing similarly affects reef-associated species from 3 Phyla. *Bulletin of Marine Science*, **55**: 388-400.

Freese, L., Auster, P. J., Heifetz, J. & Wing, B. L. 1999. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. *Marine Ecology-Progress Series*, **182**: 119-126.

Freese, L., Auster, P. J., Heifetz, J. & Wing, B. L. 2005. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. *Marine Ecology-Progress Series*, **182**: 119-126.

Frumkes, D.R. 2002. The status of the California rigs-to-reefs Programme and the need to limit consumptive fishing activities. *ICES Journal of Marine Science*, **59**: S272-S276.

Gabriele, M., Bellot, A., Gallotti, D. & Brunetti, R. 1999. Sublittoral hard substrate communities of the northern Adriatic Sea. *Cahiers de Biologie Marine*, **40**: 65-76.

Galgani, F., Leaute, J.P., Moguedet, P., Souplet, A., Verin, Y., Carpentier, A., Goraguer, H., Latrouite, D., Andral, B. & Cadiou, Y. 2000. Litter on the sea floor along European coasts. *Marine Pollution Bulletin*, **40**: 516-527.

Gardiner, C.P. & Melchers, R.E. 2003. Corrosion analysis of bulk carriers, Part I: operational parameters influencing corrosion rates. *Marine Structures*, **16**: 547-566.

Gaston, K.J. 2000. Global patterns in biodiversity. *Nature*, **405**: 220-227.

Genin, A., Dayton, P. K., Londsale, P. F. & Spiess, F. N. 1986. Coral on seamount peaks provide evidence of current acceleration over deep topography. *Nature*, **322**: 59-61.

Glasby, T.M. 1999a. Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia. *Estuarine, Coastal and Shelf Science*, **48**: 281-290.

Glasby, T.M. 1999b. Effects of shading on subtidal epibiotic assemblages. *Journal of Experimental Marine Biology and Ecology*, **234**: 275-290.

Glasby, T.M. 2001. Development of sessile marine assemblages on fixed versus moving substrata. *Marine Ecology-Progress Series*, **215**: 37-47.

Gomez-Buckley, M.C. & Haroun, R.J. 1994. Artificial reefs in the Spanish coastal zone. *Bulletin of Marine Science*, **55**: 1021-1028.

Gorham, J.C. & Alevizon, W.S. 1989. Habitat complexity and the abundance of juvenile fishes residing on small-scale artificial reefs. *Bulletin of Marine Science*, **44**: 662-665.

Grossman, G. D., Jones, G. P. & William, J. S. 1997. Do artificial reefs increase regional fish production? A review of existing data. *Fisheries*, **22**: 17-23.

Grove, R.S., Nakamura, M., Kakimoto, H. & Sonu, C.J. 1994. Aquatic habitat technology innovation in Japan. *Bulletin of Marine Science*, **55**: 276-294.

Grove, R.S., Sonu, C.J. & Nakamura, M. 1989. Recent Japanese trends in fishing reef design and planning. *Bulletin of Marine Science*, **44**: 984-996.

Grove, R. S., Sonu, C. J. & Nakamura, M. 1991. Design and Engineering of Manufactured Habitats for Fisheries Enhancement. pp 109-152. *In* Seaman, W. and Sprague, L. M. (eds), Artificial Habitats for Marine and Freshwater Fisheries, Academic Press, Inc., San Diego.

Grove, R.S. & Wilson, C.A. 1994. 5Th International-Conference on Aquatic Habitat Enhancement, 3-7 November 1991, Long-Beach, California, Usa - Introduction. *Bulletin of Marine Science*, **55**: 265-267.

Guidetti, P., Verginella, L., Viva, C., Odorico, R. & Boero, F. 2005. Protection effects on fish assemblages, and comparison of two visual-census techniques in shallow artificial rocky habitats in the northern Adriatic Sea. *Journal of the Marine Biological Association of the UK*, **85**: 247-255.

Guillen, J.E., Ramos, A.A., Martinez, L. & Lizaso, J.L.S. 1994. Antitrawling reefs and the protection of *Posidonia oceanica* (L) Delile meadows in the Western Mediterranean Sea - Demand and aims. *Bulletin of Marine Science*, **55**: 645-650.

Gutt, J., Fricke, A., Teixido, N., Potthoff, M. & Arntz, W.E. 2006. Mega-epibenthos at Bouvet Island (South Atlantic): a spatially isolated biodiversity hot spot on a tiny geological spot. *Polar Biology*, **29**: 97-105.

Hall, S. J., Robertson, M. R., Basford, D. & Heaney, S. D. 1993. The possible effect of fishing disturbance in the northern North Sea: an analysis of spatial patterns in community structure around a wreck. *Netherlands Journal of Sea Research*, **31**: 201-208.

Hamer, B., Gardner, J. & Runcie, R. 2000. Physical protection of the seabed and coast by artificial reefs. pp 403-417. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Haroun, R.J., Gomez, M., Hernandez, J.J., Herrera, R., Montero, D., Moreno, T., Portillo, A., Torres, M.E. & Soler, E. 1994. Environmental description of an artificial reef site in Gran Canaria (Canary Islands, Spain) prior to reef placement. *Bulletin of Marine Science*, **55**: 932-938.

Haroun, R. J. & Herrera, R. 2000. Artificial reefs of the Canary Islands. pp 235-247. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Hatcher, A.M. 1997. Comparison of biomass and percentage cover of sessile epibiota on the Poole Bay artificial reef. *Ophelia*, **47**: 55-62.

Hatcher, A.M. 1998. Epibenthic colonisation patterns on slabs of stabilised coal-waste in Pools Bay, UK. *Hydrobiologia*, **367**: 153-162.

Haydon, R. J. 1997. The concept of naturalness in natural resource and ecosystem management. Thesis Presented to The Graduate Faculty Central Washington University, 221 pp (Available online at http://members.tripod.com/haydon4/id17.htm).

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S. & Lawton, J.H. 1999. Plant diversity and productivity experiments in European grasslands. *Science*, **286**: 1123-1127.

Helvey, M. 2002. Are southern California oil and gas platforms essential fish habitat? *ICES Journal of Marine Science*, **59**: S266-S271.

Herrera, R., Espino, F., Garrido, M. & Haroun, R.J. 2002. Observations on fish colonization and predation on two artificial reefs in the Canary Islands. *ICES Journal of Marine Science*, **59**: S69-S73.

Heywood, V. H. 1995. Global biodiversity assessment. Cambridge University Press, Cambridge, UK.

Hidu, H. 1978. Settling of estuarine invertebrates in Delaware Bay, New Jersey, related to intertidal-subtidal gradients. *Internationale Revue der Gesamten Hydrobiologie*, **63**: 637-661.

Hiscock, K. 1980. Marine life on the wreck of the M.V. 'Robert'. *Report of the Lundy Field Society*, **32**: 40-44.

Hiscock, K., Tyler-Walters, H. & Jones, H. 2002. High level environmental screening study for offshore wind farm developments - Marine habitats and species project. Report from the Marine Biological Association to The Department of Trade and Industry New & Renewable Energy Programme, 92p + annexes.

Holbrook, S.J., Reed, D.C. & Bull, J.S. 2002. Survival experiments with outplanted seedlings of surfgrass (*Phyllospadix torreyi*) to enhance establishment on artificial structures. *ICES Journal of Marine Science*, **59**: S350-S355.

Houbolt, J. J. H. C. 1968. Recent sediments in the Southern Bight of the North Sea. *Geologie en Mijnbouw*, **47**: 245-273.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ, 448 pp.

Hueckel, G.J., Buckley, R.M. & Benson, B.L. 1989. Mitigating rocky habitat loss using artificial reefs. *Bulletin of Marine Science*, **44**: 913-922.

Hughes, D.J., Cook, E.J. & Sayer, M.D.J. 2005. Biofiltration and biofouling on artificial structures in Europe: The potential for mitigating organic impacts. *Oceanography and Marine Biology - An Annual Review*, **43**: 123-172.

Hughes, R. G. 1975. The distribution of epizoites on the hydroid *Nemertesia antennina* (L.). *Journal of the Marine Biological Association of the UK*, **55**: 275-294.

Hughes, R.G. 1983. The life-history of *Tubularia indivisa* (Hydrozoa: Tubulariidae) with observations on the status of *T. ceratogyne*. *Journal of the Marine Biological Association of the UK*, **63**: 467-479.

Hyde, K.D., Jones, G.E.B., Leano, E., Pointing, S.B., Poonyth, A.D. & Vrijmoed, L.L.P. 1998. Role of fungi in marine ecosystems. *Biodiversity and Conservation*, **7**: 1147-1161.

Japan Coastal Fisheries Promotion Association 1986. Coastal Fisheries Development Program structural design guide ("Engan-Gyojo Seibi-Kaihatsu-Jigyo Kozobutsu-Sekkei-Shishin"). In Japanese.

Jara, F. & Cespedes, R. 1994. An experimental evaluation of habitat enhancement on homogeneous marine bottoms in Southern Chile. *Bulletin of Marine Science*, **55**: 295-307.

Jensen, A. 1998. Final report of the European Artificial Reef Research Network (EARRN). SUDO/TEC/98/11, Southampton, UK, 18 pp.

Jensen, A. 2002a. Artificial reefs of Europe: perspective and future. *ICES Journal of Marine Science*, **59**: S3-S13.

Jensen, A., Collins, K. J. & Lockwood, P. 2000a. Current issues relating to artificial reefs in European Seas. pp 489-499. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Jensen, A., Collins, K. J. & Smith, P. 2000b. The Poole Bay artificial reef project. pp 263-287. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Jensen, A., Wickins, J. & Bannister, C. 2000c. The potential use of artificial reefs to enhance lobster habitats. pp 379-401. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Jensen, A. C. & Collins, K. J. 1995. The Poole Bay artificial reef project 1989 to 1994. *Biologia Marina Mediterranea*, **2**: 111-122.

Jensen, A.C. 2002b. The Seventh International Conference on Artificial Reefs and Related Aquatic Habitats. *ICES Journal of Marine Science*, **59**: S1-S2.

Jensen, A.C., Collins, K.J., Lockwood, A.P.M., Mallinson, J.J. & Turnpenny, W.H. 1994. Colonization and fishery potential of a coal-ash artificial reef, Poole-Bay, United-Kingdom. *Bulletin of Marine Science*, **55**: 1263-1276.

Johannesson, K. 1988. The paradox of Rockall: why is a brodding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*). *Marine Biology*, **99**: 507-513.

Johannesson, K. & Warmoes, T. 1990. Rapid colonization of belgian breakwaters by the direct developer, *Littorina saxatilis* (Olivi) (Prosobranchia, Mollusca). *Hydrobiologia*, **193**: 99-108.

Johnson, T.D., Barnett, A.M., Demartini, E.E., Craft, L.L., Ambrose, R.F. & Purcell, L.J. 1994. Fish production and habitat utilization on a Southern California artificial reef. *Bulletin of Marine Science*, **55**: 709-723.

Jones, L. A., Coyle, M. D., Evans, D., Gilliland, P. M. & Murray, A. R. 2004. Southern North Sea Marine Natural Area Profile: a contribution to regional planning and management of the seas around England. English Nature, Peterborough, UK, 102 pp.

Jorgensen, T., Lokkeborg, S. & Soldal, A.V. 2002. Residence of fish in the vicinity of a decommissioned oil platform in the North Sea. *ICES Journal of Marine Science*, **59**: S288-S293.

Kaiser, M.J. & Pulsipher, A.G. 2005. Rigs-to-reef programs in the Gulf of Mexico. *Ocean Development and International Law*, **36**: 119-134.

Kaiser, M.J., Spence, F.E. & Hart, P.J.B. 2000. Fishing-gear restrictions and conservation of benthic habitat complexity. *Conservation Biology*, **14**: 1512-1525.

Kerckhof, F. & Houziaux, J.-S. 2003. Biodiversity of the Belgian marine areas. pp 350-389. *In* Peeters, M., Franklin, A., and Van Goethem, J. L. (eds), Biodiversity in Belgium, Royal Belgian Institute of Natural Sciences, Brussels.

Kim, C.G. 2001. Artificial reefs in Korea. *Fisheries*, **26**: 15-18.

Kim, C.G., Lee, J.W. & Park, J.S. 1994. Artificial reef designs for Korean coastal waters. *Bulletin of Marine Science*, **55**: 858-866.

Kirke, B. 2003. Enhancing fish stocks with wave-powered artificial upwelling. *Ocean and Coastal Management*, **46**: 901-915.

Knott, N.A., Underwood, A.J., Chapman, M.G. & Glasby, T.M. 2004. Epibiota on vertical and on horizontal surfaces on natural reefs and on artificial structures. *Journal of the Marine Biological Association of the UK*, **84**: 1117-1130.

Koryakova, M.D., Filonenko, N.Y. & Kaplin, Y.M. 1995. Barnacle-induced corrosion of high-alloyed steels. *Protection of Metals*, **31**: 200-202.

Kress, N., Tom, M. & Spanier, E. 2002. The use of coal fly ash in concrete for marine artificial reefs in the southeastern Mediterranean: compressive strength, sessile biota, and chemical composition. *ICES Journal of Marine Science*, **59**: S231-S237.

Leewis, R. J. 1991. Environmental impact of shipwrecks in the North Sea. II. Negative aspects: hazardous substances in shipwrecks. *Water Science Technology*, **24**: 299-300.

Leewis, R. J. & Hallie, F. 2000. An artificial reef experiment off the Dutch Coast. pp 289-306. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Leewis, R. J., van Moorsel, G. W. N. M. & Waardenburg, H. W. 2000. Shipwrecks on the Dutch Continental Shelf as artificial reefs. pp 419-434. *In* Jensen, A. C, Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publishers, Dordrecht.

Leewis, R. J. & Waardenburg, H. W. 1991. Environmental impact of shipwrecks in the North Sea. I. Positive effects: epifauna of North Sea shipwrecks. *Water Science Technology*, **24**: 297-298.

Leeworthy, V.R., Maher, T. & Stone, E.A. 2006. Can artificial reefs alter user pressure on adjacent natural reefs? *Bulletin of Marine Science*, **78**: 29-38.

Leichter, J.J. & Witman, J.D. 1997. Water flow over subtidal rock walls: Relation to distributions and growth rates of sessile suspension feeders in the Gulf of Maine - Water flow and growth rates. *Journal of Experimental Marine Biology and Ecology*, **209**: 293-307.

Leonhard, S. B., Pedersen, J. & Moeslund, B. 2004. Hard bottom substrate monitoring. Horns Rev Offshore Wind Farm. Annual status report 2003. Bio/consult as, Copenhague, Denmark, 62 pp.

Leonhard, S. B., Pedersen, J. & Moeslund, B. 2005. Hard bottom substrate monitoring. Horns Rev Offshore Wind Farm. Annual status report 2004. Bio/consult as, Copenhague, Denmark, 79 pp.

Lin, H.J. & Shao, K.T. 2002. The development of subtidal fouling assemblages on artificial structures in Keelung Harbor, northern Taiwan. *Zoological Studies*, **41**: 170-182.

Lin, J.C. & Su, W.C. 1994. Early phase of fish habitation around a new artificial reef off southwestern Taiwan. *Bulletin of Marine Science*, **55**: 1112-1121.

Lindberg, W. J. 1997. Can science resolve the attraction-production issue? *Fisheries*, **22**: 10-13-

Lindberg, W. J., Frazer, T. K. & Stanton, G. R. 1990. Population effects of refuge dispersion for adult stone crabs (Xanthidae, *Menippe*). *Marine Ecology-Progress Series*, **66**: 239-249.

Lindquist, D.G., Cahoon, L.B., Clavijo, I.E., Posey, M.H., Bolden, S.K., Pike, L.A., Burk, S.W. & Cardullo, P.A. 1994. Reef fish stomach contents and prey abundance on reef and sand substrata associated with adjacent artificial and natural reefs in Onslow Bay, North-Carolina. *Bulletin of Marine Science*, **55**: 308-318.

Lindquist, D.G. & Pietrafesa, L.J. 1989. Current vortices and fish aggregations - the current field and associated fishes around a tugboat wreck in Onslow Bay, North-Carolina. *Bulletin of Marine Science*, **44**: 533-544.

Liu, C.C.K., Dai, J.J., Lin, H.S. & Guo, F. 1999. Hydrodynamic performance of wave-driven artificial upwelling device. *Journal of Engineering Mechanics-Asce*, **125**: 728-732.

Lok, A., Metin, C., Ulas, A., Duzbastilar, F.O. & Tokac, A. 2002. Artificial reefs in Turkey. *ICES Journal of Marine Science*, **59**: S192-S195.

Lok, A. & Tokac, A. 2000. Turkey: A New Region for Artificial Habitats. pp 21-30. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Lokkeborg, S., Humborstad, O.B., Jorgensen, T. & Soldal, A.V. 2002. Spatio-temporal variations in gillnet catch rates in the vicinity of North Sea oil platforms. *ICES Journal of Marine Science*, **59**: S294-S299.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D. A. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**: 804-808.

Love, M., Hyland, J., Ebeling, A., Herrlinger, T., Brooks, A. & Imamura, E. 1994. A pilot-study of the distribution and abundances of rockfishes in relation to natural environmental-factors and an offshore oil and gas-production platform off the coast of Southern California. *Bulletin of Marine Science*, **55**: 1062-1085.

Love, M.S., Caselle, J. & Snook, L. 1999. Fish assemblages on mussel mounds surrounding seven oil platforms in the Santa Barbara Channel and Santa Maria Basin. *Bulletin of Marine Science*, **65**: 497-513.

Love, M.S., Schroeder, D.M. & Lenarz, W.H. 2005. Distribution of bocaccio (*Sebastes paucispinis*) and cowcod (*Sebastes levis*) around oil platforms and natural outcrops off California with implications for larval production. *Bulletin of Marine Science*, **77**: 397-408.

Love, M.S. & York, A. 2005. A comparison of the fish assemblages associated with an oil/gas pipeline and adjacent seafloor in the Santa Barbara Channel, southern California bight. *Bulletin of Marine Science*, **77**: 101-117.

Lozano-Alvarez, E., Briones-Fourzan, P. & Negrete-Soto, F. 1994. An evaluation of concrete block structures as shelter for juvenile Caribbean Spiny Lobsters, *Panulirus argus*. *Bulletin of Marine Science*, **55**: 351-362.

Lukens, R. & Christian, R. 2000. Coastal state artificial reef programs - Fifty years of state/federal cooperation in enhancing marine fisheries and fishing opportunities. *Fisheries*, **25**: S26-S27.

Mac Arthur, R. H. & Wilson, E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ, 203 pp.

Maes, F., Cliquet, A., Seys, J., Meire, P. & Offringa, H. 2000. Limited atlas of the Belgian part of the North Sea. Federal Office for Scientific, Technical and Cultural Affairs (OSTC), 31 pp.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Science Ltd, Oxford, UK, 256 pp.

Mallinson, J. J., Collins, K. J. & Jensen, A. C. 1999. Species recorded on artificial and natural reefs, Poole Bay, 1989-1996. *Dorset Proceedings*, **121**: 113-122.

Maruyama, S., Tsubaki, K., Taira, K. & Sakai, S. 2004. Artificial upwelling of deep seawater using the perpetual salt fountain for cultivation of ocean desert. *Journal of Oceanography*, **60**: 563-568.

Melchers, R.E. & Jeffrey, R. 2004. Influence of water velocity on marine immersion corrosion of mild steel. *Corrosion*, **60**: 84-94.

Metz, S. & Trefy, J. H. 1988. Trace metal considerations in experimental oil ash reefs. *Marine Pollution Bulletin*, **19**: 633-636.

Miller, M.W. 2002. Using ecological processes to advance artificial reef goals. *ICES Journal of Marine Science*, **59**: S27-S31.

Milon, J.W. 1989. Artificial marine habitat characteristics and participation behavior by sport anglers and divers. *Bulletin of Marine Science*, **44**: 853-862.

Milon, J. W. 1991. Social and economic evaluation of artificial aquatic habitats. pp 237-270. *In* Seaman, W. and Sprague, L. M. (eds), Artificial habitats for marine and freshwater fisheries, Academic Press, Inc., San-Diego, California.

Milon, J. W., Holland, S. M. & Whitmarsh, D. J. 2000. Social and economic evaluation method. pp 165-194. *In* Seaman, W. (ed), Artificial reef evaluation with application to natural marine habitats, CRC Press LLC, Boca Raton, Florida.

Molles, M. C. 1978. Fish species diversity on model and natural reef patches: experimental insular biogeography. *Ecological Monographs*, **48**: 289-305.

Monteiro, C. C. & Santos, N. M. 2000. Portugese artificial reefs. pp 249-261. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Moore, P. H. 1977. Additions to the littoral fauna of Rockall, with a description of *Araeolaimus penelope* sp. nov. (Nematoda: Axonolaimidae). *Journal of the Marine Biological Association of the UK*, **57**: 191-200.

Moreno, I. 2000. Artificial reef programme in the Balearic Islands: Western Mediterranean Sea. pp 219-233. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Moreno, I. 2002. Effects of substrate on the artificial reef fish assemblage in Santa Eulalia Bay (Ibiza, western Mediterranean). *ICES Journal of Marine Science*, **59**: S144-S149.

Moreno, I., Roca, I., Renones, O., Coll, J. & Salamanca, M. 1994. Artificial reef program in Balearic Waters (Western Mediterranean). *Bulletin of Marine Science*, **55**: 667-671.

Müller, Y. 1994. Faune des épaves du littoral Nord-Pas de Calais. *Nouvelles de l'ADMS*, **15**: 8-10.

Müller, Y. 1999. Quelques aspects de la faune des épaves du littoral. *De Strandvlo*, **19**: 71-81.

Müller, Y. 2004. Mieux connaître les peuplements benthiques associés aux substrats durs au large du littoral Nord-Pas de Calais. Patrimoine Naturel Marin et Terrestre, Region Nord-Pas de Calais, 91 pp.

Myers, A. A. & Southgate, T. 1980. Artificial substrates as a mean of monitoring rocky shore cryptofauna. *Journal of the Marine Biological Association of the UK*, **60**: 963-975.

Nelson, W.G., Savercool, D.M., Neth, T.E. & Rodda, J.R. 1994. A comparison of the fouling community-development on stabilized oil-ash and concrete reefs. *Bulletin of Marine Science*, **55**: 1303-1315.

Nybakken, J. W. 1997. Marine biology: an ecological approach. Fourth edition, Addison-Wesley Educational Publishers Inc, Menlo Park, California, 481pp.

Ogawa, Y. & Kuroki, T. 1982. Various reef attributes and swarming activities of fish (translated from Japanese by J.Y. Haga). pp 127-128. *In* Vik, S. F. (ed), Japanese artificial reef technology, Aquabrio Inc. Tech. Rep. 604, Annapolis, Maryland.

Osenberg, C.W., St Mary, C.M., Wilson, J.A. & Lindberg, W.J. 2002. A quantitative framework to evaluate the attraction-production controversy. *ICES Journal of Marine Science*, **59**: S214-S221.

Osman, R. W. 1977. The establishment and development of marine epifaunal community. *Ecological Monographs*, **47**: 37-63.

Otsuka, C. & Dauer, D. M. 1982. Fouling community dynamics in Lynnhaven Bay, Virginia. *Estuaries*, **5**: 10-22.

Page, H. M., Dugan, J. E., Dugan, D. S., Richards, J. B. & Hubbard, D. M. 1999. Effects of an offshore oil platform on the distribution and abundance of commercially important crab species. *Marine Ecology-Progress Series*, **185**: 47-57.

Palmer-Zwahlen, M.L. & Aseltine, D.A. 1994. Successional development of the turf community on a quarry rock artificial reef. *Bulletin of Marine Science*, **55**: 902-923.

Perkol-Finkel, S. & Benayahu, Y. 2004. Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-development. *Marine Environmental Research*, **59**: 79-99.

Perkol-Finkel, S., Shashar, N., Barneah, O., David-Zaslow, R., Oren, U., Reichart, T., Yacobovich, T., Yahel, G., Yahel, R. & Benayahu, Y. 2005. Fouling reefal communities on artificial reefs: Does age matter? *Biofouling*, **21**: 127-140.

Picken, G. 1986. Moray Firth fouling communities. *Proceedings of the Royal Society of Edinburgh B*, **91**: 213-220.

Picken, G., Baine, M., Heaps, L. & Side, J. 2000. Rigs to reefs in the North Sea. pp 331-342. *In* Jensen, A. C., Collins, K. J, and Lockwood, A. P. M. (eds), Aritificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Pinn, E.H., Mitchell, K. & Corkill, J. 2005. The assemblages of groynes in relation to substratum age, aspect and microhabitat. *Estuarine, Coastal and Shelf Science*, **62**: 271-282.

Polovina, J. J. 1991. Fisheries applications and biological impacts of artificial habitats. pp 153-175. *In* Seaman, W. and Sprague, L. M. (eds), Artificial habitats for marine and freshwater fisheries, Academic Press, Inc., San-Diego, California.

Polovina, J.J. & Sakai, I. 1989. Impacts of Artificial Reefs on Fishery Production in Shimamaki, Japan. *Bulletin of Marine Science*, **44**: 997-1003.

Pondella, D.J., Allen, L.G., Craig, M.T. & Gintert, B. 2006. Evaluation of eelgrass mitigation and fishery enhancement structures in San Diego Bay, California. *Bulletin of Marine Science*, **78**: 115-131.

Pondella, D.J. & Stephens, J.S. 1994. Factors affecting the abundance of juvenile fish species on a temperate artificial reef. *Bulletin of Marine Science*, **55**: 1216-1223.

Pondella, D.J., Stephens, J.S. & Craig, M.T. 2002. Fish production of a temperate artificial reef based on the density of embiotocids (Teleostei : Perciformes). *ICES Journal of Marine Science*, **59**: S88-S93.

Ponti, M., Abbiati, M. & Ceccherelli, V.U. 2002. Drilling platforms as artificial reefs: distribution of macrobenthic assemblages of the "Paguro" wreck (northern Adriatic Sea). *ICES Journal of Marine Science*, **59**: S316-S323.

Pratt, J.R. 1994. Artificial habitats and ecosystem restoration - managing for the future. *Bulletin of Marine Science*, **55**: 268-275.

Pype, H. 1911. Over Visscherij. De Nederlandsche Boekhandel (ed), Antwerpen, Belgium, 102 pp.

Ramos, J., Santos, M.N., Whitmarsh, D. & Monteiro, C.C. 2006a. Patterns of use in an artificial reef system: A case study in Portugal. *Bulletin of Marine Science*, **78**: 203-211.

Ramos, J., Santos, M.N., Whitmarsh, D. & Monteiro, C.C. 2006b. The usefulness of the analytic hierarchy process for understanding reef diving choices: A case study. *Bulletin of Marine Science*, **78**: 213-219.

Ramos-Espla, A. A., Guillen, J. E., Bayle, J. T. & Sanchez-Jerez, P. 2000. Artificial anti-trawling reefs off Alicante, South-Eastern Iberian Peninsula: evolution of reef block and set designs. pp 195-218. *In* Jensen, A., Collins, K. J, and

Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Reed, D.C., Schroeter, S.C., Huang, D., Anderson, T.W. & Ambrose, R.F. 2006. Quantitative assessment of different artificial reef designs in mitigating losses to kelp forest fishes. *Bulletin of Marine Science*, **78**: 133-150.

Reggio, V., Van Sickle, V. & Wilson, C. 1986. Rigs to reef. *Louisiana conservationist*, **38**: 4-7.

Relini, G. 2000a. Coal ash for artificial habitats in Italy. pp 343-364. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Relini, G. 2000b. The Loano artificial reef. pp 129-149. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Relini, G. & Relini, L.O. 1989. Artificial reefs in the Ligurian Sea (Northwestern Mediterranean) - Aims and results. *Bulletin of Marine Science*, **44**: 743-751.

Relini, G., Relini, M., Torchia, G. & De Angelis, G. 2002a. Trophic relationships between fishes and an artificial reef. *ICES Journal of Marine Science*, **59**: S36-S42.

Relini, G., Relini, M., Torchia, G. & Palandri, G. 2002b. Ten years of censuses of fish fauna on the Loano artificial reef. *ICES Journal of Marine Science*, **59**: S132-S137.

Relini, G., Tixi, F., Relini, M. & Torchia, G. 1998. The macrofouling on offshore platforms at Ravenna. *International Biodeterioration and Biodegradation*, **41**: 41-55.

Relini, G., Zamboni, N., Tixi, F. & Torchia, G. 1994. Patterns of sessile macrobenthos community - Development on an artificial reef in the Gulf of Genoa (Northwestern Mediterranean). *Bulletin of Marine Science*, **55**: 745-771.

Render, J.H. & Wilson, C.A. 1994. Hook and line mortality of caught and released Red Snapper around oil and gas platform structural habitat. *Bulletin of Marine Science*, **55**: 1106-1111.

Revenga, S., Fernandez, F., Gonzales, J. L. & Santaella, E. 2000. Artificial reefs in Spain: the regulatory framework. pp 185-194. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Richmond, M. D. & Seed, R. 1991. A review of marine macrofouling with special reference to animal fouling. *Biofouling*, **3**: 151-168.

Ricklefs, R. E. & Miller, G. L. 2000. Ecology. Fourth Edition. W.H. Freeman and Company, USA, 822 pp.

Riggio, S., Badalamenti, F. & D'Anna, G. 2000. Artificial reefs in Sicily: an overview. pp 65-73. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Rostad, A., Kaartvedt, S., Klevjer, T. A. & Melle, W. 2006. Fish are attracted to vessels. *ICES Journal of Marine Science*, **63**: 1431-1437.

Russel, B. C. 1975. The development and dynamics of a small artificial reef community. *Helgolander Wissenschaftliche Meeresuntersuchungen*, **27**: 298-312.

Sampaolo, A. & Relini, G. 1994. Coal ash for artificial habitats in Italy. *Bulletin of Marine Science*, **55**: 1277-1294.

Sanchez-Jerez, P., Gillanders, B.M., Rodriguez-Ruiz, S. & Ramos-Espla, A.A. 2002. Effect of an artificial reef in *Posidonia* meadows on fish assemblage and diet of *Diplodus annularis*. *ICES Journal of Marine Science*, **59**: S59-S68.

Sanjeeva Raj, P. J. 1996. Artificial reefs for a sustainable coastal ecosystem in India, involving fisherfolk participation. *Bulletin of the Central Marine Fisheries Research Institute*, **48**: 1-3.

Santos, M.N. & Monteiro, C.C. 1997. The Olhao artificial reef system (south Portugal): Fish assemblages and fishing yield. *Fisheries Research*, **30**: 33-41.

Santos, M.N. & Monteiro, C.C. 1998. Comparison of the catch and fishing yield from an artificial reef system and neighbouring areas off Faro (Algarve, south Portugal). *Fisheries Research*, **39**: 55-65.

Santos, M.N., Monteiro, C.C. & Gaspar, M.B. 2002. Diurnal variations in the fish assemblage at an artificial reef. *ICES Journal of Marine Science*, **59**: S32-S35.

Sauriau, P. G., Merceron, M. & Goulletquer, P. 1997. Aménagement, pollution et exploitation de ressources : bilan, enseignement et menaces sur les biocénoses - Aquaculture marine et littorale. pp 195-206. *In* Dauvin, J.-C. (ed), Les biocénoses marines et littorales françaises des côtes Atlantique, Manche et Mer du Nord, synthèse, menaces et perspectives, Collections Patrimoines Naturels, Vol 18, MNHN, Paris.

Sayer, M.D.J. & Wilding, T.A. 2002. Planning, licensing, and stakeholder consultation in an artificial reef development: the Loch Linnhe reef, a case study. *ICES Journal of Marine Science*, **59**: S178-S185.

Scarborough Bull, A. & Kendall, J. 1994. An indication of the process - offshore platforms as artificial reefs in the Gulf of Mexico. *Bulletin of Marine Science*, **55**: 1086-1098.

Schratzberger, M., Dinmore, T.A. & Jennings, S. 2002. Impacts of trawling on the diversity, biomass and structure of meiofauna assemblages. *Marine Biology*, **140**: 83-93.

Schroeder, D.M. & Love, M.S. 2004. Ecological and political issues surrounding decommissioning of offshore oil facilities in the Southern California Bight. *Ocean and Coastal Management*, **47**: 21-48.

Schroepfer, R.L. & Szedlmayer, S.T. 2006. Estimates of residence and site fidelity for red snapper *Lutjanus campechanhus* on artificial reefs in the northeastern Gulf of Mexico. *Bulletin of Marine Science*, **78**: 93-101.

Sconfietti, R. 1983. Contributo all'ecologia degli anfipodi: Punta Salute (Laguna di Venezia). *Atti del Museo Civico di Storia Naturale di Trieste*, **35**: 235-252.

Sconfietti, R. & Marino, R. 1989. Patterns of zonation of sessile macrobenthos in a lagoon estuiary (northern Adriatic Sea). *Scientia Marina*, **53**: 655-661.

Seaman, W. 2000. Artificial reef evaluation with application to natural marine habitats. CRC Press, Boca Raton, 246 pp.

Seaman, W., Buckley, R.M. & Polovina, J.J. 1989a. Advances in knowledge and priorities for research, technology and management related to artificial aquatic habitats. *Bulletin of Marine Science*, **44**: 527-532.

Seaman, W. & Jensen, A. C. 2000. Purposes and practices of artificial reef evaluation. pp 1-19. Artificial reef evaluation with application to natural marine habitats, CRC Press LLC.

Seaman, W., Lindberg, W.J., Gilbert, C.R. & Frazer, T.K. 1989b. Fish habitat provided by obsolete petroleum platforms off Southern Florida. *Bulletin of Marine Science*, **44**: 1014-1022.

Seaman, W. & Sprague, L. M. 1991. Artificial habitat practices in aquatic systems. pp 1-29. *In* Seaman, W. and Sprague, L. M. (eds), Artificial habitats for marine and freshwater fisheries, Academic Press, Inc., San-Diego, California.

Sheng, Y. P. 2000. Physical characteristics and engineering at reef sites. pp 51-94. *In* Seaman, W. (ed), Artificial reef evaluation with application to natural marine habitats, CRC Press LLC, Boca Raton, Florida.

Shieh, C.S. & Duedall, I.W. 1994. Chemical behavior of stabilized oil ash artificial reef at sea. *Bulletin of Marine Science*, **55**: 1295-1302.

Shifler, D.A. 2005. Understanding material interactions in marine environments to promote extended structural life. *Corrosion Science*, **47**: 2335-2352.

Smith, I.P., Jensen, A.C., Collins, K.J. & Mattey, E.L. 2001. Movement of wild European lobsters *Homarus gammarus* in natural habitat. *Marine Ecology-Progress Series*, **222**: 177-186.

Smith, S.D.A. & Rule, M.J. 2002. Artificial substrata in a shallow sublittoral habitat: do they adequately represent natural habitats or the local species pool? *Journal of Experimental Marine Biology and Ecology*, **277**: 25-41.

Soldal, A.V., Svellingen, I., Jorgensen, T. & Lokkeborg, S. 2002. Rigs-to-reefs in the North Sea: hydroacoustic quantification of fish in the vicinity of a "semi-cold" platform. *ICES Journal of Marine Science*, **59**: S281-S287.

Spanier, E. 2000. Artificial reefs off the Mediterranean coast of Israel. pp 1-19. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Spehn, E.M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Jumpponen, A., Koricheva, J., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Palmborg, C., Pereira, J.S., Pfisterer, A.B., Prinz, A., Read, D.J., Schulze, E.D., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S. & Lawton, J.H. 2005. Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs*, **75**: 37-63.

Stanley, D.R. & Wilson, C.A. 1989. Utilization of offshore platforms by recreational fishermen and scuba-divers off the Louisiana Coast. *Bulletin of Marine Science*, **44**: 767-776.

Stanley, D.R. & Wilson, C.A. 1996. Abundance of fishes associated with a petroleum platform as measured with dual-beam hydroacoustics. *ICES Journal of Marine Research*, **53**: 473-475.

Stanley, D.R. & Wilson, C.A. 2000. Variation in the density and species composition of fishes associated with three petroleum platforms using dual beam hydroacoustics. *Fisheries Research*, **47**: 161-172.

Steimle, F., Foster, K., Kropp, R. & Conlin, B. 2002. Benthic macrofauna productivity enhancement by an artificial reef in Delaware Bay, USA. *ICES Journal of Marine Science*, **59**: S100-S105.

Steimle, F. W. & Zetlin, C. 2000. Reef habitats in the middle Atlantic Bight: abundance, distribution, associated biological communities, and fishery resource use. *Marine Fisheries Review*, **62**: 24-42.

Stephan, C.D. & Lindquist, D.G. 1989. A comparative-analysis of the fish assemblages associated with old and new Shipwrecks and fish aggregating devices in Onslow Bay, North-Carolina. *Bulletin of Marine Science*, **44**: 698-717.

Stone, R. B., McGurrin, J. M., Sprague, L. M. & Seaman, W. 1991. Artificial habitats of the world: synopsis and major trends. pp 31-60. *In* Seaman, W. and Sprague, L. M. (eds), Artificial habitats for marine and freshwater fisheries, Academic Press, Inc., San diego, California.

Sun, H.Y., Ma, S.D., Hou, B.R., Zhang, J.L., Huang, G.Q. & Zhu, X.R. 2003. Mathematical analysis of long term fouling corrosion in sea water. *Corrosion Engineering, Science and Technology*, **38**: 223-227.

Sutterer, R. A. & Szedlmayer, S.T. 2005. Comparisons of fish communities on artificial habitats with and without epibenthic communities. 8th International Conference on Artificial Reefs and Artificial Habitats, pp 69, Biloxi, USA.

Svane, I. & Petersen, J.K. 2001. On the problems of epibioses, fouling and artificial reefs, a review. *Marine Ecology*, **22**: 169-188.

Talbot, F. H., Russel, B. C. & Anderson, G. R. V. 1978. Coral reef fish communities: unstable, high-diversity systems? *Ecological Monographs*, **48**: 425-440.

Thanner, S.E., McIntosh, T.L. & Blair, S.M. 2006. Development of benthic and fish assemblages on artificial reef materials compared to adjacent natural reef assemblages in Miami-Dade County, Florida. *Bulletin of Marine Science*, **78**: 57-70.

Thiel, M. 2003. Rafting of benthic macrofauna: important factors determining the temporal succession of the assemblage on detached macroalgae. *Hydrobiologia*, **503**: 49-57.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science*, **277**: 1300-1302.

Tilman, D., Wedin, D. & Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**: 718-720.

Tilman, D. 2000. Causes, consequences and ethics of biodiversity. *Nature*, **405**: 208-211.

Todd, C. D., Bentley, M. G. & Kinnear, J. A. M. 1992. Torness artificial reef project. pp 15-22. *In* Baine, M. (ed), Proceedings of the First British Conference on Artificial Reefs and Restocking, Orkney, UK.

Tsemel, A., Spanier, E. & Angel, D.L. 2006. Benthic communities of artificial structures: Effects of mariculture in the Gulf of Aqaba (Eilat) on development and bioaccumulation. *Bulletin of Marine Science*, **78**: 103-113.

UNEP 2006. Marine and coastal ecosystems and human wellbeing: A synthesis report based on the findings of the Millennium Ecosystem Assessment. UNEP, 76 pp.

van Moorsel, G. W. N. M., Sips, H. J. J. & Waardenburg, H. W. 1988. De fauna op en rond wrakken in de Noordzee in 1988. Bureau Waardenburg bv, Culemborg, The Netherlands, 21 pp.

van Moorsel, G. W. N. M. & Waardenburg, H. W. 1990. De fauna op en rond wrakken in de Noordzee in 1989. Bureau Waardenburg bv, Culemborg, The Netherlands, 27 pp.

van Moorsel, G. W. N. M., Waardenburg, H. W. & van der Horst, J. 1991. Het leven op en rond scheepswrakken en andere harde substraten in de Noordzee (1986 T/M 1990) - een synthese. Rapport 91.19, Bureau Waardenburg bv, Culemborg, 49 pp.

Videla, H.A. 1994. Biofilms and corrosion interactions on stainless-steel in seawater. *International Biodeterioration and Biodegradation*, **34**: 245-257.

Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. 1997. Human domination of earth's ecosystems. *Science*, **277**: 494-499.

Waardenburg, H. W. 1987. De fauna op een aantal scheepswrakken in de Noordzee in 1987. Bureau Waardenburg bv, Culemborg, The Netherlands, 27 pp.

Watanuki, N. & Gonzales, B.J. 2006. The potential of artificial reefs as fisheries management tools in developing countries. *Bulletin of Marine Science*, **78**: 9-19.

Watling, L. & Norse, E.A. 1998. Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conservation Biology*, **12**: 1180-1197.

Watson, D.I. & Barnes, D.K.A. 2004. Temporal and spatial components of variability in benthic recruitment, a 5-year temperate example. *Marine Biology*, **145**: 201-214.

Wendt, P. H., Knott, D. M. & Van Dolah, R. F. 1989. Community structure of the sessile biota on five artificial reefs of different ages. *Bulletin of Marine Science*, **44**: 1106-1122.

West, J.E., Buckley, R.M. & Doty, D.C. 1994. Ecology and habitat use of juvenile rockfishes (*Sebastes* spp.) associated with artificial reefs in Puget-Sound, Washington. *Bulletin of Marine Science*, **55**: 344-350.

Wilding, T.A. & Sayer, M.D.J. 2002a. Evaluating artificial reef performance: approaches to pre- and post-deployment research. *ICES Journal of Marine Science*, **59**: S222-S230.

Wilding, T.A. & Sayer, M.D.J. 2002b. The physical and chemical performance of artificial reef blocks made using quarry by-products. *ICES Journal of Marine Science*, **59**: S250-S257.

Wilson, E. O. 1988. Biodiversity. National Academy Press, Washington DC.

Wilson, K.D.P., Leung, A.W.Y. & Kennish, R. 2002. Restoration of Hong Kong fisheries through deployment of artificial reefs in marine protected areas. *ICES Journal of Marine Science*, **59**: S157-S163.

Woodhead, P. M. J. & Jacobson, M. E. 1985. Epifaunal settlement, the processes of community development and succession over two years on an artificial reef in the New York Bight. *Bulletin of Marine Science*, **37**: 364-376.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J. & Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science*, **314**: 787-790.

Chapter II - Structure of the thesis

Photograph of quadrat on a community dominated by *Tubularia indivisa*.

1. Why studying the fauna of shipwrecks?

The introduction highlighted that the artificial reefs are a current hot topic for scientists. Most of the research efforts concentrate on fish populations around reefs basically because they are an immediate source of incomes or food for many people around the world and because a lot of fish stocks are at or close to their rupture point. The Food and Agriculture Organization plans to have a shortage of fish supply for the next decade (FAO, 2004) and the global collapse of all taxa currently fished is predicted for the mid–21st century (Worm *et al*, 2006.). However, fish aggregation is not the only biological consequence of artificial reef deployments. They are a source of hard substrate for the development of benthic communities. When they replace natural habitats (like along most of coastal area among developed countries) or when they are placed on natural habitats dominated by soft sediments, potentially new species for the area will thrive in this habitat, increasing locally the biodiversity. Shipwrecks were not intended as artificial reefs but they act in such a way and it would be wrong not to consider them as true hard substrate available for colonizing species. Actually, a single dive on one of these shipwrecks suffices to be convinced that they represent a very special habitat, especially when the diver first gets lost for a while on the neighbouring seabed. The contrast is striking. Little is still known about these communities globally and in the Southern North Sea in particular. However, the species inhabiting shipwrecks must recruit and find the suitable environmental conditions to eventually reproduce and disseminate for some of them. Leewis *et al.* (2000) are the only team who worked on this habitat but with the drawback of having done few direct collection of material and so missing a part of the onsite diversity. The aim of this work will be to assemble the basic levels of scientific understanding that are essential to catch the role that shipwrecks may play in the North Sea ecosystem. These basic levels are obligatory largely descriptive in nature. It is only after a sound description of α-diversity that hypotheses can be adequately formulated and tested.

2. Questions addressed in this work

- What is the density and distribution of the network created by shipwrecks on Belgian waters and to what extend can these spots be considered as isolated hard substrates?
- What is the macrofaunal (>1 mm) composition of these shipwrecks and do these species tell us something about the role of artificial hard substrates for the dispersal/distribution of these species?

- Are these communities distinct from those dominating the Belgian continental shelf and consequently can shipwrecks be considered as distinct ecosystems?
- Are all shipwrecks identical in terms of assemblages or is there a pattern in their spatial distribution? If yes, can we link this pattern to any environmental factor?
- Is there key species structuring the shipwreck communities?
- Is there a potential for shipwrecks to impact regional halieutic resources?

3. Structure of the work

Here we briefly describe the different chapters composing the thesis. This work is a compilation of published, submitted and *in prep.* papers. An introducing note will be given at the beginning of each paper in the text.

Chapter III – Species inventory

This chapter presents a paper with the very first results available from epifauna collected on shipwrecks. It stress the high species richness observed on the relatively low area prospected and also qualitatively describes the two main communities encountered on shipwrecks on Belgian waters. A second paper gives the full species list from the ten shipwrecks investigated during this study with information on spatial dispersion and abundance pattern. This species list is qualitatively compared to the existing information regarding natural hard substrate communities in the area.

Chapter IV – Identity of artificial reef communities

Chapter III gave important information on the species composition of shipwreck communities and we believe that it was important to stress the isolated identity of these communities in the context of the Belgian marine area. In this chapter, a paper is intended to formally describe shipwrecks as new habitat for the Belgian waters which are strongly dominated by soft-sedimented seabed. It qualitatively and quantitatively contrasts the structural and functional biodiversity associated with shipwrecks and the surrounding soft sediment communities.

Chapter V – Spatial and temporal community structure on shipwrecks

Following chapters III and IV which indicated that each shipwreck site held a typical association of species, two papers deal in this section with spatial (at the scale of the Belgian waters) and temporal (at the seasonal scale) variation of α-diversity, density and biomass pattern of communities on shipwrecks. Abiotic characterization of the variation scale under study will try to explain the variation in species assemblage structures.

Chapter VI – Shipwrecks and ecosystem functioning

This chapter covers the first attempt to understand the role of shipwrecks in their ecosystem. The first paper analyzes the use of shipwrecks as a source of food for important commercial fish species. The second paper describes and discusses the dispersal of a barnacle species new for the Southern North Sea in the context of unplanned artificial reefs (like shipwrecks) and global warming.

Chapter VII and VIII – General discussion and perspectives

The major results of this work will be summarized in the general discussion and recommendations for future work developed in the perspective chapter.

3. Working on artificial reefs in the North Sea

Many constrains exist if you intend to work on shipwrecks from North Sea waters. The first one resides in the accessibility of these sites which is largely dependant on the often poor meteorological conditions and the consequent availability of ship-time to go at sea. Secondly, the structure of a shipwreck prevent us from using conventional instruments (Grabs, trawlers, traps) to collect samples and the way out is to work with divers. This hardens even more the required meteorological conditions onsite to avoid diver injuries. For safety reasons, divers work on the no-decompression limit which results in bottom time ranging from 50' at 15 m to 10' at 40 m for the first dive of the day, but less for the second dive due to residual nitrogen in body tissue from the first dive. The bottom time is significantly improved by using oxygen enriched gas (NITROX) but qualification of the staff and further equipment adapted to oxygen use is needed. Bottom time is also constrained by a semi-diurnal tidal cycle. Considering the high current velocities encountered in the area, it is only possible to dive during windows of about one hour and a half every six hours when slack water occurs.

The visibility conditions are unforeseeable and often limited (0.5 to 5 m), changing with distance from the coast, season and even time of the day. Most of the time, it prevents divers from precisely locate themselves on the shipwreck.

Besides these main constrains, divers have also to experience cold waters for half of the year and the danger of being trapped by hooking lines or fishing nets which are commonly found on each site.

Most of our protocol is based on the scraping of the epifauna from the surface of the wreck. These samples can be considered as semi-quantitatives. After scraping, the organisms were transferred to plastic bags. This protocol would have been improved by using a finely-meshed bag directly attached to a fixed frame to avoid loosing any organisms during the scraping/transfer steps. However, it would have complicated a little bit more the underwater protocol with other practical problems. Furthermore, most of the small organisms stayed in close contact to their substrate, preventing them to be washed away by currents and easily transferred to the plastic bag. However, the encrusting fauna was not easily sampled, especially the calcareous species (like the tube-worms *Pomatoceros triqueter* and *Sabellaria spinulosa* and the barnacle *Balanus crenatus*) which form a crust difficult to manually scrap. Also, a large amount of encrusting sponges (mainly *Halichondria panicea*) was present between these calcareous species and we were unable to sample them quantitatively. As a consequence, the abundances noted for these species have to be considered as minimum if not underestimated.

In the future, the use of long lasting experiment protocols like colonization panels, automated traps or video recordings should be feasible in the condition that an agreement with recreational diving and fishing boats can be concluded to avoid loss of material.

References

FAO 2004. State of World Fisheries and Aquaculture (SOFIA). FAO Fisheries Department publications, 159 pp.

Leewis, R. J., van Moorsel, G. W. N. M. & Waardenburg, H. W. 2000. Shipwrecks on the Dutch Continental Shelf as artificial reefs. pp 419-434. In Jensen, A. C, Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publishers, Dordrecht.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J. & Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 314: 787-790.

Chapter III - Species inventory

Trivia monacha moving on *Tubularia indivisa*. White sea anemone: *Actinothoe sphyrodeta*.

ARTICLE 1: EPIFAUNAL INVENTORY OF TWO SHIPWRECKS FROM THE BELGIAN CONTINENTAL SHELF

This article was published in *Hydrobiologia* and is a first attempt to describe the faunal diversity found on Belgian shipwrecks. It was written soon after the beginning of the thesis. It is based on a relatively low number of samples taken on two shipwrecks. These samples had either vertical or horizontal orientations. This large number of variables compared to the low number of samples prevented statistical analysis to be adequately performed on the dataset. Consequently, we acknowledge that all conclusions associated with this paper have to be considered as resulting from observations rather than sound inference. Nevertheless, this paper provides the reader with a first global view of the typical fauna that could be observed on artificial hard substrates in our waters.

Hydrobiologia (2006) 555:207–219 _ Springer 2006
H. Queiroga, M.R. Cunha, A. Cunha, M.H. Moreira, V. Quintino, A.M. Rodrigues, J. Sero' dio & R.M. Warwick (eds),
Marine Biodiversity: Patterns and Processes, Assessment, Threats, Management and Conservation
DOI 10.1007/s10750-005-1117-1

EPIFAUNAL INVENTORY OF TWO SHIPWRECKS FROM THE BELGIAN CONTINENTAL SHELF

Vincent Zintzen[1,2,*], Claude Massin[2], Alain Norro[3] & Jérôme Mallefet[1]

[1]Catholic University of Louvain, Laboratory of Marine Biology, Place Croix du Sud 3, Kellner's building, B-1348, Louvain-la-Neuve, Belgium
[2]Royal Belgian Institute of Natural Sciences, Malacology Section, 29 Vautier street, B-1000, Brussels, Belgium
[3]Royal Belgian Institute of Natural Sciences, Management Unit of Mathematical Model of the North Sea, 100 Gulledelle, B-1200, Brussels, Belgium
(*Author for correspondence: E-mail: vincent.zintzen@naturalsciences.be)

KEYWORDS

shipwrecks, Belgian Continental Shelf, hard substrata, epifauna

ABSTRACT

Shipwrecks are almost the only subtidal substrata available for epifaunal colonization along the Belgian coastal waters and have never been scientifically prospected up to now. Two shipwrecks have been investigated during the summers of 2001 and 2002. *De visu* observations and examination of 14 scraped surfaces of 0.0625 m^2 allowed the identification of a total of 121 macrofauna species. Species richness cumulative curves provide an estimated number of 150 to 280 species. Both shipwrecks are dominated by Cnidarians. The tube-dwelling amphipod *Jassa herdmani* was also particularly abundant. Striking differences were observed between shipwrecks. Different faunal assemblages were observed on vertical and horizontal surfaces. Species richness could not been correlated with diversity indices. Samples with high species diversity were observed when the Hydrozoan *Tubularia indivisa* was dominant. On the contrary, when the Anthozoan *Metridium senile* was dominant, samples showed a very low species richness. Finally, the Poriferan *Dysidea fragilis* has to be considered as a new species for the Belgian fauna.

1. INTRODUCTION

Since the second part of the 19th century, the benthos of the Southern Bight of the North Sea has been intensively studied. The first intensive campaigns performed by Gilson (1900) gave an insight on the faunal diversity of the Belgian coasts but it is only since the early seventies that various researchers described the benthic communities of that region (Heip & Decraemer, 1974; Jensen, 1976; Govaere *et al.*, 1980 and Vincx, 1981). Focussing respectively on the macro and meiobenthos, Vanosmael *et al.* (1982) and Willems *et al.* (1982) stressed the ecological value of the Belgian Continental Shelf (BCS) sandbanks, south-west / north-east oriented. They suggested that those banks act as possible islands and generate a range of habitats for marine fauna. More recently, Beyst *et al.* (2001) listed the species of the surf zone occurring on Belgian sandy beaches and raised the question of their nursery function. Dewicke *et al.* (2003) emphasized an onshore-offshore gradient in the density and biomass of the hyperbenthos, here defined as the small animals living close to the sea bed. In 2004, Van Hoey summarized the large-scale spatial distribution of the macrobenthos of the BCS by combining a large amount of data collected from 1994 to 2000. All these researches directly concern the benthic fauna of soft bottoms. Despite the studies of Daro (1969, 1970), De Pauw & Van Damme (1992) and Volckaert *et al.* (2002) on the faunal and floral assemblage of intertidal structures along the coast, there is a paucity of available data devoted to communities of hard substrata on the BCS. This lack of information is a consequence of hydrodynamic schemes. Indeed fine sediments dominate the Southern part of the North Sea due to a hydrodynamic decrease after the Dover Strait (Prygiel *et al.*, 1988) while epifauna associated with pebbles is still well represented in the Strait (Davoult, 1990).

Assuming that *Asterias rubens* mainly feeds on molluscs (Mytilus edulis L.) that need hard substrata to develop (Castilla & Crisp, 1973), the findings of this echinoderm could indirectly reveal the presence of hard substrata. Only a few limited places where concentrations of the starfish *A. rubens* occur on the BCS were documented by De Clerck *et al.*, (1973, 1974a, 1974b, 1975) and therefore could be assigned to hard substrate regions. Moreover, Maertens (1989) and Deleu (2002) confirmed the presence of such regions on the BCS but so far studies on the fauna of these areas have never been performed (Kerckhof & Houziaux, 2003). Finally, Degraer (1999) and Van Hoey (2004) mention a very special macrobenthic community with high density of the Bivalve *Barnea candida* (L.) in outcropping tertiary clay layers near Oostende. As a consequence, the question of epifaunal assemblages on hard substrata for the Belgian waters has been hardly addressed. Although unnatural, shipwrecks represent another type of hard substrate and more than 200 recent shipwrecks which are a potential threat to navigation or fisheries are recorded along the Belgian coast (Norro, pers. communication). Moreover, it has been recently estimated that 10.000 wrecks lie in the Dutch sector of the North Sea (Leewis *et al.*, 2000). Theses structures represent substrata available for the colonization of subtidal sessile epibenthic communities in Belgian coastal waters. Even if the fauna living on these structures could be regarded as exotic, shipwrecks represent nevertheless a part of the habitat diversity that cannot be neglected. Technical problems are certainly the main reason why the fauna of shipwrecks have scarcely been studied (Massin *et al.*, 2002). This fauna has been prospected along the Dutch Continental Shelf (Leewis *et al.*, 2000) and on a single shipwreck near the Isle of Lundy (Bristol Channel, England; Hiscock, 1980) but this has never been done for the BCS. This paper presents the first results of a detailed study aiming to understand the possible role of such structures in the biological diversity of the Southern Bight of the North Sea. These preliminary results present a first estimation of the fauna of two shipwrecks from the BCS with a distinction between horizontal and vertical surfaces in order to determine whether different associations could be due to sedimentation. We intend to describe the basic features of the dominant communities found on shipwrecks with emphasis on some species of special interest.

2. MATERIAL AND METHOD

The macrofauna (fauna retained on a 1 mm sieve) of two BCS shipwrecks was investigated from July to the beginning of September during the years 2001 and 2002 on board of the A.962 'RV Belgica'. These two shipwrecks were chosen according to the following criteria: (i) large size thus ease of location, (ii) good state allowing safe working conditions, (iii) location out of navigation roads, and (iv) sunk for at least ten years to reach a mature community (Leewis *et al.*, 2000). The first shipwreck investigated was the Birkenfels, 156 m long, 42 m depth, sunk in 1966 and lying 30 nautical miles from the coast (WGS-84 coordinates: N 51°38',989 - E 02°32',268). The second one was the Bourrasque, 106 m long, 16 m depth, sunk in 1940 and lying 8 nautical miles from the coast (WGS-84 coordinates: N 51°14',964 - E 02°33',026). The Birkenfels is located in open sea conditions with a maximum current speed during neap and spring tides of 0.9 and 1.7 knots respectively. The Bourrasque lies between the Buiten Ratel sandbank and the Kwintebank close to the shore.

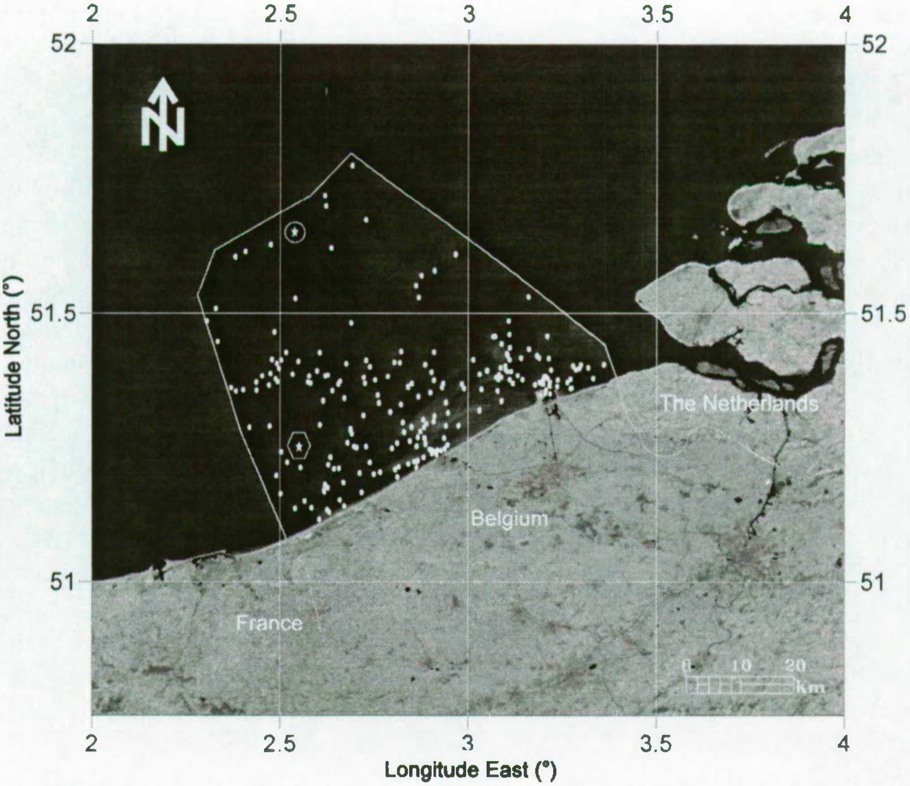


Figure 1. Location of the 231 inventoried wrecks of the Belgian Continental Shelf. The shipwreck of the Birkenfels is outlined by a circle; the shipwreck of the Bourrasque by a hexagon. Coordinates are WGS-84. Source: Afdeling Waterwegen Kust (AWK), Belgium. Map background by Image courtesy of MODIS Rapid Response Project at NASA/GSFC.

Table 1. Date, depth and orientation of the samplings.

Bourrasque			Birkenfels		
Date	**Depth (m)**	**Orientation**	**Date**	**Depth (m)**	**Orientation**
04/07/02	18	Horizontal	11/07/01	29	Horizontal
04/07/02	18	Vertical	11/07/01	27	Horizontal
05/07/02	20	Vertical	11/07/01	22	Horizontal
05/07/02	18	Horizontal	04/09/02	23	Horizontal
05/07/02	20	Vertical	04/09/02	23	Vertical
05/07/02	18	Vertical	04/09/02	23	Vertical
05/07/02	20	Horizontal	04/09/02	23	Vertical

The maximum current speeds during neap and spring tides are 0.8 and 1.3 knots respectively. These two wrecks lie in different water conditions according to the distance from the coast, since the BCS displays a gradient from turbid, nutrient rich and well-mixed inshore waters towards more oceanic, less turbid and less productive offshore waters (Cattrijsse & Vincx, 2001). Figure 1 shows the location of the two chosen shipwrecks among the other wrecks of the Belgian Continental Shelf.

Teams of three divers sampled vertical and horizontal oriented surfaces in order to document the possible faunal differences due to sedimentation process. During a tidal cycle (≈12 hours), currents turn around wrecks so that all external surfaces are exposed. Due to the large size of the wrecks and the poor underwater visibility (1-4 m), it was impossible to sample the same locations twice; therefore, all the sampling spots must be considered as differently exposed areas. As a consequence, on these exposed surfaces the most important factor for the settlement of sessile epifauna should be governed by the orientation (horizontal/vertical) of surfaces to the current. A total of 7 samples has been taken on each shipwreck (table 1) representing a total surface of 0.875 m^2.

Sampling of protected surfaces such as overhangs and more sheltered areas inside the shipwrecks was not undertaken. Moreover, abiotic parameters being quite similar for all collection times (July and September 2001, 2002), it is assumed that no seasonal or annual effects influence the observed variations in fauna.

A three step procedure was adopted in order to assess the macrofauna of the shipwrecks. First, each team randomly placed a 50 x 50 cm frame on a vertical or horizontal surface and digital pictures of the frame were taken. Then, a *de visu* inventory of the dominant visible species was performed within the 50 x 50 cm frame. Finally, a subsurface of 25 x 25 cm was scraped and transferred into plastic bags for further analysis. Divers also identified fish and jellyfish around the shipwrecks but these were not included in the analysis although they are listed for the reader's information.

On board, animals were relaxed in 3.5 % $MgCl_2$ solution for two hours and then transferred to buffered formalin solution (final concentration 4 %, pH 8.2-8.4). Later on, specimens were transferred to 70 % buffered alcohol for permanent storage. The samples were then sorted and species counted and identified to the lowest possible taxonomic level. All the collected material is deposited in the collections of the Royal Belgian Institute of Natural Sciences under the IG number 29462. Additional species were identified by examination of digital pictures. Colonies of taxa such as Hydrozoans or Bryozoans were each counted as one individual.

Species richness was estimated through species accumulation curves based on two non-parametric estimators: the Jack2 estimator (Burnham & Overton, 1978, 1979) and ACE (Abundance based Coverage Estimator) (Chazdon *et al.*, 1998). ACE is a modified version of the Chao2 estimator developed by Chao & Lee (1992) that takes into account the overestimation in species richness of the Chao2, especially when a small number of samples is used. The estimates were computed with EstimateS using 100 randomizations without replacement (Colwell, 1997). The sample's diversity was described using Hill numbers N_0, N_1, N_2 and N_∞. N_0 is the species richness, N_1 the exponential Shannon-Wiener index, N_2 the reciprocal of Simpson's index and N_∞ the reciprocal of the proportional abundance of the most common species (reciprocal of Berger-Parker index) (Hill, 1973).

3. RESULTS

3.1. Species richness, abundance and diversity

The total number of taxa identified is 121 (see appendix). Among them 22 were identified *de visu* by divers: three Scyphozoans, two Actinarians, one Hydrozoan, three Opisthobranchia, two Decapoda and 11 species of fish. The other 99 taxa were identified from the scraped surface, with 65 and 74 taxa for the Birkenfels and Bourrasque, respectively. Estimates of cumulative species richness against sampling effort showed no sign of approaching asymptotic values (figure 2). Nearly 100 species were observed while the estimated number of species for ACE and Jack2 are respectively 131 and 160. Fitting a log regression on the number of species ($R^2 = 0.99$), predicted values for 100 samples are respectively 156 for Sobs, 205 for Jack2 and 280 for ACE.

The mean, minimum and maximum number of species for the shipwrecks is presented in table 2. The number and density of species for both shipwrecks are similar with more variation among samples for the Bourrasque. The huge mean and standard error for the density is due to a single species, the tube-dwelling amphipod *Jassa herdmani* (Walker). Its density ranges from 100 to 101,120 ind/m^2.

Figure 3 shows the rank/abundance graph by shipwreck. Both are dominated by a small number of species with many 'rare' species. The dominance of *J. herdmani* reaches 76% when all samples are pooled together. Table 3 shows the cumulative dominance for pooled samples when *J. herdmani* is excluded: 81 % of the dominance is due to the 10 most abundant species.

The most represented phyla in terms of species diversity for both shipwrecks are Polychaets, Crustaceans, Molluscs and Cnidarians (table 4). Less than 50% of the species are common to both wrecks (table 5). The Spearman rank correlation between species richness (N_0) of samples and the other Hill numbers (N_1, N_2 and N_∞) is not significant ($p>0.05$) (table 6). The low value for the dominance index indicates a high degree of unevenness but this does not hamper high species richness. On the contrary, the samples containing most species (sample 4 and 14, with 33 and 41 species, respectively) have low values for the N_1, N_2 and N_∞. A dense mat of a Hydrozoan species, *Tubularia indivisa* L. is the common feature of these two samples. The erect perisarc of this species, which can reach 15-20 cm long, creates a third dimension onto the two-dimensional shipwreck surface.

3.2. Faunal assemblage description

We observed two main communities on both shipwrecks. The first one is dominated by the hydrozoan *Tubularia indivisa* associated with *Jassa herdmani* (Amphipoda). The second one is dominated by *Metridium senile* (L.) (Anthozoa). Cnidarians are the dominant phylum represented particularly by three very abundant species: *T. indivisa* (Hydrozoa), *M. senile* (Anthozoa) and *Diadumene cincta* Stephenson (Anthozoa). *T. indivisa* is always associated with *Jassa herdmani*. This amphipod builds a tube made of sediment that aggregates around the perisarc and sometimes even completely covers it. Samples with high species diversity are, as previously mentioned, linked to an important development of *T. indivisa* colonies. One can assume that the perisarc acts as a new colonization surface for a wide range of animals. On the contrary, concentration of *M. senile* does not permit the development of other species and therefore surfaces where *M. senile* is dominant are characterized by very few species.

At the prospected depth there was no algal development. The animal community was dominated by carnivores/scavengers and passive suspension-feeders. For the active suspension-feeders, only a few bivalve species were found as juveniles and in low densities; moreover, only three species of sponges and one tunicate were identified, all in low densities.

The ophiuroid *Ophiotrix fragilis* (Abildgaard) is mainly found offshore on the Birkenfels where it can form dense aggregations up to 2,000 ind/m^2. The Serpulid *Pomatoceros triqueter* (L.) covers the metal sheet of that shipwreck while *Balanus crenatus* Bruguiére is found on all onshore samples (Bourrasque). *Phyllodoce mucosa* (Oersted) occurred at a density ranging between 16 ind/m^2 to 900 ind/m^2 on the Birkenfels and between 160 ind/m^2 to 1,680 ind/m^2 on the Bourrasque. The Anomuran crab *Pisidia longicornis*

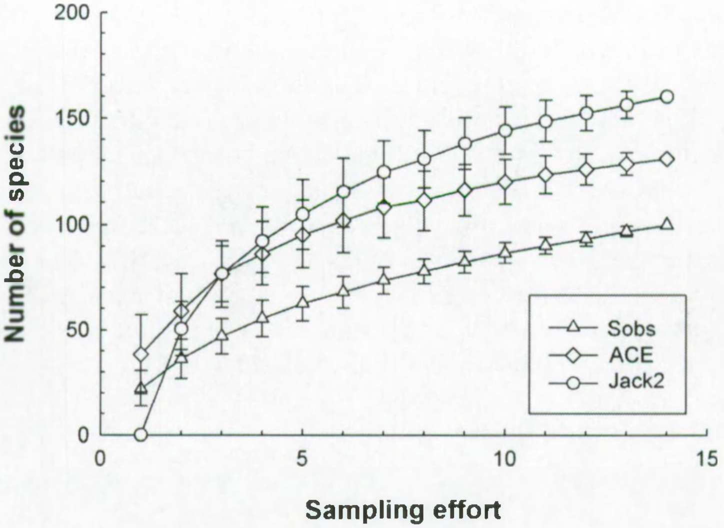


Figure 2. Species accumulation curves. Estimators of the species richness are the total number of observed species (Sobs), the Abundance based Coverage Estimator (ACE) and the Jacknife 2 Estimator of true richness. Plotted values are mean ± SD of 100 estimates based on 100 randomizations.

Table 2. Number of species (N_0) and density on the two shipwrecks. Mean is expressed with it standard error.

Shipwreck		N_0	Density (ind/m^2)
Birkenfels			
	Mean	25±5	18,460±28,930
	Min	18	3,950
	Max	33	77,056
Bourrasque			
	Mean	19±11	20,300±43,810
	Min	11	1,870
	Max	41	119,540

(L.) is common at both sites, being represented by juveniles with densities ranging between 32 to 4,860 ind/m^2. Only juveniles of *Psammechinus miliaris* (Gmelin) were found (maximum test length of 10 mm).

Differences between the faunal associations on vertical and horizontal surfaces were observed. Sedimentation on horizontal surface favours some soft sediment species. On these surfaces tubes of the Polychaeta *Lanice conchilega* (Pallas) were observed at a maximum density of 3,680 ind/m^2. *Nassarius incrassatus* (Ström) was only found on horizontal surface of the Birkenfels. The Polychaet *Phyllodoce mucosa* was preferentially found on horizontal surfaces.

The mollusc *Epitonium clathratulum* (Kanmacher) has been found in densities ranging from 32 to 144 ind/m^2 on horizontal surfaces on both shipwrecks but more frequently on the Birkenfels. The Poriferan *Dysidea fragilis* (Montagu) is recorded for the first time in Belgian waters.

4. DISCUSSION

In this study the total sampled area on both shipwrecks only represents 0.875 m^2, nevertheless 65 and 74 macrofauna species have already been identified on the offshore and onshore sites respectively. The species accumulation curves indicate that more intensive sampling will certainly add more species to the list. With only two shipwrecks and 14 samples we already reached the species richness mentioned by Leewis *et al.* (2000) (127 species) for a five year study covering 21 Dutch shipwrecks. The low species richness observed by Leewis *et al.* (2000) might be related to the fact that the sampling was mainly made by de-visu methods with a potential information loss on small macrofauna species. On the other hand, Hiscock (1980) identified a total of 187 taxa on a 1.4 m^2 horizontal surface of a shipwreck from the isle of Lundy (SW of England) sunk 5 years previously. The expected species richness of the two shipwrecks prospected in the present study is closer to the value given by Hiscock (1980).

Cattrijse & Vincx (2001) reviewed the Belgian data on macrobenthos for soft bottoms and found that species richness for a site varied from 4 to 33 and that species richness for a zone (sites pooled for 9 defined zones on the BCS) ranged from 19 to 87. Comparison with our data indicates that average macrobenthos biodiversity on the BCS is at least ten times higher on hard substrata than on soft substrata.

The pebble communities in the Dover Straits have a pooled species diversity of 211 species for the coastal zone and 128 species for the offshore zone (Davoult, 1990). The observed faunal assemblage on shipwrecks shows some resemblance to sites subjected to high hydrodynamics in the Dover

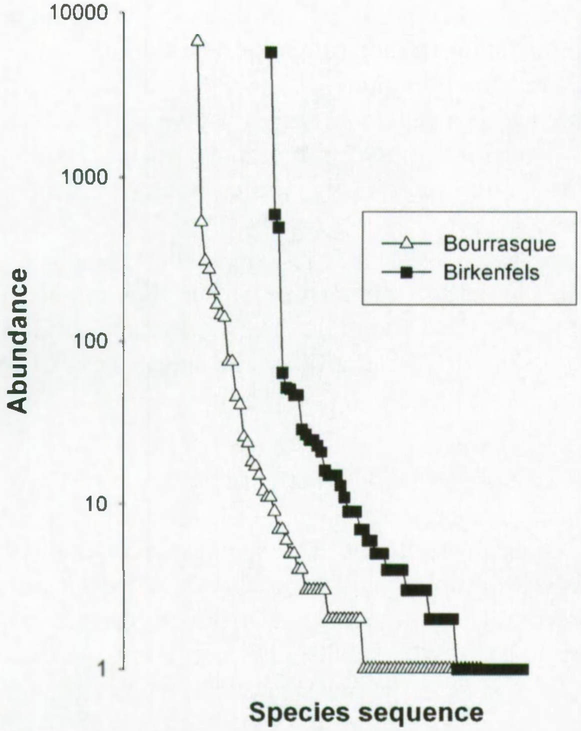


Figure 3. Rank abundance plot for the onshore (Bourrasque) and offshore (Birkenfels) shipwrecks.

Table 3. Main dominant species of the complete dataset. Colonial species (Hydrozoa and Bryozoa) and the amphipod *Jassa herdmani* are excluded.

Species	Dominance (%)	Cumulative dominance (%)
Pisidia longicornis	19.1	19.1
Phtisica marina	13.8	32.9
Ophiotrix fragilis	12.6	45.6
Phyllodoce maculata	8.2	53.8
Lanice conchilega	8.2	61.9
Diadumene cincta	6.3	68.2
Metridium senile	4.8	73.1
Balanus crenatus	3.5	76.6
Stenothoe valida	2.6	79.3
Eumida sanguinea	1.9	81.2

Strait. In this community, epifauna is the dominant group of organisms. Four dominant species are common to pebble communities and studied shipwrecks: *Ophiotrix fragilis*, *Pisidia longicornis*, *Lepidonotus squamatus* (L.) and *Psammechinus miliaris*. On the contrary, pebble communities are not dominated by Hydrozoan and Anthozoan species.

The absence of macro algal development at the studied depth is probably due to the low light intensity reaching the wrecks. The animal community is dominated by carnivores/scavengers and passive suspension-feeders and only very few active suspension-feeding species were observed. This situation can be compared with what has been described on hard substrata in the Oosterschelde (SW Netherlands). Leewis & Waardenburg (1990) studied the faunal assemblages after the construction of a storm surge barrier in the mouth of the Oosterschelde estuary. They found that *Metridium senile* and *Tubularia indivisa* communities dominate the area close to the dam, where the current velocity is the strongest. Away from the dam, under low current conditions, communities with Porifera and Tunicata develop. Indeed, these active filter-feeders are more competitive when the current velocity is low (de Kluijver & Leewis, 1994). In another study in the Adriatic Sea (Italy, Mediterranean Sea) a community on outcrops and shipwrecks in low current conditions was also dominated by active suspension filter-feeders: Tunicata, Bivalvia and Porifera accounted for 55 % of the species diversity while passive suspension filter-feeders represented only 10 % of the species (Gabriele *et al.*, 1999). It is likely that the more sheltered parts of the shipwrecks (mainly inside the shipwrecks themselves) might harbour active suspension filter-feeders but this part of the shipwrecks has not been investigated so far. In both shipwrecks, the amphipod *Jassa herdmani* was found in huge densities up to 100,000 ind/m^2. They inhabit self-constructed tubes from which they extend the anterior half of their bodies to gather detritus and filter suspended particles and plankton (Conlan, 1989). The construction of these tubes prevents them from being washed out by strong currents (Ulrich *et al.*, 1995). They are known as important fouling organisms. This species seems to out-compete most of the other amphipods that are represented by three species of the genus Stenothoe and five species of Caprellidea. The members of the genus Stenothoe are filter feeders (Barnard, 1969) and some are known to live on Hydrozoa ramifications (Lewis, 1992). Caprellidea are mainly filter feeders but some species adopt a scraping feeding strategy (Guerra-Garcia, 2002). Our results indicated that poor species assemblages are associated with the huge development of the Anthozoan *M. senile* in some places; a phenomenon already described by de

Table 4. Distribution of the organisms among taxonomic groups for both shipwrecks (nr: not represented).

Phylum	Birkenfels (%)	Bourrasque (%)
Polychaeta	33.3	37.8
Crustacea	21.2	21.6
Mollusca	19.7	13.5
Cnidaria	9.1	17.6
Echinodermata	6.1	4.1
Bryozoa	4.5	2.7
Nemertea	1.5	nr
Porifera	1.5	1.4
Sipunculia	1.5	1.4
Tunicata	1.5	nr

Table 5. Shared species based on taxonomic groups by the two shipwrecks

Phylum	Number of species		% shared
	Birkenfels	Bourrasque	
Sipunculia	1	1	100
Mollusca	13	10	53
Crustacea	14	16	43
Echinodermata	4	3	40
Polychaeta	22	28	39
Cnidaria	6	13	36
Bryozoa	3	2	25
Nemertea	1	0	0
Porifera	2	1	0
Tunicata	1	0	0

Kluijver & Leewis (1994). One possible reason is the asexual mode of reproduction of this anthozoan by basal laceration (Manuel, 1981) that tends to overgrow other organisms (Bucklin, 1987). Another reason could be toxin production (Anderluh & Macek, 2002) and exudation preventing larval settlement (Koh, 1997).

The hard substrata provide attachment sites and microhabitats for a range of species typically not found in the surrounding soft sediments. As with other artificial structures, shipwrecks raise the question of the 'attraction versus production' debate (see among others Hall *et al.*, 2000; Jensen *et al.*, 2000; Page *et al.*, 1999; Bortone, 1998; Bohnsack *et al.*, 1997; Pickering & Whitmarsh, 1997). Although not quantified, the increased density of fish around the shipwreck was probably important since 11 species were encountered; among them, the commercially important species *Gadus morhua* L.

Finally, some species have to be considered as having conservation value because of their scarcity or rareness. Several living specimens of the amphipod *Caprella tuberculata* Guérin were found on the Birkenfels. This species does not seem to be uncommon but is scarce along the British coasts (Isaac *et al.*, 1990) and has been mentioned only very recently for the Belgian marine fauna (Massin *et al.*, 2002). *Epitonium clathratulum* is a rare species for the Belgian marine fauna; it was only known from a few stranded specimens (Balckeljau, 1986 and Vanhaelen, 1989) and one single living specimen collected on a breakwater (Jonckheere, 2001). In the Netherlands, the first record of a living specimen was made by Eisma (1966) and more recently it was found in the Osterschelde (The Netherlands) (Wetsteyn & Nieuwenhuize, 1996). During the present study, *E. clathratulum* was observed on both shipwrecks, the species being more frequent on the Birkenfels. *E. clathratulum* was found only on horizontal surfaces were a thin layer of sediment occurs. This observation highlights the importance of sedimentation on horizontal surfaces that seems to favour some soft sediment molluscs and polychaeta species such as *Lanice conchilega*. The Epitonidae are carnivorous and known to feed on Anthozoa (Graham, 1988). But compared to other horizontal samples, relatively few Anthozoa (*M. senile* and *D. cincta*) were present in the samples where *E. clathratulum* was found. The Poriferan *Dysidea fragilis* is recorded for the first time in the Belgian waters. This species is widespread but seldom dominant in the British Isles and can be found along the Atlantic coast of Europe and in the Mediterranean Sea (Ackers *et al.*, 1992).

Table 6. Hill numbers values for the 14 samples with indication on the orientation of the sampling surface. N_0 is the species richness, N_1 the exponential Shannon-Wiener index, N_2 the reciprocal of Simpson's index and N_∞ the reciprocal of the proportional abundance of the commonest species (reciprocal of Berger-Parker index).

	N_0	N_1	N_2	N_∞
Birkenfels				
Horizontal	11	4,23	3,10	2,00
	15	6,22	4,18	2,30
	21	7,59	5,27	3,16
	23	4,63	2,14	1,47
Vertical	11	5,43	4,04	2,66
	13	5,59	4,00	2,58
	41	2,14	1,39	1,18
Bourrasque				
Horizontal	18	2,01	1,43	1,21
	23	5,00	2,85	1,77
	25	10,07	6,51	3,15
	33	1,37	1,10	1,05
vertical	22	5,27	3,80	2,79
	28	6,08	3,97	2,50
	28	8,58	5,91	3,69

As a conclusion, these preliminary results emphasize spots of high species richness for the sessile and slow moving epifauna. The two investigated sites show striking differences in terms of species assemblage but more intensive sampling is needed in order to discern ecological patterns. The possible role of such 'hard substrata islands' in an environment dominated by soft bottom sediments needs further research in order to evaluate their impact on the reproduction, dissemination and protection of North Sea species. In this respect, two separate questions need to be addressed. First, what is the origin of the species present on shipwrecks in the Belgian waters? Second, do shipwrecks allow these species to develop, reproduce and disseminate? We do not know anything about natural hard substrata available on the BCS for the colonization of subtidal epifauna. It seems that if present, they occur in very localized and limited areas. A comparison between the fauna encountered on these natural and unnatural outcrops could be helpful in order to know if shipwrecks are discrete spots where a natural fauna occurs or if shipwrecks play an important role for the dissemination of some species that would otherwise not be present. In this later case, shipwrecks, even if hotspots for diversity, could favour the dissemination of possibly harmful exotic species and act as stepping-stones to put in touch different populations of a single species. This could lead to a loss of genetic diversity and fitness for all or part of these populations.

ACKNOWLEDGEMENTS

It is our pleasure to thank Drs Y. Laitat, A. Simon, D. Delbare and Mrs J.P. De Blauwe, J. Haelters, A. Vanhaelen & P. Van de Steen for their help on the field. Drs J. Bouillon (Hydrozoa), Cl. De Broyer (Crustacea), Th. Backeljau (Mollusca), Ph. Willenz (Porifera) & K. Wouters (Crustacea) and Mrs G. Van Hoey (Polychaeta) and Fr. Kerckhof (Mollusca, Crustacea) for their help in species identification; our sincere thanks to officers and crew of the RV Belgica for their help during the 2001 and 2002 cruise, to RBINS (malacology section and MUMM department) for logistical support. Special thanks to Ir Vincent Tigny for his help in the mapping process, to two anonymous reviewers who made suggestions in order to improve our paper and to C. Vanderlinden for English revision. This study has been supported by a 'plan Action II' grant from the Federal Office for Scientific, Technical and Cultural Affairs (OSTC).

REFERENCES

Ackers, R.G., Moss, D. & B.E. Picton, 1992. Sponges of the British Isles: a colour guide and working document. Marine Conservation Society, Herefordshire: 175 pp.

Anderluh, G. & P. Macek, 2002. Cytolytic peptide and protein toxin from sea anemones (Anthozoa: Actiniaria). Toxicon 40: 111-124.

Backeljau, T., 1986. Lijst van de recente mariene mollusken van Belgïe. Studiedocumenten Koninklijk Belgisch Instituut voor Natuurwetenschappen 29: 1-106.

Barnard, J. L., 1969. The family and genera of marine gammaridean amphipod. U.S. National Museum Bulletin 271: 1-535.

Beyst, B., Hostens, K. & J. Mees, 2001. Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: temporal variation. Journal of Sea Research 46: 281-294.

Bohnsack, J. A., Ecklund, A. M. & A. M. Szmant, 1997. Artificial reef research: Is there more than the attraction-production issue? Fisheries 22: 14-16.

Bortone, S. A., 1998. Resolving the attraction-production dilemma in artificial reef research: Some yeas and nays. Fisheries 23: 6-10.

Bucklin, A., 1987. Adaptative advantages of patterns of growth and asexual reproduction of the sea anemone *Metridium senile* (L.) in intertidal and submerged populations. Journal of Experimental Marine Biology and Ecology 110: 225-243.

Burnham, K. P. & W. S. Overton, 1978. Estimation of the size of a closed population when capture probabilities vary among animals. Biometrika 65: 623-633.

Burnham, K. P. & W. S. Overton, 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60: 927-936.

Castilla, J. C. & D. J. Crisp, 1973. Responses of *Asterias rubens* to water currents and their modification by certain environmental factors. Netherlands Journal of Sea Research 7: 171-190.

Cattrijsse, A. & M. Vincx, 2001. Sustainable management of the North Sea: Biodiversity of the benthos and the avifauna of the Belgian coastal waters. Federal Office for Scientific, Technical and Cultural Affairs, Brussels: 48 pp.

Chao, A. & S.-M. Lee, 1992. Estimating the number of classes via sample coverage. Journal of the American Statistical Association 87: 210-217.

Chazdon, R. L., Colwell, R. K., Denslow, J. S. & M. R. Guariguata, 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In Dallmeier, F. & Comiskey, J. A. (eds.), Forest biodiversity research, monitoring and modelling: conceptual background and Old World case studies, Parthenon Publisher, Paris: 285-309.

Colwell, R. K., 1997. EstimatesS: Statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Conlan, K. E., 1989. Delayed reproduction and adult dimorphism in males of the amphipod genus *Jassa* (Corophioidea: Ischyroceridae): an explanation for systematic confusion. Journal of Crustacean Biology, 9: 601-625.

Costello, M. J., Emblow C. S. & R. White (eds), 2001. European Register of Marine Species. A check-list of marine species in Europe and a bibliography of guides to their identification. Patrimoines naturels 50: 463 pp.

Daro, M., 1969. Etude écologique d'un brise-lame de la côte belge. 1. Description et zonation des organismes. Annales de la Société Royale Zoologique de Belgique 99: 112-152.

Daro, M., 1970. Etude écologique d'un brise-lame de la côte belge. 2. Biologie et développement saisonnier des espèces. Annales de la Société Royale Zoologique de Belgique 100: 159-189.

Davoult, D., 1990. Biofaciès et structure trophique du peuplement des cailloutis du Pas-de-Calais (France). Oceanologica Acta 13: 335-348.

De Clerck, R., Cloet, N. & N. Redant, 1973. Bestandopname langsheen de Belgische kust. 7. Mededelingen van het Rijkstation voor Zeevisserij, Ghent.

De Clerck, R., Cloet, N. & N. Redant, 1974a. Bestandopname langsheen de Belgische kust. 9. Mededelingen van het Rijkstation voor Zeevisserij, Ghent.

De Clerck, R., Cloet, N. & N. Redant, 1974b. Bestandopname langsheen de Belgische kust. 8. Mededelingen van het Rijkstation voor Zeevisserij, Ghent.

De Clerck, R., Cloet, N. & N. Redant, 1975. Bestandopname langsheen de Belgische kust. 10. Mededelingen van het Rijkstation voor Zeevisserij, Ghent.

Degraer, S., Vincx, M., Meire, P. & Offringa, 1999. The macrozoobenthos of an important wintering area of the common scoter (Melanitta nigra). Journal of the Marine Biological Association of the UK 79: 243-251.

de Kluijver, M. J. & R. J. Leewis, 1994. Changes in the sublittoral hard substrate communities in the Oosterschelde estuary (SW Netherlands), caused by changes in the environmental parameters. Hydrobiologia 283: 265-280.

Deleu, S., 2002. Tide-topography interactions near the kink in the Westhinder sandbank (Southern North Sea). M. Sc. Thesis, Gent University: 43 pp.

De Pauw, N. & Van Damme 1992. Mariene Fauna en Flora. MER Study. Elektriciteitcentrale Zeebrugge (N.V. ELECTRABEL - S.P.E.), Zeebrugge.

Dewicke, A., Cattrijsse, A., Mees, J. & M. Vincx, 2003. Spatial patterns of the hyperbenthos of subtidal sandbanks in the southern North Sea. Journal of Sea Research 49: 27-46.

Eisma, D., 1966. The distribution of benthic marine molluscs off the main Dutch coast. Netherlands Journal of Sea Research 3: 107-163.

Gabriele, M., Bellot, A., Gallotti, D. & R. Brunetti, 1999. Sublittoral hard substrate communities of the northern Adriatic Sea. Cahiers de Biologie Marine 40: 65-76.

Gilson, G., 1900. Exploration de la mer sur les côtes de la Belgique. Mémoire du Muséum d'Histoires naturelles de Belgique 1: 1-81.

Govaere, J. C. R., Van Damme, D., Heip, C. & L. A. P. De Coninck, 1980. Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring. Helgolander Wissenschaftliche Meeresuntersuchungen 33: 507-521.

Graham, A., 1988. Mollusca, Prosobranch and Pyramidellid Gastropods. Synopses of the British fauna (New series), N°2, Academic Press, London: 662 pp.

Guerra-Garcia, M., 2002. Re-descriptions of *Caprella linearis* (Linnaeus, 1767) and *C. septentrionalis* Kröyer, 1838 (Crustacea: Amphipoda: Caprellidea) from Scotland, with an ontogenetic comparison between the species and a study of the clinging behaviour. Sarsia 87: 216-235.

Hall, S. J., Gray, S. A. & Z. L. Hammett, 2000. Biodiversity-productivity relations: an experimental evaluation of mechanisms. Oecologia 122: 545-555.

Heip, C. & W. Decraemer, 1974. The diversity of nematode communities in the Southern North Sea. Journal of the Marine Biological Association of the UK 54: 251-255.

Hill, M. O., 1973. Diversity and evenness: a unifying notation and its consequence. Ecology 54: 427-431.

Hiscock, K., 1980. Marine life on the shipwreck of the M.V. 'Robert'. Report of the Lundy Field Society 32: 40-44.

Isaac, M. J., Making, P., Naylor, E., Smaldon, G. & R. G. Withers, 1990. Crustacea II: Malacostraca Peracarida. In Hayward, P. J. & Ryland, J. S. (eds.), The marine fauna of the British Isles and North-West Europe, Volume 1, Oxford University Press, Oxford: 362-488.

Jensen, A. C., Collins, K. J. & A. P. M. Lockwood, 2000. Artificial reefs in European seas. Kluwer Academic Publishers, Dordrecht, The Netherlands, 508 pp.

Jensen, P., 1976. Free-living marine nematodes from a sublittoral station in the North Sea off the Belgian coast. Biologisch Jaarboek 44: 231-255.

Jonckheere, I., 2001. Witte wenteltrap *Epitonium clathratulum* levend op een golfbreker te Koksijde. Strandvlo 21: 53-57.

Kerckhof, F. & J.-S. Houziaux, 2003. Biodiversity of Belgian marine areas. In: Peeters, M., Franklin, A. and Van Goethem, J.L. (eds), Biodiversity in Belgium. Royal Belgian Insitute of Natural Sciences, Brussels: 350-385.

Koh, E. G. L., 1997. Secretion of bioactive compounds by a scleractinian coral. Proceedings of the 8th International Coral Reef Symposium, 24-29 June 1996. Lessios, H. A. & MacIntyre, I. G. (eds), Smithsonian Tropical Research Institute, Balboa, Republic of Panamá: 1263-1266.

Leewis, R. J. & H. W. Waardenburg, 1990. Flora and fauna of the sublittoral hard substrata in the Oosterchelde (The Netherlands) - interactions with the North Sea and the influence of a storm surge barrier. Hydrobiologia 195: 189-200.

Leewis, R. J., van Moorsel, G.W.N.M. & H.W. Waardenburg, 2000. Shipwrecks on the Dutch continental shelf as artificial reefs. Artificial reefs in European seas. Jensen, A. C, Collins, K. J, & Lockwood, A. P. M. (eds), Kluwer Academic Publishers, 419-434.

Lewis, B. L., 1992. Abundance, distribution and behaviour of a commensal amphipod *Stenothoe valida* Dana on the hydrocoral Millepora complanata Lamarck. Bulletin of Marine Science 51: 245-249.

Manuel, R. L., 1981. British Anthozoa. Synopses of the British Fauna (New series), N°18, Academic Press, London, 241 pp.

Maertens, D., 1989. Ecological monitoring of the new dumping area on the Belgian Continental Shelf. In: Pichot, G. (ed.), Progress in Belgian Oceanographic Research 1989. Proceedings of the North Sea symposium held in Ghent, 14 February 1989. Prime Minister's Services. Science Policy Office, Brussels: 297-324.

Massin Cl., Norro A. & J. Mallefet, 2002. Biodiversiy of a shipwreck from the Belgian Continental Shelf: monitoring using scientific diving. Preliminary results. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 72: 67-72.

Page, H. M., Dugan, J. E., Dugan, D. S., Richards, J. B. & D. M. Hubbard, 1999. Effects of an offshore oil platform on the distribution and abundance of commercially important crab species. Marine Ecology - Progress Series 185: 47-57.

Pickering, H. & D. Whitmarsh, 1997. Artificial reefs and fisheries exploitation: a review of the 'attraction versus production' debate, the influence of design and its significance for policy. Fisheries Research 31: 39-59.

Prygiel, J., Davoult, D., Dewarumez, J. M., Glaçon, R. & A. Richard, 1988. Description et richesse des peuplements benthiques de la partie française de la Mer du Nord. Comptes Rendus de l'Académie des Sciences, Série III 306: 5-10.

Ulrich, I., Anger, K. & U. Schöttler, 1995. Tube-building in two epifaunal amphipod species, *Corophium insidiosum* and *Jassa falcata*. Helgolander Wissenschaftliche Meersuntersuchungen, 49: 393-398.

Vanhaelen, M.-T., 1989. Enkele waarnemingen van het strand tussen Koksijde en Oostduinkerke tijdens en na de warme zomer van 1989. Strandvlo 9: 117-120.

Van Hoey, G., Degraer, S. & Vincx, 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. Estuarine, Coastal and Shelf Science 59: 599-613.

Vanosmael, C., Willems, K. A., Claeys, D., Vincx, M. & C. Heip, 1982. Macrobenthos of a sublittoral sandbank in the Southern Bight of the North Sea. Journal of the Marine Biological Association of the UK, 62: 521-534.

Vincx, M., 1981. New and little known nematodes from the North Sea. Cahiers de Biologie Marine, 22: 431-451.

Volckaert, A., Engledow, S., Degraer, S., Vincx, M., Coppejans, E. & M. Hoffmann, 2002. The epilithic macrofauna and macroalgae of the hard substrates along the Belgian coast. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 72 - Supplément: 13-15.

Wetsteyn, L. P. M. J. & J. Nieuwenhuize, 1996. *Epitonium clathratulum* (Kanmacher, 1798) (Gasteropoda, Prosobranchia: Epitoniidae), new for the Oosterschelde (The Netherlands), and some remarks on its presence in the Dutch Delta area. Basteria 59: 239-240.

Willems, K. A., Vanosmael, C., Claeys, D., Vincx, M. & C. Heip, 1982. Benthos of a sublittoral sandbank in the southern bight of the North Sea: general considerations. Journal of the Marine Biological Association of the UK 62: 549-557.

Appendix. List of species found only in the Birkenfels, Bourrasque and common to both shipwrecks. Species designated by 'photo' were not collected but identified by mean of digital pictures. Species designated by * were identified *in-situ* by divers. The taxonomy is based on the 'European Register of Marine Species' (Costello *et al.*, 2001).

		Birkenfels specific taxa	**Bourrasque specific taxa**	**Common taxa to both shipwrecks**
PORIFERA		*Dysidea fragilis* (Montagu, 1818) *Halichondria* cf *panicea* (Pallas, 1766)	*Haliclona* sp.	
CNIDARIA	Hydrozoa		*Bougainvillia muscus* (Allman, 1863) *Campanularia volubilis* (Linnaeus, 1758) *Clytia gracilis* (Sars, 1850) *Clytia hemisphaerica* (Linnaeus, 1767) *Hydrallmania falcata* (Linnaeus, 1758) *Laomedea flexuosa* Alder 1857 *Nemertesia antennina* (Linnaeus, 1758) *Obelia dichotoma* (Linnaeus, 1758) *Sertularia cupressina* Linnaeus, 1758 *Tubularia larynx* Ellis & Solander, 1786	*Hydractinia echinata* (Flemming, 1828) *Obelia bidentata* Clarke, 1875 *Sarsia eximia* (Allman, 1859) *Tubularia indivisa* Linnaeus, 1758
	Schyphozoa	*Aequorea vitrina* Gosse, 1853* *Chrysaora hysoscella* (Linnaeus, 1767)*		*Cyanea lamarcki* Péron & Lesueur,1810*
	Anthozoa	*Alcyonium digitatum* Linnaeus, 1758 *Anemonia* sp. (photo) *Sagartia* sp. (photo) *Urticina felina* (Linnaeus, 1767) (photo)	*Sagartia* sp. *	*Diadumene cincta* Stephenson, 1925 *Metridium senile* (Linnaeus, 1767) *Sagartia troglodytes* (Price *in* Johnston, 1847)
NEMERTEA		Nemertinea sp.		
ANNELIDA	Polychaeta	*Alentia gelatinosa* (M. Sars, 1835) *Eulalia* cf *fucescens* de Saint Joseph, 1888	Pectinariidae *Cirratulus filiformis* Keferstein, 1862	*Autolytus* sp. *Eumida sanguinea* (Oersted, 1843)

		Birkenfels specific taxa	**Bourrasque specific taxa**	**Common taxa to both shipwrecks**
		Nereis zonata Malmgren, 1867	*Eteone picta* Quatrefages, 1865	*Eupolymnia nesidensis* (Delle Chiaje, 1828)
		Poecilochaetus serpens Allen, 1904	*Eulalia* sp.	*Eusyllis blomdstrandi* Malmgren, 1867
		Procerastea halleziana Mallaquin, 1893	*Eulalia viridis* (Linnaeus, 1768)	*Harmothoe extenuata* (Grube, 1840)
		Syllis armillaris (O.F. Müller, 1776)	*Gattyana cirrhosa* (Pallas, 1766)	*Harmothoe* sp.
		Thelepus cincinnatus (Fabricius, 1780)	*Nereimyra punctata* (O.F. Müller, 1788	*Kefersteinia cirrata* (Keferstein, 1862)
			Nicomache sp.	*Lanice conchilega* (Pallas, 1766)
			Ophelia sp.	*Lepidonotus squamatus* (Linnaeus, 1758)
			Phyllodoce maculata (Linnaeus, 1767)	*Nereis pelagica* Linnaeus, 1758
			Phyllodoce sp.	*Nereis* sp.
			Polydora sp.	*Pomatoceros triqueter* (Linnaeus, 1758)
			Sabellaria spinulosa Leuckart, 1849	*Phyllodoce mucosa* (Öersted, 1843)
			Scoloplos armiger (O.F. Müller, 1776)	*Procerastea perieri* Gravier, 1900
			Thelepus setosus (Quatrefages, 1865)	*Syllis gracilis* Grube, 1840
MOLLUSCA	Bivalvia	*Heteranomia squamula* (Linnaeus, 1758)		*Aequipecten opercularis* (Linnaeus, 1758)
		Venerupis geographica (Gmelin, 1791		*Mytilus edulis* Linnaeus, 1758
				Mysella bidentata (Montagu, 1803)
	Gasteropoda	*Archidoris pseudoargus* (Rapp, 1827)	*Cuthona* sp.	Aeolidiidae
		Coryphella verrucosa (M. Sars, 1829)	*Nassarius reticulatus* (Linneaus, 1758)	*Crepidula fornicata* (Linnaeus, 1758)
		Dendronotus frondosus (Ascanius, 1774)		*Epitonium clathratulum* (Kanmacher, 1798)
		Euspira pulchella (Risso, 1826)		*Eubranchus* sp.
		Flabellinidae sp. (photo)		Rissoidae
		Nassarius incrassatus (Ström, 1768)		
SIPUNCULIA				*Sipunculus* sp.
CRUSTACEA	Decapoda	*Hias araneus* (Linneaus, 1758)		*Cancer pagurus* Linneaus, 1758
		Macropodia rostrata (Linnaeus, 1761)		*Liocarcinus holstatus* (Fabricius, 1798)
		Paguridae		*Liocarcinus* sp.
				Necora puber (Linnaeus, 1767)*

		Birkenfels specific taxa	**Bourrasque specific taxa**	**Common taxa to both shipwrecks**
				Pagurus berhnardus (Linnaeus, 1758) *Pilumnus hirtellus* (Linnaeus, 1761) *Pisidia longicornis* (Linneaus, 1767)
	Amphipoda	*Caprella tuberculata* Guérin, 1836	*Pseudoprotella phasma* (Montagu, 1804) *Pariambus typicus* (Kroyer, 1844) *Stenothoe marina* (Bate, 1856) *Stenothoe* sp.	*Caprella linearis* (Linnaeus, 1767) *Jassa herdmani* (Walker, 1893) *Phtisica marina* Slabber, 1769 *Stenothoe monoculoides* (Montagu, 1815) *Stenothoe valida* Dana, 1855
	Cirripedia		*Balanus crenatus* Bruguière, 1789	
	Cumacea		Cumacea	
	Copepoda		Copepoda	
BRYOZOA		*Disporella hispida* (Fleming, 1828)	*Conopeum seurati* (Canu, 1928)	*Electra pilosa* (Linnaeus, 1767)
ECHINO-DERMATA	Asteroidea	*Asterias rubens* Linnaeus, 1758		
	Echinoidea		Clypeasteroidea	*Psammechinus miliaris* (Gmelin, 1778)
	Ophiuroidea	*Ophiura albida* Forbes, 1839		*Ophiotrix fragilis* (Abildgaard,1789)
TUNICATA		*Molgula* cf *occulta* Kupffer, 1875		

	Birkenfels specific taxa	**Bourrasque specific taxa**	**Common taxa to both shipwrecks**
PISCES	*Gadus morhua* Linnaeus, 1758* *Pollachius pollachius* (Linnaeus, 1758)* *Scomber scombrus* Linnaeus, 1758* *Trisopterus luscus* (Linnaeus, 1758)* *Trisopterus minutus* (Linnaeus, 1758)* *Trachurus trachurus* (Linnaeus, 1758)*	*Dicentrarchus labrax* (Linnaeus, 1758)* *Myoxocephalus scorpius* (Linnaeus, 1758)* *Parablennius gattorugine* (Linnaeus, 1758)*	*Pollachius virens* (Linnaeus, 1758)* *Pomatoschistus* sp. (photo)*

ARTICLE 2: SPECIES INVENTORY OF SHIPWRECKS FROM THE BELGIAN PART OF THE NORTH SEA: A COMPARISON WITH THE EPIFAUNA ON ADJACENT NATURAL SUBSTRATES

It seemed essential to compare the shipwreck fauna with what is known from the surrounding natural hard substrates. One of the main reasons to work on these issues is to give arguments to answer the following question: can shipwrecks be taken as a surrogate for natural hard substrate or, on the contrary, does their structure allow for the development of totally different communities? These considerations may have important impacts on the conservation priorities that could be decided regarding shipwreck fauna.

At the time of writing, comparison between the communities from shipwrecks and those from natural grounds was only possible through species list comparison. In the near future, we hope being able to analyze these habitats within a more complex framework including species composition by sampling stations. This will allow for example, the formal testing of the variation of taxonomic diversity thanks to the availability of replicates (i.e. samples). This paper should thus be seen first, as an exhaustive list of species from shipwrecks on the Belgian waters with information on their repartition, density and rareness for the Belgian and surrounding countries fauna, and then, as a preliminary comparison of species occurrence on this habitat with subtidal natural hard substrate habitats occurring in the same area.

Data from natural epifaunal communities are still fragmentary for the Belgian waters. A project is currently re-analyzing the historical data collected from Gilson (Gilson, 1900) who largely sampled the Belgian waters during the early XXth century with a two meter beam trawl (Houziaux, SPSD II, research contract EV/36/45A). A number of these samples, especially in the region of the Hinder Banks comprised gravely sediments which allowed for the development of epifaunal species. The characterization of these samples for the sessile species (Porifera, Cnidaria, Bryozoa) is ongoing. Some information exists for the Crustacea, Echinodermata and Mollusca. Re-sampling of some of these stations occurred on 2005 and the samples are currently being processed. Only gross tendency were available for these last samples and we decided not to use them in the following paper.

SPECIES INVENTORY OF SHIPWRECKS FROM THE BELGIAN PART OF THE NORTH SEA: A COMPARISON WITH THE EPIFAUNA ON ADJACENT NATURAL SUBSTRATES

Vincent ZINTZEN [1,2]

[1] Royal Belgian Institute of Natural Sciences, Malacology Section, Rue Vautier 29, B-1000 Brussels, Belgium.

[2] University of Louvain, Biology Laboratory, Kellner Building, place Croix du Sud 3, B-1348 Louvain-la-Neuve, Belgium.

1. INTRODUCTION

On the Belgian part of the North Sea lies a large number of artificial structures which are mainly shipwrecks (Zintzen *et al.*, 2006). While the sea bottom is mostly represented by soft sediments, patches of gravels (grain size above 4 mm; Krumbein, 1941) also occur (Lanckneus *et al.*, 2001; Kerckhof & Houziaux, 2003). Another area largely dominated by pebbles exists around the Dover Strait because of the high current speed and nature of the seabed in the area (Cabioch & Glaçon, 1975). It is essential to compare the communities (being focussed on fish or epifauna) which develop on artificial structures with those from natural habitats. Most of the time, artificial structures have been deployed purposely and their performance has to be evaluated. For example, to determine how well artificial reefs mitigate for the losses due to human activities on natural reefs, their performance should be evaluated using contemporaneous comparisons with relatively undisturbed natural reef (Carr & Hixon, 1997). However in this case, the artificial structures were not planned and shipwrecks were not deployed with any purpose in mind. Nevertheless, they are still a source of hard substrate which allow for the development of an epifaunal community which will locally increase the species richness. This might have potential implications on the repartition, dissemination and genetic variability for these species.

Several studies compared epifauna from natural and artificial substrata (Myers & Southgate, 1980; Wendt *et al.*, 1989; Edgar, 1991; Aseltine-Neilson *et al.*, 1999; Gabriele *et al.*, 1999; Smith & Rule, 2002; Badalamenti *et al.*, 2002; Perkol-Finkel & Benayahu, 2004; Perkol-Finkel *et al.*, 2005). They all showed that natural and artificial reef epifauna were not similar, sometimes only because of species cover/dominance differences and not variations in species presence/absence (Myers & Southgate, 1980; Edgar, 1991).

In this paper, we will present an exhaustive list of the macrospecies recorded on 10 shipwrecks from the Belgian waters and qualitatively compare it with the current knowledge that we have from the species occurring on natural hard substrate in the same area.

2. MATERIAL AND METHOD

Ten shipwreck sites from the Belgian waters were investigated from 2001 to 2005. The ten boats (Table 1) had sunk since at least 40 years and consequently we considered that their communities had reached a mature state (van Moorsel *et al.*, 1991; Leewis *et al.*, 2000). Quantitative sampling was achieved by scraping all the living fauna within frames of 25 x 25 cm selected at random on years 2001 to 2004. On 2005, samples were mostly taken on vertical surfaces in a *Tubularia* spp. community. On board, animals were relaxed in a 3.5 % $MgCl_2$ solution for two hours and then transferred to a buffered formalin solution (final concentration 4 %, pH 8.2-8.4). Later on, specimens were transferred to 70 % buffered alcohol for permanent storage. The samples were then sorted under a binocular and macro-species (>1 mm) were identified to the lowest possible taxonomic level and counted. Most of the samples were taken between March and September. The species only recorded between October and February will be presented in a separate table and are not taken into account for the comparison with natural habitats. Some species were also noted from *in situ* observation by divers and digital picture analysis. They will be presented in a separate table and will not be taken into account for the analysis as well.

In the region of the Hinder Banks in Belgian waters, video recording confirmed the presence of gravely sediments which allow for the development of epifaunal species. During these campaigns ten stones (up to 20 cm length) were picked up by hand at two stations (WGS84 N51° 19,5568 - E 002° 32,6273 and WGS84 N 51°25,103 - E 002°30,383). Species present on these stones were identified. Since the information for the pebble community on the Belgian Part of the North Sea is still far from complete, we will use it only for global tendency analysis of species patterns.

In the region of the Dover Strait, a community of sessile epifauna on pebbles is described by Cabioch & Glaçon (1975), Souplet & Dewarumez (1980), Souplet & Dewarumez (1980) and Davoult (1980). The station sampled by Cabioch were re-sampled in 2004 and a species list for the sessile (Foveau, 2005) and vagile epifauna (Alizier, 2005) is now available. In March and April 2004, 46 stations were sampled with a 'Rallier du Baty' grab which allow for a qualitative sampling of the pebble community. A sample was composed of 30 litres of sediments which were sieved over a 2 mm size sieve, transferred to formalin for fixation and then to ethanol (70%) for conservation. The samples where then sorted and species identified to the lowest possible taxonomic level. Fish species were excluded from the analysis.

Taxa with potential misidentifications were lumped to higher taxonomic levels, i.e. *Harmothoe* spp., *Eumida* spp., *Musculus* spp. and *Molgula* spp. Taxa will further be referred as species. Total species richness of both habitats and the repartition of species into the large taxonomic subdivision will be analyzed.

3. RESULTS

3.1 Shipwrecks species richness

The Annex 1 presents the species richness and average density range for the different investigated shipwrecks between March and September (2001-2005). It totalizes 193 species. Another 9 species were only sampled between October and February (Annex 2) and 22 more species were observed *in situ* or after examination of digital pictures (Annex 3). The current pooled species richness for Belgian shipwrecks is then 224 spp. Among these species, 48 should be provisionally considered as new for the Belgian fauna (Annex 4). An indication on the distribution is given in this table. Most of these species have records on the north and south of the Belgian area, but some species are meridional inhave a southern origin and their presence on shipwrecks extend their actual distribution to the north (*Actinothoe sphyrodeta*, *Eulalia aurea*, *Thelepus setosa*, *Procerastea nematodes*, *Pseudoprotella phasma, Callipallene emacinata*, *Acasta spongites* or *Tritonia* cf *manicata*).

3.2 Shipwrecks and the pebble community from Belgian waters

The species found on the stones sampled by divers are compiled on table 2. We identified 50 species of which 72% were also observed on shipwrecks. The general cover noted by divers was that the pebbles were not dominated by a single species and that the repartition of species was rather patchy. Certainly, there was no dominance of *Tubularia* sp. The Campanulariidae and Actiniaria species were well represented.

Table 1. Baseline information on studied shipwreck sites.

Shipwreck sites	WGS-84 Coordinates	Depth (MLLWS) (m)	Date of sunk	Sampling years
Birkenfels	N 51°38',989 E 02°32',268	37	1966	01-02-03-04-05
Callisto	N 51°41',950 E 02°37',330	28	1959	04-05
Garden City	N 51°29',170 E 02°18',320	26	1969	05
John Mahn	N 51°28',930 E 02°41',350	29	1942	05
Duc de Normandie	N 51°25',524 E 02°36',345	29	1942	05
LCT 457	N 51°24',670 E 02°43',720	21	1944	05
Kilmore	N 51°23',730 E 02°29',790	30	1906	03-04-05
Bourrasque	N 51°14',964 E 02°33',026	18	1940	02-03-04-05
LST 420	N 51°15',510 E 02°40',830	8	1944	05
Sperrbrecher	N 51°16',650 E 02°49',780	9	1942	04

Table 2. Species identified on pebbles from the Belgian waters by divers in situ observations and the sorting of some sampled pebbles. * taxa also identified on shipwrecks.

CNIDARIA
- *Abietinaria abietina* (Linnaeus, 1758) *
- *Alcyonium digitatum* Linnaeus, 1758 *
- *Calycella syringe* (Linnaeus, 1758)
- *Clytia hemisphaerica* (Linnaeus, 1767) *
- *Diadumene cincta* Stephenson, 1925 *
- *Hydractinia echinata* (Flemming, 1828) *
- *Metridium senile* (Linnaeus, 1767) *
- *Nemertesia antennina* (Linnaeus, 1758) *
- *Obelia longissima* (Pallas, 1766)
- *Obelia* sp. *
- *Sagartia* sp. *
- *Sarsia tubulosa* (M. Sars, 1835)
- *Sertularia* sp.
- *Tubularia larynx* Ellis & Solander, 1786 *

ANNELIDA
- *Eulalia ornata* de Saint Joseph, 1888
- *Eulalia viridis* (Linnaeus, 1768) *
- *Harmothoe* sp. *
- *Kefersteinia cirrata* (Keferstein, 1862) *
- *Lanice conchilega* (Pallas, 1766) *
- *Pomatoceros triqueter* (Linnaeus, 1758) *
- *Sabellaria spinulosa* Leuckart, 1849 *
- *Sphaerodopsis flavum* Oersted, 1843
- *Syllis gracilis* Grube, 1840 *

MOLLUSCA
- *Aequipecten opercularis* (Linnaeus, 1758) *
- *Coryphella* sp.
- *Cuthona* sp. *
- *Doto pinnatifida* (Montagu, 1804) *
- *Epitonium clathratulum* (Kanmacher, 1798) *
- *Epitonium clathrus* (Linnaeus, 1758)
- *Eubranchus* cf *tricolor* Forbes, 1838
- *Facelina bostoniensis* (Couthouy, 1838) *
- *Lomanotus marmoratus* (Alder & Hancock, 1845)

CRUSTACEA
- *Abludomelita obtusata* (Montagu, 1813) *
- *Aora gracilis* (Bate, 1857)
- *Caprella linearis* (Linnaeus, 1767) *
- *Caprella tuberculata* Guérin, 1836 *
- *Jassa herdmani* (Walker, 1893) *
- *Liocarcinus marmoreus* (Leach, 1814)
- *Macropodia* sp. *
- *Monocorophium sextonae* Crawford, 1937 *
- *Phtisica marina* Slabber, 1769 *
- *Pisidia longicornis* (Linneaus, 1767) *
- *Pseudoprotella phasma* (Montagu, 1804) *
- *Stenothoe marina* (Bate, 1856) *

PYCNOGONIDE
- *Anoplodactylus petiolatus* (Kroyer, 1844)

BRYOZOA
- *Conopeum reticulum* (Linnaeus, 1767)
- *Electra pilosa* (Linnaeus, 1767) *

ECHINODERMATA
- *Amphipholis squamata* (Delle Chiaje, 1829) *
- *Asterias rubens* Linnaeus, 1758 *
- *Echinocyamus pusillus* (Müller, 1776)
- *Ophiothrix fragilis* (Abildgaard,1789) *
- *Ophiura albida* Forbes, 1839 *
- *Psammechinus miliaris* (Gmelin, 1778) *

3.3 Shipwrecks and the pebble community from the Dover Strait

Species richness for sessile and vagile epifauna taken on shipwrecks between March and September (2001-2005) was 193 spp. The sessile and vagile species represented 23% and 77% of the species, respectively. The pebble community species richness was 281 with 43% and 57% belonging to the sessile and vagile taxa, respectively.

The figure 1 presents the repartition of species on a simplified taxonomic hierarchy. Both habitats shared 10 phyla (Annelida, Arthropoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Mollusca, Nemertea, Porifera, Sipuncula). Platyhelminthes were only noted on shipwrecks and Rhodophyta (*Lithotamnium* sp.) only on pebbles. Both habitats had the same number of classes (24) and shared 79% of these. At the level of order and below, the diversity of pebbles was higher than on shipwrecks.

On both habitats, the Annelida, Arthropoda, Mollusca, Cnidaria and Bryozoa were the best represented phyla in terms of species richness (Figure 2). They accounted for 86% and 89% of the total species richness on shipwrecks and pebbles, respectively. However, Cnidaria and Bryozoa species were proportionally better represented on pebbles than on shipwrecks. The proportion of Annelida species on shipwrecks was largely above what was observed on pebbles. Porifera, Echinodermata, Chordata and the minor groups were equally represented on both habitats.

The combined species richness of shipwrecks and pebbles were 404 species with 17% (70 species) being shared (Table 3). Shared species belonged to the Porifera, Cnidaria, Annelida, Arthropoda, Mollusca, Bryozoa, Echinodermata and Chordata.

Concerning the sessile epifauna of the Dover Strait, the following species dominated the assemblages: Annelida (*Pomatoceros* spp. and *Spirorbis* spp.), Cnidaria (*Actinaria* spp. and *Alcyonium digitatum*), Crustacea (*Balanus crenatus* and *Verruca stroemia*), Mollusca (*Modiolus modiolus*), Bryozoa (*Disporella hispida*, *Escharella variolosa*, *Microporella ciliata*, *Reptadeonella violacea*, *Schizomavella auriculata* and *Turbicellepora avicularis*) and Tunicata (*Dendrodoa grossularia* and *Molgula* spp.). The major part of the zone (73% of the surface) was dominated by an assemblage which was characterized by *Alcyonium digitatum* and four lophophorates (*Omalosecosa ramulosa*, *Diplosolen obelia*, *Plagioecia sarniensis* and *Tubulipora liliacea*).

The largest part (70% of the stations) of the vagile fauna and endofauna belonged to a community characterized by *Ophiothrix fragilis*, *Pisidia longicornis* and *Monocorophium sextonae* which accounted for 68% of the total number of individuals. Other typical species were *Pagurus bernhardus*, *Galathea intermedia* and *Lepidonotus squamatus*.

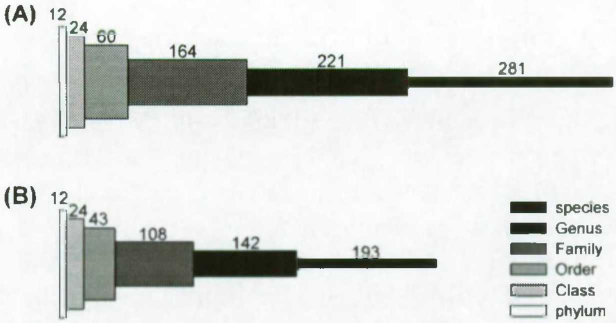


Figure 1. Taxonomic hierarchy for pebbles of the Dover Strait (A) and shipwrecks on Belgian waters (B). The figures are the number of phyla, classes, orders, families, genera and species for both habitats.

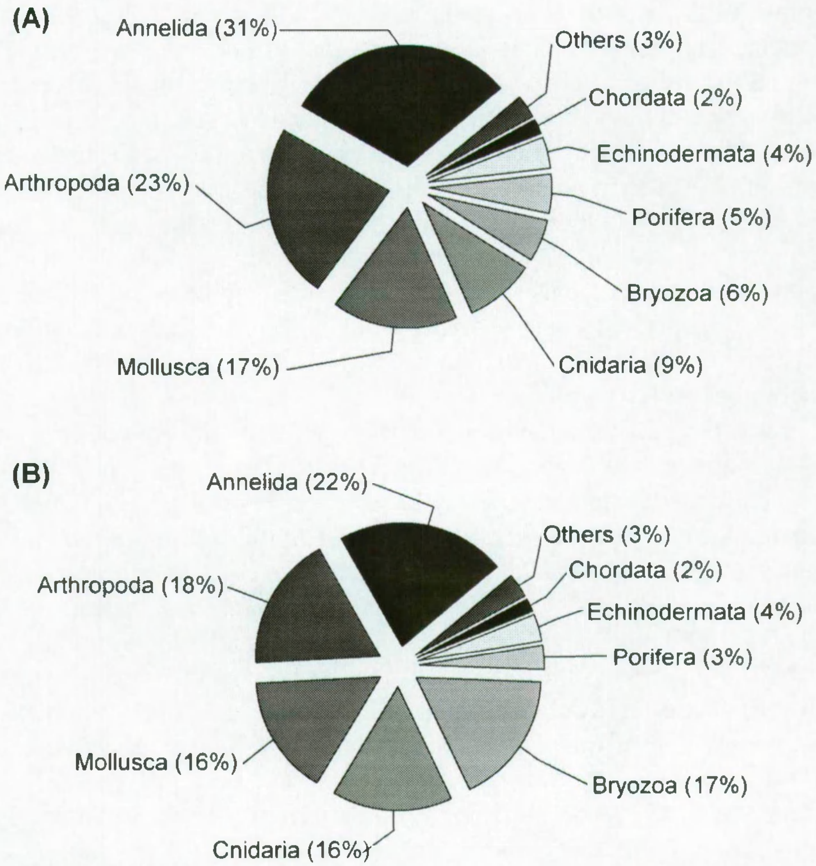


Figure 2. Repartition of species richness by phyla for shipwrecks on Belgian waters (A) and pebbles of the Dover Strait (B).

4. DISCUSSION

The current species richness of the shipwreck macrofauna was 224, including 12 fish species observed *in situ* by divers. This is in the range of the species richness observed for the soft sediment macrofauna of the Belgian continental shelf where Degraer *et al.* (2006) identified a total of 265 species from 771 samples. However, taking into account the relative small area covered by shipwrecks compared to the continental shelf, shipwrecks tended to concentrate species richness and could be consequently considered as hot spots of species richness.

The provisional number of species new for the Belgian fauna is large (48 spp.). It is not surprising to find such a large amount of new species since this is the first investigation on subtidal hard substrates which produces results in the area. Interestingly, the occurrence of these species on shipwrecks fulfils a gap in the regional distribution of sessile and mobile epibenthos. The records of several species are interrupted in the Southern Bight of the North Sea, simply because their habitat, natural hard substrates, are lacking in this area. The Paguridae *Anapagurus chiroacanthus* gives a nice example of such a distribution (Garcia-Gomez, 1994). It is present from Norway to the Azores, but is not recorded on the Southern North Sea. For these species, it may be that shipwrecks favour transfer between populations by providing adequate substrate for dissemination. Other species like the sea anemone *Actinothoe sphyrodeta*, have their northern limit extended by their presence on shipwrecks (see Williams (1997) for a review of its records).

The fauna of the Dover Strait has affinities with the fauna which is found on the shipwrecks from Belgian waters. They shared 17% of their species. However, the dominating sessile species were not the same. In the pebbles of the Dover Strait, the sessile fauna was mostly dominated by bryozoan species and *Alcyonium digitatum*, while the largest fraction of the sessile epifauna of wrecks belonged to the cnidarians (*Tubularia* spp. and *Metridium senile*) (Zintzen *et al.*, 2006). It appeared that large epibenthic species were not able to dominate the assemblages on the Dover Strait. The reasons for such a pattern could be strictly dependent on the abiotic factors which control the recruitment and development of these assemblages. The sole presence of *Lithotamnium* sp. (a red algae) in the Dover Strait waters showed that the turbidity conditions on both habitats should differ, although other factors like abrasion and source population could also play a role. No algae species were ever identified on subtidal Belgian habitats, neither on soft sediments (Van Hoey *et al.*, 2004) or on shipwrecks, except on harbours and groins (Volckaert *et al.*, 2002). The strong hydrodynamic in the area associated with the presence of sand can have a marked abrasive effect on species. This is highlighted by the presence of species adapted to sand abrasion like the tube annelid *Sabellaria spinulosa*. Other possible reason for the absence of algae may be that the quantity of light reaching the seabed is below the compensation point of algae, that the distance of shipwrecks from any source population is beyond the dispersal capacity of spores, that the competition for space by hydroids prevents the settlement of spores or that echinids (*Psammechinus miliaris*) in large abundance on shipwrecks eat all the algae population before attaining a observable size.

(Davoult & Clabaut, 1988). Since shipwrecks offer a structure which protrudes from several meters above the seabed, they could well provide a habitat more protected to sand abrasion than pebbles. However, *S. spinulosa* was also identified on shipwrecks, showing that shipwrecks are not entirely protected from sand abrasion. Another factor which potentially differs from pebbles and shipwrecks is the stability of the substrate. Particularly strong currents or storm events might have a more profound effect on pebbles than on the rigid and large structure of shipwrecks (Posey *et al.*, 1996). Under the effect of these events, pebbles can be moved and the epifauna damaged. On shipwrecks, important storm events can lead to the collapsing of a part of the superstructure but frequent small scale perturbation events are unlikely to occur. Passive suspension feeding seems to be the privileged mode of nutrition on both habitats. The rate of particles filtered by a specimen is a function of particle density and current velocity. This last parameter could be enhanced on shipwrecks because current speed is higher at increasing distance from the bottom. Finally, human activities like fisheries are more intense on natural grounds like pebbles than on shipwrecks and might also lead to more frequent perturbation on pebbles. This can have strong effects on the development of epibenthic species (Engel & Kvitek, 1998; Fraschetti *et al.*, 2001).

Interestingly the three species dominating the vagile/endo- fauna of the Dover Strait, *Ophiothrix fragilis*, *Pisidia longicornis* and *Monocorophium sextonae* were also very common and abundant on Belgian shipwrecks. However, the amphipod *Jassa herdmani* which is the more abundant species on shipwrecks, was even not mentioned in the species list from the pebble community. Like *M. sextonae*, *J. herdmani* is a tube builder and a suspension feeder which is often found linked to hydroids (*T. indivisa* on shipwrecks) but which can also directly build its tubes on any hard substrate available (Conlan, 1989). On shipwrecks, the overall densities of *J. herdmani* were 60 times higher than the densities of *M. sextonae*. The existence of a competition between these two species was indicated by the higher proportion of *M. sextonae* when the densities of *J. herdmani* decreased (mainly during winter). It is difficult to explain why *J. herdmani* is not represented in the Dover Strait pebbles on natural substrates. It is well present in the area since *Jassa* species (most probably *J. herdmani*) was identified on shipwrecks from the Dover Strait (Müller, 2004). When its tube is not fixed with another species, this species seems to have strong affinities for artificial material (harbour wall, groins,...). One of the differences between shipwreck structures and pebbles which could explain the low abundance of *J. hermani* in the Strait lies in the critical size of surface provided by both habitats. Shipwrecks (like most other artificial structures) offer a relatively large and homogenous area compared to the patchy nature of pebbles. This area may be necessary to have a population size large enough to be viable. This hypothesis is supported by the reproductive system in the genus *Jassa*. The mating is polygynous and there is a continuous and asynchronous reproduction by the females (Conlan, 1989). However, the males delay their reproduction to the last instar, meaning that they are reproductively active for only 10% of their life span (Nair & Anger, 1979). It is then possible that a critic population size has to be realized to allow an effective fecundation of the female pool. The advantages to delaying sexual activity would be (1) a reduction in competition for receptive females, (2) maximization of growth output to achieve successful mating later, (3) avoiding too large energy expenditure in both sexual outputs and molting

Table 3. Taxa shared by shipwrecks from the Belgian waters and pebble community from the Dover Strait.

- **PORIFERA (3 SP.)**
  - *Dysidea fragilis*
  - *Haliclona oculata*
  - *Sycon ciliatum*
- **CNIDARIA (11 SP.)**
  - *Alcyonium digitatum*
  - *Campanularia volubilis*
  - *Clytia gracilis*
  - *Clytia hemisphaerica*
  - *Halecium* sp.
  - *Hydractinia echinata*
  - *Hydrallmania falcata*
  - *Metridium senile*
  - *Nemertesia antennina*
  - *Sertularia cupressina*
  - *Tubularia indivisa*
- **ANNELIDA (17 SP.)**
  - Cirratulidae
  - *Eteone longa*
  - *Eumida* sp.
  - *Gattyana cirrhosa*
  - *Harmothoe* sp.
  - *Lanice conchilega*
  - *Lepidonotus squamatus*
  - *Marphysa sanguinea*
  - *Nicolea venustula*
  - *Owenia fusiformis*
  - *Pomatoceros triqueter*
  - *Sabellaria spinulosa*
  - *Sphaerodoropsis flavum*
  - *Sthenelais boa*
  - Syllidae
  - *Syllis gracilis*
  - *Thelepus setosus*
- **ARTHROPODA (17 SP.)**
  - *Abludomelita obtusata*
  - *Balanus crenatus*
  - *Caprella linearis*
  - *Ebalia tumefacta*
  - *Inachus phalangium*
  - *Janira maculosa*
  - *Liocarcinus holsatus*
  - *Macropodia rostrata*
  - *Metopa alderi*
  - *Monocorophium sextonae*
  - *Necora puber*
  - *Nymphon rubrum*
  - *Pilumnus hirtellus*
  - *Pisidia longicornis*
  - *Pycnogonum littorale*
  - *Thoralus cranchii*
  - *Verruca stroemia*
- **MOLLUSCA (10 SP.)**
  - *Archidoris pseudoargus*
  - *Dendronotus frondosus*
  - *Doto pinnatifida*
  - *Epitonium clathratulum*
  - *Euspira pulchella*
  - *Musculus* sp.
  - *Mytilus edulis*
  - *Nassarius incrassatus*
  - *Raphitoma linearis*
  - *Tritonia plebeia*
- **BRYOZOA (5 SP.)**
  - *Bicellariella ciliata*
  - *Crisia aculeata*
  - *Disporella hispida*
  - *Electra pilosa*
  - *Plagioecia patina*
- **ECHINODERMATA (5 SP.)**
  - *Amphipholis squamata*
  - *Asterias rubens*
  - *Ophiothrix fragilis*
  - *Ophiura albida*
  - *Psammechinus miliaris*
- **CHORDATA (2 SP.)**
  - *Ascidiacea*
  - *Molgula* sp.

instars, (4) limiting the increased probability of mortality from predation or current dislodgement when reproductively active males venture out of their tubes (Conlan, 1989).
O. fragilis and *P. longicornis* are both suspension feeders. The first species is found forming dense aggregations (beds) in the Dover Strait (Holme, 1984) while it is intimately associated with the perisarc of *T. indivisa* on shipwrecks. The second species lives under boulders on the Strait (Carpentier *et al.*, 2005) and also protected from current in the dense aggregation of *T. indivisa* on shipwrecks. Since both of these species have a relatively long planktonic stage (Jenson, 1991; Robinson & Tully, 2000; Lefebvre & Davoult, 2000) and since the residual tidal currents are running north-east (Pingree & Maddock, 1977), the population of the Dover Strait may be a source for the shipwreck populations.

The comparison of the shipwreck epifauna with the fauna from gravel habitat from the Belgian waters is currently hampered by the lack of information concerning this last habitat. The first results from the few stones collected *in situ*, the diver observations onsite and the inspection of underwater video images gave indications that the species shared by both habitats may be high (72%). It is also clear that large erect species were not a common feature of gravel habitat. *Tubularia* spp. were present but not dominant like on shipwrecks, allowing for the development of a more diverse set of hydroid species. The detailed analysis of this fauna will give a more complete picture on the similarity/dissimilarity of the shipwreck fauna compared to their natural counterpart assemblages. This matter turns out to be essential for determining the protection status which should be allocated to both habitats and to study the interactions which exist between them. More precisely, the question of which habitat for which species represents a source for the other would be particularly pertinent in this context.

ACKNOWLEDGEMENTS

The author wish to thanks the station marine de Wimereux for providing species list from the Dover Strait pebble community and to JS Houziaux for providing data from the gravel area of the Belgian waters. The authors wish also to thank the crews of the RV Zeeleeuw and RV Belgica for their help during the sampling campaigns and to Céline Delforge for the great help during the sorting process. It's also our pleasure to thank all the people who helped collecting the samples: Drs Y. Laitat, A. Simon, D. Delbare, E. Vanden Bergh, T. Schils, Mss C. Delforge and R. Gyssens and Mrs P.B. Demoulin, G. Rooms, D. Marsham, F. Cray, M. Van Espen, Y. Verkemping, M. Backx, J. Haelters, F. Hernandez, F. Darchambeau, G. Van Hoydonck,

A. Vanhaelen, R. Knuts & P. Van de Steen. This study has been financially supported by a 'plan Action II' grant (contract N° WI/36/C04) from the Belgian Science Policy and by the BEWREMABI project (Belgian Science Policy).

REFERENCES

Alizier, S. 2005. Evolution spatio-temporelle de l'épifaune vagile et de l'endofaune du peuplement des cailloutis à épibiose sessile dans le Détroit du Pas de Calais. Rapport de Diplôme Superieur de Recherche, Océanologie biologique, Station Marine de Wimereux, 78 pp.

Aseltine-Neilson, D.A., Bernstein, B.B., Palmer-Zwahlen, M.L., Riege, L.E. & Smith, R.W. 1999. Comparisons of turf communities from Pendleton Artificial Reef, Torrey Pines Artificial Reef, and a natural reef using multivariate techniques. *Bulletin of Marine Science*, **65**: 37-57.

Badalamenti, F., Chemello, R., D'Anna, G., Ramos, P.H. & Riggio, S. 2002. Are artificial reefs comparable to neighbouring natural rocky areas? A mollusc case study in the Gulf of Castellammare (NW Sicily). *ICES Journal of Marine Science*, **59**: S127-S131.

Cabioch, L. & Glaçon, R. 1975. Distribution des peuplements benthiques en Manche Orientale, de la Baie de Somme au Pas-de-Calais. *Comptes Rendus des Séances de l'Académie des Sciences*, **280**: 491-494.

Carpentier, A., Vaz, S., Martin, C. S., Coppin, F., Dauvin, J.-C., Desroy, N., Dewarumez, J. M., Eastwood, P. D., Ernande, B., Harrop, S., Kemp, Z., Koubbi, P., Leader-Williams, N., Lefèbvre, A., Lemoine, N., Loots, C., Meaden, G. J., Ryan, N. & Walkey, M. 2005. Eastern Channel habitat atlas for marine resource management (CHARM). Interreg IIIA, 225 pp.

Carr, M.H. & Hixon, M.A. 1997. Artificial reefs: the importance of comparisons with natural reefs. *Fisheries*, **22**: 28-33.

Conlan, K. E. 1989. Delayed reproduction and adult dimorphism in males of the amphipod genus *Jassa* (Corophioidea: Ischyroceridae): an explanation for systematic confusion. *Journal of Crustacean Biology*, **9**: 601-625.

Davoult, D. 1990. Biofaciès et structure trophique du peuplement des cailloutis du Pas-de-Calais (France). *Oceanologica acta*, **13**: 335-348.

Davoult, D. & Clabaut, P. 1988. Le passage des fonds sableux de la baie de Wissant aux fonds caillouteux du large et les peuplements benthiques associées. *Journal de la Recherche Océanographique*, **1-2**: 32-35.

Degraer, S., Wittoeck, J., Appeltans, W., Cooreman, C., Deprez, T., Hillewaert, H., Hostens, K., Mees, J., Vanden Berghe, E. & Vincx, M. 2006. The macrobenthos atlas of the Belgian Part of the North Sea. Belgian Science Policy, D/2005/1191/6, CD-ROM

Edgar, G. J. 1991. Artificial algae as habitats for mobile epifauna: factors affecting the colonization in a Japanese *Sargassum* bed. *Hydrobiologia*, **226**: 111-118.

Engel, J. & Kvitek, R. 1998. Effects of otter trawling on a benthic community in monterey bay national marine sanctuary. *Conservation Biology*, **12**: 1204-1214.

Foveau, A. 2005. Evolution des fonds à *Modiolus modiolus* dans le détroit du Pas de Calais. Rapport de stage d'un Master Recherche 2 EDEL, La Rochelle, Station Marine de Wimereux, 45 pp.

Fraschetti, S., Bianchi, C.N., Terlizzi, A., Fanelli, G., Morri, C. & Boero, F. 2001. Spatial variability and human disturbance in shallow subtidal hard substrate assemblages: a regional approach. *Marine Ecology-Progress Series*, **212**: 1-12.

Gabriele, M., Bellot, A., Gallotti, D. & Brunetti, R. 1999. Sublittoral hard substrate communities of the northern Adriatic Sea. *Cahiers de Biologie Marine*, **40**: 65-76.

Garcia-Gomez, J. 1994. The systematics of the genus *Anapagurus* Henderson, 1886, and a new genus for *Anapagurus drachi* Forest, 1966 (Crustacea: Decapoda: Paguridae). *Zoologische Verhandelingen*, **295**: 1-131.

Gilson G. 1900. Exploration de la mer sur les côtes de la Belgique. *Mémoire du Muséum d'Histoires naturelles de Belgique* **1**:1-81.

Holme, N. A. 1984. Fluctuations of *Ophiothrix fragilis* in the Western English Channel. *Journal of the Marine Biological Association of the UK*, **64**: 351-378.

Jenson, G. C. 1991. Competency, settling behavior, and postsettlement aggregation by porcelain crab megalopae (Anomura: Porcellanidae). *Journal of Experimental Marine Biology and Ecology*, **153**: 49-61.

Kerckhof, F. & Houziaux, J.-S. 2003. Biodiversity of the Belgian marine areas. pp 350-389. *In* Peeters, M., Franklin, A., and Van Goethem, J. L. (eds), Biodiversity in Belgium, Royal Belgian Institute of Natural Sciences, Brussels.

Krumbein W. C. 1941. Measurement and geological significance of shape and roundness of sedimentary particles. *Journal of Sedimentary Research*, **11**:64-72.

Lanckneus, J., van Lancker, V., Moerkerke, G., Van den Eynde, D., Fettweis, M., de Batist, M. & Jacobs, P. 2001. Investigation of the natural sand transport on the Belgian continental shelf (BUDGET). Final report. Federal Office for Scientific, Technical and Cultural Affairs (OSTC), 104 pp.

Leewis, R. J., van Moorsel, G. W. N. M. & Waardenburg, H. W. 2000. Shipwrecks on the Dutch Continental Shelf as artificial reefs. pp 419-434. *In* Jensen, A. C, Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publishers, Dordrecht.

Lefebvre, A. & Davoult, D. 2000. Larval distribution of *Ophiothrix fragilis* (Echinodermata : Ophiuroidea) in a macrotidal area, the Dover Strait (eastern English Channel, France). *Journal of the Marine Biological Association of the UK*, **80**: 567-568.

Müller, Y. 2004. Mieux connaître les peuplements benthiques associés aux substrats durs au large du littoral Nord-Pas de Calais. Patrimoine Naturel Marin et Terrestre, Region Nord-Pas de Calais, 91 pp.

Myers, A. A. & Southgate, T. 1980. Artificial substrates as a mean of monitoring rocky shore cryptofauna. *Journal of the Marine Biological Association of the UK*, **60**: 963-975.

Nair, K. K. C. & Anger, K. 1979. Experimental studies on the life cycle of *Jassa falcata* (Crustacea, Amphipoda). *Helgolander Wissenschaftliche Meeresuntersuchungen*, **32**: 444-452.

Perkol-Finkel, S. & Benayahu, Y. 2004. Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-development. *Marine Environmental Research*, **59**: 79-99.

Perkol-Finkel, S., Shashar, N., Barneah, O., David-Zaslow, R., Oren, U., Reichart, T., Yacobovich, T., Yahel, G., Yahel, R. & Benayahu, Y. 2005. Fouling reefal communities on artificial reefs: Does age matter? *Biofouling*, **21**: 127-140.

Pingree, R. D. & Maddock, L. 1977. Tide residuals in the English Channel. *Journal of the Marine Biological Association of the UK*, **57**: 339-354.

Posey, M., Lindberg, W., Alphin, T. & Vose, F. 1996. Influence of storm disturbance on an offshore benthic community. *Bulletin of Marine Science*, **59**: 523-529.

Robinson, M. & Tully, O. 2000. Spatial variability in decapod community structure and recruitment in sub-tidal habitats. *Marine Ecology-Progress Series*, **194**: 133-141.

Smith, S.D.A. & Rule, M.J. 2002. Artificial substrata in a shallow sublittoral habitat: do they adequately represent natural habitats or the local species pool? *Journal of Experimental Marine Biology and Ecology*, **277**: 25-41.

Souplet, A. & Dewarumez, J. M. 1980. Les peuplements benthiques du littoral de la région de Dunkerke. *Cahiers de Biologie Marine*, **21**: 23-39.

Van Hoey, G., Degraer, S. & Vincx, M. 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuarine, Coastal and Shelf Science*, **59**: 599-613.

van Moorsel, G. W. N. M., Waardenburg, H. W. & van der Horst, J. 1991. Het leven op en rond scheepswrakken en andere harde substraten in de Noordzee (1986 T/M 1990) - een synthese. Rapport 91.19, Bureau Waardenburg bv, Culemborg, 49 pp.

Williams, R. B. 1997. *Actinothoe sphyrodeta* (Cnidaria, Actiniaria): the first records from Portugal and the Mediterranean Sea. *Journal of the Marine Biological Association of the UK*, **77**: 245-248.

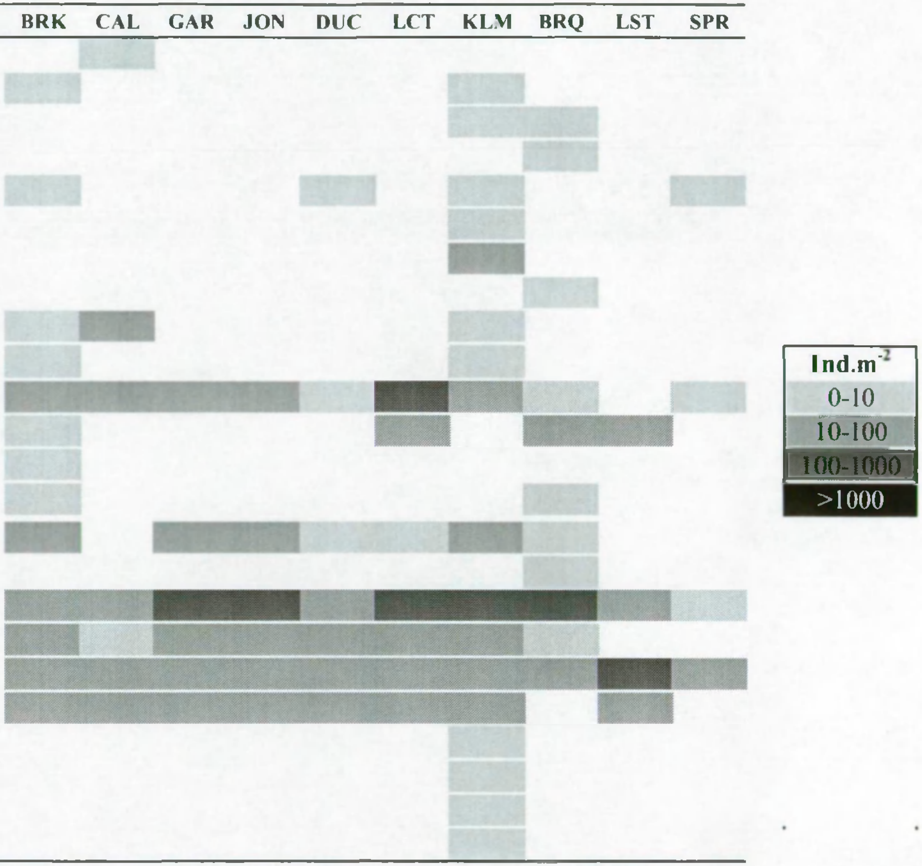
Annex 1. Distribution of the epifaunal species on the ten shipwrecks investigated. Only the data collected between April and September are used. Sites are ordered from offshore to coastal zone. BRK: Birkenfels (N=25), CAL: Callisto (N=7), GAR: Garden City (N=3), JON: John Mahn (N=3), LCT: LCT 457 (N=3), KLM: Kilmore (N=32), BRQ: Bourrasque (N=23), LST: LST 420 (N=3), SPR: Sperrbrecher (N=6). A simplified scale of dominance was attributed to the uncountable species: • present, •• abundant, ••• dominant. *: species also identified on the Dover Strait hard substrates communities.

	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
PORIFERA										
Dysidea fragilis (Montagu, 1818) *	•	•			•		•			
Esperiopsis fucorum (Esper, 1794)				•	•		•			
Halichondria cf *panicea* (Pallas, 1766)					••		•			
Haliclona oculata (Pallas, 1766) *					•		•			
Haliclona sp.	•						•	•		
Hymeniacidon perlevis (Montagu, 1818)		•					•			
Leucosolenia sp. (Montagu, 1818)		•	•	•		•	•			
Myxilla rosacea (Lieberkühn, 1859)					••		•			
Phorbas plumosus (Montagu, 1818)							•			
Sycon ciliatum (Fabricius, 1780) *	•	••	•	••	••	••	••			
CNIDARIA										
Hydrozoa										
Bougainvillia muscus (Allman, 1863)								•		
Campanularia volubilis (Linnaeus, 1758) *	•							•		
Clytia gracilis (Sars, 1850) *								•		
Clytia hemisphaerica (Linnaeus, 1767) *	•						•	•		
Halecium sp. *							•			
Hydractinia echinata (Flemming, 1828) *	•							•	•	

Ind.m^{-2}
0-10
10-100
100-1000
>1000

	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Hydrallmania falcata (Linnaeus, 1758) *								•		
Laomedea flexuosa Alder 1857								•		
Nemertesia antennina (Linnaeus, 1758) *							•	•		
Obelia bidentata Clarke, 1875	•						•	•	•	
Sarsia eximia (Allman, 1859)		•								
Sertularia cupressina Linnaeus, 1758 *								••		
Tubularia indivisa Linnaeus, 1758 *	•••	•••	•••	•••	•••	•••	•••	••	•••	
Tubularia larynx Ellis & Solander, 1786	••					••	••	••		
Anthozoa										
Actiniaria	▓	▓	▓	▓	▓	▓	▓	▒	▓	▓
Alcyonium digitatum Linnaeus, 1758 *	░	░	▒				▒			
Diadumene cincta Stephenson, 1925	▒						▓	▓		
Metridium senile (Linnaeus, 1767) *	░						░	▓	▒	▓
PLATYHELMINTHE										
Eurylepta cornuta (O.F. Müller, 1776)					░					
Turbellaria			░			▒	░			
NEMERTEA										
Baseodiscus delineatus (Delle Chiaje, 1825)		▒	░			▒	▒			
Nemertinata sp.		░				▓				
Oerstedia dorsalis (Abildgaard, 1806)	▒	▒	▒	▒	▓	▓	▓	▒	▓	
ANNELIDA										
Polychaeta										
Alentia gelatinosa (M. Sars, 1835)	░									
Autolytus sp.	▒	░		░			▒	░		

Ind.m^{-2}
░ 0-10
▒ 10-100
▓ 100-1000
█ >1000



	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Cirratulidae		0-10								
Cirratulus cirratus (O.F. Müller, 1776)	0-10						0-10			
Cirratulus filiformis Keferstein, 1862							0-10	0-10		
Cirratulus sp.								0-10		
Cirriformia tentaculata (Montagu, 1808)	0-10				0-10		0-10			0-10
Dipolydora coeca (Oersted, 1843)							0-10			
Eteone longa (Fabricius, 1780) *							10-100			
Eteone picta Quatrefages, 1865								0-10		
Eulalia aurea Gravier, 1896	0-10	10-100					0-10			
Eulalia sp.	0-10						0-10			
Eulalia viridis (Linnaeus, 1768)	10-100	10-100	10-100	10-100	0-10	100-1000	10-100	0-10		0-10
Eumida sp.	0-10					10-100		10-100	10-100	
Eupolymnia nebulosa (Montagu, 1818)	0-10									
Eupolymnia nesidensis (Delle Chiaje, 1828)	0-10							0-10		
Eusyllis blomstrandi Malmgren, 1867	10-100		10-100	10-100	0-10	0-10	10-100	0-10		
Gattyana cirrhosa (Pallas, 1766)								0-10		
Harmothoe sp.	10-100	10-100	100-1000	100-1000	10-100	100-1000	100-1000	100-1000	10-100	0-10
Kefersteinia cirrata (Keferstein, 1862)	10-100	0-10	10-100	10-100	10-100	10-100	10-100	0-10		
Lanice conchilega (Pallas, 1766) *	10-100	10-100	10-100	10-100	10-100	10-100	10-100	10-100	100-1000	10-100
Lepidonotus squamatus (Linnaeus, 1758)	10-100	10-100	10-100	10-100	10-100	10-100	10-100		10-100	
Lumbrineris latreilli Audouin & Milne-Ed., 1834							0-10			
Lumbrineris sp.							0-10			
Marphysa sanguinea (Montagu, 1815) *							0-10			
Neoamphitrite figulus (Dallyell, 1853)							0-10			

Ind.m^{-2}
0-10
10-100
100-1000
>1000

	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Nereimyra punctata (O.F. Müller, 1788)								░		
Nereis pelagica Linnaeus, 1758	▒	▒	▒		░	░	░	▒		▒
Nicolea venustula (Montagu, 1818) *							░			
Nicomache sp.								░		
Ophelia sp.								░		
Owenia fusiformis Delle Chiaje, 1842							░			
Pectinaria koreni (Malmgren, 1866)							▒			
Pholoe inornata Johnston, 1839	▒	░					▒			
Phyllodoce longipes Kinberg, 1866	░									
Phyllodoce mucosa Oersted, 1843	▓	░	░	▓	▒	█	▓	▓	▓	▓
Phyllodoce sp.							░	░		
Pista cristata (O.F. Müller, 1776)	░									
Poecilochaetus serpens Allen, 1904							░	░		
Polycirrus sp.							░			
Polydora hoplura Claparède, 1870	░									
Polydora sp.	░						░	░		
Pomatoceros triqueter (Linnaeus, 1758) *	▒	▒	▒	▒	▒	▒	▒	░		░
Proceraea sp.								░		
Procerastea halleziana Mallaquin, 1893	▒						▓	░		
Procerastea nematodes Langerhans, 1884	░							░		
Sabellaria spinulosa Leuckart, 1849 *	▒	▓	▒	░	▓	▒	▒	░		
Scoloplos armiger (Allman, 1859)							░	░		
Sphaerodoropsis flavum Oersted, 1843 *						░	░			
Sphaerosyllis bulbosa Southern, 1914							░			

$Ind.m^{-2}$
░ 0-10
▒ 10-100
▓ 100-1000
█ >1000

	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Sphaerosyllis sp.	░									
Sthenelais boa (Johnston, 1833) *		░					░	░		
Subadyte pellucida (Ehlers, 1864)	░	░	▒	▒			░			
Syllidae	░									
Syllis armillaris (O.F. Müller, 1776)	▒	░	▒			░	▒			░
Syllis gracilis Grube, 1840	▒	▒	▒	░	▒	▓	▒	▒		▒
Terebellidae	▒									
Thelepus cincinnatus (Fabricius, 1780)	▒						░			
Thelepus setosus (Quatrefages, 1865) *							░	░		
MOLLUSCA										
Gastropoda										
Aeolidiidae	░					░		░		
Archidoris pseudoargus (Rapp, 1827) *	░						░			
Catriona gymnota (Couthouy, 1838)								▒		
Cerithiopsis tubercularis (Montagu, 1803)	░	░					░			
Crepidula fornicata (Linnaeus, 1758)	░						░			
Cuthona amoena (Alder & Hancock, 1845)							░			
Cuthona concinna (Alder & Hancock, 1843)							░			
Cuthona sp.	▒	░	░	▒	▒	▒	▒	░	▒	
Dendronotus frondosus (Ascanius, 1774) *	░		▒	▒	▒	▒	▒	░	░	
Doto pinnatifida (Montagu, 1804) *							░			
Epitonium clathratulum (Kanmacher, 1798) *	▒	░	▒					▒		
Eubranchus pallidus (Alder & Hancock, 1842)							░			
Eubranchus sp.	░						░	░	▒	

Ind.m^{-2}
░ 0-10
▒ 10-100
▓ 100-1000
█ >1000

	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Euspira pulchella (Risso, 1826) *	░	▒					░	░		
Facelina bostoniensis (Couthouy, 1838)	░					▒	░	░		
Lamellaria latens (O.F. Müller O.F., 1776)							░			
Nassarius incrassatus (Ström, 1768) *	▒	▒	▒		░		▒			░
Nassarius reticulatus (Linneaus, 1758)	░							▒		
Raphitoma linearis (Montagu, 1803)	░						░			
Rissoidae	▒	▒					▒	░		
Tergipes tergipes (Forskal, 1775)							░			
Tritonia cf *manicata* Deshayes, 1853							░			
Tritonia plebeia Johnston, 1828		░								
Trivia monacha (da Costa, 1778)							░			
Bivalvia										
Aequipecten opercularis (Linnaeus, 1758)	▒	▒	▓	░			▒	░		
Heteranomia squamula (Linnaeus, 1758)	▒	▒	▒	░	▒		░			
Musculus sp.	░	▒	▒	░			░			
Mysella bidentata (Montagu, 1803)	░							░		
Mytilus edulis Linnaeus, 1758 *	▓	▓	▓	▓	▓	▓	█	▒	▒	
Ostreidae							░			
Venerupis geographica (Gmelin, 1791)	▒									
Venerupis sp.	▓	░					░	░		
SIPUNCULA										
Golfingiida							░			

Ind.m^{-2}
░ 0-10
▒ 10-100
▓ 100-1000
█ >1000

	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
CRUSTACEA										
Copepoda										
Copepoda	░						░	▒		
Cirripedia										
Acasta spongites (Poli, 1795)							░			
Balanus crenatus Bruguiére, 1789 *	▒				▒		░	▓		▒
Verruca stroemia O.F. Müller, 1776 *							░			
Cumacea										
Cumacea	░							░		
Isopoda										
Janira maculosa Leach, 1814 *							░			
Pleurocrypta porcellanae Hesse, 1876							░			
Amphipoda										
Abludomelita obtusata (Montagu, 1813) *									░	
Atylus swammerdami (Milne-Edwards, 1830)			░					░	░	
Caprella linearis (Linnaeus, 1767) *	░							░		
Caprella tuberculata Guérin, 1836	▓	█	█	▒	█		█	░		
Iphimedia nexa Myers & McGrath, 1987	░	░					░			
Jassa herdmani (Walker, 1893)	█	█	█	█	█	█	█	█	█	█
Lysianassa ceratina (Walker, 1889)	░									
Melita hergensis Reid, 1939									░	
Metopa alderi (Bate, 1857)	░	▓	▓	▓	▓	▓	▒	░	░	
Monocorophium acherusicum (Costa, 1851)								▓	▓	█

Ind.m^{-2}
░ 0-10
▒ 10-100
▓ 100-1000
█ >1000

	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Monocorophium sextonae (Crawford, 1937) *	▓	▒	▓	▓	█	█	█	█	▒	
Pariambus typicus (Kroyer, 1844)								░		
Phtisica marina Slabber, 1769	▒	▓	█	█	▓	█	█	▓	▒	
Pseudoprotella phasma (Montagu, 1804)								░		
Stenothoe marina (Bate, 1856)	▒	▒	▒	▓	▓	▓	▓	▒	▓	
Stenothoe monoculoides (Montagu, 1815)	▓	▓	▓	▓	▓	█	█	░	▒	
Stenothoe sp.	▒	▓					▓	▒		░
Stenothoe valida Dana, 1855	▒	▓	▓	█	▓	█	▒	░		
Decapoda										
Anapagurus chiroacanthus (Lilljeborg, 1856)	░									
Atelecyclus rotundatus (Olivi, 1792)	░									
Ebalia tumefacta (Montagu, 1808) *							░			
Hyas araneus (Linneaus, 1758)	░									
Inachus phalangium (Fabricius, 1775) *							░			
Liocarcinus arcuatus (Leach, 1814)							░			
Liocarcinus holsatus (Fabricius, 1798) *								░		
Liocarcinus sp.	▒	▒					▒	░		░
Macropodia parva Van Noort & Adema, 1985							░		░	
Macropodia rostrata (Linnaeus, 1761)	░									
Macropodia sp.							░			
Necora puber (Linnaeus, 1767) *	░						░			
Paguridae	░			░				░		
Pilumnus hirtellus (Linnaeus, 1761)	▒	▓	▒	▒	▒	▒	▓	░	▒	▒
Pisidia longicornis (Linneaus, 1767) *	█	█	█	█	▓	▓	█	▓	▒	▓

Ind.m^{-2}
░ 0-10
▒ 10-100
▓ 100-1000
█ >1000

	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Thoralus cranchii (Leach, 1817)							░			
CHELICERATA										
Pyconogonida										
Achelia sp.			░				▒			
Callipallene emacinata (Dohrn, 1881)							░			
Nymphon rubrum Hodge, 1865 *							░			
Pycnogonum littorale (Strom, 1762)			░					░		
BRYOZOA										
Cyclostomatida										
Crisia aculeata Hassall, 1841 *							░ •			
Disporella hispida (Fleming, 1828) *	░ •									
Plagioecia patina (Lamarck, 1816) *	░ •						░ •			
Cheilostomatida										
Bicellariella ciliata (Linnaeus, 1758) *							░ ••			
Conopeum cf *seurati* (Canu, 1928)								░		
Electra pilosa (Linnaeus, 1767) *	░ •	░ ••	░ ••	░ ••	░ ••	░ ••	░ ••	░ •	░ •	
Scruparia chelata (Linnaeus, 1758)	░ •									
Scrupocellaria scruposa (Linnaeus, 1758)	░ •	░ •					░ ••			
Ctenostomatida										
Alcyonidium cellarioides Calvet, 1900	░ •						░ •			
Nolella pusilla (Hincks, 1880)	░ •									
Vesicularia spinosa (Linnaeus, 1967)								░		
ECHINODERMATA										
Asteroidea										

Ind.m^{-2}
░ 0-10
▒ 10-100
▓ 100-1000
█ >1000

	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Asterias rubens Linnaeus, 1758 *	░	▒			░		▒	░	░	▒
Asterias rubens juv. Linnaeus, 1758 *		▒	▓	▓	▓	▓	▒		▓	
Echinoidea										
Clypeasteroidea							░	░		
Psammechinus miliaris (Gmelin, 1778)	▓	▓	▒	▒		▒	▒	░		
Ophiuroidea										
Amphipholis squamata (Delle Chiaje, 1829) *	▒	▓	▓	▒	▒	▒	▓	░	░	
Ophiothrix fragilis (Abildgaard,1789) *	▓	▓	█	▓	▓	▓	█	▒	▒	░
Ophiura albida Forbes, 1839 *	░									
Ophiura sp.							░			
CHORDATA										
Tunicata										
Ascidiacea	░									
Diplosoma sp.		░ •	░ ••	░ ••	░ ••		░ ••			
Molgula cf *occulta* occulta Kupffer, 1875	░	▒					▒			
Polyclinum aurantium Milne-Edwards, 1841		░ ••					░ ••			

$Ind.m^{-2}$
░ 0-10
▒ 10-100
▓ 100-1000
█ >1000

Annex 2. Distribution of the epifaunal species exclusively recorded between October and March. Sites are ordered from offshore to coastal zone. BRK: Birkenfels (N=7), KLM: Kilmore (N=14), BRQ: Bourrasque (N=12). A simplified scale of dominance was attributed to the uncountable species: •: present, ••: abundant, •••: dominant.

	BRK	KLM	BRQ
PORIFERA			
Mycale cf *macilenta* (Bowerbank, 1866)	•		
Suberites ficus (Esper, 1794)			•
ANNELIDA			
Polychaeta			
Eunicidae		░	
Lysidice ninetta Audouin & Milne-Ed., 1833	░		
NERMERTEA			
Tubulanus sp.		░	
MOLLUSCA			
Gasteropoda			
Tergipes tergipes (Forskal, 1775)		░	
CRUSTACEA			
Cumacea			
Bodotria arenosa Goodsir, 1843		░	
Amphipoda			
Amphilochus manudens Bate, 1862		░	░
Decapoda			
Pagurus cuanensis Bell, 1845		░	

Ind.m^{-2}
0-10
10-100
100-1000
>1000

Annex 3. List of additional species not sampled but observed by divers on shipwreck sites.

CNIDARIA
  Anthozoa
    Urticina felina (Linnaeus, 1767)
    Sagartia sp.
    Sagartiogeton undatus (O.F. Müller, 1788)
    Actinothoe sphyrodeta (Gosse, 1858)
CRUSTACEA
  Decapoda
    Cancer pagurus Linnaeus, 1758
MOLLUSCA
  Cephalopoda
    Loligo vulgaris Lamarck, 1798 – eggs
    Acanthodoris pilosa (Abildgaard in O.F. Müller, 1789)
BRYOZOA
  Cyclostomatida
    Bugula cf *turbinata* Alder, 1857
CHORDATA
  Tunicata
    Ascidiella scabra (O.F. Müller, 1776)
    Clavelina lepadiformis O.F. Müller, 1776
PISCES
    Dicentrarchus labrax (Linnaeus, 1758)
    Gadus morrhua Linnaeus, 1758
    Myoxocephalus scorpius (Linnaeus, 1758)
    Parablennius gattorugine (Linnaeus, 1758)
    Pollachius pollachius (Linnaeus, 1758)
    Pollachius virens (Linnaeus, 1758)
    Pomatoschistus sp.
    Scomber scombrus Linnaeus, 1758
    Spondyliosoma cantharus (Linnaeus, 1758)
    Trisopterus luscus (Linnaeus, 1758)
    Trisopterus minutus (Linnaeus, 1758)
    Trachurus trachurus (Linnaeus, 1758)

Annex 4. Provisional list of species from shipwrecks which are new for the Belgian fauna. SNSS: Southern North Sea species, NSSP: Northern North Sea species, NC: species found in neighbouring countries, SS: Southern species, NS: Northern species, ES: European species, COS: cosmopolite species. ?: unavailable information.

TAXON	SNSS	NNSS	NC	SS	NS	ES	COS
PORIFERA							
Dysidea fragilis	+	+	+	+	+	+	
Phorbas plumosus	+		+			+	
CNIDARIA							
Actinothoe sphyrodeta	-	-	+	+	-	+	
Diadumene cincta	+	+	+				+
PLATYHELMINTHE							
Eurylepta cornuata	+			+		+	+
NEMERTEA							
Oerstedia dorsalis	+	+	+				+
POLYCHAETA							
Alentia gelatinosa	+	+	+			+	
Cirratulus cirratus	+	+	+				+
Cirriformia tentaculata	+	+	+				+
Dipolydora caeca	+	+	+			+	
Eteone picta	+	-	+			+	
Eulalia aurea	-	-	+	+		+	
Eupolymnia nebulosa	+	+	+		+	+	
Eupolymnia nesidensis	?	+	+			+	
Kefersteinia cirrata	+	-	+				+
Lysidice ninetta	-	-	+	+			+
Marphysa sanguinea	+	-	+	+	-		+
Neamphitrite figulus	+	+	+			+	
Nereimyra punctata	+	+	+		+	+	
Pholoe inornata	-	+	+				+
Phyllodoce longipes	+	-					+
Pista cristata	-	+	+				+
Polydora hoplura	+	+	+				+
Procerastea halleziana	-	+	+			+	
Procerastea nematodes	-	-	+	+		+	
Sphaerodoropsis flavum	?	+	+				+
Sphaerosyllis bulbosa	+	-	+	+		+	
Subadyte pellucida	+	+	+				+
Thelepus cincinnatus	+	?	+	+			+
Thelepus setosa	-	-	+	+			+
GASTROPODA							
Cuthona amoena	+	-	+	+		+	
Cuthona concinna	-	+			+	+	

TAXON	SNSS	NNSS	NC	SS	NS	ES	COS
Raphitoma linearis	-	+				+	
Tritonia cf *manicata*	-	-	+	+		+	
CRUSTACEA							
Acasta spongites	-	-	+	+	-		
Caprella tuberculata	+	+	+	+			
Lysianassa ceratina	-	-	+			+	
Pleurocrypta porcellanae	+	-	+	+		+	
Pseudoprotella phasma	-	-	+	+		+	
Anapagurus chiroacanthus	-	+	+				
Macropodia parva	+	+	+		+	+	
PYGNOGONIDE							
Callipallene emacinata	-	-		+		+	
BRYOZOA							
Crisia aculeata	+	+	+			+	
Conopeum cf *seurati*		+	+	+			
Alcyonidium cellarioides	+	-	+	+		+	
Nolella pusilla	+	-	+	+		+	
TUNICATA							
Clavelina lepadiformis	+	-	+			+	
Polyclinum aurantium	+	+	+			+	

Annex 5. Species from Belgian shipwrecks which can be considered as rare for the Belgian fauna (mentioned only one or two times).

PORIFERA
- *Hymeniacidon perlevis*
- *Esperiopsis fucorum*

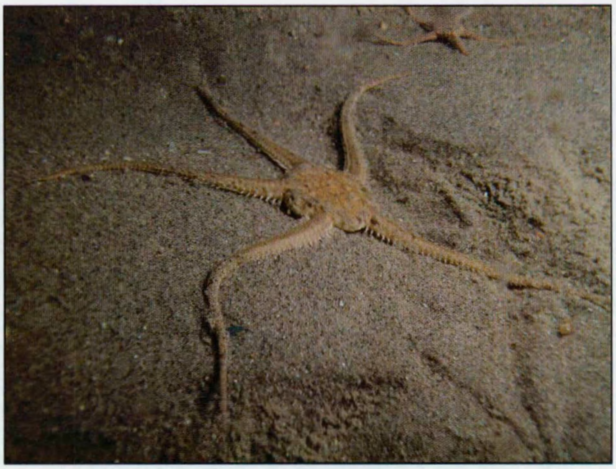
CNIDARIA
- *Sagartiogeton undatus*

CRUSTACEA
- *Iphimedia nexa*
- *Atelecyclus rotundatus*
- *Inachus phalangium*

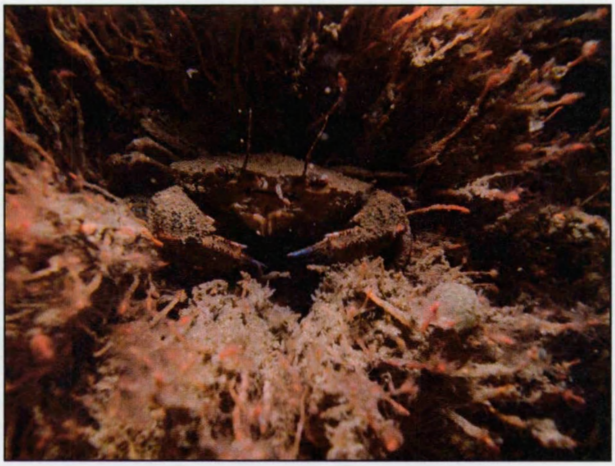
PYCNOGONIDE
- *Pycnogonum littorale*

TUNICATA
- *Ascidiella scabra*

Chapter IV - Identity of artificial reef communities



Ophiura sp. from soft sediments on the Belgian Part of the North Sea.



Necora puber around a dense turf of *Tubularia indivisa* (Kilmore shipwreck).

ARTICLE 3: ARTIFICIAL HARD SUBSTRATES INCREASE STRUCTURAL AND FUNCTIONAL BIODIVERSITY IN SOFT SEDIMENT SEA BEDS

Chapter III gave important information on the species composition of shipwreck communities. The fauna was typified by a large fraction of species typically associated with hard substrates. We believe that it was important to stress the isolated identity of these communities in the context of the Belgian marine area. To characterize the degree of isolation of shipwrecks communities among the Belgian continental shelf, it is essential to contrast them with the communities from the habitat surrounding them. In this chapter, a paper is intended to formally describe shipwrecks as a new habitat for the Belgian waters which are strongly dominated by soft-sedimented seabed. It qualitatively and quantitatively contrasts the structural and functional biodiversity associated with shipwrecks and the surrounding soft sediment communities. We will see that both the abundance and biomass patterns are distinct and that the trophic organization is different with possible consequences for the inherent stability of shipwrecks communities.

ARTIFICIAL HARD SUBSTRATES INCREASE STRUCTURAL AND FUNCTIONAL BIODIVERSITY IN SOFT SEDIMENT SEA BEDS

Vincent Zintzen[1,2], Steven Degraer[3], Claude Massin[1], Jérôme Mallefet[2]

[1] Royal Belgian Institute of Natural Sciences, Rue Vautier 29, B-1000 Brussels, Belgium.
[2] University of Louvain, Biology Laboratory, Kellner Building, place Croix du Sud 3, B-1348 Louvain-la-Neuve, Belgium.
[3] Ghent University, Biology Department, Marine Biology Section, Krijgslaan 281-S8, B9000 Gent, Belgium.

Corresponding author: Vincent Zintzen
Email: vincent.zintzen@naturalsciences.be
Tel: +32(0)2 627.43.38, Fax: +32(0)2 627.41.41
Royal Belgian Institute of natural Sciences
Rue Vautier, 29
1000 Brussels
Belgium

ABSTRACT

Shipwrecks are patches of hard substrate in sea beds dominated by soft sediments. We investigated the structural and functional diversity of the epifaunal communities developing on these artificial hard substrates in the context of a soft sediment sea bed in the Southern Bight of the North Sea. The hard substrate available for the colonization of the epifauna represents between 0.025% and 0.043% of the area under investigation. The results indicate that few species are shared by the two habitats (9.6%) and that their faunal assemblages are distinct. There is a shift from a habitat dominated by bivalves and polychaetes in soft sediments to shipwrecks dominated by crustaceans, polychaetes and cnidarians. Diversity indices show that shipwrecks are more species rich and that their taxonomic diversity is also higher than on soft sediments. Faunal abundance and biomass are a thousand and a hundred times higher than on soft sediments. Shipwrecks are strongly dominated by suspension feeders and have consequently a distinct and less diversified trophic structure than what is found on the surrounding sediments. In consequence, shipwrecks stress the impacts of human activities on natural communities at sea by adding a source of added structural and functional diversity in soft sediment bottoms.

KEYWORDS

Soft sediment, shipwrecks, species diversity, invertebrate zoology, trophic structure, biomass

1. INTRODUCTION

The relative effect on species diversity and abundance of artificial structures at sea is still poorly understood (Connell & Glasby, 1999). Even though scientific publications about the topic are limited, there is a general agreement that these sites harbour a large amount of epibenthic organisms and associated motile species living on them. This is particularly striking when artificial substrates are lying on soft sediment sea beds because their fauna looks entirely different (Steimle & Zetlin, 2000). However, quantification of this difference is generally lacking. Several studies already proved that marked differences exist between community structures on natural and artificial substrata (Connell, 2000; Connell, 2001; Smith & Rule, 2002) and there are several potential ecological implications which raise from the presence of shipwrecks. These differences can have several impacts on the structural and functional aspects of ecosystems dominated by soft sediments.

First, a set of new species are susceptible to colonize these substrates. The presence of a stable habitat will inevitably allow the settlement of a set of typically sessile species which would otherwise not be found in the vicinity. A few studies described the epibenthic communities of this kind of submerged structures and described a fauna typical of hard substrates (e.g. on temperate waters Bulloch, 1965; Hiscock, 1980; Wendt *et al.*, 1989; van Moorsel *et al.*, 1991; Gabriele *et al.*, 1999; Massin, 2002; Zintzen *et al.*, 2006). In this context, stepping stone effect may occur, especially for those species having a low dispersal capacity and if the network of hard substrate is dense enough. Consequently, the dispersal of some species could be impacted by facilitated spreading in area dominated by unfavourable habitat (i.e. soft sediments).

Secondly, following the settlement of sessile species and associated fauna, the diversity and biomass of species can locally increase (Leewis *et al.*, 2000; Bially & Macisaac, 2000) and could in turn attract predators (Sutterer & Szedlmayer, 2005). The attraction of fish populations by artificial reefs is a well known phenomenon (Osenberg *et al.*, 2002) and is indeed the main reason why artificial reefs have been studied although what makes a reef attractive is still mostly unanswered (Bohnsack & Sutherland, 1985).

Another impact is directly related to the increased biomass on artificial reefs compared to the surrounding soft sediments (Foster *et al.*, 1994) and to the expected dominance of filter feeders on these sites. Filter feeders have been shown to diminish phytoplankton concentrations as water passes over them (Wildish & Kristmanson, 1984; Tweddle *et al.*, 2005). This leads to horizontal gradients in phytoplankton concentration, with higher concentrations upstream of the suspension feeders, and lower concentrations downstream with consequences on food availability for downstream communities.

Finally, besides the effect of the artificial reef itself, the sediments directly surrounding the shipwreck are potentially protected from fishing pressure and could harbour communities with a lower degree of disturbance (Hall *et al.*, 1993; Danovaro *et al.*, 2002).

To assess the impact of artificial hard substrates in soft sediment sea beds, a first step is to quantitatively stress the structural and functional differences that characterize both habitats. In this paper, we will specifically quantify the structural and functional diversity of shipwrecks in a context dominated by soft sediment communities. The specific questions to be answered are: to what extend (1) the structure of species assemblages (patterns of alpha-diversity, density and biomass) on both habitats differs and (2) does the trophic structure differs between both habitats?

2. MATERIAL AND METHOD

2.1. Study area

The Belgian part (3460 km^2) of the North Sea (BPNS) is an epicontinental sea with a mean depth of 20 m and a maximum depth of 40 m (Figure 1). The region is strongly governed by tidal currents which have a strong influence on the distribution of sediments and benthic communities (Larsonneur *et al.*, 1982). Current velocities are gradually decreasing from west to east. Around the Dover Strait, where the distance between France and England is the shortest, strong currents up to 3 knots occur during spring tides and pebbles dominate the sea bottom (Pingree & Maddock, 1977). To the east, current is decreasing allowing for the sedimentation of finer sediments. Soft sediments dominate on the Belgian Part of the North Sea but because of the presence of numerous sandbanks a high geomorphological and sedimentological diversity is found (Degraer *et al.*, 1999). Most of its hard substrates are artificial, such as shipwrecks: natural hard substrates such as pebbles are rare and only occur in some places in gullies between sandbanks (Lanckneus *et al.*, 2001). Officially, the Belgian waters harbour a total number of 231 recorded obstructions for navigation or fisheries (Administration for Navigation and Coast, unpublished data, Figure 1), most of them being shipwrecks.

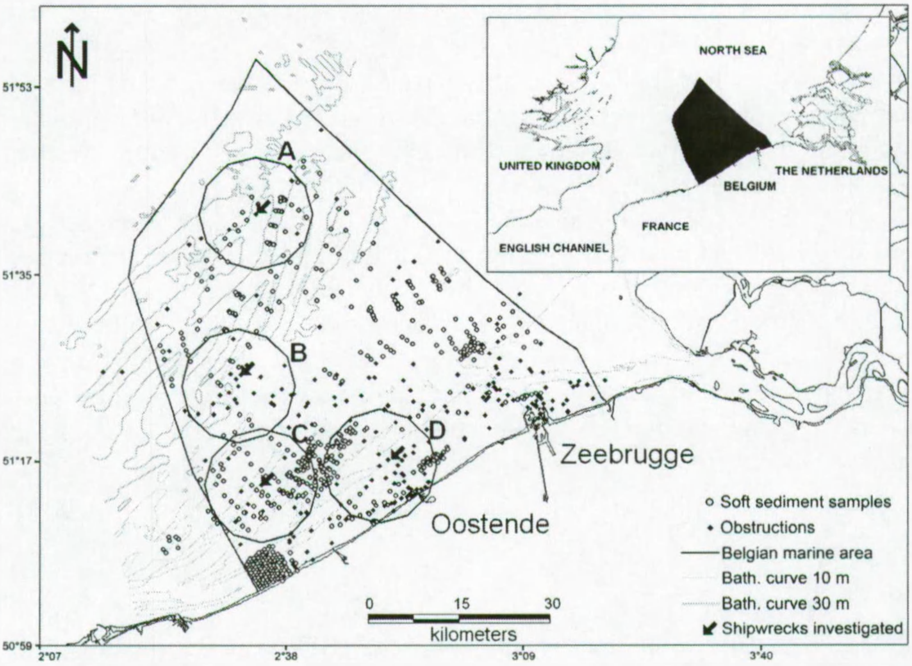


Figure 1. Localisation of the 231 subtidal obstructions on the BPNS officially recognised by the Administration for Navigation and Coast (AWZ) and sampling sites of soft sediment. (A) Birkenfels, (B) Kilmore, (C) Bourrasque and (D) Sperrbrecher 142. A 5 nautical miles circle is delimited around each investigated shipwreck. Map background layers provided by the MUMM.

2.2. Data origin

Two data sets (soft and hard substrates) on macrobenthic assemblages from the subtidal zone were used in the analysis. The macrobenthos in soft sediments was defined as all taxa retained on a 1 mm mesh-sized sieve while the macrobenthos of hard substrate was defined as all taxa with a body size bigger than 1 mm as measured under a binocular.

The first data set was composed of soft sediment samples covering the major part of the BPNS (MS Access MACRODAT database, Ghent University, Marine Biology Section) and collected within the framework of several studies between 1994 and 2004. We considered this data set as representing the most recent picture of the soft sediment assemblages constituting the BPNS. Samples were taken with a Van Veen Grab (sampling surface area: 0.1 m^2) and sieved alive over a 1 mm mesh-sized sieve. After transfer to 8 % buffered formalin, the taxa were identified to the lowest possible taxonomic level and counted. This raw data set, comprising 196 species for 685 samples (Figure 1), was used for species accumulation curves and species richness estimators analysis (see below). For all other analyses, all rare taxa (present as single specimens in samples and occurring in less than 2% of the samples) were excluded because of their probable unreliable density and distribution estimates (Cao *et al.*, 2001). This latter data set consisted of 685 samples and 118 taxa (further referred to as species). From this data set, Degraer (unpublished data) distinguished four subtidal communities: an *Abra alba* community, a *Macoma baltica* community, a *Nephtys cirrosa* community and an *Ophelia limacina-Glycera capitata* community (see Van Hoey *et al.*, 2004 for a detailed description of these communities). This data set is further referred to as the 'soft sediments' data set.

A second data set originates from samples taken on artificial hard substrates found on the BPNS. Four shipwrecks, located along a cross-shore transect were sampled from 2001 until 2004 (Figure 1, Table 1). The four ships had sunk since at least 40 years and consequently we considered that their communities had reached a mature state (van Moorsel *et al.*, 1991; Leewis *et al.*, 2000). All the living fauna within frames of 25 x 25 cm selected at random were scraped on the surface of shipwrecks by SCUBA divers. On board, animals were relaxed in a 3.5 % $MgCl_2$ solution for two hours and then transferred to a buffered formalin solution (final concentration 4 %, pH 8.2-8.4). Later on, specimens were transferred to 70 % buffered alcohol for permanent storage. The samples were then sorted under a binocular and macro-species (>1 mm) were identified to the lowest possible taxonomic level and counted. Colonial species were considered as present or absent. The raw data set is composed of 80 samples for 181 taxa (further referred to as species). This raw data set was again used for species accumulation curves and species richness estimators analysis. A total of 57 species were considered as rare species (see above) and were consequently excluded from the remaining of the analysis. The final data set held 80 samples and 124 taxa and was further referred to as the 'hard substrate' data set.

The taxonomy followed Costello *et al.* (2001). Taxa with potential misidentifications were lumped to higher taxonomic levels (e.g. to the genus level: *Eulalia* spp., *Eumida* spp., *Harmothoe* spp., *Liocarcinus* spp., *Molgula* spp.; to the family level: Paguridae, Cirratulidae; to the order level: Actiniaria, Golfingiida).

2.3. The extend and repartition of artificial hard substrate on the BPNS

The amount of hard substrate available for colonization of epifauna was estimated from the obstruction data set of the Administration for Navigation and Coast of Belgium. This data set is a compilation of the possible obstruction to navigation or to fishery for the BPNS. As a consequence, it is not an exhaustive list of subtidal hard substrates. For the 231 records which were almost exclusively shipwrecks, the length of 73 shipwrecks (average length: 80.9 m) and the width of 70 shipwrecks (average width: 11.4 m) were known from measurements done with multi-beam sonar. In order to calculate the total surface of these hard substrates, we used van Moorsel *et al.* (1988) estimations. In their work on shipwrecks representative of the Dutch coast, they calculated that the ratio of shipwreck surface against its projected area lay between 4 and 7. The projected area was calculated by multiplying the length by the width. For shipwrecks where these values were unknown, we used mean values estimated from the pool of known dimensions.

Obstruction points were incorporated into a SIG (Mapinfo V6.5) and analyzed for their spatial allocation in relation to distance from the coast, navigation routes, harbours and mean distance between them.

2.4. Data analysis

Analysis of data collected by two different methods poses inevitably methodological problems. However, in both datasets, the size of the sample unit and type of technique used were chosen to adequately sample the habitat under investigation. Except for the rare species whose repartition is too patchy to estimate correctly their abundance pattern, the density of the other species should be correctly estimated and it is then reasonable to compare abundance data and patterns of abundance (Magurran, 2004). In all following analysis, the abundances from both datasets were scaled to a common unit of area. We do think that it is meaningful to compare species assemblages originating from the same environment and from the same size range (>1 mm), their only intrinsic difference being the substrate they live on/in.

2.4.1. Univariate analysis

For univariate statistics, a subset of the soft sediment samples surrounding each shipwreck was extracted from the initial database. All samples within 5 nautical miles from the shipwrecks were selected, being a trade-off between representativity of the soft-sedimented macrobenthic communities around shipwrecks and sample availability. Univariate summary variables used were the species richness (S), the Simpson index (D) (Magurran, 2004), the average taxonomic distinctness (Δ^+) and the variation in taxonomic distinctness (Λ^+) (Clarke & Warwick, 1998a; Clarke & Warwick, 2001a). Δ^+ has to be seen as the average taxonomic distance apart of all the pairs of species in a sample. Λ^+ is the variance of the taxonomic distances between each pair of species about their mean value Δ^+. The taxonomic distances were here evaluated through a taxonomic tree built on standard Linnean classification. The distance was defined by the sum of the branch length between two species. Using the taxonomy proposed by Costello *et al.* (2001), we extracted a simplified tree: the retained taxonomic levels were species, genus, family, order, class and phylum. The default weights between step length of the Linnean tree was set to constant (i.e. weights were 16.7 for species in the same genus, 33.3 for species in different genus but the same family, 50 for species in different family but the same order, 66.7 for species in different orders but the same class, 83.3 for species in different class but the same phylum and 100 for species in different phyla). These indices were calculated using the DIVERSE procedure of the PRIMER statistical software package and compared across habitats using a permutation test based on Monte Carlo simulations (Sokal and Rohlf, 1995).

True species richness was estimated with the Chao2 nonparametric estimator (Chao & Lee, 1992). Chao2 was defined as Chao2 = $S_{obs} + (Q_1^2/2Q_2)$ where S_{obs} was the observed species richness, Q_1 was the number of species that occur in one sample and Q_2 was the number of species that occur in two samples. Since this estimator was based on the rare taxa present in samples,

Table 1. Localization of the four shipwrecks under study.

Site	Wreck name	WGS-84 Coordinates	Date of sinking	Coastal distance (nautical miles)	Length (m)	Depth (MWLS) (m)	Number of samples
A	Birkenfels	N 51°38',989 E 02°32',268	1966	29	156	37	33
B	Kilmore	N 51°23',730 E 02°29',790	1906	17	87	30	19
C	Bourrasque	N 51°14',964 E 02°33',026	1940	8	74	18	24
D	Sperrbrecher 142	N 51°16',650 E 02°49',780	1942	4	51	8	4

we used the data sets without omitting rare taxa. Species accumulation curves were constructed using the EstimateS software (Version 7.5, R. K. Colwell, http://purl.oclc.org/estimates). Difference for dominance pattern across habitats was tested by comparing the slope of the rank/abundance plot (Whittaker, 1965) using Kolmogorov-Smirnov two-sample test (Sokal & Rohlf, 1995).

2.4.2. Biomass analysis

During the spring and summer periods, samples (N=35) from the four shipwrecks were scraped for biomass analysis. The epifauna inside a 0.0625 m^2 frame was removed and transferred to plastic bags. Onboard, the samples were directly frozen (-80°C). Dry weight was measured after constant weight was attained in an oven at 80°C. Since the samples were often large, ash fee dry weights were measured on a subsample. Ashes were obtained after burning the subsample in a furnace at 500°C for 12h. Ash free dry weight was the difference between dry weight and the weight after the burning process.

The biomass of soft sediment from the coastal area (<5 nautical miles from the coast) were estimated from Van Veen grabs (S=0.1026 m^2, N=50). The animals were sieved alive over a 1 mm mesh-sized sieve. Ash-free dry weight per higher taxon and per sample was determined by drying the individuals for 72 hours at 60 °C to a constant dry weight and then combusting them for 2 hours at 500 °C. The AFDW was determined by subtracting the ash weight from the dry weight.

2.4.3. Multivariate analysis

A Bray-Curtis similarity matrix was created with abundance data of species of the pooled data set (Kruskal, 1964). Prior to analysis, abundances were fourth root transformed. Another similarity matrix based on taxonomic dissimilarity from presence/absence data which is the natural extension of the Kulczynski presence/absence dissimilarity was set up (Clarke & Warwick, 1998b). These matrix were then used to explore the pattern of community structure among samples by means of ordination with non-metric multidimensional scaling (nMDS) and clustering by group-averaging (Clarke, 1999). The goodness-of-fit of the resulting 2-dimensional nMDS plot was measured using Kruskal's stress formula I (Kruskal & Wish, 1978). Difference between habitats were tested through one-way ANOSIM which is a multivariate test based on the corresponding rank similarities between samples in the underlying triangular similarity matrix (Clarke & Warwick,

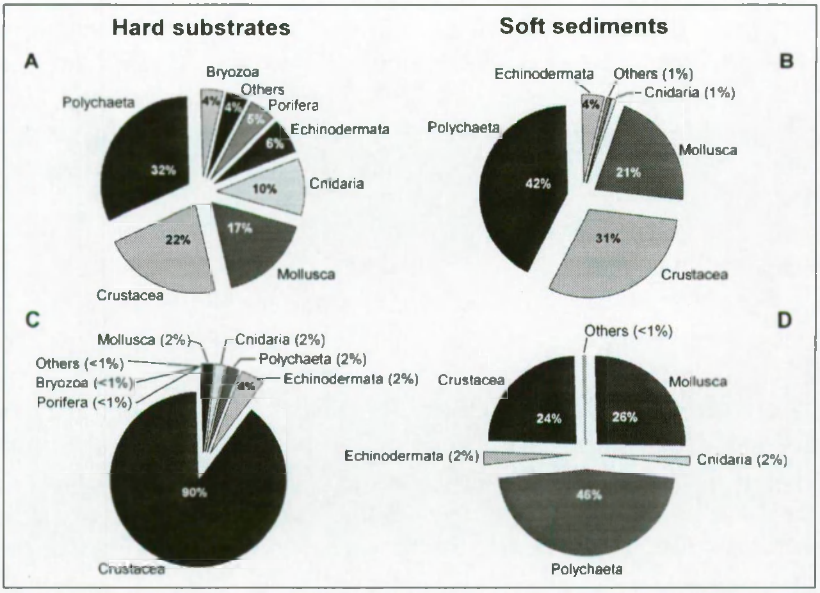


Figure 2. Species richness distribution (A and B) and abundance (C and D) on hard substrates and soft sediments. Others: Chordata (Tunicata), Nemertea and Sipuncula.

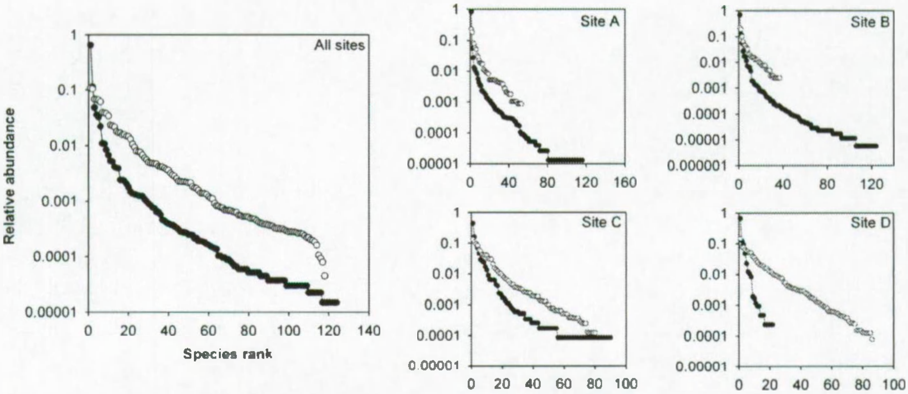


Figure 3. Rank/abundance plot based on count of species on hard substrates (●) and selected soft sediments (○) around hard substrate sites (distance: circle of 5 nautical miles, number of samples: site A (38), B (14), C (90), D (118))

2001b). The trophic status of each taxon was assigned by classification into feeding groups according to literature data (e.g. Fauchald & Jumars, 1979; Lincoln, 1979; Graham, 1988; Eleftheriou & Basford, 1989; Dauwe *et al.*, 1998; Roth & Wilsson, 1998; Desrosiers *et al.*, 2000). There still exists considerable uncertainty about the diet of many species and those species were assigned to the category 'unknown' trophic status. If several feeding habits were possible, the species was assigned to the prevailing mode of nutrition. A new data set based on trophic status was created from the initial species data set. Each sample was consequently characterized by its abundance-weighted trophic structure. The multivariate pattern of this matrix was again analyzed by nMDS and clustering (agglomerative hierarchical group-averaging) based on Bray-Curtis similarities calculated on square root transformed data. The contribution of each trophic status to total density was compared between shipwrecks and soft sediment samples around shipwrecks within a circle of five nautical miles.

3. RESULTS

3.1. Spatial allocation of artificial hard substrate on the Belgian waters

The mean estimated dimensions for shipwrecks were 80.9 m in length and 11.4 m in width. The projected area of this mean wreck was 919.5 m^2 and its real surface was estimated to be between 3,677.8 m^2 and 6,436.2 m^2. The 231 obstructions of the entire Belgian continental shelf totalised an area available for epibenthos colonization lying between 0.85 km^2 and 1.49 km^2. These estimations represented 0.025% and 0.043% of the surface of the BPNS. 19% of shipwrecks lay under the navigation routes and 23% at less than two nautical miles from harbours. 83% of the shipwrecks were at less than 30 km from the coast. It means that generally, a wreck could be found at each node of a grid of 3.87 km side, but on the coastal zone, this grid would have had a size of 3.01 km and offshore a size of 6.64 km.

3.2. Species richness and abundance of the macrobenthos

3.2.1. General trend

In both soft and hard substrates, polychaetes, crustaceans and molluscs were the dominant higher taxa in terms of number of species (Figure 2). For hard substrates, 71% of the species belonged to these three taxa and 94% for soft sediments. No algae were found. Some groups, not recorded from soft sediments, were well represented in hard substrates (bryozoans, poriferans,

Table 2. Dominance pattern across the different habitats. % cum is the cumulative dominance. The value between brackets is the cumulative dominance without taking into account *Jassa herdmani* for the sites strongly dominated by this species. CNI: Cnidaria. CRU: Crustacea. ECH: Echinodermata. MOL: Mollusca. POL: Polychaeta. Hard substrates state for all samples from wreck pooled together.

SOFT SEDIMENTS

Taxa	Group	% Cum
Spiophanes bombyx	POL	10
Magelona sp.	POL	21
Scoloplos armiger	POL	28
Abra alba	MOL	34
Mysella bidentata	MOL	41
Lanice conchilega	POL	47
Nephtys cirrsa	POL	51
Pariambus typicus	CRU	55
Eumida spp.	POL	59
Cirratulidae	POL	62

HARD SUBSTRATES (HS)

Taxa	Group	% Cum
Jassa herdmani	CRU	64
Phtisica marina	CRU	76 (32)
Caprella tuberculata	CRU	81 (46)
Pisidia longicornis	CRU	84 (56)
Ophiothrix fragilis	ECH	88 (65)
M. sextonae[†]	CRU	90 (72)
Actiniaria	CNI	91 (75)
Mytilus edulis	MOL	92 (78)
Amphipholis squamata	ECH	93 (80)
Stenothoe monoculoides	CRU	93 (82)

HS - SITE A

Taxa	Group	% Cum
Jassa herdmani	CRU	83
Pisidia longicornis	CRU	88 (31)
Ophiothrix fragilis	ECH	91 (47)
Caprella tuberculata	CRU	92 (54)
M. sextonae[†]	CRU	93 (61)
Actiniaria	CNI	94 (66)
Phtisica marina	CRU	95 (70)
Mytilus edulis	MOL	95 (74)
Pomatoceros triqueter	POL	96 (76)
Psammechinus miliaris	ECH	96 (78)

HS - SITE B

Taxa	Group	% Cum
Jassa herdmani	CRU	53
Phtisica marina	CRU	73 (43)
Caprella tuberculata	CRU	81 (60)
Ophiothrix fragilis	ECH	85 (68)
M. sextonae[†]	CRU	88 (75)
Pisidia longicornis	CRU	90 (79)
Amphipholis squamata	ECH	92 (82)
Actiniaria	CNI	93 (85)
Stenothoe monoculoides	CRU	94 (87)
Mytilus edulis	MOL	95 (89)

HS - SITE C

Taxa	Group	% Cum
Jassa herdmani	CRU	31
Metridium senile	CNI	44 (18)
Phyllodoce mucosa	POL	50 (28)
Phtisica marina	CRU	57 (37)
Diadumene cincta	CNI	63 (46)
Pisidia longicornis	CRU	69 (54)
M. acherusicum[§]	CRU	74 (63)
Harmothoe spp.	POL	79 (70)
Balanus crenatus	CRU	82 (74)
Stenothoe valida	CRU	84 (77)

HS - SITE D

Taxa	Group	% Cum
M. acherusicum[§]	CRU	37
Mytilus edulis	MOL	61
Phyllodoce mucosa	POL	76
Metridium senile	CNI	83
Jassa herdmani	CRU	88
Actiniaria	CNI	92
Pisidia longicornis	CRU	95
Syllis gracilis	POL	98
Balanus crenatus	CRU	98
Lanice conchilega	POL	98

[†] *Monocorophium sextonae.* [§] *Monocorophium acherusicum.*

nemertineans and sipunculans). The abundance of specimens on hard substrates was dominated by crustaceans (90%, mainly the amphipod *Jassa herdmani*), while a more balanced situation prevailed on soft sediments where again polychaetes (46%) dominated followed by an equal proportion of molluscs (26%) and crustaceans (24%). Generally, hard substrates were more strongly dominated by a few crustacean species compared to soft sediments which were dominated by polychaete species (Table 2). The difference in evenness of the two distributions was clearly illustrated by the rank/abundance plots (Figure 3). On hard substrates, a few species had a high abundance while the distribution of abundance classes was more uniform on soft sediments. The abundance pattern of species among the two substrates was different. The Kolmogorov-Smirnov test for differences in the distribution of the two samples was highly significant ($p<0.001$), even when omitting the most abundant species (*J. herdmani*) from the hard substrates dataset. The abundance of individuals was on average 25 times higher on shipwrecks than on soft sediments (Table 3). The maximum abundance observed on shipwrecks was over 280,000 ind.m^{-2} and 1076 ind.m^{-2} for soft sediments.

Combined species richness of both habitats was 220. Although not directly comparable, the macrofauna species richness of samples for soft sediments ranged from 1 to 50 (average: 11 spp.sample^{-1}) and from 2 to 52 (average 24 spp.sample^{-1}) for hard substrates (Table 3). Comparison of species richness was realized through species accumulation curves (Figure 4). As well for hard substrates as for soft sediments, these curves showed no sign of approaching asymptotic value and consequently had to be seen as minimum estimates. The chao2 estimate of true species richness for hard substrates peaked at 261 ± 20 sp. and at 224 ± 20 sp. for soft sediments at the respective maximal sampling intensity. Again, none of these estimates are close to reach an asymptote. The mean number of species (± s.d.) observed per square meter was 106 ± 6 and 44 ± 5 for hard substrates and soft sediments, respectively. However, if we look at species richness as a function of accumulated number of individuals, we observe that species richness on soft sediments is higher than on hard substrates. For example, at a sampling effort of 50,000 individuals, Chao2 for soft sediments is 184 ± 14 sp and 165 ± 20 for hard substrates.

3.2.2. Among sites comparisons

Looking at the higher taxa repartition by wreck (Figure 5), sites A and B had a very similar pattern with all groups well represented while the site close to coast (site D) was less diverse and missed some groups (bryozoans,

Table 3. Species richness and abundance of soft sediment and hard substrate samples.

	Species richness			Abundance (ind.m^{-2})		
	Mean (± s.d.)	Min	Max	Mean (± s.d.)	Min	Max
Soft sediments	11 ± 9	1	50	1076 ± 2442	8	26,508
Hard substrates (HS)	24 ± 12	2	52	27,014 ± 55,748	44	281,172
HS - site A	24 ± 8	11	49	27,628 ± 55,206	966	240,182
HS - site B	36 ± 10	7	52	49,030 ± 73,094	256	281,172
HS - site C	13 ± 8	2	39	2,659 ± 4,165	44	18,774
HS - site D	10 ± 5	3	16	5,540 ± 3,743	1,320	10,432

Table 4. Shared species by soft sediment and hard substrate samples. CNI: Cnidaria, CRU: Crustacea, ECH: Echinodemata, POL: Polychaeta. Mean abundance (ind.m^{-2}) and standard deviation (s.d.) are calculated for the samples where the species is present. % occurrence is the ratio of the number of samples where the species is present by the total number of samples.

	Species	Faunal group	Mean abundance ± s.d. (% occurrence among samples)			
			Soft sediment		Hard substrate	
1	Actiniaria	CNI	90 ±130	(19%)	419 ± 3127	(70%)
2	*Aequipecten opercularis*	MOL	34 ± 7	(<1%)	90 ± 511	(41%)
3	*Asterias rubens*	ECH	56 ± 86	(1%)	50 ± 253	(35%)
4	*Autolytus* sp.	POL	36 ± 42	(10%)	89 ± 446	(30%)
5	*Crepidula fornicata*	MOL	27 ± 22	(4%)	56 ± 86	(5%)
6	*Eteone longa*	POL	41 ± 76	(13%)	160 ± 159	(2%)
7	*Harmothoe* sp.	POL	36 ± 56	(7%)	157 ± 1176	(68%)
8	*Lanice conchilega*	POL	282 ± 965	(23%)	29 ± 115	(23%)
9	*Mysella bidentata*	MOL	329 ± 770	(22%)	80 ± 83	(2%)
10	*Mytilus edulis*	MOL	42 ± 57	(8%)	388 ± 3047	(74%)
11	*Nassarius reticulatus*	MOL	37 ± 43	(8%)	103 ± 423	(6%)
12	*Nereis* sp.	POL	34 ± 39	(12%)	34 ± 155	(30%)
13	*Pectinaria koreni*	POL	47 ± 55	(13%)	264 ± 226	(2%)
14	*Phtisica marina*	CRU	140 ± 393	(2%)	3995 ± 34,157	(77%)
15	*Phyllodoce mucosa*	POL	109 ± 236	(22%)	262 ± 1565	(42%)
16	*Pisidia longicornis*	CRU	16 ± 9	(2%)	1202 ± 1948	(80%)
17	*Poecilochaetus serpens*	POL	63 ± 105	(8%)	27 ± 29	(4%)
18	*Polydora* sp.	POL	26 ± 22	(3%)	19 ± 34	(7%)
19	*Pomatoceros triqueter*	POL	41 ± 38	(2%)	108 ± 713	(51%)
20	*Scoloplos armiger*	POL	158 ± 447	(47%)	48 ± 38	(2%)
21	*Stenothoe marina*	CRU	56 ± 155	(2%)	371 ± 2117	(38%)
22	*Sthenelais boa*	POL	50 ± 75	(10%)	16 ± 21	(5%)
23	*Syllis armillaris*	POL	21 ± 15	(1%)	34 ± 158	(31%)

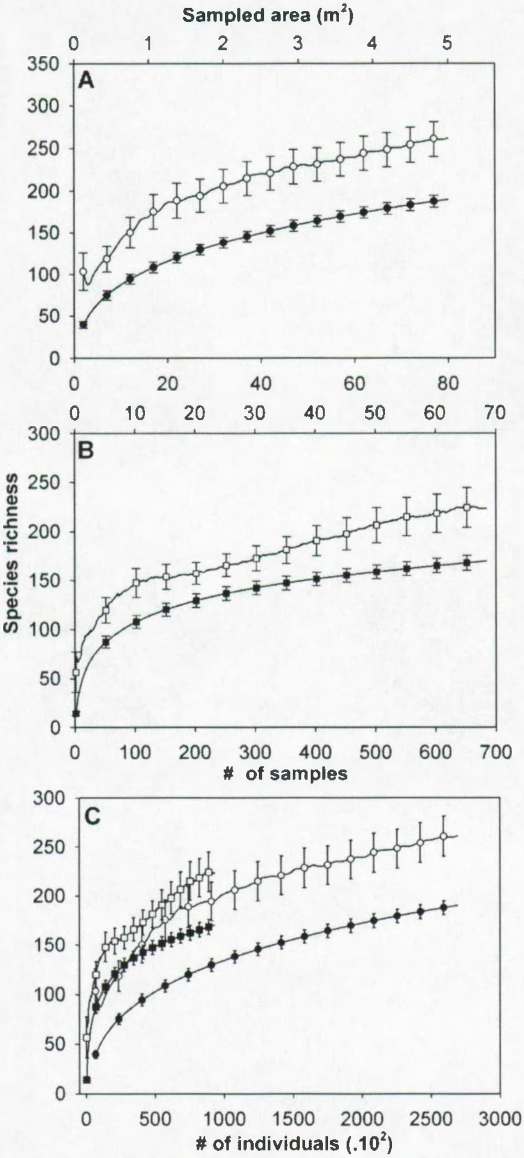


Figure 4. Species accumulation curves for the entire datasets. Estimators of the species richness are the total number of all species (Sobs, • and ▪) and the Chao2 estimator of true richness (○ and □). Results are mean ± s.d. for a selection of points based on 50 randomizations (without replacement). (A) Accumulated number of samples on hard substrates. (B) Accumulated number of samples on soft sediments (square symbol). (C) Accumulated number of individuals on hard substrate (○ and •) and soft sediments (□ and ▪).

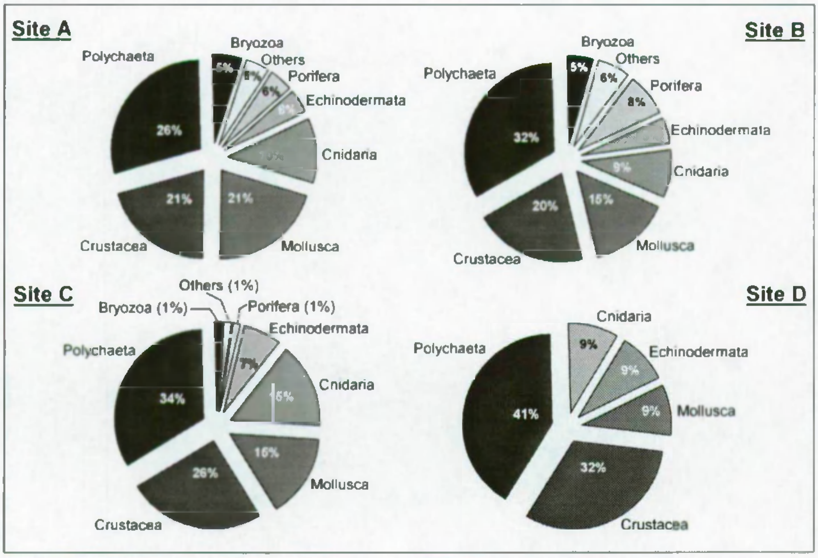


Figure 5. Species richness distribution on hard substrate sites. Others: Chordata (Tunicata), Nemertea and Sipuncula.

poriferans, nemerteans, chordates (tunicates) and sipunculids). These missing groups were found on the intermediate site (site C) but with a lower representation compared to sites A and B.

On all sites, the rank/abundance plots showed that the hard substrate sites were more strongly dominated by a few species than soft sediments (Figure 3). The abundance pattern of species among the two substrates differed on all sites (Kolmogorov-Smirnov test for differences in the distribution of the two samples: $p<0.001$ on all sites). The species richness of offshore soft-sedimented sites (A and B) was far under the species richness on hard substrates. Closer to the coast, species richness were equal on site C and higher on soft sediments for site D. However, this pattern of species richness could solely be due to the number of soft-sediment samples that were selected around shipwrecks. Less samples were available on site A (n=38) and B (n=14) than on sites C (n=90) and D (n=118).

Many species were common to all hard substrate sites and especially for the two wrecks far from the coast (Sites A and B) which were both strongly dominated by the amphipod *J. herdmani* (Table 2). At sites close to the coast this amphipod was less numerous but other species tended to appear (like the sea anemone *Metridium senile*). In order to compare species richness by site, the species accumulation curves on hard substrate and from the surrounding sediments around it are presented on figure 6. On sites A, B and C, species richness and estimators of true species richness on hard substrates are superior to what is observed on soft sediments. There are no sign of asymptotes on these sites. On site D, there is a lack of samples from hard substrates to effectively compare the curves. However, the species richness and estimator converge around this shipwreck to a common value of 85 species, indicating that sampling around this site is close to be exhaustive.

3.3. Species pattern

3.3.1. Univariate analysis

The two data sets shared 23 species (9.6% of the total number of species) (Table 4). Most of them were polychaetes (54%), molluscs (22%) and crustaceans (13%). The occurrence of species from both habitats showed an inverse correlation (Spearman's and Kendall rank correlation with $p<0,05$): frequency of occurrence of shared species which was high on one habitat was generally low on the other habitat (Table 4).

There was no obvious trend in the Simpson index (Figure 7). Only its value for site D was significantly under the one of the surrounding sediments. The average taxonomic diversity was significantly higher on all the hard

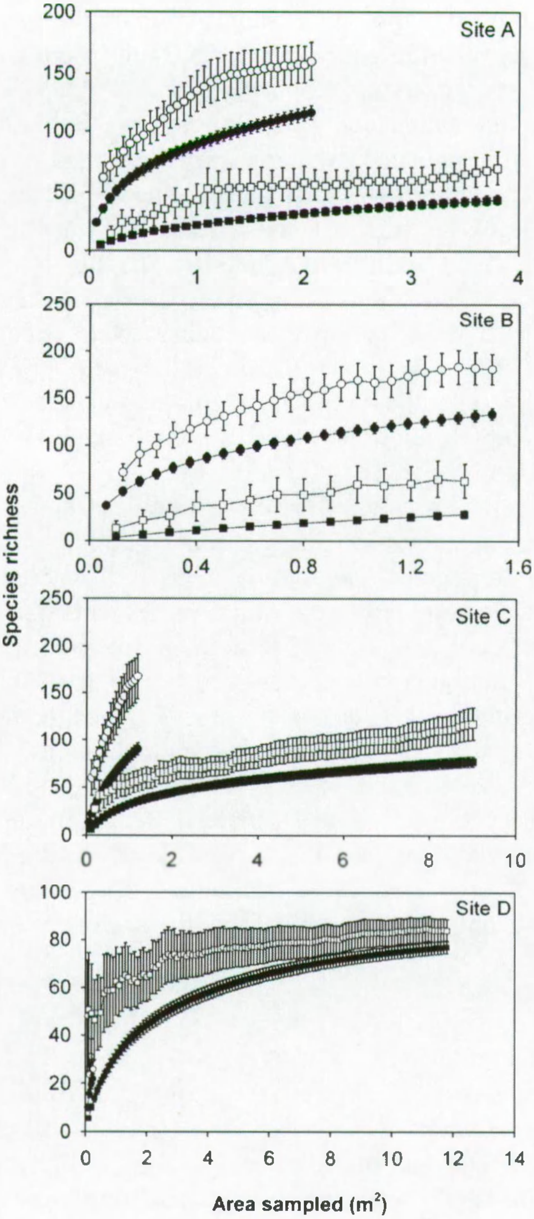


Figure 6. Species accumulation curves by sites (± s.d., 50 randomizations without replacements). ● Species richness on hard substrates, ○ Chao2 estimator of true richness on hard substrates, ■ Species richness on soft sediments, □ Chao2 on soft sediments.

substrate sites than on the surrounding soft sediments (Figure 7). Site D had a low value of variation in taxonomic distinctness and inversely the soft sediments close to the coasts displayed a rather high value meaning that their assemblages were dominated by many species belonging to the same low taxonomic level (Figure 7).

3.3.2. Biomass

The mean biomass for the hard substrates was 628 g AFDW.m^{-2} with site values ranging from 195 to 1174 g.m^{-2} (Figure 8). Minimal sample biomass was 30 g.m^{-2} and maximal value was 3,148 g.m^{-2}, both on site D. This last sample was exclusively composed of *Metridium senile*. There was an apparent decreasing average biomass from coastal to offshore sites. The soft sediment samples had an average biomass of 7.4 g.m^{-2}. Minimal and maximal biomass were 0.02 g.m^{-2} and 65 g.m^{-2}, respectively.

3.3.3. Multivariate analysis

Multidimensional scaling and clustering (not shown) based on Bray-Curtis similarity index from fourth root transformed abundances showed a clear differentiation between samples originating from soft sediments and from hard substrates (Figure 9,A). This differentiation was further confirmed by the result of the ANOSIM analysis (global R: 0.738, $p<0.001$). The pair-wise comparison of ANOSIM was significant ($p<0.001$) for each group except for site C with site D ($p=0.103$). Apart from these two sites that ANOSIM test did not differentiate, all hard substrate sites were different from soft sediments assemblages and from each other. The MDS based on the taxonomic similarity also differentiated the soft sediment and hard substrate samples and was confirmed by the ANOSIM analysis (global R: 0.831, $p<0.001$) (Figure 9,B).

3.4. Trophic structure

The ordination plot based on Bray-Curtis similarity index from square root transformed data again showed a separation of the soft sediments from hard substrates trophic organization (Figure 10). When superimposing the discerned soft sediment communities, the *Abra alba* community was the most closely associated with hard substrates. It is confirmed by the cluster analysis (not shown). The reason was a higher dominance of some suspension feeders associated with this community. However, an ANOSIM test confirmed (Global R: 0.387, $p<0.001$) that the trophic structure of the soft sediment was significantly different from those of hard substrates. The ANOSIM test for each trophic structure from soft sediment communities

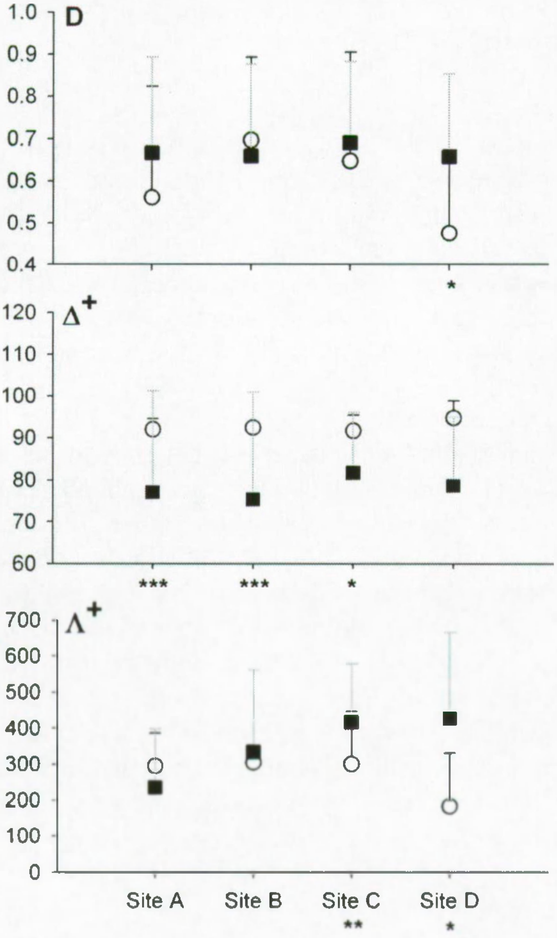


Figure 7. Diversity index comparison of hard substrate (○) with selected soft sediment (■) samples around hard substrates (distance: circle of 5 nautical miles, number of samples: site A (38), B (14), C (90), D (118)). Values are mean values + standard error. D is the Simpson index; $\Delta+$ is the average taxonomic distinctness; $\Lambda+$ is the variation in taxonomic distinctness. Significant difference between means tested with Monte Carlo permutation (999 randomizations) (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

with the hard substrate samples showed also significant differences for all pair-wise comparisons.

Except for deposit feeders, all the other trophic groups were significantly different between soft sediments and hard substrates (Mann-Whitney U test, figure 11). The general pattern for hard substrates was clearly dominated by suspension feeders, even when suppressing the effect of the dominant species *J. herdmani*, which belongs to this trophic category. This dominance was mainly due to amphipods such as *Phtisica marina*, *Caprella tuberculata* and *Monocorophium sextonae*, to the anomur *Pisidia longicornis*, and to actiniarian species (Table 5). The second most important trophic group were predators. These were mainly represented by polychaetes such as *Phyllodoce mucosa*, *Harmothoe* spp., *Pholoe inornata*, *Lepidonotus squamatus* and other members of Phyllodocidae, Nereidae and Syllidae families. Other abundant predators were nemertean, pycnogonid and nudibranch species. Sand licker feeding type was absent from hard substrates and subsurface deposit feeder was represented by only two species (*Pectinaria koreni* and *Cumacea* sp.). In general, each hard substrate site individually held the same type of trophic organization.

There was no such a clear-cut dominance of one feeding group for soft sediments macrofauna. Suspension feeders were never dominating and were represented by caprellid amphipods (*Pariambus typicus* and *Phtisica marina*), bivalves (*Spisula subtruncata*, *Ensis* sp., *Montacuta ferruginosa*, *Venerupis pullastra*, *Donax vittatus*, *Mytilus edulis*) and actiniarians (Table 5). Interface feeders were abundant and represented by spionids (*Spiophanes bombyx*, *Magelona* sp., *Spio* sp.) and terebellids (*Lanice conchilega*) and by bivalves (*Abra alba*, *Mysella bidentata*, *Tellina fabula*). Species from varied taxa contributed to the predator group with the polychaetes being dominant in association with some decapods (*Liocarcinus* sp., *Crangon crangon*). Around the site B, the dominance of predators was due to the polychaetes *Nephtys cirrosa* and *Hesionura elongata* while around the site D, the good representation of subsurface deposit feeder was linked to high abundance of *Scoloplos armiger*.

4. DISCUSSION

4.1. The occurrence of artificial hard substrates

With less than 0.05%, the total hard surface available from shipwrecks for the colonization of the epibenthos is low compared to natural substrates and we can consider their allocation in space as patchy. The density of

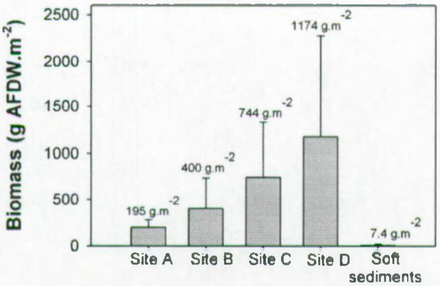


Figure 8. Biomass on hard substrates (sites A to D) and soft sediments.

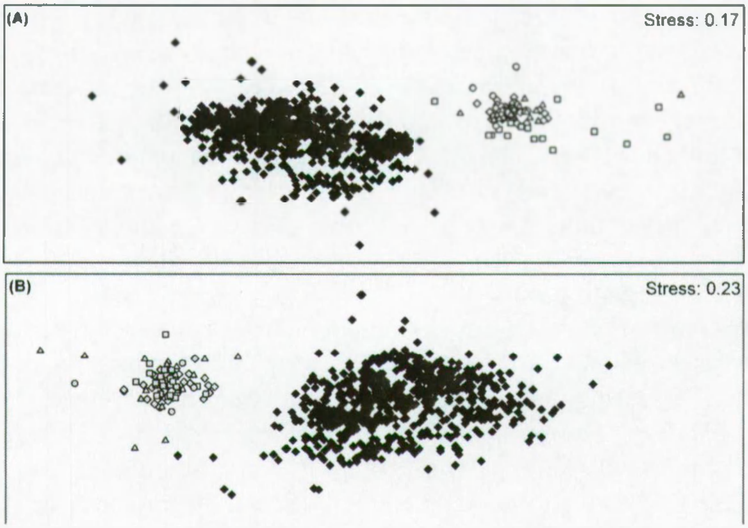


Figure 9. Multidimensional scaling ordination of macrobenthos samples. (A) Bray-Curtis similarity index based on fourth root transformed abundance data. (B) taxonomic dissimilarity. ◆ : soft sediments, ◊ : hard substrates (HS) site A, Δ : HS site B, □ : HS site C, ○ : HS site D.

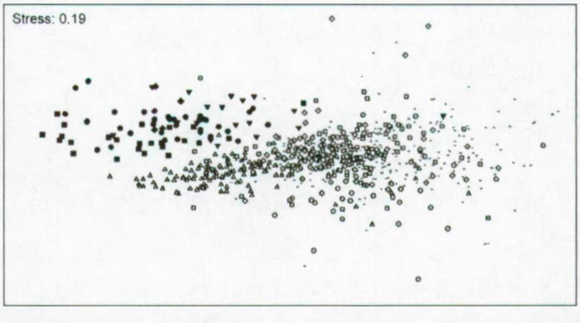


Figure 10. Multidimensional scaling ordination of the trophic organization of macrobenthos samples from hard substrates (black symbols) and soft sediments (grey symbols). Each sample is characterized by its trophic structure. Bray-Curtis similarity index based on square root transformed abundance data. Hard substrate site A: ●, site B:■, site C: ▼, site D: ♦. Soft sediment communities: *Abra alba* (Δ), *Macoma baltica* (○), *Nephtys cirrosa* (□) and *Ophelia limacina-Glycera capitata* (◊) communities. - indicates transitional samples between soft sediment communities.

obstructions on Belgian waters was around 0.06 obs.km^{-2} while values from French Atlantic coast were around 0.02 obs.km^{-2} (SHOM, 2001). Leewis *et al.* (2000) stated that more than 10.000 shipwrecks may lie on the Dutch waters which results in a density of 0.2 obs.km^{-2}. However, the official number of shipwrecks from the Dutch waters was around 2000 leading to a comparable density with the Belgian observations (0.04 obs.km^{-2}). Their allocation in space was strongly influenced by navigation routes where they were more abundant. Offshore, their density decreased. The English Channel and Southern Bight of the North Sea was and is one of the most heavily navigated route in the world. The origin of shipwrecks goes from collision and storm events to war destruction. All the wrecks studied have been under water for at least 40 years. One of them has been underwater for almost 100 years (Kilmore). On relatively protected conditions, the life span of shipwrecks is potentially long and further enhanced by the presence of fouling organisms which prevent the direct exposure of steel to sea water (Gabriele *et al.*, 1999; Sun *et al.*, 2003). This is particularly true for organisms strongly attached to the surface by calcification such as barnacles or serpulid polychaetes (Ma, 1989). These organisms were abundant on the studied shipwrecks. As a consequence, shipwrecks have the potential to provide a stable habitat for the establishment of mature assemblages and their abundance is not anecdotic.

4.2 Impact of artificial hard substrates on alpha diversity

This study demonstrated marked differences in the macrofauna composition of hard substrates with the surrounding sediments. There was a low number of shared taxa between these two habitats (9.6%) and, hence, soft sediments seemed to be a source of hard substrate organisms for only a few taxa. The species typically shared by both habitats were living on the sediments trapped by the hydroid or actiniarian growths on hard substrates. Some taxa such as actiniarians were only shared at this high level of taxonomic resolution. Actiniarians in soft sediments were mainly *Sagartia troglodytes* and *Urticina felina* while shipwrecks supported a variety of species such as *Metridium senile*, *Diadumene cincta*, *Sagartia elegans*, *Actinothoe sphyrodeta* and *Urticina felina*. A common and important feature of soft sediments was the sand mason polychaete (*Lanice conchilega*) which is a tube builder providing structure to the sediments (Jones & Jago, 1993). On hard substrates, this species was invariably found attached and alongside the perisarc of *Tubularia indivisa* (hydrozoan). Other polychaetes includedcommon predators of the Atlantic and North Sea waters (*Harmothoe* spp., *Eumida* spp., *Eulalia* spp.). Some crustaceans were important features

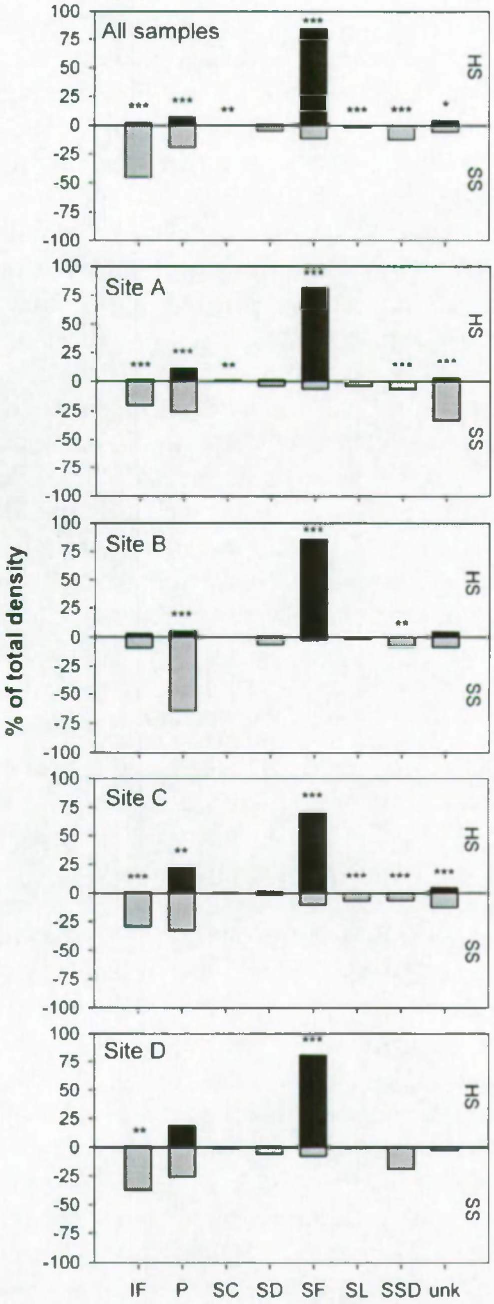


Figure 11. Contribution of the different trophic groups to total density. The soft sediment samples selected around hard substrate sites are within a circle of 5 nautical miles. On hard substrates, the dominant species *Jassa herdmani* is excluded from calculation. IF: interface feeder, P: predator, SC: scavenger, SD: deposit feeder, SF: suspension feeder, SL: sand licker, SSD: subsurface deposit feeder, Unk: unknown type. *** $p<0.001$, ** $p<0.01$, * $p<0.05$ (significance level of a Mann-Whitney U test).

of shipwrecks (*Phtisica marina*, *Pisidia longicornis*, and *Stenothoe* sp.) and were occasionally associated with soft sediments whenever they found some element to cling to (on stones or as epifauna). Considering the large densities of these taxa encountered on shipwrecks and the fact that they were reproductively active, it is likely that they could act as a source population for soft sediments.

There was an apparent shift from a habitat dominated by bivalves and polychaetes on soft sediments to shipwrecks dominated by crustaceans, polychaetes and cnidarians. The representation of cnidarians, especially hydrozoans, was not well estimated by abundance data because most of them were uncountable. However, the cover of these taxa was the most striking feature of shipwreck assemblages and they modified their spatial heterogeneity allowing for the settlement of a range of new species (Hughes, 1975; Ardizzone *et al.*, 1989).

Natural hard substrates in Southern North Sea in general and Belgian waters in particular are rare (Kerckhof & Houziaux, 2003). Large pebble fields in the English Channel were described by Cabioch & Glaçon (1975), Davoult & Richard (1988) and Davoult (1990). These assemblages provide a potential source of species for the Belgian shipwrecks since the residual current is running north-east. Lefebvre *et al.* (2003) studied the dispersal of ophioplutei larvae from *Ophiotrix fragilis* population in the Dover Strait using a 2D Lagrangian model. He concluded that the dispersal of larvae was under the strong influence of the wind forcing conditions imposed to the model and that depending on the population, dispersal capability was very variable but potentially large. In Belgian waters, there exists some area with pebbles (Lanckneus *et al.*, 2001; Houziaux, pers. com.) mainly located in the gullies between sandbanks. The first results of recent investigations (pers. obs.) showed that these assemblages are very different both in terms of dominant species and biomass. The possibility that these areas could act as a source population for shipwrecks is difficult to estimate due to our limited current knowledge.

The strong difference in species composition on artificial hard substrates from the surrounding natural soft-sedimented area and probably also from the natural pebble/gravel fields lead to the conclusion that shipwrecks other artificial hard structures in the BPNS are different habitats. The major factors leading to the differentiation of assemblages on soft and hard substrates has to be looked in the inherent stability of the latter, allowing for the settlement of a large set of sessile species. Shipwrecksrepresent also a very large topographic feature compared to what is observed on natural habitats in the region (both soft and hard). They consequently offer a protection from sand scouring, at least for animals at some distance from the seabed. They finally alter the water movement and the further contact of species with their environment (see discussion below).

Species typically associated with hard substrates could use the network created by shipwrecks to disperse more easily. Shipwrecks have the potential to act as stepping stones with potential impacts on species repartition and/or on the genetic diversity by allowing an easier transfer of allele from normally unconnected populations.

4.3. Impact of artificial hard substrates on species pattern and diversity

Species richness estimators were slightly higher for hard substrates (261 spp.) than for soft sediments (224 spp.) at the respective maximal sampling intensity. There was no sign of asymptote in the species and richness estimator accumulation curves. As a consequence, the global species richness of both habitats cannot readily be compared (Gotelli & Colwell, 2001; Magurran, 2004) and these estimates should be seen as minimum estimates of true species richness (Longino *et al.*, 2002). However, if we look at the species richness as a function of individuals, we can see that diversity on soft sediments is above diversity on hard substrates. Nevertheless, if both values were in the same order of magnitude, they stand for very different spatial scales. Shipwrecks concentrated many species on a relative small area, and add a substantial number of new species to the diversity of Belgian waters (Zintzen *et al.*, 2006). More interestingly, the taxonomic diversity of shipwrecks was superior to what was revealed on soft sediments. Taxa belonging to higher taxonomic resolution found the right habitat to thrive and the taxonomic breadth was also higher at lower level (Family, Genus). Certainly the most striking feature when comparing hard substrates with soft sediments was the abundance patterns. The order of magnitude for densities was a thousand times higher on hard substrates than on soft sediments. This was mainly due to a typical fouling amphipod species, *Jassa herdmani*, which needs a hard substrate to build the tube where it is living (Conlan, 1989).

Other workers showed the effect that the presence of artificial reefs can have on the closely surrounding soft sediment communities. Artificial reefs will change the hydrodynamic regime in the sediment surrounding it. As a consequence, they can potentially alter species abundance and distribution on the surrounding soft sediments through changes in current intensity and direction, erosion and sedimentation rates, grain-size distributions, organic content of sediments, and attraction of predators (Ambrose & Anderson, 1990; Hiscock *et al.*, 2002). This effect can be limited in space (<20 m) (Ambrose & Anderson, 1990) or more dispersed (200 m) (Davis *et al.*, 1982) depending on the size and structure of the reef. Species macrobenthic diversity and assemblages variability has been noted to increase close to artificial reef (Barros *et al.*, 2001). The densities of the infauna species can be enhanced or depleted in their vicinity (Ambrose & Anderson, 1990). This may either be due to a change in sedimentology or to foraging of reef associated predators (Davis *et al.*, 1982; Ambrose & Anderson, 1990). Jensen *et al.* (1994) did not find any evidence that the presence of the reef would create a 'feeding halo' of low abundance and diversity by grazing pressure of the infauna (Poole Bay artificial reef (UK)). They rather observed that the most abundant fish species (pouting, *Trisopterus luscus*) feeds on *Crangon crangon* (L.) (a surface dwelling shrimp) and small crustaceans, an activity that is not susceptible to alter the infaunal population. We observed during diving operations a large population of pouting together with cod (*Gadus morhua*) and seabass (*Dicentrarchus labrax*). These species typically feed on soft sediment species (Svetovidov, 1986) and could prey upon soft sediment species. Other predators and scavengers (Portunidae, Nassariidae and Paguridae) had a high density next to the shipwrecks, indicating a source of food. However, this accumulation of organic compounds could find their origin as well from dead specimens falling from shipwrecks as from an increased density of soft sediment species.

4.4. Impact of artificial hard substrates on biomass repartition

The biomass on Belgian shipwrecks has a mean value of about 628 g AFDW.m^{-2} with maximal value peaking at 3,148 g AFDW.m^{-2}. The biomass on hard substrates is on average 85 times larger than on soft sediments from the coastal area. The values from literature for the macrofauna of soft sediments in the Southern North Sea are around 10 g.m^{-2} (Duineveld *et al.*, 1991; Heip *et al.*, 1992) and around 30-50 g.m^{-2} for the *Abra alba* community (Prygiel *et al.*, 1988). In the view of the few studies describing biomass values on temperate artificial reefs, our results are in the superior range of these results. In Delaware (Atlantic USA coast), the wet biomass raised to 24,580 g.m^{-2} when mussels dominated the community and dropped to a mean value of 596 g.m^{-2} afterwards. It represents 147 to 895 times the mean biomass of the surrounding sediments (Foster *et al.*, 1994). On the

Dutch shipwrecks, the highest biomass values were obtained on a community dominated by *Metridium senile*. They peaked at 1,954 g AFDW.m^{-2}. The mean biomass was 642 g.m^{-2}, 209-364 times the mean biomass of the surrounding sediments (Leewis *et al.*, 2000). In the North Sea wind farms of Denmark, mean biomass (wet weight) was 3,364 g.m^{-2} on mono-piles and 236 g.m^{-2} on the scouring protections two years after immersion (Leonhard *et al.*, 2005). The high mono-pile values are due to *Mytilus edulis*. In the Northern Adriatic Sea, the biomass of two outcrops was compared with the biomass of two artificial reefs (one shipwreck and one barrier of concrete blocks) (Gabriele *et al.*, 1999). Artificial reefs (391 g AFDW.m^{-2}) had a significant larger value of biomass than natural outcrops (135 g AFDW.m^{-2}). However, the reefs were also located in more turbid waters which could potentially lead to increased biomass through the promotion of some species from the epifauna.

When combining the ratio of biomass on hard substrates and soft sediments with the occurrence of hard substrate, the biomass on artificial structures from the BPNS represents about 4 % of the total biomass from the BPNS. This is a gross estimation but never the less it proves that the species from artificial habitats can represent a significant part of the biomass on coastal area. Hydroids are known to play an important role in the transfer of energy from the plankton to the benthos (Gili & Hughes, 1995). Tubulariid species have a high prey-capture rate, together with high assimilation efficiency (Gili *et al.*, 1996) and may be an important component of bentho-pelagic coupling (Orejas *et al.*, 2000).

4.5. Impact of artificial reefs on trophic organization

There was a strong dominance of suspension feeders on shipwrecks compared to the feeding habits in the surrounding soft sediments. In this respect, shipwreck communities have a clear affinity with the 'pebbles with epifauna' community described on the Dover Strait (Prygiel *et al.*, 1988; Davoult, 1990; Migne & Davoult, 1997). However, the species representing the bulk of the biomass were *Ophiothrix fragilis* and *Alcyonium digitatum* in pebbles. *O. fragilis* was present on shipwrecks mainly on offshore sites and was not the dominant species. Only very young colonies (a few polypes) of *A. digitatum* were found attached to the perisarc of *Tubularia indivisa*.

Flow velocity has a marked effect on structuring benthic community. Flach *et al.* (1998) noted that an increased density of suspension feeders was observed where flow velocity increased. Sessile suspension feeders rely on the movement of water to fulfil their food requirement. The potential food available to the taxa is a function of particle concentration and rate at which particle can be delivered. When suspension feeders are active on or near the almost smooth and featureless sea bed, they have to feed on the boundary layer. The presence of other substrata such as shipwrecks modifies the pattern of moving waters, thereby altering the selection of feeding type by fauna (Baynes & Szmant, 1989; Leichter & Witman, 1997). Varying obstacles ranging from hydroids to seamounts can induce an increased productivity at their peaks/tops due to current acceleration (Hughes, 1975; Genin *et al.*, 1986; Leichter & Witman, 1997).

The large biomass values and dominance of suspension feeders on shipwrecks may lead a local change in bentho-pelagic coupling with a diminution of food concentration downstream the hard substrates. It has been observed that consumption of phytoplankton by mussel beds reduced water-column concentration and resulted in a pronounced horizontal gradient (Wildish & Kristmanson, 1984; Tweddle *et al.*, 2005). However, this impact should only be localized since the dimension of the shipwrecks never exceeds 150 m.

Moreover, the general food web organization for these two substrates could be quite different. Both depend on exogenous food source but the bioaccumulation of organic matter on soft sediments is partly realized by surface and sub-surface deposit feeder. This step is virtually inexistent on shipwrecks certainly because water movement and turbulence do not favour the deposition of particles (Davoult & Gounin, 1995). We also note that most of the food web transfer on shipwrecks depends on a restricted set of species (*Tubularia indivisa* and *Jassa herdmani*). We postulate that the degradation of the *T. indivisa* populations could result in a dramatic change in community composition on shipwrecks. First because this species provides structure and hence microhabitats to shipwrecks and then because its regression would be followed by a rapid decline of *J. herdmani* population which are probably an essential source of food for many predators found on shipwreck sites. Contrary to this, soft sediment communities have probably a larger stability due to their reduced dependence to a single species.

4.6. Conclusion: impact of artificial hard substrate on soft-sedimented sea beds

Species, trophic and biomass analysis of this study showed that soft sediments and artificial hard substrates (shipwrecks) are distinct habitats. The presence of these hard substrate patches in a soft sediment dominated sea bed increased the structural (new species) as well as functional diversity (different abundance and biomass patterns, different trophic structure) of the

Belgian waters. However, the naturalness of these communities and the question of whether shipwrecks represent a novel habitat need to be addressed in the light of the natural hard substrates in the Southern Bight of the North Sea. Pebble fields are the only known source of natural hard substrate in Belgian waters. Their specific composition is not published yet (Houziaux, pers com.). Studying these natural hard substrates communities would permit to achieve a more balanced view of the macrobenthic sessile species of the BPNS. This aspect is particularly important especially when a number of offshore wind mill projects are ongoing and will add a substantial amount of artificial hard substrate to the sea bed. There are chances that natural and artificial communities share a large number of species but with largely different abundance patterns. Connell (2001) stressed the importance of artificial structures as new habitats in the marine environment and the creation of patches in areas lacking such habitats.

ACKNOWLEDGEMENT

The authors wish to thank the crews of the RV Zeeleeuw and RV Belgica for their help during the sampling campaigns and to Céline Delforge for the great help during the sorting process. It's also our pleasure to thank all the people who helped collecting the samples: Drs Y. Laitat, A. Simon, D. Delbare, E. Vanden Bergh, T. Schils, Mss C. Delforge and R. Gyssens and Mrs P.B. Demoulin, G. Rooms, D. Marsham, F. Cray, M. Van Espen, Y. Verkemping, M. Backx, J.P. De Blauwe, J. Haelters, F. Hernandez, F. Darchambeau, G. Van Hoydonck, A. Vanhaelen, R. Knuts & P. Van de Steen. This study has been financially supported by a 'plan Action II' grant (contract N° WI/36/C04) from the Belgian Science Policy.

REFERENCE LIST

Ambrose, R. F. & Anderson, T. W. 1990. The influence of an artificial reef on the surrounding infaunal community. *Marine Biology*, **107**: 41-52.

Ardizzone, G. D., Gravina, M. F. & Belluscio, A. 1989. Temporal development of epibenthic communities on artificial reefs in the central Mediterranean Sea. *Bulletin of Marine Science*, **44**: 592-608.

Barros, F., Underwood, A. J. & Lindegarth, M. 2001. The influence of rocky reefs on structure of benthic macrofaunain nearby soft-sediments. *Estuarine Coastal and Shelf Science*, **52**: 191-199.

Baynes, T. W. & Szmant, A. M. 1989. Effects of current on the sessile benthic community structure of an artificial reef. *Bulletin of Marine Science*, **44**: 545-566.

Bially, A. & Macisaac, U.G.H.J. 2000. Fouling mussels (*Dreissena spp.*) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. *Freshwater Biology*, **43**: 85-97.

Bohnsack, J. A. & Sutherland, J. P. 1985. Artificial reef research: a review with recommendations for future priorities. *Bulletin of Marine Science*, **37**: 11-39.

Bulloch, D. K. 1965. The development of the wreck *Pinta* as a marine habitat. *Underwater Naturalist.Bulletin of the American Littoral Society*, **31**: 17-32.

Cabioch, L. & Glaçon, R. 1975. Distribution des peuplements benthiques en Manche Orientale, de la Baie de Somme au Pas-de-Calais. *Comptes Rendus des Séances de l'Académie des Sciences*, **280**: 491-494.

Cao, Y., Larsen, D.P. & Thorne, R.S. 2001. Rare species in multivariate analysis for bioassessment: some considerations. *Journal of the North American Benthological Society*, **20**: 144-153.

Chao, A. & Lee, S.-M. 1992. Estimating the number of classes via sample coverage. *Journal of the American Statistical Association*, **87**: 210-217.

Clarke, K.R. 1999. Nonmetric multivariate analysis in community-level ecotoxicology. *Environmental Toxicology and Chemistry*, **18**: 118-127.

Clarke, K. R. & Warwick, R. M. 1998a. A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, **35**: 523-531.

Clarke, K.R. & Warwick, R.M. 1998b. Quantifying structural redundancy in ecological communities. *Oecologia*, **113**: 278-289.

Clarke, K.R. & Warwick, R.M. 2001a. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology-Progress Series*, **216**: 265-278.

Clarke, K. R. & Warwick, R. M. 2001b. Change in marine communities: an approach to statistical analysis and interpretation. 2nd edition. PRIMER-E, Plymouth, UK, 172 pp.

Conlan, K. E. 1989. Delayed reproduction and adult dimorphism in males of the amphipod genus *Jassa* (Corophioidea: Ischyroceridae): an explanation for systematic confusion. *Journal of Crustacean Biology*, **9**: 601-625.

Connell, S.D. 2000. Floating pontoons create novel habitats for subtidal epibiota. *Journal of Experimental Marine Biology and Ecology*, **247**: 183-194.

Connell, S.D. 2001. Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. *Marine Environmental Research*, **52**: 115-125.

Connell, S.D. & Glasby, T.M. 1999. Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Marine Environmental Research*, **47**: 373-388.

Costello, M. J., Emblow, C. S. & White, R. 2001. European Register of Marine Species. A check-list of the marine species in Europe and a bibliography of guides to their identification. *Patrimoines naturels*, **50**: 1-463.

Danovaro, R., Gambi, C., Mazzola, A. & Mirto, S. 2002. Influence of artificial reefs on the surrounding infauna: analysis of meiofauna. *ICES Journal of Marine Science*, **59**: S356-S362.

Dauwe, B., Herman, P.M.J. & Heip, C.H.R. 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Marine Ecology-Progress Series*, **173**: 67-83.

Davis, N., VanBlaricom, G. R. & Dayton, P. K. 1982. Man-made structures on marine sediments: effects on adjacent benthic communities. *Marine Biology*, **70**: 295-303.

Davoult, D. 1990. Biofaciès et structure trophique du peuplement des cailloutis du Pas-de-Calais (France). *Oceanologica acta*, **13**: 335-348.

Davoult, D. & Gounin, F. 1995. Suspension-feeding activity of a dense *Ophiothrix fragilis* (Abildgaard) population at the water-sediment interface: time coupling of food availability and feeding behaviour of the species. *Oceanologica acta*, **41**: 567-577.

Davoult, D. & Richard, A. 1988. Les ridens, haut-fond rocheux isolé du Pas de Calais: un peuplement remarquable. *Cahiers de Biologie Marine*, **29**: 93-108.

Degraer, S., Vincx, M., Meire, P. & Offringa, H. 1999. The macrozoobenthos of an important wintering area of the common scoter (*Melanitta nigra*). *Journal of the Marine Biological Association of the UK*, **79**: 243-251.

Desrosiers, G., Savenkoff, C., Olivier, M., Stra, G., Juniper, K., Caron, A., Gagné, J.-P., Legendre, L., Mulsow, S., Grant, J., Roy, S., Grehan, A., Scaps, P., Siverberg, N., Klein, B., Tremblay, J.-E. & Therriault, J.-C. 2000. Trophic structure of macrobenthos in the Gulf of St. Lawrence and the Scotian Shelf. *Deep-Sea Research part II - Tropical Studies in Oceanography*, **47**: 663-698.

Duineveld, G., Kunitzer, A., Niermann, U., Dewilde, P.A.W.J. & Gray, J.S. 1991. The macrobenthos of the North Sea. *Netherlands Journal of Sea Research*, **28**: 53-65.

Eleftheriou, A. & Basford, D. 1989. The macrobenthic infauna of the offshore northern North Sea. *Journal of the Marine Biological Association of the UK*, **69**: 123-143.

Fauchald, K. & Jumars, P. A. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology - An Annual Review*, **17**: 193-284.

Flach, E., Lavaleye, M., de Stigter, H. & Thomsen, L. 1998. Feeding types of the benthic community and particle transport across the slope of the NW European Continental Margin (Goban Spur). *Progress in Oceanography*, **42**: 209-231.

Foster, K.L., Steimle, F.W., Muir, W.C., Kropp, R.K. & Conlin, B.E. 1994. Mitigation potential of habitat replacement - concrete artificial reef in Delaware Bay - preliminary results. *Bulletin of Marine Science*, **55**: 783-795.

Gabriele, M., Bellot, A., Gallotti, D. & Brunetti, R. 1999. Sublittoral hard substrate communities of the northern Adriatic Sea. *Cahiers de Biologie Marine*, **40**: 65-76.

Genin, A., Dayton, P. K., Londsale, P. F. & Spiess, F. N. 1986. Coral on seamount peaks provide evidence of current acceleration over deep topography. *Nature*, **322**: 59-61.

Gili, J.M. & Hughes, R.G. 1995. The ecology of marine benthic hydroids. *Oceanography and Marine Biology - An Annual Review*, **33**: 351-426.

Gili, J.M., Hughes, R.G. & Alva, V. 1996. A quantitative study of feeding by the hydroid *Tubularia larynx* Ellis and Solander, 1786. *Scientia Marina*, **60**: 43-54.

Gotelli, N.J. & Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**: 379-391.

Graham, A. 1988. Mollusca, Prosobranch and Pyramidellid Gastropods. Synopses of the British fauna (New Series) No 2 (2nd Edition), Academic Press, London, 662 pp.

Hall, S. J., Robertson, M. R., Basford, D. & Heaney, S. D. 1993. The possible effect of fishing disturbance in the northern North Sea: an analysis of spatial patterns in community structure around a wreck. *Netherlands Journal of Sea Research*, **31**: 201-208.

Heip, C., Basford, D., Craeymeersch, J.A., Dewarumez, J.M., Dorjes, J., Dewilde, P., Duineveld, G., Eleftheriou, A., Herman, P.M.J., Niermann, U., Kingston, P., Kunitzer, A., Rachor, E., Rumohr, H., Soetaert, K. & Soltwedel, T. 1992. Trends in biomass, density and diversity of North Sea macrofauna. *ICES Journal of Marine Research*, **49**: 13-22.

Hiscock, K. 1980. Marine life on the wreck of the M.V. 'Robert'. *Report of the Lundy Field Society*, **32**: 40-44.

Hiscock, K., Tyler-Walters, H. & Jones, H. 2002. High level environmental screening study for offshore wind farm developments - Marine habitats and species project. Report from the Marine Biological Association to The

Department of Trade and Industry New & Renewable Energy Programme, 92p + annexes.

Hughes, R. G. 1975. The distribution of epizoites on the hydroid *Nemertesia antennina* (L.). *Journal of the Marine Biological Association of the UK*, **55**: 275-294.

Jensen, A.C., Collins, K.J., Lockwood, A.P.M., Mallinson, J.J. & Turnpenny, W.H. 1994. Colonization and fishery potential of a coal-ash artificial reef, Poole-Bay, United-Kingdom. *Bulletin of Marine Science*, **55**: 1263-1276.

Jones, S. E. & Jago, C. F. 1993. In situ assessment of modification of sediment properties by burrowing invertebrates. *Marine Biology*, **115**: 133-142.

Kerckhof, F. & Houziaux, J.-S. 2003. Biodiversity of the Belgian marine areas. pp 350-389. *In* Peeters, M., Franklin, A., and Van Goethem, J. L. (eds), Biodiversity in Belgium, Royal Belgian Institute of Natural Sciences, Brussels.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika*, **29**: 115-129.

Kruskal, J. B. & Wish, M. 1978. Multidimensional scaling. Sage University Paper series on Quantitative Applications in the Social Sciences n°11. Sage Publications, Beverly Hills and London., 86 pp.

Lanckneus, J., van Lancker, V., Moerkerke, G., Van den Eynde, D., Fettweis, M., de Batist, M. & Jacobs, P. 2001. Investigation of the natural sand transport on the Belgian continental shelf (BUDGET). Final report. Federal Office for Scientific, Technical and Cultural Affairs (OSTC), 104 pp.

Larsonneur, C., Bouysse, P. & Auffret, J.-P. 1982. The superficial sediments of the English Channel and its Western Approaches. *Sedimentology*, **29**: 851-864.

Leewis, R. J., van Moorsel, G. W. N. M. & Waardenburg, H. W. 2000. Shipwrecks on the Dutch Continental Shelf as artificial reefs. pp 419-434. *In* Jensen, A. C, Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publishers, Dordrecht.

Lefebvre, A., Ellien, C., Davoult, D., Thie, E. & Salomon, J.C. 2003. Pelagic dispersal of the brittle-star *Ophiothrix fragilis* larvae in a megatidal area (English Channel, France) examined using an advection/diffusion model. *Estuarine, Coastal and Shelf Science*, **57**: 421-433.

Leichter, J.J. & Witman, J.D. 1997. Water flow over subtidal rock walls: Relation to distributions and growth rates of sessile suspension feeders in the Gulf of Maine - Water flow and growth rates. *Journal of Experimental Marine Biology and Ecology*, **209**: 293-307.

Leonhard, S. B., Pedersen, J. & Moeslund, B. 2005. Hard bottom substrate monitoring. Horns Rev Offshore Wind Farm. Annual status report 2004. Bio/consult as, Copenhague, Denmark, 79p.

Lincoln, R. J. 1979. British marine amphipoda: Gammaridea. British Museum (Natural History), London, 658 pp.

Longino, J.T., Coddington, J. & Colwell, R.K. 2002. The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology*, **83**: 689-702.

Ma, S. D. 1989. The corrosive effect of barnacles on low alloy steels. *Chinese Journal of Oceanology and Limnology*, **7**: 31-33.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Science Ltd, Oxford, UK, 256 pp.

Massin, C. 2002. Biodiversity of a wreck from the Belgian Continental Shelf: Monitoring using scientific diving. Preliminary results. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Biologie*, **72**: 67-72.

Migne, A. & Davoult, D. 1997. Quantitative distribution of benthic macrofauna of the Dover Strait pebble community (Eastern English channel, France). *Oceanologica acta*, **20**: 453-460.

Orejas, C., Gili, J.M., Alva, V. & Arntz, W. 2000. Predatory impact of an epiphytic hydrozoan in an upwelling area in the Bay of Coliumo (Dichato, Chile). *Journal of Sea Research*, **44**: 209-220.

Osenberg, C.W., St Mary, C.M., Wilson, J.A. & Lindberg, W.J. 2002. A quantitative framework to evaluate the attraction-production controversy. *ICES Journal of Marine Science*, **59**: S214-S221.

Pingree, R. D. & Maddock, L. 1977. Tide residuals in the English Channel. *Journal of the Marine Biological Association of the UK*, **57**: 339-354.

Prygiel, J., Davoult, D., Dewarumez, J. M., Glaçon, R. & Richard, A. 1988. Description et richesse des peuplements benthiques de la partie française de la Mer du Nord. *Comptes Rendus de l'Académie des Sciences, Série III*, **306**: 5-10.

Roth, S. & Wilsson, J. G. 1998. Functional analysis by trophic guilds of macrobenthic community structure in Dublin Bay, Ireland. *Journal of Experimental Marine Biology and Ecology*, **222**: 195-217.

SHOM 2001. Les épaves des côtes de France (métropole). Service Hydrographique et Océanographique de la Marine, CD-ROM.

Smith, S.D.A. & Rule, M.J. 2002. Artificial substrata in a shallow sublittoral habitat: do they adequately represent natural habitats or the local species pool? *Journal of Experimental Marine Biology and Ecology*, **277**: 25-41.

Sokal, R. & Rohlf, F. J. 1995. Biometry. Third edition, W.H. Freeman and Company, New-York, USA, 887 pp.

Steimle, F. W. & Zetlin, C. 2000. Reef habitats in the middle Atlantic Bight: abundance, distribution, associated biological communities, and fishery resource use. *Marine Fisheries Review*, **62**: 24-42.

Sun, H.Y., Ma, S.D., Hou, B.R., Zhang, J.L., Huang, G.Q. & Zhu, X.R. 2003. Mathematical analysis of long term fouling corrosion in sea water. *Corrosion Engineering, Science and Technology*, **38**: 223-227.

Sutterer, R. A. & Szedlmayer, S.T. 2005. Comparisons of fish communities on artificial habitats with and without epibenthic communities. 8th International Conference on Artificial Reefs and Artificial Habitats, pp 69, Biloxi, USA.

Svetovidov, A. N. 1986. Gadidae. pp 680-710. *In* Whitfield, A. K., Bauchot, M.-L., Hureau, J-C., Nielsen, J., and Tortonese, E. (eds), Fishes of the north-eastern Atlantic and the Mediterranean, UNESCO, Paris.

Tweddle, J.F., Simpson, J.H. & Janzen, C.D. 2005. Physical controls of food supply to benthic filter feeders in the Menai Strait, UK. *Marine Ecology-Progress Series*, **289**: 79-88.

Van Hoey, G., Degraer, S. & Vincx, M. 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuarine, Coastal and Shelf Science*, **59**: 599-613.

van Moorsel, G. W. N. M., Waardenburg, H. W. & van der Horst, J. 1991. Het leven op en rond scheepswrakken en andere harde substraten in de Noordzee (1986 T/M 1990) - een synthese. Rapport 91.19, Bureau Waardenburg bv, Culemborg, 49 pp.

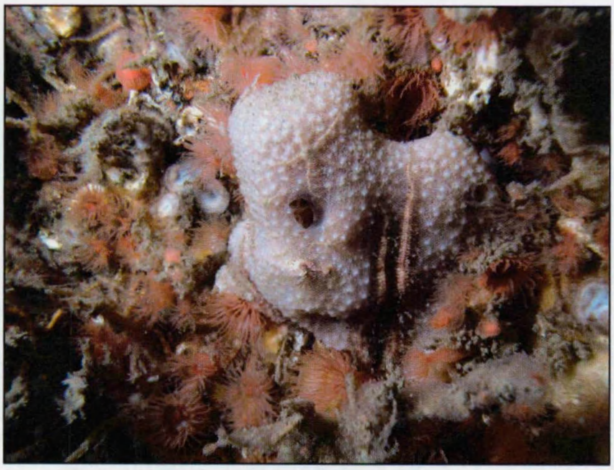
Wendt, P. H., Knott, D. M. & Van Dolah, R. F. 1989. Community structure of the sessile biota on five artificial reefs of different ages. *Bulletin of Marine Science*, **44**: 1106-1122.

Whittaker, R. H. 1965. Dominance and diversity in land plant communities. *Science*, **147**: 250-260.

Wildish, D. J. & Kristmanson, D. D. 1984. Importance to mussels of the benthic boundary layer. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**: 1618-1625.

Zintzen, V., Massin, Cl., Norro, A. & Mallefet, J. 2006. Epifaunal inventory of two shipwrecks from the Belgian Continental Shelf. *Hydrobiologia*, **555**: 207-219.

Chapter V - Spatial and temporal community structure on shipwrecks



Recruits of *Ophiothrix fragilis* on *Dysidea fragilis* and *Haliclona oculata*.

ARTICLE 4: SPATIAL VARIABILITY OF EPIFAUNAL COMMUNITIES FROM ARTIFICIAL HABITAT: SHIPWRECKS IN THE SOUTHERN BIGHT OF THE NORTH SEA

The article 3 indicated that shipwrecks were distinct habitats within a continuous system dominated by soft-sedimented habitats. Another result of this paper was that the species assemblages of the four investigated shipwrecks seemed to be different from each other. The samples used in the previous article were collected on different sites, but also on different period of the year, different years and vertically/horizontally oriented surfaces. These three factors introduce variability in the data set that could hamper the detection of community pattern primarily due to spatial variables. Consequently, it was decided to concentrate a massive effort of sampling during a short period of time and for a large set of environmental condition (and so locations) encountered on the Belgian waters. The chosen period was Mai-June, mostly for practical rather than ecological reasons (water temperature allowing work in good conditions, best period of the year to enjoy correct visibility and thus allowing the use of photographic techniques, relative mild weather and sea conditions, available ship time, and finally outside the holyday period to have enough diver helping for sample collection).

With the previous knowledge we had from shipwrecks communities, we estimated that two scales of analysis would be useful to give a precise overview of spatial patterns. First, the various assemblages developing at the scale of one shipwreck could only be apprehended through photographic techniques. However, it was evident from the previous analysis of samples, that most of the diversity on shipwrecks would be made available through direct sampling (scraping) because many species were small sized. This second method was then used to estimate the species richness at the scale of one assemblage dominated by the hydrozoans *Tubularia indivisa* or *T. larynx*. These species were strongly suspected to be present on each site. It was also deemed necessary to use both densities and biomass as units of abundances, since many important species were uncountable (like the tubulariids, for example).

Specific questions to be answered here were:

- Is there a pattern in community structure on shipwrecks at the scale of the Belgian continental shelf? The null hypothesis being that all shipwreck sites harbour identical assemblages.
- If yes, is this pattern ordered along a cross-shore gradient?
- Is this pattern consistent at the scale of the shipwreck and at the scale of a particular assemblage whose key species are tubulariids?
- Explore the different environmental parameters that could explain differences in pattern.

SPATIAL VARIABILITY OF EPIFAUNAL COMMUNITIES FROM ARTIFICIAL HABITAT: SHIPWRECKS IN THE SOUTHERN BIGHT OF THE NORTH SEA

Vincent Zintzen[1,2], Alain Norro[3], Claude Massin[1], Jérôme Mallefet[2]

[1] Royal Belgian Institute of Natural Sciences, Rue Vautier 29, B-1000 Brussels, Belgium.
[2] University of Louvain, Biology Laboratory, Kellner Building, place Croix du Sud 3, B-1348 Louvain-la-Neuve, Belgium.
[3] Royal Belgian Institute of Natural Sciences, Management Unit of the North Sea Mathematical Models,100 Gulledelle,1200 Brussels, Belgium.

Corresponding author: Vincent Zintzen
Email: vincent.zintzen@naturalsciences.be
Tel: +32(0)2 627.43.38, Fax: +32(0)2 627.41.41
Royal Belgian Institute of natural Sciences
Rue Vautier, 29
1000 Brussels
Belgium

ABSTRACT

We investigated the cover, community structure and abiotic environment of nine shipwrecks lying at increasing distances from the Belgian coast. Results indicated that all shipwrecks were strongly dominated by cnidarians in terms of biomass and by amphipods in terms of abundances. Based on epifaunal composition, three groups of shipwrecks could be determined. *Metridium senile* dominated a species poor community of the coastal sites in association with a more diversified *Tubularia larynx* community. This latter community had a lower biomass value (102 g AFDW.m^{-2}) and significantly lower species richness compared to the other sites. These sites were characterized by periodic salinity decreases, large seasonal temperature fluctuation, high total suspended matter load and reduced current velocity. Channel water masses influence the offshore sites causing a more stable temperature and salinity environment, less turbid waters and high current speed. *Tubularia indivisa* dominated this community, with an average biomass of 229 g AFDW.m^{-2}. Intermediate sites were also dominated by *T. indivisa*, but a higher biomass (424 g AFDW.m^{-2}) was observed. They showed intermediate results for the abiotic parameters and fast current velocities. Hypotheses for the observed variation in community structures are discussed in the light of the abiotic characterization of the shipwrecks.

KEYWORDS

Artificial habitat, shipwrecks, biomass, *Tubularia*, *Metridium senile*, North Sea

1. INTRODUCTION

Artificial hard substrates have increasingly occurred at sea since man started using the sea and its resources (Connell *et al.* 1999). Certainly, the most profound and visible effect of this action are coastal constructions that dramatically changed the nature and extent of hard substrates both in shallow-water and intertidal areas (Glasby *et al.* 1999, Bacchiocchi *et al.* 2003). At sea, a large number of artificial reefs have been created for several purposes like fishery enhancement, coastal protection, recreational activities (mostly diving and fishing), and also scientific research. Other man made marine structures like offshore platforms were originally not intended as artificial reefs, but they are increasingly seen as a tool for fishery improvement or protection (Scarborough Bull *et al.* 1994, Relini *et al.* 1998, Stanley *et al.* 2000, Picken *et al.* 2000, Soldal *et al.* 2002, Jorgensen *et al.* 2002, Lokkeborg *et al.* 2002, Cripps *et al.* 2002, Fabi *et al.* 2002, Ponti *et al.* 2002, Fabi *et al.* 2004, Love 2005). Lost cargos or shipwrecks form a less conspicuous range of artificial hard substrates that lie on the seabed as results of unintentional processes (Bulloch 1965, Hiscock 1980, Leewis *et al.* 2000, Steimle *et al.* 2000, Massin *et al.* 2002). A range of pioneer organisms colonize these wrecks soon after sinking (Forteath *et al.* 1982) and an epibenthic fauna and/or flora develops that may mature into a stable community (Forteath *et al.* 1982, Picken 1986). Indications exist that these communities are distinct from those maturing on natural grounds surrounding them (Carr *et al.* 1997, Glasby 2001, Smith *et al.* 2002, Badalamenti *et al.* 2002, Knott *et al.* 2004). Not only new hard substrates may be added to the sea but novel habitats are created, distinct from those naturally occurring in the area (Connell 2000, Connell 2001, Holloway *et al.* 2002).

In areas dominated by soft sediments, shipwrecks form a patchy network of hard substrates (Zintzen *et al.* 2006) whose interconnections are unknown (Bacchiocchi *et al.* 2003). Transfer must occur between these populations but the rate and frequency at which it happens have not yet been studied. Identifying spatial patterns and species associations is a first step towards understanding the relationships that exist within these networks of disconnected marine habitats. In this paper, we investigate the spatial variation of the epifaunal community structure of nine shipwrecks located at short distances from each others (< 50 km) and in a coastal macrotidal environment.

2. MATERIAL AND METHOD

2.1. General description of the study sites

Studied shipwrecks are located in Belgian coastal waters in the Southern Bight of the North Sea. In the region, maximum depth is about 40 m and tides highly influence the distribution of sediments and their benthic communities (Larsonneur *et al.* 1982). Mean spring tide amplitudes are around 4 m. East of the Dover Strait, current velocities decrease as a result of the increasing opening between continental Europe and UK, allowing for the sedimentation of finer particles. Soft sediments dominate the seabed of the Belgian part of the North Sea (BPNS) where the presence of several subtidal sandbanks has caused a high geomorphological and sedimentological diversity (Degraer *et al.* 1999). Natural hard substrate like pebbles are rare and only occur locally in the swales between sandbanks (Lanckneus *et al.* 2001).

On the 3,640 km^2 of the BPNS, 231 obstructions were recorded, most of them being shipwrecks. A detailed map of these obstructions can be found in Zintzen *et al.* (2006). For this study, nine shipwrecks (Table 1) have been selected on basis of four criteria: (1) the vessels should have sunken at least 40 years ago, allowing for a mature state of the epifauna, (2) they are in a good condition and large enough for easy localisation, (3) they are situated outside navigation roads for safety reasons and (4) they are maximally distributed on the BPNS.

2.2. Sampling strategy and sample processing

The nine sites were sampled during a two months period (May and June 2005) avoiding seasonal variation in community structure. Preliminary studies showed that both photographic documentation and collection of organisms were needed to provide useful information on the epifauna communities of subtidal artificial hard substrates.

Sampling was achieved during day time. Photographic techniques were used to assess general features of the different communities at the scale of the individual shipwreck. A 30 m tape was deployed by divers on the upper structures of each shipwreck and digital pictures of 0.5 x 0.5 m quadrats

Table 1. Localization and basic information on the nine shipwrecks under study.

Wreck	WGS-84 Coordinates	Date of sunk	Coast distance (nautical miles)	Length x Width x Height[a] (m)	Depth (MLLWS) (m)	Orien-tation
A-Birkenfels	N 51°38',989 E 02°32',268	1966	29	156 x 18 x 22	37	174°
B-Callisto	N 51°41',950 E 02°37',330	1959	29	146 x 19 x 8	28	28°
C-Garden city	N 51°29',170 E 02°18',320	1969	25	160 x 21 x 14	26	27°
D-Kilmore	N 51°23',730 E 02°29',790	1906	17	87 x 13 x 8	30	46°
E-John Mahn	N 51°28',930 E 02°41',350	1942	17	46 x 9 x 4	29	104°
F-Duc de Normandie	N 51°25',524 E 02°36',345	1942	16	51 x 11 x 7	29	164°
G-LCT 457	N 51°24',670 E 02°43',720	1944	12	63 x 10 x ?	21	67°
H-Bourrasque	N 51°14',964 E 02°33',026	1940	8	74 x 12 x 3	18	81°
I-LST 420	N 51°15',510 E 02°40',830	1944	6	109 x 13 x 4	8	128°

[a] The height as estimated from multibeam sonar images i.e. the highest structure above the seabed level.

? Unavailable data

were taken every 5 m with a digital camera recorder (Sony PC 330, 3.2 Mpix) in a Mako housing and lighting (Light & Motion). After completion of the first set of pictures, the tape was deployed in the opposite direction of the first transect and the process started again. Due to the very poor visibility conditions, it was often impossible for the divers to locate themselves precisely on the shipwrecks.

The changing and often poor visibility conditions on sites prevented for detailed analysis of pictures. The independent collection by SCUBA of a selected faunal assemblage allowed for detailed species identification and enumeration in the laboratory. Since it was practically unfeasible to manually sample all the communities on shipwrecks, these samples were randomly taken on an *a priori* defined faunal assemblage dominated by the hydrozoan *Tubularia indivisa* and/or *Tubularia larynx* on each shipwreck site. These assemblages are known to harbour a diverse faunal association on these sites (Zintzen *et al.* 2006) and were present on all investigated sites. All organisms within quadrats of 0.25 x 0.25 m were scraped off of vertical surfaces in triplicate. All organisms were carefully collected in a plastic bag. The loss of vagile material by currents was kept low because most of the species were in close contact to the tubulariids and tended to protect themselves by staying close to their substrate. On board, the organisms were anaesthetised in a 3.5% $MgCl_2$ solution for one hour and then transferred to buffered formalin solution (final concentration 4%, pH 8.2-8.4). After 5-7 days, specimens were transferred to 70% buffered alcohol for permanent storage. The samples were sorted under a binocular microscope and macro-species (>1 mm) were identified to the lowest possible taxonomic level and counted. Colonial species were noted as present or absent.

Ash free dry weights (AFDW) were calculated for each species in each sample. First, wet weight (in alcohol) per species was determined to the nearest mg. Prior to weighting, specimens were blotted on absorbent paper to remove excess alcohol. Specimens weighting less than 1 mg were given the assigned value of 1 mg. For the taxa represented by low biomass values, ash free dry weights were calculated by using conversion factors found in the literature (Rumohr *et al.* 1987, Ricciardi *et al.* 1998, Galéron *et al.* 2000). For the more important taxa in terms of biomass, we calculated our own wet weights to ash free dry weights conversion factors. Therefore, taxa were weighted wet, dried (48h at 70°C), re-weighted (dry weight) and then burned at 500°C for 12h. Ash free dry weight is the difference between dry weight and the weight after the burning process. Specimens were kept in preservatives which have a known effect on their biomass (Brey 1986, Rumohr *et al.* 1987, Gaston *et al.* 1996, Pakhomov 2003, Wetzel *et al.*

2005). The sorting and taxonomic work did not allow freezing of the samples for conservation. In this case, Gaston *et al.* (1996) recommended fixing organisms in a formalin solution prior to transfer them into alcohol for sample processing. However, there is no agreement on which factor to apply to correct weight loss. Consequently, we multiplied our values by a factor of 1.2 as estimated by Rumohr *et al.* (1987) and used by Cusson *et al.* (2005). This factor has to be considered as a minimum one.

2.3. Abiotic data

The following abiotic data were made available for this study: water temperature, salinity, turbidity, vertically averaged current velocity and direction, depth (Mean lower low water springs level), orientation of the shipwreck on the seabed, chlorophyll *a* content of water above shipwreck and chlorophyll *a* content of sediments on shipwreck.

Seawater temperature and salinity data were extracted from the data acquisition system onboard the R/V Belgica where a seabird SBE 21 thermosalinograph reads temperature and salinity data at a depth of 3 m. Data were collected between 1993-2006 and extracted for perimeters of five nautical miles around each wreck (see table 1). Monthly mean sub-surface temperature and salinity values as well as minima and maxima were computed. Due to the well-mixed water column, these sub-surface values remain representative for the complete water column.

Turbidity estimates were obtained through satellite imagery collected between September 1997 and March 2004. For each site, the mean total suspended matter ($mg.l^{-1}$) was calculated using the MODerate resolution Imaging Spectro-radiometer (MODIS) aboard the satellite EOS AQUA. A bio-optical model calibrated for the Belgian coastal waters, following the method described in Nechad *et al.* (2003), was applied to MODIS readings.

On each sampling date, water transparency was measured with a Secchi disk during slack period.

Data on the currents present at each site were obtained using a three-dimensional operational model (Pison *et al.* 2003). The model is based on the COHERENS code (Luyten *et al.* 1999) and run on a daily basis forced by meteorological forecast provided by the UK Met Office. The grid size of the model is 750 m square. Boundary conditions were provided by larger scale model using the nesting methods. Outputs of the model included profiles of the current at each shipwrecks as well as depth averaged values. Currents roses were constructed on depth averaged values of the current that were computed every 10 minutes. The runs started in august 2004, resulting in at least 230 days of data for each shipwreck site.

Water samples (3 x 1 L) were taken at 50 cm above the shipwreck surfaces and the sediment found on the shipwreck surface was transferred to plastic recipient by divers in triplicate. The chlorophyll *a* concentration in water and sediment samples was determined by High Performance Liquid Chromatography (Gilson) using the method described by Wright *et al.* (1997). For water samples, the results were expressed as µg per litre and the sediment samples as µg per gram of sediments.

From this abiotic dataset, we retained the following parameters for multivariate analysis: (1) mean temperature and salinity for February (T1, S1), June (T2, S2) and October (T3,S3), (2) minimal and maximal temperature (Tmin, Tmax) and salinity (Smin, Smax), (3) annual monthly mean minimal and maximal salinity (SMmin, SMmax), (4) mean total suspended matter for January-February (TSM-1), May-June (TSM-2) and August-September (TSM-3), (5) Secchi depth (Sec), (6) depth, (7) chlorophyll *a* content in water (W-pig) and sediments (S-pig), (8) proportion of current velocities (>1, 1-0.75, 0.75-0.50, 0.50-0.25, 0.2-0.10, <0.10 $m.s^{-1}$) (C100, C100-75, C75-50, C50-25, C25-10, C10) and (9) angular difference between heading of the shipwreck and dominant current direction (Head-Dir).

2.4. Data analysis

2.4.1. Tubularia association collected by SCUBA

Species richness (S), the Simpson index (D) (as recommended by Magurran 2004), the average taxonomic distinctness (Δ^+) and the variation in taxonomic distinctness (Λ^+) (Clarke *et al.* 1998, Clarke *et al.* 2001a) were used as univariate summary variables. The taxonomic distances were evaluated through a taxonomic tree built on standard Linnean classification. We used the taxonomy proposed by Costello *et al.* (2001) from which we extracted a simplified tree: the retained taxonomic levels were species, genus, family, order, class and phylum. The default weights between step length of the Linnean tree were set to constant (i.e. weights were 16.7 for species in the same genus, 33.3 for species in different genus but the same family, 50 for species in different family but the same order, 66.7 for species in different orders but the same class, 83.3 for species in different class but the same phylum and 100 for species in different phyla). These indices were calculated using the DIVERSE procedure of the PRIMER statistical software package and compared across sites using the post-hoc Student-Newman Keuls test for comparisons of means (Keuls 1952). Normality of the data was tested with Shapiro-Wilk W test prior to analysis (Shapiro *et al.* 1965).

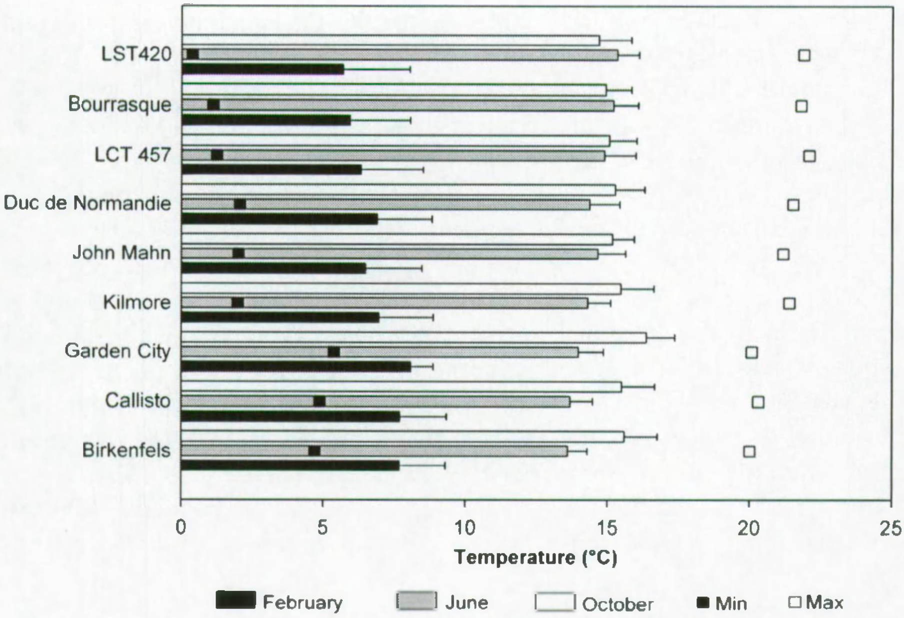


Figure 1. Water temperature on the nine shipwrecks. The mean monthly values (+s.d.) for February, June and October are presented together with minimal and maximal observed temperature. Period covered: 1993-2006.

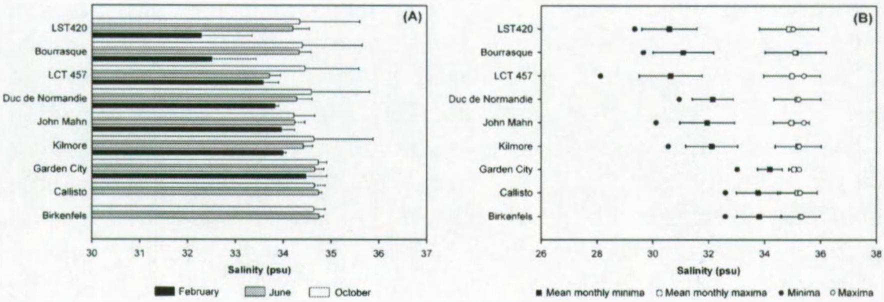


Figure 2. Water salinity on the nine shipwrecks. (A) Mean monthly values (+s.d.) for February, June and October. (B) Mean (± s.d.) monthly minima and maxima. Period covered: 1993-2006.

Multivariate exploratory analysis of the scraped samples from the *Tubularia* association was conducted on biomass data. The data were pooled by site (shipwreck) and square-root transformed. Similarity between each pair of samples was then calculated with the Bray-Curtis similarity coefficient (Bray *et al.* 1957). This matrix was used to explore the pattern of community structure among samples by means of ordination with non-metric multidimensional scaling (nMDS) and clustering by group-averaging (Clarke 1999). The goodness-of-fit of the resulting two dimensional nMDS plot was measured using Kruskal's stress formula I (Kruskal *et al.* 1978). The groups *a posteriori* defined by the cluster and ordination analysis were tested by a one-way ANOSIM which is a multivariate test based on the corresponding rank similarities between samples in the underlying triangular similarity matrix (Clarke *et al.* 2001b). Non-parametric multivariate analysis of variance was used to test for difference between sites using PERMANOVA (Anderson 2001). The matching of biotic to environmental data was done with the BIO-ENV procedure. Draftsman plot of environmental data was done to estimate skewness of data and transformation applied if necessary. Environmental data with strong colinearity (Spearman rank correlation > 0.90) were grouped prior to analysis. Analyses were performed with the Primer 6.0 software package.

The groups of sites resulting from the multivariate analysis were characterized by their indicator species. We used the indicator value (IndVal) coefficient developed by Dufrêne *et al.* (1997). A species is indicator of a group if it occurs on most of the samples from this group (specificity) and if it is poorly represented on the other groups (fidelity). The IndVal coefficient combines both the species relative abundance with its relative frequency of occurrence in the defined groups of sites. The statistical significance of the species indicator values was evaluated using a randomization procedure (999 randomizations). A species is considered indicator of a group if the results of two tests are significant at a level of 0.05: a t-test computing the weighted distance between randomized values and the observed value, and the rank of the observed value among the decreasing ordered randomized value distribution. The calculations were made using the IndVal program.

2.4.2. Photographic quadrats

Per site, 7 to 13 pictures were found of a quality high to allow identification. The percentage cover of epibiota from each quadrat was estimated by

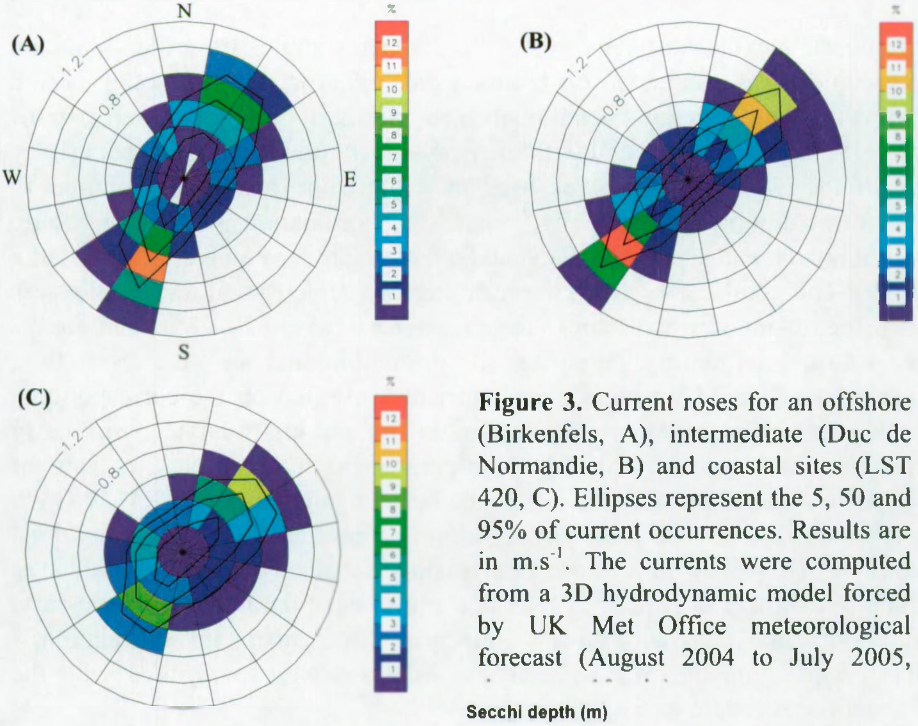


Figure 3. Current roses for an offshore (Birkenfels, A), intermediate (Duc de Normandie, B) and coastal sites (LST 420, C). Ellipses represent the 5, 50 and 95% of current occurrences. Results are in m.s^{-1}. The currents were computed from a 3D hydrodynamic model forced by UK Met Office meteorological forecast (August 2004 to July 2005,

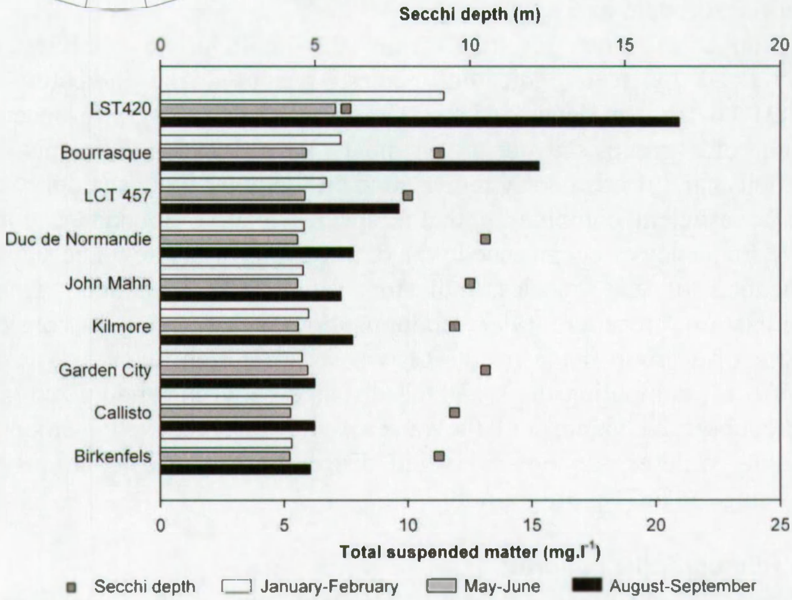


Figure 4. Mean total suspended matter by period of the year and by site estimated from Modis satellite imagery (period covered: July 2002 to October 2005) and Secchi depth taken on the sampling dates.

identifying taxa under 196 regularly spaced points with CPCe software (Kohler *et al.* 2006). This number of points was chosen after tests on three representative quadrats and varying grid size (100, 144, 169, 196, 225 and 256 points per quadrat). The 196 point grid was needed to identify all the recognizable features of the pictures and more points did not add any more information. Besides epifauna, bare surface (metal, sand or mud) and fishing lines/nets could be recognized. The amount of unidentifiable features or empty spaces was kept low.

The data were fourth square-root transformed because the data set was strongly dominated by some of the variables. It was then submitted to a Principal Component Analysis on covariance matrix. Similarity between sites was estimated also by the Bray-Curtis index calculated from double-square-root transformed data and tested by an ANOSIM procedure (Clarke *et al.* 2001b). A SIMPER breakdown was performed to determine the epibenthic categories that contribute most to the average similarity within sites (Clarke *et al.* 2001b).

3. RESULTS

3.1. Abiotic data

Depth and orientation of the shipwrecks are presented on table 1. Obviously, offshore shipwrecks are located in deeper waters while coastal sites are shallower. There was no preferential orientation of the shipwrecks on the seabed.

Temperature varied between 0.4 and 22.1 °C (Figure 1). Water temperature showed a lower seasonal fluctuation at offshore sites than inshore. Temperatures were colder in winter and hotter in summer for the coastal sites than further offshore. The three offshore sites (Garden City, Birkenfels and Callisto) which are under the influence of Channel water differed strongly from the other sites by having higher minimum temperatures and lower maximum temperatures. The minimal and maximal water temperature differences were 14.7 °C for an offshore site (Garden City) and 21.5 °C for a coastal site (LST 420).

Salinity ranged from 28.1 to 35.4 psu (Figure 2). In February, the coastal sites showed a decreased salinity of approximately two units compared to the intermediate and offshore sites (Figure 2,A). Salinity values recorded in October showed less variation amongst the nine sites. Three groups differentiated from the minimal and maximal salinities (Figure 2,B). Lowest salinities were recorded on the LST420, Bourrasque and LCT457 as these

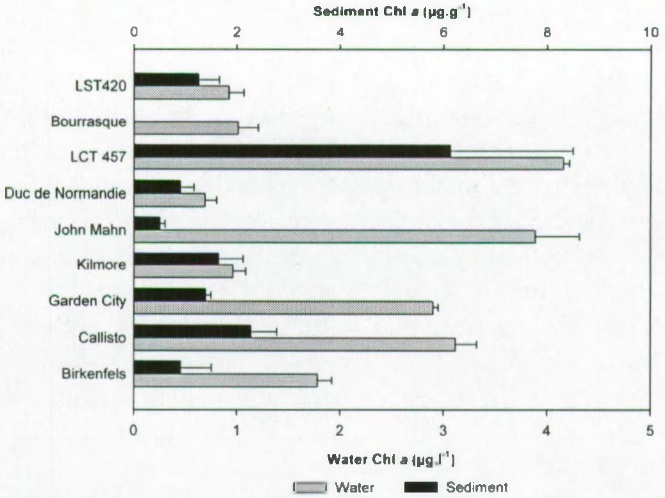


Figure 5. Chlorophyll *a* concentration (N=3, ± s.d.) of water and sediment samples from the shipwreck sites.

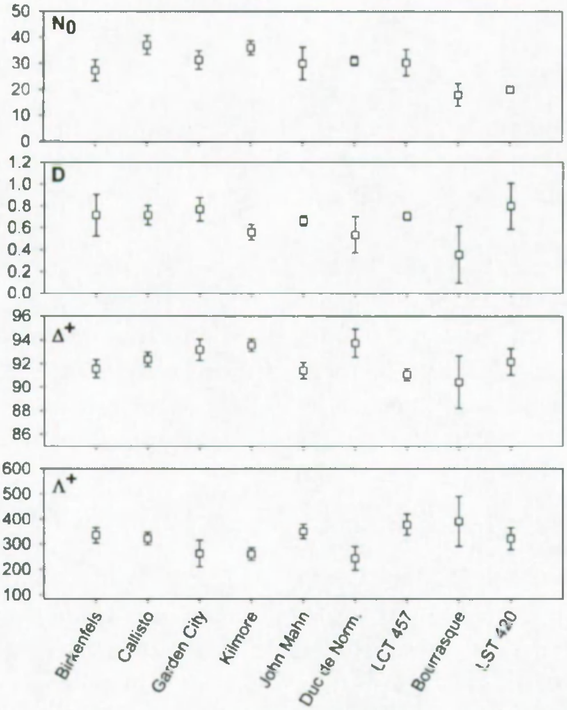


Figure 6. Mean number of species (N_0), Simpson index (D), taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) for each shipwreck site (Number of replicates=3, ± s.d.).

received periodically an input of freshwater from continental rivers. The difference between minima and maxima recorded salinities was lowest for the offshore sites (Garden City, Birkenfels and Callisto). The remaining sites had an intermediate salinity regime.

The current velocities and directions of the nine sites were oriented along a coastal-offshore gradient. Figure 3 presents typical examples of coastal (LST 420), intermediate (Duc de Normandie) and offshore (Birkenfels) current roses. Current ellipses showed preferential directions: NE (22.5-67.5°) and SW (202.5-247.5°). The prevailing direction was oriented to 22.5-40° and 202.5° for Birkenfels, Callisto and Garden City, to 45° and 225° for the Kilmore, Duc de Normandie, LCT457 and John Mahn, to 45-67.5° and 225° for the Bourrasque and to 45-67.5° and 202.5-225° for LST420. This last site, together with the Bourrasque had sparsely current above 0.8 $m.s^{-1}$, compared to the other and further offshore sites. Only the Garden City, Kilmore and Duc de Normandie had sparsely current velocities above 1 $m.s^{-1}$. For all sites, the frequency of low current velocity (<0.2 $m.s^{-1}$) was comprised between 9.0 and 15.1 % and the period of very low current velocity (calms, <0.1 $m.s^{-1}$) was always under 1.1 %. The most occurring current velocity was comprised between 0.6 and 1.0 $m.s^{-1}$, except for the LST420 and Bourrasque where current velocity in the range 0.4-0.8 $m.s^{-1}$ was the most frequent.

Total suspended matter (TSM) decreased in May-June and reached highest values during August-September. This pattern was more pronounced for the coastal sites and tended to be attenuated further offshore with less fluctuating concentration over time. There was a clear spatial trend of decreasing TSM with distance from the coast. During late summer, TSM values for the coastal wrecks, LST420 and Bourrasque were 20.9 $mg.l^{-1}$ and 15.3 $mg.l^{-1}$, respectively, while reaching 9.7 $mg.l^{-1}$ at LCT457. Values for the Kilmore, Duc de Normandie and John Mahn fell between 7.3 and 7.8 $mg.l^{-1}$. At the Garden City, Birkenfels and Callisto, late summer TSM values of 6.1 to 6.2 $mg.l^{-1}$ were found. Secchi readings confirmed TSM measurements (Figure 4). The lowest transparency was measured on the LST420 (6.0 m) while the highest was found on the Garden City and Duc de Normandie (10.5 m).

Chlorophyll *a* concentrations of water samples taken close to the shipwrecks ranged between 1.0 and 4.2 $\mu g.l^{-1}$ (Figure 5). The sediments contained chlorophyll *a* in concentration ranging from 0.9 to 6.1 $\mu g.g^{-1}$. Data for sediment samples are missing for the Bourrasque. The further offshore sites (Garden City, Birkenfels and Callisto) and especially the John Mahn were characterized by a high ratio of chlorophyll in water to chlorophyll in sediments. The other sites had comparable and lower ratios.

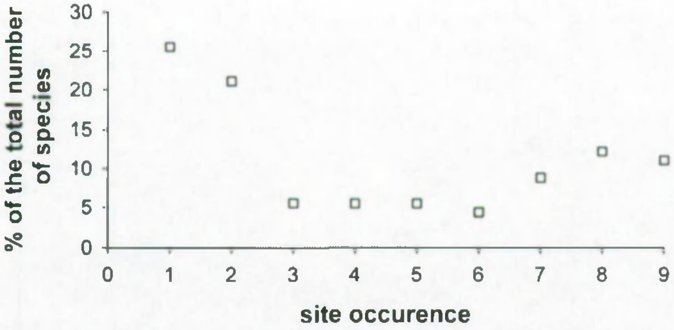


Figure 7. Repartition of shared species on the shipwrecks sites. The x-axis represents the number of sites where the species are present.

Table 2. Dispersion (site occupation), global (all sites) and maximal local mean abundances of the 20 most dominant taxa. CRU: Crustacea, CNI: Cnidaria, ECH: Echinodermata, MOL: Mollusca, NEM: Nemertea, POL: Polychaeta,

Species		**Global mean abundance (ind.m^{-2})**	**Dispersion (%site)**	**Local mean abundance (ind.m^{-2})**	**Site of maximal mean abundance**
Jassa herdmani	CRU	63,029	100	116,997	Kilmore
Caprella tuberculata	CRU	3,219	78	22,677	Kilmore
Phtisica marina	CRU	1,343	100	4,315	John Mahn
Stenothoe valida	CRU	1,253	89	4,192	LCT457
Pisidia longicornis	CRU	950	100	1,909	Callisto
Ophiothrix fragilis	ECH	831	100	1,269	Garden City
Stenothoe monoculoides	CRU	823	89	3,643	Kilmore
Phyllodoce mucosa	POL	804	89	6,533	LCT457
Mytilus edulis	MOL	516	100	2,971	Kilmore
Asterias rubens juv.	ECH	363	67	885	LCT457
Actiniaria	CNI	345	100	581	Duc de Nor.
Stenothoe marina	CRU	334	100	731	LCT457
Monocorophium sextonae	CRU	299	89	1,435	LCT457
Metopa alderi	CRU	245	89	944	John Mahn
Harmothoe spp.	POL	152	100	427	John Mahn
Oerstedia dorsalis	NEM	141	100	427	LST420
Sabellaria spinulosa	POL	121	89	555	Callisto
Amphipholis squamata	ECH	107	78	624	Kilmore
Eulalia viridis	POL	74	78	475	LCT57
Pilumnus hirtellus	CRU	63	89	144	Callisto

3.2. The *Tubularia* community from SCUBA sampling

3.2.1. Diversity and abundance of epifauna

A total of 90 species were recorded. Species diversity ranged from 13 to 40 species per site with a mean value of 29 species. The species number (N_0) was significantly lower at the Bourrasque and LST 420 shipwrecks (SNK, $p < 0.05$ and figure 6). The Simpson index (D), the average taxonomic distinctness (Δ^+) and the variation in taxonomic distinctness (Λ^+) showed little variations between sites. The following significant differences were found ($p < 0.05$): LST 420 and Bourrasque for D, Kilmore and Bourrasque for Δ^+, Duc de Normandie and Bourrasque for Δ^+ and for Λ^+.

47% of the species were present in only one (23 species) or two sites (19 species) (Figure 7). 32% of the species were present on 7 to 9 sites. Species found on an intermediate number of sites (3-5) were the least common (21%).

The dominant species were generally observed in the majority of the sites (Table 2). The amphipods accounted for 94% of the specimens in our samples. A large fraction (89%) of these amphipods were *Jassa herdmani* which had an average density (±s.d.) of 116,997±31,700 ind.m^{-2} and a maximal density of 180,000 ind.m^{-2} in one Kilmore sample. Other caprellid species and species of the genus *Stenothoe* were also abundant. Four polychaetes were numerically abundant (*Phyllodoce mucosa*, *Harmothoe* spp., *Eulalia viridis* and *Sabellaria spinulosa*). Echinoderms were represented by three species that were abundant (*Ophiothrix fragilis*, juveniles of *Asterias rubens* and *Amphipholis squamata*). The nemertean *Oerstedia dorsalis* was reported on all sites.

3.2.2. Biomass

The mean biomass recorded on the shipwrecks was 288 g AFDW.m^{-2} (Figure 8). This value does not include the biomass from tubes built by amphipods (*Jassa herdmani*). These tubes were made of organic material collected from surrounding waters. On average, the biomass accumulated in these tubes was 92 g AFDW.m^{-2}. The hydrozoans *Tubularia indivisa* and *Tubularia larynx* accounted for 69% of the recorded biomass. Crustaceans, mainly amphipods species and the anomuran decapod *Pisidia longicornis*, constituted another 21% of the recorded biomass. Echinoderms, mainly *Ophiothrix fragilis*, represented 4% of the total biomass. Three sites, the Kilmore, the LCT 457 and the John Mahn shared high biomass values of 584±207, 474±597 and 471±391 g AFDW.m^{-2}, respectively. Lowest biomass

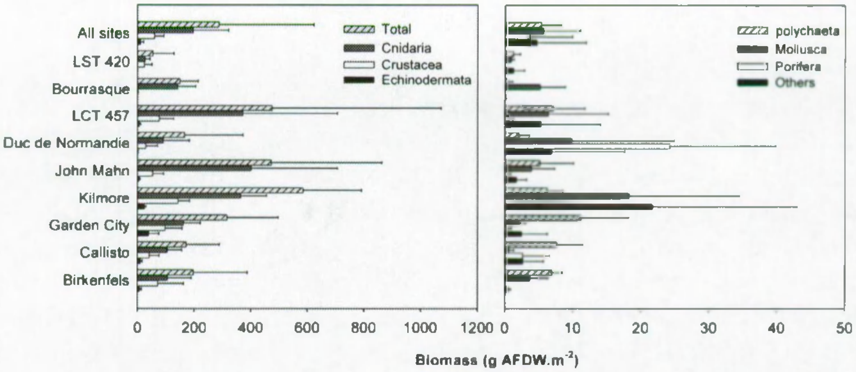


Figure 8. Mean biomass values (Number of replicates=3, + s.d.) of shipwrecks sites for main taxonomic groups. Others: Tunicata, Nemertea, Bryozoa and Turbellaria.

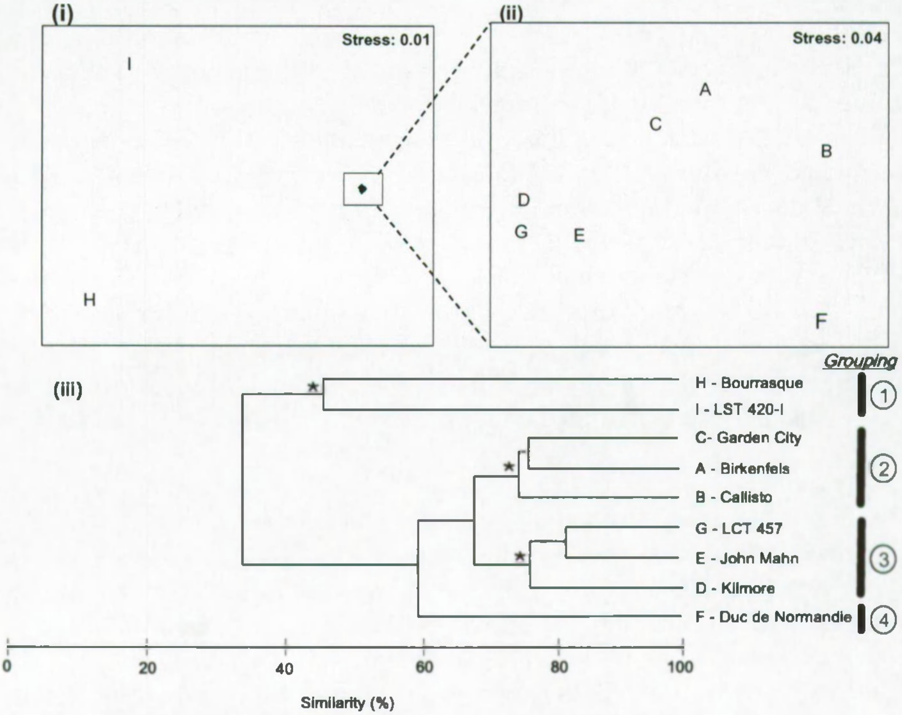


Figure 9. Multivariate analysis of similarity between sites (Bray-Curtis coefficient on square root transformed biomass data). (i) nMDS of all sites; H: Bourrasque, I: LST 420. (ii) nMDS of indiscernible sites in (A); A: Garden City, B: Birkenfels, C: Callisto, D: Kilmore, E: Duc de Normandie, F: John Mahn, G: LCT 457. (iii) Clustering of sites; * significant at $p<0.05$ after SIMPROF (Permutations for mean profile: 2000, Simulation permutations: 999).

Table 3. BIO-ENV results from root-transformed abundance data. Bray-Curtis similarity was used for biotic data and Euclidean distance for normalized abiotic data. Correlation based on spearman rank coefficient. Combination with maximal five factors are showed. Significance test was calculated based on 999, 499 and 199 random permutations of sample names for 1-2, 3 and 4-5 variables, respectively. See text for parameter abbreviations.

# variables	Correlation	Variables	Permutation test sign.
1	0.581	TSM-1	0.1%
1	0.570	C100-75	0.1%
1	0.552	C50-25	0.1%
1	0.519	S1	0.1%
2	0.589	Depth, C100-75	0.1%
3	0.612	TSM-1, C100-75, C75-50	0.2%
4	0.635	T2, W-pig, C100-75, C75-50	0.4%
5	0.635	T2, TSM-1, C100-75, C75-50, Head-Dir	0.4%

Table 4. Indicator species values (IndVal), mean biomass (g AFDW.m^{-2}) and presence of species at different clustering levels. Only species with IndVal > 50% are considered. The first figure is the mean biomass for the three samples of the site; if the mean biomass is lower than 0.1 g AFDW.m^{-2}, it is rounded to 0. The second figure is the number of samples where the species is present for the site under consideration. Species in bold have reached their maximum indicator value. ** Significant at $p < 0.05$ level for the two randomization tests. * Significant at $p < 0.05$ level for only one of the two randomization tests.

SPECIES	**Ind-Val (%)**	**Birkenfels**	**Callisto**	**Garden city**	**Kilmore**	**John Mahn**	**Duc de Noman.**	**LCT457**	**Bourrasque**	**LST420**
All sites										
Tubularia indivisa	100	100.7/3	92.5/3	153.4/3	361.6/3	399.6/3	86.4/3	366.1/3	20.3/3	20/3
Jassa herdmani	96	65.6/3	29.5/2	86/3	123.3/3	41.2/3	26.2/3	67.8/3	1.1/3	23.6/3
Phtisica marina	96	0.1/3	0.3/3	0.6/3	1.3/3	1.7/3	0.2/3	0.6/3	0.1/2	0/3
Actiniaria	92	3.9/3	13.5/3	9.3/3	2.6/3	1.9/3	4.8/3	5.2/3	0.2/2	0.7/2
***Harmothoe* spp.**	92	0.6/3	0.8/3	2.2/3	3.2/3	4.1/3	0.4/3	2.5/3	0/1	0.7/3
Ophiothrix fragilis	92	7.7/3	10.5/3	38.9/3	24.9/3	5/3	1.7/3	5.5/3	0/2	0.1/2
Mytilus edulis	88	1.7/3	0/2	0.4/3	1.9/3	0.1/3	0.1/3	0.4/3	0/2	0.1/2
Stenothoe marina	88	0.3/2	0.1/3	0/1	0/3	0.3/3	0.2/3	0.3/3	0.6/3	0.1/3
Monocorophium sextonae	81	0.2/3	0.1/3	0/3	0/3	0.1/3		0.5/3	0/3	0/1
Oerstedia dorsalis	81	0.3/2	0.3/2	0.2/2	1.3/3	0.5/2	0.8/3	0.4/3	0.1/2	1.2/3
Pisidia longicornis	81	4.3/2	9.3/3	9.6/3	9.5/3	7/3	1.3/3	3.5/3	0/1	0/1
Stenothoe valida	81	0.4/3	0.5/3	0.3/3	0.8/3	1.9/3	0.2/3	3.7/3	0/1	
Electra pilosa	77	0.2/3	0.4/3	0.4/3	6.4/3	0.9/3	0.3/3	0.1/2		0.1/1
Pilumnus hirtellus	77	0.3/3	1.1/2	0.7/3	1.2/3	0.7/3	0.1/3	0.5/3		0/1
Lanice conchilega	74	0/1	0/1	0.2/3	0.1/3	0.1/3	0.4/3	0.1/3		0.5/3
Lepidonotus squamatus	74	0.5/3	0/2	0.2/2	1.1/3	0.2/3	0.2/3	0.4/2		0/2
Stenothoe monoculoides	70	0/2	0.1/3	0.1/3	0.5/3	0.1/3	0/1	0.1/3		0/1
Caprella tuberculata	66	1/3	0.4/3	0.6/3	6.4/3	0/2	1/3		0/1	
Metopa alderi	66	0/2	0.5/3		0.1/2	0.6/3	0.4/3	0.1/3	0/1	0/1

SPECIES	Ind-Val (%)	Birken-fels	Callisto	Garden city	Kilmore	John Mahn	Duc de Noman.	LCT457	Bourra-sque	LST420
***Asterias rubens* juv.**	62		0/2		0.2/3	0.1/3	0.1/3	0.8/3		0.3/3
Phyllodoce mucosa	62		0/2	0/1	0.1/3	0.1/2	0.1/2	3.1/3	0.4/2	0/2
Amphipholis squamata	59		0/3	0.2/3	0.3/3	0/2	0/2	0/2		0/1
Pomatoceros triqueter	59	2.8/2	2.6/3	6.7/3	1.4/2	0.5/2	0.3/2	0.4/2		
Dendronotus frondosus	55			0.7/3	15.9/3	3.8/2	9.7/3	5.7/2	0/1	0.1/1
Cuthona sp.	51	0.2/3		0/1	0.1/3	0/2	0/2	0/1		0.4/2
Eulalia viridis	51	0/2	0.1/1	0.1/1	0.1/3	0/3	0/1	0.2/3		
Psammechinus miliaris	51	0/2	0.1/2	0.6/3	0.1/3	0/2		0/2		
Sabellaria spinulosa	51	0.8/2	3.6/2	0.2/2	0.2/2	0/1	0.5/3	0.1/1	0/1	
Syllis gracilis	51	0/2	0/2	0/2	0/2	0/1	0/2	0.2/3		
Offshore sites										
Aequipecten opercularis	91**	0.3/3	0.3/3	0.5/3	0.1/2	0/1			0/1	
Pomatoceros triqueter	76**	2.8/2	2.6/3	6.7/3	1.4/2	0.5/2	0.3/2	0.4/2		
Actiniaria	68**	3.9/3	13.5/3	9.3/3	2.6/3	1.9/3	4.8/3	5.2/3	0.2/2	0.7/2
Ophiothrix fragilis	67**	7.7/3	10.5/3	38.9/3	24.9/3	5/3	1.7/3	5.5/3	0/2	0.1/2
Psammechinus miliaris	67 *	0/2	0.1/2	0.6/3	0.1/3	0/2		0/2		
Sabellaria spinulosa	58 *	0.8/2	3.6/2	0.2/2	0.2/2	0/1	0.5/3	0.1/1	0/1	
Heteranomia squamula	55**	0/2	0.1/2	0.3/2	0/3	0/1	0.1/2			
Musculus sp.	54**	0/2	0/1	0/2		0/1				
Nereis pelagica	53**	2.2/2	0.2/2	1.4/1			0/1	0.2/1		
Pisidia longicornis	52 *	4.3/2	9.3/3	9.6/3	9.5/3	7/3	1.3/3	3.5/3	0/1	0/1
Intermediate sites										

SPECIES	Ind-Val (%)	Birken-fels	Callisto	Garden city	Kilmore	John Mahn	Duc de Noman.	LCT457	Bourra-sque	LST420
Dendronotus frondosus	80**			0.7/3	15.9/3	3.8/2	9.7/3	5.7/2	0/1	0.1/1
Stenothoe valida	80**	0.4/3	0.5/3	0.3/3	0.8/3	1.9/3	0.2/3	3.7/3	0/1	
Electra pilosa	76**	0.2/3	0.4/3	0.4/3	6.4/3	0.9/3	0.3/3	0.1/2		0.1/1
Phtisica marina	71**	0.1/3	0.3/3	0.6/3	1.3/3	1.7/3	0.2/3	0.6/3	0.1/2	0/3
Tubularia indivisa	69**	100.7/3	92.5/3	153.4/3	361.6/3	399.6/3	86.4/3	366.1/3	20.3/3	20/3
Phyllodoce mucosa	65 *		0/2	0/1	0.1/3	0.1/2	0.1/2	3.1/3	0.4/2	0/2
Harmothoe spp.	62**	0.6/3	0.8/3	2.2/3	3.2/3	4.1/3	0.4/3	2.5/3	0/1	0.7/3
Asterias rubens juv.	62**		0/2		0.2/3	0.1/3	0.1/3	0.8/3		0.3/3
Stenothoe monoculoides	58 *	0/2	0.1/3	0.1/3	0.5/3	0.1/3	0/1	0.1/3		0/1
Sycon ciliatum	57**			0.1/1	4.5/3	0.1/1	6.3/2	0.4/1		
Lepidonotus squamatus	57 *	0.5/3	0/2	0.2/2	1.1/3	0.2/3	0.2/3	0.4/2		0/2
Syllis gracilis	57**	0/2	0/2	0/2	0/2	0/1	0/2	0.2/3		
Metopa alderi	53	0/2	0.5/3		0.1/2	0.6/3	0.4/3	0.1/3	0/1	0/1
Coastal sites										
Tubularia larynx	97**	2.1/1						0.7/1	59.9/3	3/3
M. acherusicum^a	83**								0/3	0.1/2
Stenothoe marina	50	0.3/2	0.1/3	0/1	0/3	0.3/3	0.2/3	0.3/3	0.6/3	0.1/3
Catriona gymnota	50**								1.7/3	
Metridium senile	50**								59.2/2	3.6/1
Obelia bidentata	50**								2/2	0/1
Birkenfels										
-	-	-	-	-	-	-	-	-	-	-

SPECIES	Ind-Val (%)	Birken-fels	Callisto	Garden city	Kilmore	John Mahn	Duc de Noman.	LCT457	Bourra-sque	LST420
Callisto										
Eulalia aurea	70**	0/1	0.1/3		0/1					
Polyclinum aurantium	64 *		1/2		0/1					
Molgula cf occulta	58 *	0.1/2	0.5/2							
Garden City										
Psammechinus miliaris	68	0/2	0.1/2	0.6/3	0.1/3	0/2		0/2		
Odontosyllis fulgurans	55**		0/1	0/3	0/1	0/1	0/1	0/1	0/1	
Kilmore										
Scrupocellaria scruposa	79**		0/2		0.2/3					
Electra pilosa	72**	0.2/3	0.4/3	0.4/3	6.4/3	0.9/3	0.3/3	0.1/2		0.1/1
Caprella tuberculata	67**	1/3	0.4/3	0.6/3	6.4/3	0/2	1/3		0/1	
Amphipholis squamata	55 *		0/3	0.2/3	0.3/3	0/2	0/2	0/2		0/1
Stenothoe monoculoides	53**	0/2	0.1/3	0.1/3	0.5/3	0.1/3	0/1	0.1/3		0/1
John Mahn										
-	-	-	-	-	-	-	-	-	-	-
Duc de Normandie										
Myxilla rosacea	74**		0.8/1		0.6/1		4.1/3			
Halichondria* cf *panacea	54 *		0.4/1				1.9/2			

SPECIES	Ind-Val (%)	Birken-fels	Callisto	Garden city	Kilmore	John Mahn	Duc de Noman.	LCT457	Bourra-sque	LST420
LCT 457										
Phyllodoce mucosa	81**		0/2	0/1	0.1/3	0.1/2	0.1/2	3.1/3	0.4/2	0/2
Syllis gracilis	75**	0/2	0/2	0/2	0/2	0/1	0/2	0.2/3		
Nemertinata sp.1	58 *		0/1					0.2/2		
Turbellaria	57 *			0/1				0.1/2		
Asterias rubens juv.	52**		0/2		0.2/3	0.1/3	0.1/3	0.8/3		0.3/3
Monocorophium sextonae	50**	0.2/3	0.1/3	0/3	0/3	0.1/3		0.5/3	0/3	0/1
Bourrasque										
Catriona gymnota	100**								1.7/3	
Tubularia larynx	91**	2.1/1						0.7/1	59.9/3	3/3
Balanus crenatus	66 *						0/1		0.5/2	
Obelia bidentata	65 *								2/2	0/1
Metridium senile	62 *								59.2/2	3.6/1
LST 420										
Eumida sp.	60**							0/1		0/3
M. acherusicum[a]	51								0/3	0.1/2

[a]: *Monocorophium acherusicum*

values were found at the LST 420 and Bourrasque (55±73 and 150±65 g AFDW.m^{-2}). However, post-hoc comparison of means could not discern for significant differences in biomass between sites because of the large variation of the biomass values noted on each sites. The fauna of the Duc de Normandie was typified by a low biomass of polychaetes and Cnidaria combined with a relative high biomass of sponges.

3.2.3. Multivariate pattern

The Bourrasque (site H) and LST 420 (site I) were found to clearly differ from the other shipwrecks in the ordination plane (Figure 9,A). Ordination and clustering identified two additional groups (Figure 9,B & C). The Kilmore (site D), LCT 457 (site G) and John Mahn (site F) comprised a first group. A second group associated the Birkenfels (site B), Callisto (site C) and Garden City (site A). One site, the Duc de Normandie (site E) did not have clear affinities with the other shipwrecks. These groupings were further confirmed by an ANOSIM test (global R: 0.823, $p < 0.001$). The NPMANOVA showed that there was a significant difference between the assemblages of the different sites ($p=0.002$), but the pair-wise comparisons between sites did not result in any significant results. The shipwrecks with similar fauna's are further referred to as coastal (Bourrasque and LST 420), offshore (Birkenfels, Garden City and Callisto) and intermediate (LCT 457, Kilmore and John Mahn) groups. The same dataset with the *Tubularia* spp. removed showed the same differentiation between the coastal and other sites. However, the distinction between the intermediate sites and offshore sites was less clear, except for the Duc de Normandie which was still clearly isolated from the other sites.

After colinearity inspection, five factors were dropped because of their strong correlation (spearman rank correlation >0.90) with other variables: mean temperature for February, mean salinity for June, monthly mean minimal salinity and mean total suspended matter for January-February. The other factors were retained for the BIO-ENV analysis. The best single factor explaining species pattern was total suspended matter for January-February ($r=0.581$, $p=0.001$), but current velocity proportion between 1 and 0.75 m.s^{-1}, current velocity proportion between 0.50 and 0.25 m.s^{-1} and salinity for January explained almost as well the relation between biotic and abiotic data (Table 3). The addition of other factors improved slightly the correlation between biotic and abiotic data. The best five factors combination comprised temperature for June, total suspended matter for January-February, current velocity proportion between 1 and 0.75 m.s^{-1}, current velocity proportion

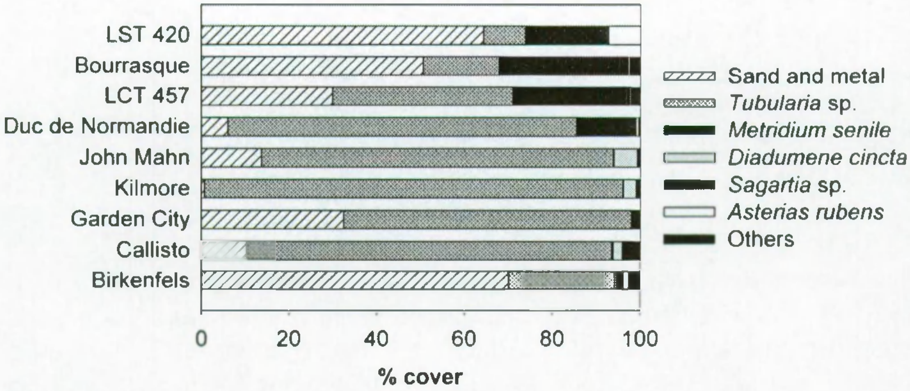


Figure 10. Mean percentage cover of epifauna on the shipwrecks estimated from photographic quadrats. Others: *Actinothoe sphyrodeta*, *Cancer pagurus*, *Dendronotus frondosus*, *Diplosoma* sp., *Porifera*, *Haliclona* sp., Jassa tubes, *Nassarius* sp., *Necora puber*, *Nemertesia antennina*, *Ophiotrix fragilis*, Paguridae, *Pomatoceros triqueter*, *Sycon ciliatum*, *Urticina felina*, fishing lines/net and unidentified features.

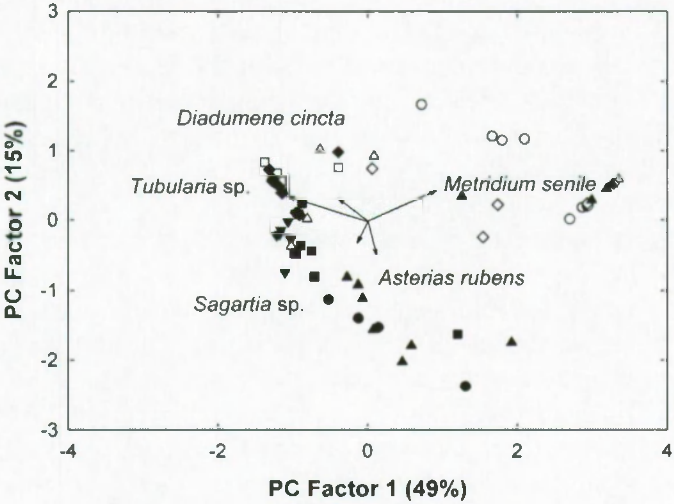


Figure 11. Principal Components Analysis biplot of the epifauna cover data (on covariance matrix, double-root-transformed data). Only the main variables and the sites with Σ Cos$^2 \geq 0.40$ are represented. Sites symbolism: ■ Bourrasque, □ LST 420, ● John Mahn, ○ Duc de Normandie, ♦ Birkenfels, ◊ Kilmore, ▲ Callisto, Δ LCT 457, x Garden City.

between 0.75 and 0.50 $m.s^{-1}$, and angular difference between heading of the shipwreck and prevailing current direction.

3.2.4. Indicator species

Shipwrecks in general were represented by a large number of indicator species (Table 4). Indicator Values (IndVal) of more than 50% were found for 29 taxa. *Tubularia indivisa* was present on all samples. Many of the highest IndVal belong to crustaceans, mainly amphipods (*Jassa herdmani, Phtisica marina, Stenothoe marina, Monocorophium sextonae, Pisidia longicornis, Stenothoe valida*). Offshore sites had 10 species with an IndVal higher than 50% which were all significant (two randomization tests) or partly significant (one randomization test) at $p < 0.05$. However, these species were not only present offshore. Most of them were also sampled in the intermediate sites but with a lower biomass. The difference with coastal sites was more pronounced, with many species being totally absent there. This situation was also encountered with the indicator species for intermediate sites. Thirteen species had high and most significant indicator values but were also present offshore with lower biomass. Only two species, the opistobranch *Dendronotus frondosus* and the sponge *Sycon ciliatum* had their maximum indicator value in this clustering level. Coastal sites had a distinct set of indicator species. *Tubularia larynx* did not occur in high abundances elsewhere. Four species were only present on coastal sites: *Monocorophium acherusicum, Catriona gymnota, Metridium senile* and *Obelia bidentata*. The Birkenfels and John Mahn shipwrecks had no species with IndVal above 50%. No more than two taxa were found in only one site: Gastropoda belonging to the Rissoidae in the Callisto and the opistobranch *Catriona gymnota* at the Bourrasque.

3.3. General characteristics of shipwrecks cover – photographic transect

Generally, the percentage of surface not covered by epifauna for the 9 sites was 30%. Epifaunal cover was generally high for the sites at an intermediate distance from the coast, medium to high for offshore sites and low for coastal sites (Figure 10). The Birkenfels showed the lowest epifaunal growth with 70% uncovered, bare surface. Due to poor visibility conditions, a limited set of features was recognizable from the underwater photography. The main taxa that were identifiable were: *Tubularia* spp. (a mixture of *T. indivisa* and *T. larynx*), *Sagartia* sp., *Asterias rubens*, *Metridium senile* and *Diadumene cincta* (Figure 10). Less common taxa identified were: *Actinothoe sphyrodeta*, *Cancer pagurus*, *Dendronotus frondosus*, *Diplosoma*

Table 5. BIO-ENV results from double square root-transformed cover data. Bray-Curtis similarity was used for biotic data and Euclidean distance for normalized abiotic data. Correlation based on spearman rank coefficient. Combination with maximal five factors are showed. Significance test was calculated based on 999, 499 and 199 random permutations of sample names for 1-2, 3 and 4-5 variables, respectively. See text for parameter abbreviations.

# variable	Correlation	Variables	Permutation test sign.
1	0.393	Depth	1%
1	0.379	TSM-1	1%
1	0.364	S1	1%
1	0.343	C100-75	1%
1	0.329	C50-25	1%
2	0.397	TSM-1, Depth	1%
3	0.398	S1, Depth, C100-75	1%
4	0.401	S1, Depth, Sec, C100-75	1%
5	0.401	Tmax, S1, Depth, Sec, C100-75	1%

sp., unidentified Porifera, *Haliclona* sp., *Jassa* tubes, *Nassarius* sp., *Necora puber*, *Nemertesia antennina*, *Ophiothrix fragilis*, *Pagurus* sp., *Pomatoceros triqueter*, *Sycon* sp. and *Urticina felina*. No macroalgae were recorded. Coastal shipwrecks had 52% of their surface covered by *M. senile* and 29% covered by a mixture of *T. indivisa* - *T. larynx* - *J. herdmani* (if excluding bare surface). The other sites were on average covered at 81% by *T. indivisa* - *J. herdmani*.

A multivariate analysis of the data on coverage is presented in figure 11. The two first axis of the Principal Component Analysis explained 64% of the total variance of the cover matrix. The third one explained 8%. The first axis was strongly correlated with the abundance/coverage of *Tubularia* spp. (contribution of 50%) and *Metridium senile* (43%). The second axis was mainly a function of the recorded density/coverage of *M. senile* (30%), *Asterias rubens* (26%), *Sagartia* sp. (15%), *Tubularia* spp. (15%) and *Diadumene cincta* (12%). The third axis was correlated with the abundance/coverage of *D. cincta* (46%), *Sagartia* sp. (20%) and *Tubularia* spp. (15%). The Callisto, Garden city, Duc de Normandie, John Mahn and Kilmore were characterized by a dominance of *Tubularia* spp., which was generally associated with *D. cincta*. The Birkenfels was closely associated with this group even if some of the quadrats showed a very low cover of *Tubularia* spp. On the offshore sites (Garden City, Birkenfels, Callisto), *Sagartia* sp. were well represented together with *D. cincta*. The LST 420, LCT 457 and Bourrasque were less dominated by *Tubularia* spp. *Metridim senile* was the dominant taxa on Bourrasque and LST 420. This species was also well represented on Duc de Normandie and LCT 457 but were here not the dominant feature. The LCT457 was particular in having equal proportions of *Tubularia* spp. and *M. senile*. These findings were confirmed by the ANOSIM and SIMPER tests.

Table 5 presents the results of the BIO-ENV analysis. Depth was the best single correlated factor ($r=0.393$). Other factors could however explain the observed variation in the biotic dataset with almost the same accuracy (total suspended matter for January-February, salinity for January, current velocity proportion between 1 and 0.75 $m.s^{-1}$ and current velocity proportion between 0.50 and 0.25 $m.s^{-1}$). The addition of other factors only slightly improved the correlation.

4. DISCUSSION

4.1. Sampling techniques

The complementary sampling techniques allowed estimating the general cover of the communities by site and describing the differences encountered in their cryptic fauna. The collection of epibenthic samples by scraping has been previously used in several studies (Migne *et al.* 1997, Guichard *et al.* 1998, Badalamenti *et al.* 2002). Being cost- and time-consuming, it remains an unavoidable method of obtaining quantitative data on epifaunal assemblages of hard structures.

Quantitative sampling in an area dominated by *Tubularia* spp. was relatively easy to implement for the major part of the fauna. Most of the species stayed in close contact to the tubulariids, preventing them to be washed away by currents. However, the encrusting fauna was not easily sampled, especially the calcareous species (like the tube-worms *Pomatoceros triqueter* and *Sabellaria spinulosa* and the barnacle *Balanus crenatus*) which form a crust difficult to manually scrape. Also, it was observed that a large amount of encrusting sponges (mainly *Halichondria panicea*) was present between these calcareous species and we were unable to sample them quantitatively. As a consequence, the values of biomass noted for these species have to be considered as minimal if not underestimated.

The general limited visibility conditions on the sites (3 to 5 m at the shipwreck depth for the period under study) and to the cryptic nature of most of the fauna caused the relatively low resolution of the photographic material.

4.2. Environmental factors

The BPNS can be effectively divided into three distinctive areas according to their environmental conditions: (1) a coastal zone characterized by shallow-waters, a high suspended matter load, reduced current speed and a freshwater influence, (2) a transition zone with intermediate depths, turbidity values and the strongest currents, (3) an offshore zone with deeper waters, lowest turbidity and high current speed. Epifaunal communities can be affected by all or part of these parameters independently. Their possible effects are discussed here under.

4.3. The *Metridium senile* community

The *Metridium senile* community dominated the coastal shipwrecks while it was at most present or poorly developed on intermediate sites and almost absent on offshore sites. On sites where *M. senile* was less abundant, it was mostly found on overhangs or on vertical surfaces with some protection from the prevailing currents. The sites where this species was most dominant were those which were in the shallower waters (LST420, Bourrasque and LCT457). They experience a decreased salinity during some period of the year. In Helgoland, *M. senile* together with *Pomatoceros triqueter* was largely represented on shallow natural hard substrates where light was sufficiently attenuated to prevent algae growth (Kluijver 1991). It was also only dominating on vertical cliffs. It was noted by divers that shipwrecks lying at 2 nautical miles from the Monterey Bay coast (California, USA) were covered with *Metridium farcimen* at a depth of 95 m and Whomersley *et al.* (2003) pointed at the dominance of *M. senile* up to depths of 140 m on offshore platforms in the North Sea. *M. senile* might prefer relatively shallow waters because of the higher production or because the hydrodynamic regime or physical environment is favourable to that species. Maybe in this environment *M. senile* finds an adaptive advantage to *Tubularia* spp., its direct competitors. The prey capture by *M. senile* is a function of both flow regime and body size (Anthony *et al.* 1995). The flux of the seston, rather than a high concentration seems to be important for the growth of *M. senile* (Lesser *et al.* 1994). However, we note that the current velocities observed on the coastal sites were lower compared to further offshore and that these waters had a high load of particulate matter. It may be that the flux of the material was above the upper limit for efficient capture in the intermediate and offshore sites.

One hypothesis explaining the success of *M. senile* in shallow-waters could be its better resistance to major climatic events. During winter time, the shallow-water sites are under the regular influence of storms (Houthuys *et al.* 1994, Posey *et al.* 1996). In deeper waters, the influence of strong winds is decreased by a diminished wave action. Hughes (1983) claimed that the detachment of *T. indivisa* was unlikely to be a significant source of mortality unless such detachment was hastened by the growth of other animals like barnacles. Barnacles (*Balanus crenatus*) were noted to be a conspicuous element of the coastal shipwrecks only. The combined effect of increased influence of storms and the abundance of *B. crenatus* in coastal waters could lead to an increased rate of winter mortality for *T. indivisa* through dislodgment. After the removal of *T. indivisa*, the bare surface may be easily colonized by *M. senile* because its asexual reproduction by pedal laceration and its capability of oriented locomotion make it a very strong competitor for space (Anthony *et al.* 1995). Further, the gamete production of *T.*

indivisa in winter is very low and not capable of fast colonization of bare spaces (Hughes 1983).

4.4. The *Tubularia* spp. community

Tubularia indivisa composed the bulk of the cover and biomass on intermediate and offshore sites, while a mixture of *T. indivisa* and *T. larynx* occurred on the coastal sites. These species are common on many waters around the world (Pyefinch *et al.* 1949, Schmidt 1983, Foster *et al.* 1994, Lemire *et al.* 1996, Orlov 1996, Steimle *et al.* 2000, Collins *et al.* 2002), but they are rarely said to be the dominant feature of a community. On the shipwrecks located a few hundreds of km north of our study sites, *T. larynx* was present only at an early colonization stage on a recent sunken vessel (Leewis *et al.* 2000) and *T. indivisa* was not covering large surfaces (van Moorsel *et al.* 1991). In UK waters, *T. indivisa* was found on circalittoral rocky habitats and could have a large cover on sounds, narrows and around tide-swept promontories in accelerated tidal streams in association with *Balanus crenatus* and *Alcyonium digitatum* (Doody *et al.* 1993). *Tubularia indivisa* was replacing *M. senile* and became dominant on UK shipwrecks where tidal currents were strong (Connor *et al.* 2004). *Tubularia* species have a chitinous cylindrical perisarc of up to 10 cm and this surface is used by a variety of epibionts. In terms of abundance (up to 180,000 ind.m^{-2}) and biomass (173 g AFDW.m^{-2}), the amphipod *Jassa herdmani* was the most common of these epibionts. Caprellids (*Caprella tuberculata* and *Phtisica marina*) were also abundant (up to 1,700 ind.m^{-2} and 9,360 ind.m^{-2}, respectively). Gili *et al.* (1996) found that *T. larynx* fed mainly on copepods, nauplii larvae and crustaceans eggs and that their prey size could reach 3 mm. Genzano (2005) studied the trophic ecology of *Tubularia crocea* and found that juveniles of *Jassa falcata* and caprellids were among its most abundant prey items. He noted that these two species were known to live in close association to the perisarc of the hydroid. The *Tubularia* species could well benefit of the large abundance of these amphipod species in its diet while in turn, the amphipods see their surface of attachment largely increased by the presence of *Tubularia* spp. However, Ostman *et al.* (1995) performed prey-capturing experiments on *T. larynx* revealing that crustaceans like *Monocorophium* sp. and caprellids were not taken by the polypes while Artemia nauplii and small planktonic crustaceans were fed upon.

4.5. Biomass on shipwrecks

The mean epifauna biomass of the nine Belgian shipwrecks was estimated at 288 g AFDW.m^{-2}. On shipwrecks in the Dutch sector of the North Sea, Leewis *et al.* (2000) found a mean biomass value of 642 g AFDW.m^{-2}. Many of their samples were taken in a *M. senile* assemblage which was only one of the discerned assemblages in their study. In Leewis' study, the average biomass of that community was 1,072 g AFDW.m^{-2} and it was the highest observed on Dutch shipwrecks. That value is comparable to the mean biomass value of 1,243 g AFDW.m^{-2} (N=14, unpublished data we recorded for the *M. senile* assemblages).

In the Oosterschelde, a marine bay with reduced tidal influence, mean epifauna biomass on a rocky seabed was estimated to be 286 g AFDW.m^{-2} (Leewis *et al.* 1994). On pebbles in the Dover Strait, Migne *et al.* (1997) measured a mean value of 281 g AFDW.m^{-2}.

Our biomass values are among the highest recorded values for epibenthic communities in temperate waters. Kuhne *et al.* (1996) recorded 30-180 g AFDW.m^{-2} for the macrofauna of a stony sand area in the German Bight of the North Sea. The dry weight of the macrofauna of hard substrates in the Bristol Channel was found to be 24.5 g.m^{-2} (dry weight) (George *et al.* 1985). Steimle (1985) also reported a lower (wet weight) value of 238 g.m^{-2} for the macrofauna in the New York Bight. In comparison, the literature values for the macrofauna of soft sediments in the Southern North Sea were around 10 g AFDW.m^{-2} (Duineveld *et al.* 1991, Heip *et al.* 1992) and around 30-50 g AFDW.m^{-2} for the *Abra alba* community (Prygiel *et al.* 1988). This highlights that even if the surface covered by shipwrecks is a very small percentage of the BPNS, they may concentrate locally a significant part of the biomass. No macroalgae were collected on the nine shipwrecks, suggesting that they were located below the compensation point for photosynthesis or that the high turbidity conditions and sand scouring would create a significant abrasion preventing their development. However, it may be possible to find encrusting red algae in such low light conditions as it is observed in the Dover Strait (Dewarumez, pers. com.). Considering the strong competition for space with barnacles, tube building annelids and tubulariids, the grazing effects of the echinid *Psammechinus miliaris* which was found in large densities on shipwrecks and the low growth rate of the encrusting red algae, it may be that these species were outcompeted in shipwrecks.

4.6. Spatial variability

Coastal sites showed a clear pattern of decreased species richness compared to the sites located further from the coast. However, species richness was not significantly different between the intermediate and offshore sites. Multivariate analysis refined the clustering of the sites by separating the coastal, intermediate and offshore sites. The primary difference on coastal and other sites was due to the dominance of *T. larynx* which replaced *T. indivisa*. The biomass of *T. indivisa* was lower on the offshore sites than on intermediate sites. This could be explained by the lower productivity of these zones linked to a decrease in suspended sediments and productivity (our results and Fettweis *et al.* 2003). The fauna of the Duc de Normandie was distinctive from intermediate sites because of a lower biomass of *T. indivisa*. The other constituents of its epifauna were however not different. Another source of variability in local epibenthic communities could find its origin in the nature of the water masses. Channel water is under the influence of the Atlantic waters and penetrates into the Southern North Sea through the English Channel. The physical, chemical and biological composition of these water masses are different from those of coastal systems (Otto *et al.* 2006). M'harzi *et al.* (1998) showed that the zooplankton composition from the Belgian offshore waters differed significantly from the coastal waters, suggesting that the larvae supply could differ between these two areas.

One of the most ecologically important gradient is the cross-shore gradient on the coastal area. In this area, environmental factors can drastically change at the scale of a few km with strong repercussions on community structure. On the BPNS, Govaere *et al.* (1980) distinguished three macrobenthic zones: a coastal zone with a set of species and abundance poor communities, a species and abundance rich transition zone and a species rich – abundance poor open sea zone. This pattern was not confirmed by the more recent and larger study of Van Hoey *et al.* (2004, 2005) who discerned an association of species rich and poor assemblages on the coastal zone and species poor offshore. The coastal sites in our results are characterized by the dominance of species poor community, while intermediate and offshore sites are richer. For the epifauna, the high productivity and high turbidity of the coastal zone do not allow for the development of species rich community, maybe because the disturbance introduced by the turbidity variable is very high and only permit the development of a limited set of species (i.e. *M. senile*).

The analysis of indicator species revealed that a large number of species were typical of shipwrecks in general. It showed that no taxa were exclusively indicative of some of the groupings, but that some taxa were more common or have a higher biomass at some locations in the BPNS.

Among these common taxa, many were carnivorous polychaetes (*Harmothoe* spp., *Lepidonotus squamatus*, *Phyllodoce mucosa*, *Eulalia viridis* and *Syllis gracilis*) certainly feeding on the large amount of available amphipods (Wolff 1973, Fauchald *et al.* 1979). Some filter feeding crustaceans were very common on shipwrecks: *Jassa herdmani*, *Monocorophium sextonae*, *Stenothoe marina*, *Stenothoe monoculoides*, *Metopa alderi*, *Phtisica marina*, *Caprella tuberculata* and *Pisidia longicornis*. All are probably adapted to a filter feeding mode of nutrition. The latter species, an anomuran, was found in large densities on pebbles in the Dover Strait (Carpentier *et al.* 2005) and could initially have colonized the shipwrecks on the BPNS. However, all these amphipod populations contained carrying eggs females, suggesting that the shipwreck populations are probably self sustaining or at least linked to each other through dispersal of larvae or juveniles.

The most indicative species of the offshore sites were *Aequipecten opercularis* and *Pomatoceros triqueter*. van Moorsel *et al.* (1991) also reported this species to be typical for offshore Dutch shipwrecks. *Aequipecten opercularis* was present as juveniles (shell of less than 15 mm) at rather high densities (mean value: 120 ind.m^{-2}). They use the perisarc of *Tubularia* spp. as an attachment site before leaving that hard substrate to start their benthic life. Actinarians (mainly represented by *Diadumene cincta*) and *Ophiothrix fragilis* were also more abundant on these sites. The mean density of the ophiuroid was 900 ind.m^{-2} with a maximum value of 3,650 ind.m^{-2} for one sample. Similar to the Mediterranean Sea (Turon *et al.* 2000), we observed a massive recruitment of juvenile *O. fragilis* on sponges. The young recruits (less than 1 mm in disc diameter) are intimately packed on the sponges. This behaviour is seen as a trophic association as *O. fragilis* takes advantage of the inhalant currents created by the sponges (Turon *et al.* 2000). *O. fragilis* is abundantly represented on the pebble areas of the deeper waters in the English Channel (Ellis *et al.* 2000) where suitable hydrodynamic conditions are met for the formation of large beds (tidal currents 10-25 cm.s^{-1} and low sedimentation rates) (Davoult 1990, Ellis *et al.* 2000). This species is known to have a gregarious behaviour (Broom 1975). It is possible that exchange with the dense population of the Dover Strait will occur. Simulation of larvae dispersal support this (Lefebvre *et al.* 2003). Populations of *O. fragilis* on Belgian shipwrecks may form an extension of the Dover Strait populations. For this species, the shipwrecks provide a recruitment surface for the juveniles, an anchorage area in the *Tubularia* spp. and favourable hydrodynamic conditions on the elevated ground.

On intermediate sites, only two species (*Dendronotus frondosus* and *Sycon ciliatum*) were typical. *D. frondosus* is a predator of *T. indivisa* (Thompson *et al.* 1976, Hughes 1983). Except for *T. larynx*, the coastal sites shared a single characteristic species: the tube building amphipod *Monocorophium acherusicum*. At the individual site level, it was a set of species with a superior level of biomass which identified the community and few species were entirely indicative of a particular location. An exception was the nudibranch *Catriona gymnota* which was observed on all samples of a single site (Bourrasque). It feeds on the stems of *T. indivisa*.

The spatial distribution pattern of some species is difficult to explain. For example, the amphipod *Caprella tuberculata* was absent from coastal sites but occurred in large numbers on the intermediate and offshore sites (average density: 3,219 ind.m^{-2}). However, on one site (John Mahn), it was found in only very low abundance (21 ind.m^{-2}) and it was absent from the LCT457. Both sites were only 16 km on the east of the Kilmore where the average density of *C. tuberculata* reached 22,677 ind.m^{-2}. One cannot exclude that the samples were taken on these intermediate sites on locations that did not favour the development of this particular species. The orientation of the shipwrecks versus the dominant direction of the water current could account for this. Another possible reason could be small scale changes in environmental parameters that do not allow for its recruitment. Caprellid species are known to be susceptible to tributyltin (TBT) exposures (Ohji *et al.* 2003a, Ohji *et al.* 2003b, Ohji *et al.* 2004). The embryo survival rate of caprellids can decline in concentration of TBT as low as what is known for the water column of the Scheldt Estuary (1-20 ng.l^{-1}, Monteyne, pers. com.). The LCT457 and John Mahn are located on the east of the anchorage area where ships wait for pilots. The residual currents run to the east of this anchorage area and the LCT 457 and John Mahn could receive increased concentrations of TBT. However, if TBT was the reason for the low density of *C. tuberculata* on these two sites, it is surprising that the Duc de Normandie, which is located in the anchorage zone, would not have been affected. Further analysis of TBT in individuals and water column would be needed to evaluate this effect. The low density of *C. tuberculata* could also originate from a low larval supply for these sites. However, it is highly unlikely that specific current patterns may prevent its dispersal to these sites since the distribution of a greater number of species would then need to be affected.

Sites located very close to each other showed nonetheless differences in their epifaunal communities. The Birkenfels and Callisto are less than three nautical miles apart while the densities of many shared taxa differed and

43% of the taxa were present in only one of the two sites. Neither wreck age, substrate type or different abiotic factors can explain this. Possibly, samples could have been collected on surfaces that favoured or excluded the occurrence of some species. Maybe the number of samples was insufficient for correctly estimating the alpha diversity. The most plausible explanation lies in the orientation and/or configuration of the shipwrecks towards the dominant current direction. The Birkenfels orientation was almost perpendicular to the dominant currents while the orientation of the Callisto differs by 35° with the Birkenfels. This may alter the settlement, recruitment and dispersion of some species as well as the sedimentation rate and seston flux (Baynes *et al.* 1989).

Acknowledgements

The authors wish to thank the crews of the RV Zeeleeuw and RV Belgica for their help during the sampling campaigns and to Céline Delforge for the great help during the sorting process. It's also our pleasure to thank all the people who helped collecting the samples: Drs Y. Laitat, A. Simon, D. Delbare, E. Vanden Bergh, T. Schils, Mss C. Delforge and R. Gyssens and Mrs P.B. Demoulin, G. Rooms, D. Marsham, F. Cray, M. Van Espen, Y. Verkemping, M. Backx, J.P. De Blauwe, J. Haelters, F. Hernandez, F. Darchambeau, G. Van Hoydonck, A. Vanhaelen, R. Knuts & P. Van de Steen. UGent (G. de Smet and M. Steyaert) helped for the pigment analysis. We thank also Dr. A. Cattrijsse for his careful reading of an early version of the manuscript. This study has been financially supported by a 'plan Action II' grant (contract N° WI/36/C04) from the Belgian Science Policy. The second author is grateful to MUMM BMDC for data, REMSEM group for the availability of satellite data and Model groups for model results availability. His participation to this study has been funded by BEWREMABI project (Belgian Science Policy).

REFERENCES

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32-46

Anthony KRN , Svane Ib (1995) Effects of substratum instability on locomotion and pedal laceration in *Metridium senile* (Anthozoa: Actiniaria). Mar Ecol Prog Ser 124:171-180

Bacchiocchi F , Airoldi L (2003) Distribtution and dynamics of epibiota on hard structures for coastal protection. Est Coast Shelf Sci 56:1157-1166

Badalamenti F, Chemello R, D'Anna G, Ramos PH, Riggio S (2002) Are artificial reefs comparable to neighbouring natural rocky areas? A mollusc case study in the Gulf of Castellammare (NW Sicily). ICES J Mar Sci 59:S127-S131

Baynes TW , Szmant AM (1989) Effects of current on the sessile benthic community structure of an artificial reef. Bull Mar Sci 44:545-566

Bray JR , Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. Ecol Monogr 27:325-349

Brey T (1986) Formalin and formaldehyde-depot chemicals: effects on dry weight and ash free dry weight of two marine bivalve species. Meeresforsch 31:52-57

Broom DM (1975) Aggregation behaviour of the brittle-star *Ophiothrix fragilis*. J Mar Biol Ass UK 55:191-197

Bulloch DK (1965) The development of the wreck *Pinta* as a marine habitat. Underw Nat Bull Am Littoral Soc 31:17-32

Carpentier A, Vaz S, Martin CS, Coppin F, Dauvin J-C, Desroy N, Dewarumez JM, Eastwood PD, Ernande B, Harrop S, Kemp Z, Koubbi P, Leader-Williams N, Lefèbvre A, Lemoine N, Loots C, Meaden GJ, Ryan N, Walkey M (2005) Eastern Channel habitat atlas for marine resource management (CHARM). Interreg IIIA

Carr MH , Hixon MA (1997) Artificial reefs: the importance of comparisons with natural reefs. Fisheries 22:28-33

Clarke KR (1999) Nonmetric multivariate analysis in community-level ecotoxicology. Environ Toxicol Chem 18:118-127

Clarke KR , Warwick RM (1998) A taxonomic distinctness index and its statistical properties. J Appl Ecol 35:523-531

Clarke KR , Warwick RM (2001a) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Mar Ecol Prog Ser 216:265-278

Clarke KR, Warwick RM (2001b) Change in marine communities: an approach to statistical analysis and interpretation. 2nd edition. PRIMER-E, Plymouth, UK

Collins KJ, Jensen AC, Mallinson JJ, Roenelle V, Smith IP (2002) Environmental impact assessment of a scrap tyre artificial reef. ICES J Mar Sci 59:S243-S249

Connell SD (2000) Floating pontoons create novel habitats for subtidal epibiota. J Exp Mar Biol Ecol 247:183-194

Connell SD (2001) Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. Mar Environ Res 52:115-125

Connell SD , Glasby TM (1999) Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. Mar Environ Res 47:373-388

Connor DW, Allen JH, Golding N, Howell KL, Lieberknecht LM, Northen KO, Reker JB (2004) The marine habitat classification for Britain and Ireland, Version 04.05, Circalittoral rock section. Joint Nature Conservation Commitee, Peterborough, UK

Costello MJ, Emblow CS, White R (2001) European Register of Marine Species. A check-list of the marine species in Europe and a bibliography of guides to their identification. Patrimoines naturels 50:1-463

Cripps SJ , Aabel JP (2002) Environmental and socio-economic impact assessment of Ekoreef, a multiple platform rigs-to-reefs development. ICES J Mar Sci 59:S300-S308

Cusson M , Bourget E (2005) Global pattern of macroinvertebrate production in marine benthic habitat. Mar Ecol Prog Ser 297:1-14

Davoult D (1990) Biofaciès et structure trophique du peuplement des cailloutis du Pas-de-Calais (France). Oceanol Acta 13:335-348

Degraer S, Vincx M, Meire P, Offringa H (1999) The macrozoobenthos of an important wintering area of the common scoter (*Melanitta nigra*). J Mar Biol Ass UK 79:243-251

Doody JP, Johnston C, Smith B (1993) Directory of the North Sea coastal margin. Joint Nature Conservation Committee, Peterborough, UK

Dufrêne M , Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345-366

Duineveld G, Kunitzer A, Niermann U, Dewilde PAWJ, Gray JS (1991) The macrobenthos of the North Sea. Neth J Sea Res 28:53-65

Ellis JR , Rogers SI (2000) The distribution, relative abundance and diversity of echinoderms in the eastern English Channel, Bristol Channel, and Irish Sea. J Mar Biol Ass UK 80:127-138

Fabi G, Grati F, Lucchetti A, Trovarelli L (2002) Evolution of the fish assemblage around a gas platform in the northern Adriatic Sea. ICES J Mar Sci 59:S309-S315

Fabi G, Grati F, Puletti M, Scarcella G (2004) Effects on fish community induced by installation of two gas platforms in the Adriatic Sea. Mar Ecol Prog Ser 273:187-197

Fauchald K , Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193-284

Fettweis M , Van den Eynde D (2003) The mud deposits and the high turbidity in the Belgian-Dutch coastal zone, southern bight of the North Sea. Cont Shelf Res 23:669-691

Forteath GNR, Picken GB, Ralph R, Williams J (1982) Marine growth studies on the North Sea oil platform Montrose Alpha. Mar Ecol Prog Ser 8:61-68

Foster KL, Steimle FW, Muir WC, Kropp RK, Conlin BE (1994) Mitigation potential of habitat replacement - concrete artificial reef in Delaware Bay - preliminary results. Bull Mar Sci 55:783-795

Galéron J, Sibuet M, Mahaut M-L, Dinet A (2000) Variation in structure and biomass of the benthic communities at three contrasting sites in the tropical Northeast Atlantic. Mar Ecol Prog Ser 197:121-137

Gaston GR, Bartlett JHW, McAllister AP, Heard RW (1996) Biomass variations of estuarine macrobenthos preserved in ethanol and formalin. Estuaries 19:674-679

Genzano GN (2005) Trophic ecology of a benthic intertidal hydroid, *Tubularia crocea*, at Mar del Plata, Argentina. J Mar Biol Ass UK 85:307-312

George CL , Warwick RM (1985) Annual macrofauna production in a hard-bottom reef community. J Mar Biol Ass UK 65:713-735

Gili JM, Hughes RG, Alva V (1996) A quantitative study of feeding by the hydroid *Tubularia larynx* Ellis and Solander, 1786. Sci Mar 60:43-54

Glasby TM (2001) Development of sessile marine assemblages on fixed versus moving substrata. Mar Ecol Prog Ser 215:37-47

Glasby TM , Connell SD (1999) Urban structures as marine habitats. Ambio 28:595-598

Govaere JCR, Van Damme D, Heip C, De Coninck LAP (1980) Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring. Helgolander Wissenschaftliche Meeresuntersuchungen 33:507-521

Guichard F , Bourget E (1998) Topographic heterogeneity, hydrodynamics, and benthic community structure: a scale-dependent cascade. Mar Ecol Prog Ser 171:59-70

Heip C, Basford D, Craeymeersch JA, Dewarumez JM, Dorjes J, Dewilde P, Duineveld G, Eleftheriou A, Herman PMJ, Niermann U, Kingston P, Kunitzer A, Rachor E, Rumohr H, Soetaert K, Soltwedel T (1992) Trends in biomass, density and diversity of North Sea macrofauna. ICES J Mar Res 49:13-22

Hiscock K (1980) Marine life on the wreck of the M.V. 'Robert'. Report of the Lundy Field Society 32:40-44

Holloway MG , Connell SD (2002) Why do floating structures create novel habitats for subtidal epibiota? Mar Ecol Prog Ser 235:43-52

Houthuys R, Trentesaux A, De Wolf P (1994) Storm influences on a tidal sandbank's surface (Middelkerke Bank, southern North Sea). Mar Geol 121:23-41

Hughes RG (1983) The life-history of *Tubularia indivisa* (Hydrozoa: Tubulariidae) with observations on the status of *T. ceratogyne*. J Mar Biol Ass UK 63:467-479

Jorgensen T, Lokkeborg S, Soldal AV (2002) Residence of fish in the vicinity of a decommissioned oil platform in the North Sea. ICES J Mar Sci 59:S288-S293

Keuls M (1952) The use of the studentized range in connection with an analysis of variance. Euphytica 1:112-122

Kluijver M (1991) Sublittoral hard substrate communities off Helgoland. Helgol Meeresunters 45:317-344

Knott NA, Underwood AJ, Chapman MG, Glasby TM (2004) Epibiota on vertical and on horizontal surfaces on natural reefs and on artificial structures. J Mar Biol Ass UK 84:1117-1130

Kohler NE , Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Comput Geosci 32:1259-1269

Kruskal JB, Wish M (1978) Multidimensional scaling. Sage University Paper series on Quantitative Applications in the Social Sciences n°11. Sage Publications, Beverly Hills and London.

Kuhne S , Rachor E (1996) The macrofauna of a stony sand area in the German Bight (North Sea). Helgol Meeresunters 50:433-452

Lanckneus J, van Lancker V, Moerkerke G, Van den Eynde D, Fettweis M, de Batist M, Jacobs P (2001) Investigation of the natural sand transport on the Belgian continental shelf (BUDGET). Final report. Federal Office for Scientific, Technical and Cultural Affairs (OSTC)

Larsonneur C, Bouysse P, Auffret J-P (1982) The superficial sediments of the English Channel and its Western Approaches. Sedimentology 29:851-864

Leewis RJ, van Moorsel GWNM, Waardenburg HW (2000) Shipwrecks on the Dutch Continental Shelf as artificial reefs. In: Jensen AC, Collins KJ, Lockwood APM (eds) Artificial reefs in European Seas. Kluwer Academic Publishers, Dordrecht, p 419-434

Leewis RJ, Waardenburg HW, Vandertol MWM (1994) Biomass and standing stock on sublittoral hard substrates in the Oosterschelde estuary (SW Netherlands). Hydrobiologia 283:397-412

Lefebvre A, Ellien C, Davoult D, Thie E, Salomon JC (2003) Pelagic dispersal of the brittle-star *Ophiothrix fragilis* larvae in a megatidal area (English Channel, France) examined using an advection/diffusion model. Est Coast Shelf Sci 57:421-433

Lemire M , Bourget E (1996) Subatratum heterogeneity and complexity influence micro-habitat selection of *Balanus sp* and *Tubularia crocea* larvae. Mar Ecol Prog Ser 135:77-87

Lesser MP, Witman JD, Sebens KP (1994) Effects of flow and seston availability on scope for growth of benthic suspension-feeding invertebrates from the Gulf of Maine. Biol Bull 187:319-335

Lokkeborg S, Humborstad OB, Jorgensen T, Soldal AV (2002) Spatio-temporal variations in gillnet catch rates in the vicinity of North Sea oil platforms. ICES J Mar Sci 59:S294-S299

Love MS (2005) More fun than working for a living - Tales of 10 years of research on the fishes of California oil platforms. Proceedings of 8th International Conference on Artificial Reefs and Artificial Habitats, Biloxi, USA, p 3

Luyten PJ, Jones JE, Proctor R, Tabor A, Tette P, Wild-Allen K (1999) COHERENS – A coupled Hydrodynamic-Ecological model for regional and shelf seas. Users documentation. Report, Management Unit of the Mathematical Models of the North Sea, Brussels

M'harzi A, Tackx M, Daro MH, Kesaulia I, Caturao R, Podoor N (1998) Winter distribution of phytoplankton and zooplankton around some sandbanks of the Belgian coastal zone. J Plankton Res 20:2031-2052

Magurran AE (2004) Measuring biological diversity. Blackwell Science Ltd, Oxford, UK

Massin Cl, Norro A, Mallefet J (2002) Biodiversity of a wreck from the Belgian Continental Shelf: monitoring using scientific diving. Preliminay results. Bull Inst r Sci nat Belg 72:67-72

Migne A , Davoult D (1997) Quantitative distribution of benthic macrofauna of the Dover Strait pebble community (Eastern English channel, France). Oceanol Acta 20:453-460

Nechad B, De Cauwer V, Park Y, Ruddick K (2003) Suspended Particulate Matter (SPM) mapping from MERIS imagery. Calibration of a regional algorithm for the Belgian coastal waters. MERIS user workshop, 10-13th November 2003 . (Frascati). European Space Agency SP549

Ohji M, Arai T, Miyazaki N (2003a) Biological effects of tributyltin exposure on the caprellid amphipod, *Caprella danilevskii*. J Mar Biol Ass UK 83:111-117

Ohji M, Arai T, Miyazaki N (2003b) Timing of sex disturbance caused by tributyltin exposure during the embryonic stage in the caprellid amphipod, *Caprella danilevskii*. J Mar Biol Ass UK 83:943-944

Ohji M, Aral T, Miyazaki N (2004) Effects of tributyltin on the survival in the caprellid amphipod *Caprella danilevskii*. J Mar Biol Ass UK 84:345-349

Orlov (1996) Biology of the White Sea hydrozoan *Tubularia indivisa* (Hydrozoa, Athecata). Zool Zh 75:1294-1303

Ostman C, Myrdal M, Nyvall P, Lindstrom J, Bjorklund M, Aguirre A (1995) Nematocysts in *Tubularia Larynx* (Cnidaria, Hydrozoa) from Scandinavia and the Northern Coast of Spain. Sci Mar 59:165-179

Otto L, Zimmermann JTF, Furnes GH, Mork M, Saetre R, Beccker G (2006) Review of the physical oceanography of the north sea. Neth J Sea Res 26:161-238

Pakhomov EA (2003) Correction of zooplankton and benthos biomass under-estimations from formaldehyde-preserved samples. Arch Fish Mar Res 50:141-148

Picken G (1986) Moray Firth fouling communities. P Roy Soc Edinburgh B 91:213-220

Picken G, Baine M, Heaps L, Side J (2000) Rigs to reefs in the North Sea. In: Jensen AC, Collins KJ, Lockwood APM (eds) Aritificial reefs in European Seas. Kluwer Academic Publisher, Dordrecht, p 331-342

Pison V, Ozer J (2003) Operational products and services for the Belgian coastal waters. In: Dalhin H, Flemings NC, Nittis K, Petersson SE (eds) Building the European capacity in operational oceanography. Proceedings of the Third International Conference on EuroGOOS. Elsevier Oceanography, series 69, p 503-509

Ponti M, Abbiati M, Ceccherelli VU (2002) Drilling platforms as artificial reefs: distribution of macrobenthic assemblages of the "Paguro" wreck (northern Adriatic Sea). ICES J Mar Sci 59:S316-S323

Posey M, Lindberg W, Alphin T, Vose F (1996) Influence of storm disturbance on an offshore benthic community. Bull Mar Sci 59:523-529

Prygiel J, Davoult D, Dewarumez JM, Glaçon R, Richard A (1988) Description et richesse des peuplements benthiques de la partie française de la Mer du Nord. Compt Rendus Acad Sci III Sci Vie 306:5-10

Pyefinch KA , Downing FS (1949) Notes on the general biology of *Tubularia larynx* Ellis & Solander. J Mar Biol Ass UK 28:21-44

Relini G, Tixi F, Relini M, Torchia G (1998) The macrofouling on offshore platforms at Ravenna. Int Biodeterior Biodegrad 41:41-55

Ricciardi A , Bourget E (1998) Weight-to-weight conversion factors for marine benthic macroinvertebrates. Mar Ecol Prog Ser 163:245-251

Rumohr H, Brey T, Ankar S (1987) A compilation of biometric conversion factor for benthic invertebrates of Baltic Sea. Balt Mar Biol Publ 9:1-56

Scarborough Bull A , Kendall J (1994) An indication of the process - offshore platforms as artificial reefs in the Gulf of Mexico. Bull Mar Sci 55:1086-1098

Schmidt GH (1983) The hydroid *Tubularia larynx* causing 'bloom' of the ascidians *Ciona intestinalis* and *Ascidiella aspersa*. Mar Ecol Prog Ser 12:103-105

Shapiro SS , Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52:591-611

Smith SDA , Rule MJ (2002) Artificial substrata in a shallow sublittoral habitat: do they adequately represent natural habitats or the local species pool? J Exp Mar Biol Ecol 277:25-41

Soldal AV, Svellingen I, Jorgensen T, Lokkeborg S (2002) Rigs-to-reefs in the North Sea: hydroacoustic quantification of fish in the vicinity of a "semi-cold" platform. ICES J Mar Sci 59:S281-S287

Stanley DR , Wilson CA (2000) Variation in the density and species composition of fishes associated with three petroleum platforms using dual beam hydroacoustics. Fish Res 47:161-172

Steimle F (1985) Biomass and estimated productivity of the benthic macrofauna in the New York Bight. Est Coast Shelf Sci 21:539-554

Steimle FW , Zetlin C (2000) Reef habitats in the middle Atlantic Bight: abundance, distribution, associated biological communities, and fishery resource use. Mar Fish Rev 62:24-42

Thompson TE, Brown GH (1976) British opistobranch molluscs. Synopses of the British Fauna, No 8, The Linnean Society of London, Academic Press, London

Turon X, Codina M, Tarjuelo I, Uriz MJ (2000) Mass recruitment of *Ophiothrix fragilis* (Ophiuroidea) on sponges: settlement patterns and post-settlement dynamics. Mar Ecol Prog Ser 2000:201-212

Van Hoey G, Degraer S, Vincx M (2004) Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. Est Coast Shelf Sci 59:599-613

Van Hoey G, Vincx M, Degraer S (2005) Small- to large-scale geographical patterns within the macrobenthic Abra alba community. Est Coast Shelf Sci 64:751-763

van Moorsel GWNM, Waardenburg HW, van der Horst J (1991) Het leven op en rond scheepswrakken en andere harde substraten in de Noordzee (1986 T/M 1990) - een synthese. Rapport 91.19, Bureau Waardenburg bv, Culemborg

Wetzel MA, Leuchs H, Koop JHE (2005) Preservation effects on wet weight, dry weight, and ash-free dry weight biomass estimates of four common estuarine macro-invertebrates: no difference between ethanol and formalin. Helgol Meeresunters 59:206-213

Whomersley P , Picken GB (2003) Long-term dynamics of fouling communities found on offshore installations in the North Sea. J Mar Biol Ass UK 83:897-901

Wolff WJ (1973) The estuary as a habitat, an analysis of data on the soft bottom macrofauna of the estuarine area of the rivers Rhine, Meuse, and Scheldt. Zool Verh 126:1-242

Wright SW, Jeffrey SW (1997) High-resolution HPLC system for chlorophylls and caretenoids of marine phytoplankton. In: Jeffrey W, Mantoura RFC, Wright SW (eds) Phytoplancton pigments in oceanography: guidelines to modern methods. UNESCO, Paris, p 327-341

Zintzen V, Massin Cl, Norro A, Mallefet J (2006) Epifaunal inventory of two shipwrecks from the Belgian Continental Shelf. Hydrobiologia 555:207-219

ARTICLE 5: THE HYDROID *TUBULARIA INDIVISA* (CNIDARIA, TUBULARIIDAE) PLAYS A STRUCTURAL ROLE ON ARTIFICIAL HABITAT COMMUNITIES

Biodiversity of communities can vary in space and time. The article 4 studied the spatial variation of the shipwreck communities. It also stressed the importance in terms of species richness of a particular assemblage whose key species is a hydrozoan, *Tubularia indivisa*. The shipwrecks located at an intermediate distance from the coast (7-15 nautical miles) were strongly dominated by this species. Indeed, this species covered almost 100% of the surface of the Kilmore, one of these intermediate sites. It was deemed necessary to study the temporal evolution of the biodiversity associated with this species. The sampling schema was first planned on a seasonal basis, but we had to deal with often difficult weather conditions which prevented us to complete all the campaigns successfully.

The specific questions to be answered in this article were:

- What is the temporal evolution of biodiversity and biomass associated with an assemblage dominated by *Tubularia indivisa*?
- Is there a temporal evolution of the assemblage associated with *T. indivisa* on a seasonal and yearly basis?
- To what extend is *T. indivisa* itself responsible for the faunal diversity of these assemblages?
- What could be the environmental variables which are the most responsible for the observed patterns?

TEMPORAL

THE HYDROID *TUBULARIA INDIVISA* (CNIDARIA, TUBULARIIDAE) PLAYS A STRUCTURAL ROLE ON ARTIFICIAL HABITAT COMMUNITIES

Vincent Zintzen[1,2], Alain Norro[3], Claude Massin[1], Jérôme Mallefet[2]

[1] Royal Belgian Institute of Natural Sciences, Rue Vautier 29, B-1000 Brussels, Belgium.
[2] University of Louvain, Biology Laboratory, Kellner Building, place Croix du Sud 3, B-1348 Louvain-la-Neuve, Belgium.
[3] Royal Belgian Institute of Natural Sciences, Management Unit of the North Sea Mathematical Models,100 Gulledelle,1200 Brussels, Belgium.

Corresponding author: Vincent Zintzen
Email: vincent.zintzen@naturalsciences.be
Tel: +32(0)2 627.43.38, Fax: +32(0)2 627.41.41
Royal Belgian Institute of natural Sciences
Rue Vautier, 29
1000 Brussels
Belgium

ABSTRACT

We analyzed the composition, diversity, density and biomass of a temporal series of samples taken in a *Tubularia indivisa* community which dominates a shipwreck in the North Sea waters (N 51°23',730 - E 02°29',790, 17 nautical miles from the coast, 30 m depth). This shipwreck has structures emerging up to 8 m above the seabed. Water temperature ranged from 4.2°C in March to 20.3°C in August. Salinity showed few variations around 33.9 psu. Bottom tidal currents followed a semi-diurnal cycle and were preferentially NE oriented with 84% of them in the range 0.25-0.75 $m.s^{-1}$. Mean value for total suspended matter was 6.2 $mg.l^{-1}$ with large variation at a monthly scale. The species richness varied from 15 in October to 42 in August with a mean value of 33 species per sample. Diversity indices were higher during autumn and winter because of the strong dominance of a few crustacean species. The total density ranged from 6,500 $ind.m^{-2}$ in October to 445,800 $ind.m^{-2}$ in July, most of these individuals being the amphipod *Jassa herdmani*. The biomass of the *T. indivisa* community varied from 9 g $AFDW.m^{-2}$ in October to 1,106 g $AFDW.m^{-2}$ in July, with *T. indivisa* itself constituting between 59 and 82% of the total biomass. The biomass of *T. indivisa* was positively correlated with species richness and density of *J.*

herdmani and negatively correlated with the Shannon-Wiener index and the Simpson index. The number of species associated with *T. indivisa* was generally superior to 55% of the sorted species. Multivariate analysis confirmed the temporal evolution of the community. These findings support the conclusion that shipwrecks in Belgian waters allow for the development of assemblages with high density and biomass which show large monthly variations under an apparent repetitive annual cycle.

KEYWORDS

Tubularia indivisa, temporal variability, shipwrecks, hard substrate, North Sea, biomass, epifauna.

1. INTRODUCTION

Hard substrates in the marine environment are bi-dimensional structures in nature, but a third dimension generally develops through the growth of sessile species. These structural aspects are important factors controlling the subsequent settlement and/or survivorship of species (Dean, 1981). The modification of the colonization pattern following sessile species development can be influenced by an alteration of the flow characteristics (Baynes & Szmant, 1989), the provision of additional surface area (Genzano, 1998), more secure/attractive attachment surfaces (Schmidt, 1983) and refuge from predation (Walters & Wethey, 1996).

Hydroids in general and the species of the genus *Tubularia* in particular are among the first species to colonize bare surfaces (Dean & Hurd, 1980). *Tubularia* species are described as pioneer because they are one of the first settler on newly available hard substrate and are short-lived (Hughes, 1983). They are often found on recently submerged substrata (Bulloch, 1965; Forteath *et al.*, 1982; Woodhead & Jacobson, 1985; Sampaolo & Relini, 1994; Leewis *et al.*, 2000; Leewis & Hallie, 2000; Jensen *et al.*, 2000; Leonhard *et al.*, 2004). Sometimes they are only transient species which are replaced by climatic species (Forteath *et al.*, 1982; Claereboudt *et al.*, 1994; Whomersley & Picken, 2003), but in other cases, these are fixed elements of an annual cycle and tend to dominate during the warmer months of the year (Caine, 1987).

Tubularia species are known to enhance the settlement of a set of other sessile and motile taxa (Caine, 1987; Bourget & Harvey, 1998; Genzano, 1998) and applications for commercially important scallop species have been tested (Harvey *et al.*, 1993; Harvey *et al.*, 1995a; Harvey *et al.*, 1997). Some information is known about the epibionts of *Tubularia crocea* (Genzano,

1998) and the association of this species with a number of commensal pycnogonids and polychaetes (Genzano & San Martin, 2002; Genzano, 2002).

Among the genus *Tubularia*, the species *T. indivisa* is typically a subtidal species although some isolated individuals can be found on the intertidal zone (Goss-Cusard *et al.*, 1979; Kaandorp, 1982). It is common on all North-East Atlantic coast and has a widespread history records on natural highly turbulent and tide swept subtidal habitats around UK and Ireland (Doody *et al.*, 1993; Connor *et al.*, 2004; MarBEF, 2004). While Hughes (1983) detailed the annual cycle of *Tubularia indivisa*, there are currently no study analyzing the temporal variation of the assemblages associated with this species.

On shipwrecks from the Belgian part of the North Sea, it has been observed that *T. indivisa* was strongly dominating the epifauna observed in June (Zintzen *et al.*, submitted). This dominance has been reported for many years by local divers. Combined to the apparent continuity of this community, the interesting particularity of these artificial hard substrates is that they are lying on a seabed dominated by soft sediments and that they are consequently located at great distance from any natural hard bottoms. In this study, the hypothesis was to evaluate if *T. indivisa* was an essential species structuring the communities of artificial habitats in the Southern Bight of the North Sea. To test this, we analyzed the composition, diversity, density and biomass of a temporal series of samples taken on a community dominated by *Tubularia indivisa* and developing on a shipwreck from the Belgian waters. Specific questions were: (1) did the abundance of *T. indivisa* display a temporal pattern on artificial habitats, (2) what were the species associated with this community, how did this assemblage vary in time and what were their seasonal characteristic species, (3) to what extend could *T. indivisa* be considered as a micro-habitat for other species?

2. MATERIAL AND METHOD

2.1 General description of the study site

The Belgian part of the North Sea (BPNS) covers 3,640 km^2 and its seabed is dominated by soft sediments. It harbours a high geomorphological and sedimentological diversity because of the presence of numerous sandbanks (Degraer *et al.*, 1999) and a large number of obstructions, most of them being shipwrecks, are widely dispersed on the bottom (Zintzen *et al.*, 2006). Natural hard substrates such as pebbles are rare and only occur in some places in gullies between sandbanks (Lanckneus *et al.*, 2001).

From the Belgian Administration for Navigation and Coast, the Kilmore (WGS 84, N 51°23',730 - E 02°29',790, 17 nautical miles from the coast) is the oldest shipwreck made of steel known on the Belgian waters. It sunk in 1906 and its dimension are 87 by 12 m. Depth of the seabed is 30 m (Mean lower low water springs) and this shipwreck has structures emerging up to 8 m above the seabed. Despite its relative long time of submersion, it is in very good state and the major parts of its structure can still be observed. The major part of the vessel is covered by a community dominated by the hydrozoan *Tubularia indivisa* (Zintzen *et al.*, submitted) and all the samples were made within this community.

2.2 Sampling and sample processing

Initially, the shipwreck had to be sampled on a seasonal basis from December 2003 to December 2005. However, adverse weather conditions prevented sampling on many occasions and the Kilmore was sampled on height dates: December 2003, April 2004, July 2004, October 2004, March 2005, June 2005, August 2005 and October 2005.

On each date, all the living fauna within frames of 25 x 25 cm selected at random in the *T. indivisa* community were scraped on the surface of shipwrecks using SCUBA. This was achieved three times on each sampling occasion and on surface vertically oriented. On board, animals were relaxed in a 3.5% $MgCl_2$ solution for two hours and then transferred to a buffered formalin solution (final concentration 4%, pH 8.2-8.4). Later on, specimens were transferred to 70 % buffered alcohol for permanent storage. The samples were then sorted under a binocular and macro-taxa (>1 mm) were identified to the lowest possible taxonomic level and counted. Colonial taxa were considered as present or absent. From *in situ* and laboratory observations, systematically attached taxa or taxa invariably found living in association with *T. indivisa* were noted. Taxa were further considered as species in the text.

From every sample, wet weight (in alcohol) of the nine most important species in term of biomass was weighted individually to the nearest mg with an OHAUS Adventurer balance. These nine most important taxa were determined from a complete weighting of the samples from June 2005. Prior to weighting, specimens were blotted on Whatman qualitative filters with absorbent paper under it to remove excess alcohol. We calculated wet weights to ash free dry weights conversion factors in triplicate for each species. Taxa were weighted wet, dried (48h at 70°C), re-weighted (dry weight) and then burned at 500°C for 12h. Ash free dry weight (AFDW) is the difference between dry weight and the weight after the burning process.

Specimens were kept in preservatives which have a known effect on their biomass (Brey, 1986; Rumohr *et al.*, 1987; Gaston *et al.*, 1996; Pakhomov, 2003; Wetzel *et al.*, 2005). The sorting and taxonomic work hampered to freeze the samples for conservation. In this case, Gaston *et al.* (1996) recommended fixing the animals in formalin solution prior to transfer them into alcohol for sampling processing. However, there is no agreement on which factor to apply to correct weight loss. Consequently, we multiplied our results by a factor of 1.2 as suggested by Rumohr *et al.* (1987) and used by Cusson & Bourget (2005). This factor has to be considered as a minimum one.

2.3 Environmental data

The following abiotic data were collected in order to characterize the physical environment around shipwrecks in the Southern Bight of the North Sea: temperature, salinity, current velocity and direction and turbidity.

The temperatures series were obtained from the Afdeling Waterwegen Kust (AWK) permanent station on the Westhinder sandbank which is located 3.8 nm West from the Kilmore. Salinity data were provided by underway data from R/V Belgica. Data were sorted for the period 1993-2006 and for location inside a 5 nautical miles square centred on wreck position. Seabird SBE 21 system was used onboard. Temperature and salinity values used here are sub-surface values (3m). Due to the well mixed water column featuring the Belgian zone, these values have to be considered as representative for all depth.

Turbidity estimates were obtained through satellite imagery collected between September 1997 and March 2004. For each site, the mean total suspended matter ($mg.l^{-1}$) was calculated using the MODerate resolution Imaging Spectro-radiometer (MODIS) aboard the satellite EOS AQUA. A bio-optical model calibrated for the Belgian coastal waters, following the method described in Nechad *et al.* (2003), was applied to MODIS readings.

On each sampling date, water transparency was measured with a Secchi disk during slack period.

Data on the currents present at each site were obtained using a three-dimensional operational model (Pison *et al.* 2003). The model is based on the COHERENS code (Luyten *et al.* 1999) and run on a daily basis forced by meteorological forecast provided by the UK Met Office. The grid size of the model is 750 m square. Boundary conditions were provided by larger scale model using the nesting methods. The results of the model were available by layers of 1.6 m and we used the four bottom layers (4x1.6 m) to only consider the current parameters which had a direct effect on the shipwreck.

Currents roses were constructed with values of the current that were computed every 10 minutes. The runs started in august 2004, resulting in at least 230 days of data for each shipwreck site.

2.4 Temporal pattern analysis

Species richness and diversity index

Univariate summary statistics used were the species richness (S) (here defined as the number of species by sample unit), the Shannon-Wiener index (H', log$_e$), the Simpson index (1-D) (Magurran, 2004), the average taxonomic distinctness (Δ^+) and the variation in taxonomic distinctness (Λ^+) (Clarke & Warwick, 1998; Clarke & Warwick, 2001). The taxonomic distances were evaluated through a taxonomic tree built on standard Linnean classification. We used the taxonomy proposed by Costello *et al.* (2001) from which we extracted a simplified tree: the retained taxonomic levels were species, genus, family, order, class and phylum. The default weights between step length of the Linnean tree were set to constant (i.e. weights were 16.7 for species in the same genus, 33.3 for species in different genus but the same family, 50 for species in different family but the same order, 66.7 for species in different orders but the same class, 83.3 for species in different class but the same phylum and 100 for species in different phyla). These indices were calculated using the DIVERSE procedure of the PRIMER statistical software package and compared across dates using Kruskal-Wallis non parametric ANOVA.

Multivariate pattern

Multivariate analysis of the scraped samples was conducted on abundance and biomass data. Similarity between each pair of samples was calculated with the Bray-Curtis similarity coefficient (Bray & Curtis, 1957) for abundance data and Euclidean distance for the biomass data. Prior to analysis, a set of transformations (√√ or presence/absence) were applied to the raw data set to put more weight on the less abundant species. This matrix was then used to explore the pattern of community structure among samples by means of ordination with non-metric multidimensional scaling (nMDS) (Clarke, 1999). The goodness-of-fit of the resulting two dimensional nMDS plot was measured using Kruskal's stress formula I (Kruskal & Wish, 1978). Non parametric multivariate analysis of variance was used to test for difference between dates using PERMANOVA (Anderson, 2001). Significance test of pair-wise comparisons between each date could not be calculated through traditional permutation method because of the low number of replicates for each date (N=3). The P value was then calculated using Monte Carlo simulation (Anderson & Robinson, 2003). Again, the Bray-Curtis similarity index was used for abundance data and Euclidean distance for the biomass data.

Indicator species

Indicator species for each season were characterized by mean of the Indicator Value (IndVal) coefficient (Dufrêne & Legendre, 1997). A species is indicator of a group if it occurs on most of the samples from this group (specificity) and if it is poorly represented on the other groups (fidelity). The IndVal coefficient combines both the species relative abundance with its relative frequency of occurrence in the defined groups of sites. The statistical significance of the species indicator values is evaluated using a randomization procedure (9999 randomizations). A species was considered an indicator of a group if the results of two tests were significant at a level of 0.05: a t-test computing the weighted distance between randomized values and the observed value, and the rank of the observed value among the decreasing ordered randomized value distribution. The calculations were made using the IndVal program.

2.5 Value of *T. indivisa* as microhabitat

Correlation between biomass values of *T. indivisa* and univariate diversity statistics and between biomass of *T. indivisa* and abundance of species were analyzed by non parametric methods (Spearman rank correlation coefficient) since the normality of the variables could not be obtained even after transformations (graphical examination of the residuals and Shapiro-Wilk's W test, Shapiro & Wilk, 1965).

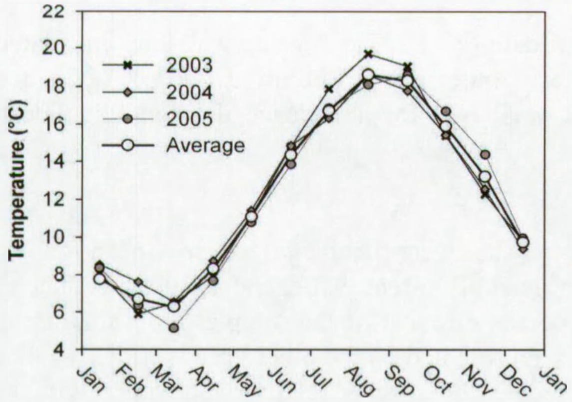


Figure 1. Mean monthly temperature on the Westhinder station (3.8 nm from the Kilmore) for the period June 2001 to May 2006. Data from AWK.

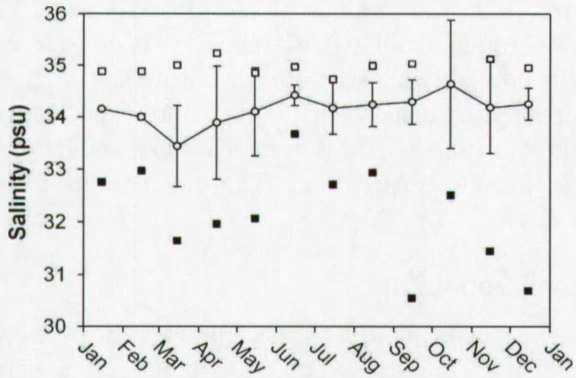


Figure 2. Mean (±s.d.) (○), Min (■) and Max (□) monthly salinity values on the Kilmore for the period 1993 to 2006 R/V Belgica underway data. Salinity measures were made at less than 5 nautical miles from the shipwreck.

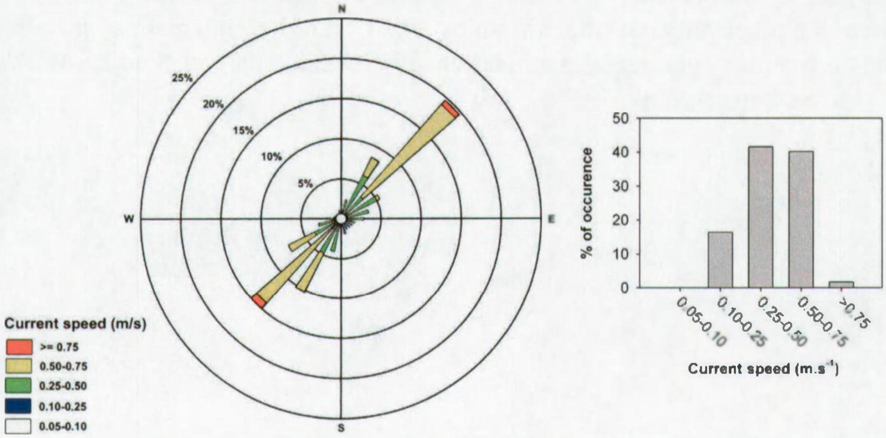


Figure 3. Current roses and current velocity occurrence for the Kilmore (July 2005). MUMM operational three-dimensional model (10 min. time step, 750 m grid size, UK Met Office weather forecast forcing).

3. RESULTS

3.1 Environmental characterization

The temperature on the Kilmore ranged from 4.2°C (March 2006) to 20.3°C (August 2003) with an average value of 12.2°C (Figure 1). March was the coldest month except for 2003 where temperatures started to rise from February. The highest temperatures were read during August except for 2005 where they were observed on September. The temperature displayed a cycle which was repeated from years to years (2001-2006) with small variations.

The salinity was constant between months and was comprised between 33.2 and 34.5 psu (Figure 2) so that the Kilmore did not seem to suffer from periodic marked low salinity due to fresh water income from the Rhine-Meuse and Scheldt estuaries.

The hydrodynamic of the area is constrained by semi-diurnal tides resulting in the emergence of strong tidal currents. Minimum tidal currents occur on the Kilmore generally three hours before and after the local high tide. The current roses for each month were closely similar and a typical example is presented for the month of July on figure 3. The current was preferentially oriented along a SW-NE axis (66% of the occurrence). It was also along these directions that the currents were the strongest (up to 0.86 $m.s^{-1}$). For other directions, the velocity of the currents did not rise above 0.50 $m.s^{-1}$. There was no current under 0.10 $m.s^{-1}$ and the proportion of current under 0.30 $m.s^{-1}$ was 18%. The 0.25-0.50 $m.s^{-1}$ current velocity class was the most frequent (42%), followed by the 0.50-0.75 $m.s^{-1}$ class (40%).

Mean value for total suspended matter on the Kilmore is 6.2 $mg.l^{-1}$. Total suspended matter was clearly lower from May to September with value around 5.5 $mg.l^{-1}$ (Figure 4). The turbidity rose from September to November and then remained constant until February at 8.0 $mg.l^{-1}$. From February to April, the turbidity was sharply decreasing. The deviation around the mean values were sometimes high (March and September), indicating large monthly fluctuations of suspended matter at the monthly temporal scale.

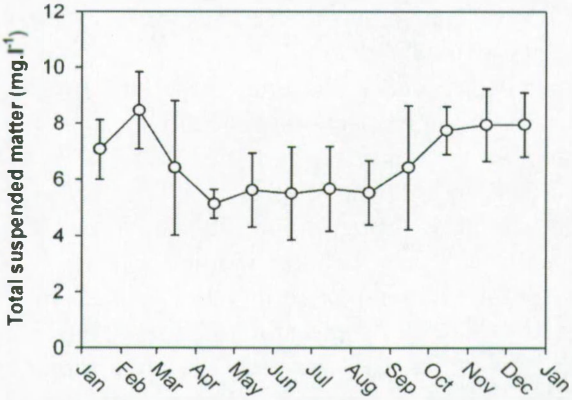


Figure 4. Mean monthly total suspended matter (±s.d.) on the Kilmore obtained from Modis satellite imagery for the period July 2002 to October 2005 (Number of observations = 199).

3.2 Temporal pattern

Species richness and diversity index

The univariate indices of diversity are presented on figure 5. The total number of species was 104. The species richness (N_0) varied from 15 in October to 42 in August with a mean value of 33 species per sample. All the other species richness values lay between 30 and 40 species with the exception of the samples from March 2005 (28 sp). The results of the Kruskal-Wallis ANOVA was significant at $p<0.03$, indicating that species richness was different from date to date. The Shannon-Wienen (H', $\log_e$) and Simpson (1-D) index displayed a very similar pattern. The samples from the fall and winter periods shared high diversity index values while spring and summer samples were strongly dominated by a few species. The Kruskal-Wallis ANOVA is significant at $p<0.03$ and $p<0.04$ for H' and 1-D, respectively. The taxonomic distinctness (Δ^+) values had no distinct pattern linked to time of the year. The average taxonomic distance between two species taken at random did not change with time. The variation in taxonomic distinctness (Λ^+) was also rather constant. Only two values, one at the end of 2004 and the other at the beginning of 2005 were lower, indicating a more homogeneous repartition of the species in the taxonomy of these samples.

Density and biomass

The total density of the macrobenthos displayed a clear temporal variation with larger values during the spring and summer period (Figure 6). It ranged (mean ± s.d.) from 6,500±56 ind.m^{-2} in October 2004 to 445,800±189,800 ind.m^{-2} in July 2004. A major part of these individuals were due to the amphipod *Jassa herdmani* (Figure 6). Its density ranged from 1,000±385 ind.m^{-2} in October 2004 to 398,500±189,800 ind.m^{-2} in July 2004 and closely followed the pattern of the total density. The abundance of Crustacea (*J. herdmani* omitted) and Echinodermata had a peak of abundance during the spring and summer months (4,600±1,340 ind.m^{-2} and 12,100±8,120 ind.m^{-2} in June 2005 and July 2004, respectively; Figure 6). For the Crustacea, the decapod *Pisidia longicornis* and the caprellids *Phtisica marina* and *Caprella tuberculata* were the most contributing species to the observed abundances (Figure 6). Stenothoidae were also abundant. *Ophiothrix fragilis* dominated the Echinodermata (Figure 6). Annelida, Cnidaria and Mollusca had a very close pattern of temporal abundances. They were all more abundant in spring and summer with maximal

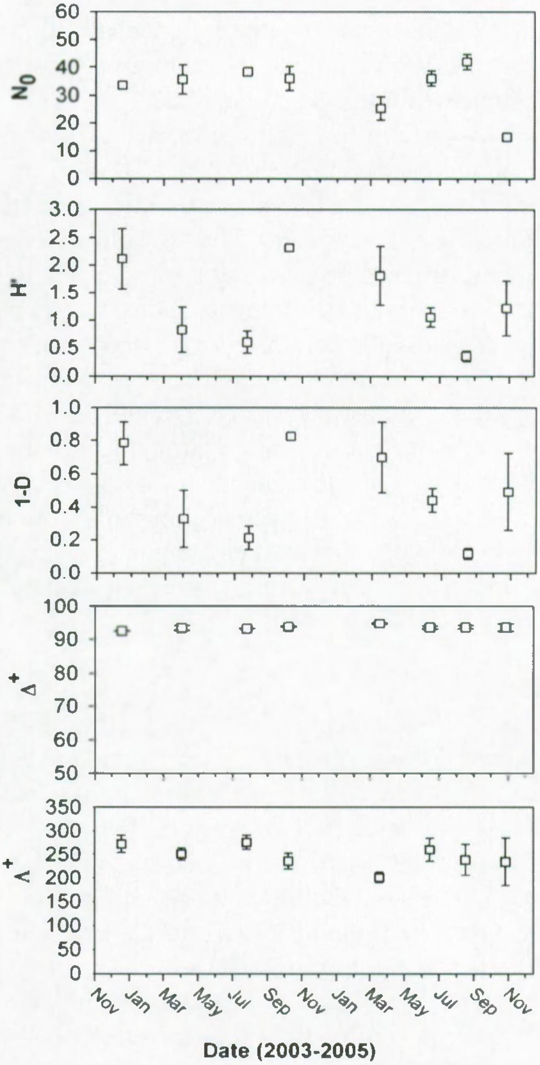


Figure 5. Temporal variation of diversity index on the Kilmore shipwreck. Values are means ±s.d. N_0 is the species richness, H' is the Shannon-wiener index (natural log), 1-D is the Simpson index, Δ^+ is the taxonomic distinctiveness, Λ^+ is the variation in taxonomic distinctiveness.

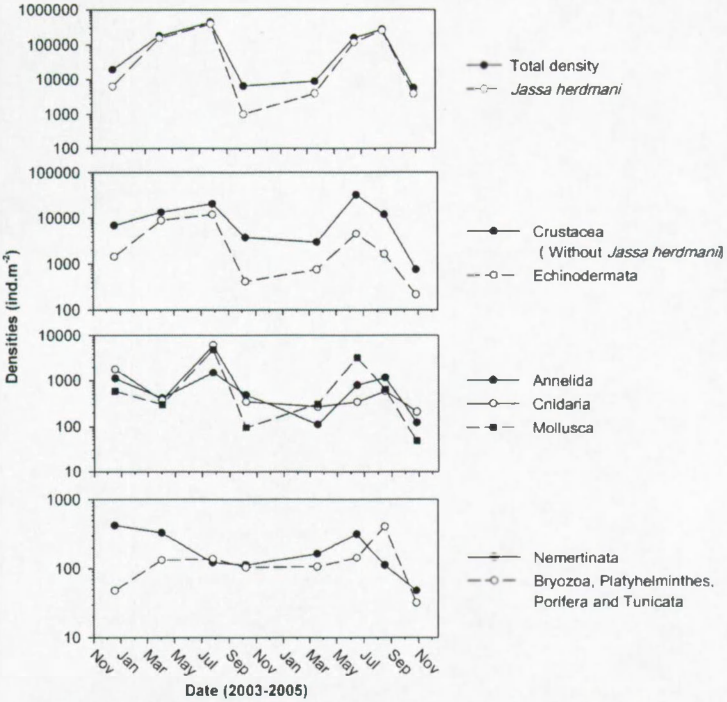


Figure 6. Temporal variation of densities on the Kilmore shipwreck. Y axes are presented on a log scale.

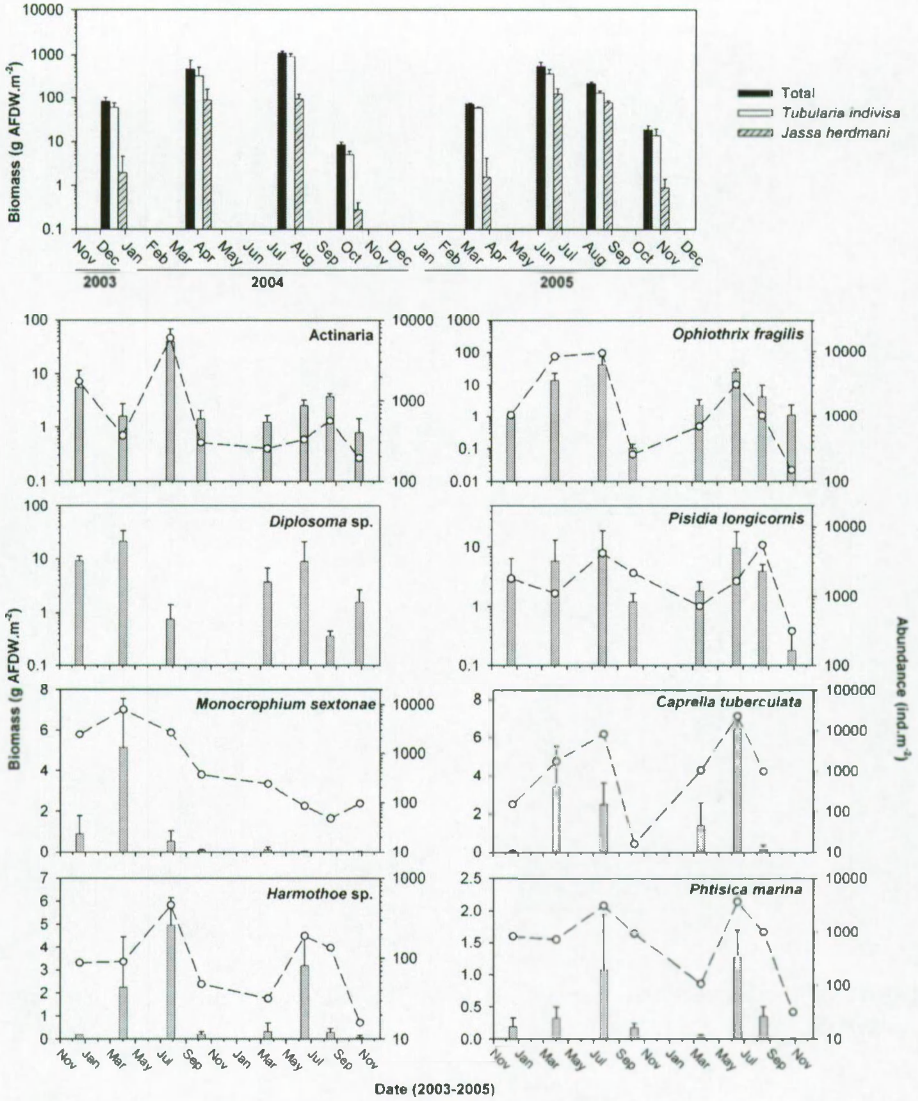


Figure 7. Temporal variation of biomass (mean ash-free dry weights, ±s.d.) and abundance of dominant species on the Kilmore shipwrecks. Abundance for *Diplosoma* sp. is not presented because this species is not countable. For readability, Y axes of Actinaria, *Ophiothrix fragilis*, *Diplosoma* sp. and *Pisidia longicornis* are presented on a logarithmic scale.

abundances of 1,500 ind.m^{-2} for Annelida, 6,100 ind.m^{-2} for Cnidaria and 5,000 ind.m^{-2} for Mollusca. However, some of the cnidarians species were not readily countable and were not adequately represented by abundance data. Groups with low abundance like Nemertea, Porifera, Platyhelminthes, Bryozoa and Tunicata did not show any clear temporal pattern.

The total biomass varied from 9 g.m^{-2} in October 2004 to 1,106 g.m^{-2} in July 2004 (Figure 7; all biomass values are expressed as ash-free dry weights). The variation in total biomass was under the strong dependence of the biomass of *Tubularia indivisa* which constituted between 59 and 82% of the total biomass (Figure 7). Its development was already important at the end of winter (60-324 g.m^{-2}) and increasing until the first part of the summer period (362-912 g.m^{-2}). Afterwards, its biomass was decreasing with its minimal development being around October (5-14 g.m^{-2}). The biomass of the most abundant species, *J. herdmani*, displayed the same pattern with biomass ranging from 0.3 to 123.3 g.m^{-2} (Figure 7). The eight most abundant species have their biomass values presented on figure 7. For June 2005, with *T. indivisa* and *J. herdmani*, they accounted for 93% of the biomass measured from each individual on the samples. Except the amphipod *Monocorophium sextonae* and the tunicate *Diplosoma* sp., they all had a peak of biomass at the end of spring. The last two species were more represented at the end of winter.

Generally, the biomass values on 2004 were higher than on 2005. In July 2004, the biomass of *T. indivisa* was 912 g.m^{-2} while they were 362 and 129 g.m^{-2} in June and August 2005, respectively (Figure 7).

Multivariate patterns of differences among assemblages

The non-metric multidimensional scaling ordination plot (abundance data) of the assemblages from each date showed a good consistency for the samples taken on the same dates (Figure 8). Only the variance for the samples from December 2005 was larger. The samples from spring and summer grouped together, especially with the $\sqrt{}\sqrt{}$ transformation on abundance data (Figure 8,A). When ordinating the samples on the presence/absence of species, they still isolated but less sharply. With presence/absence data, the weights of the abundant species found during spring and summer was not dominant anymore and the similarity between samples tended to increase. The samples from December 2003 and October 2004 and 2005 had a different assemblage pattern from each other and from the other samples (Figure 8,B).

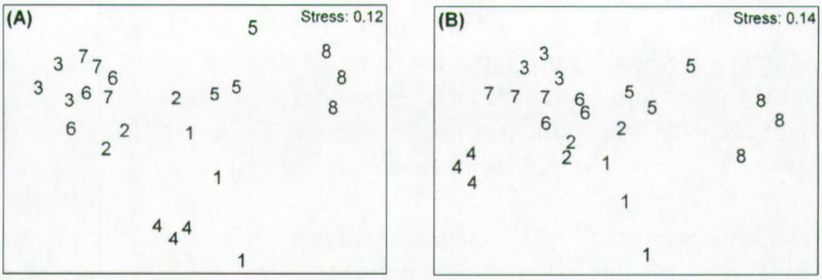


Figure 8. non-Metric Multidimensional Scaling based on Bray-Curtis similarity from √√ abundance data (A) and presence/absence data (B). 1: December 2003, 2: April 2004, 3: July 2004, 4: October 2004, 5: March 2005, 6: June 2005, 7: August 2005, 8: October 2005.

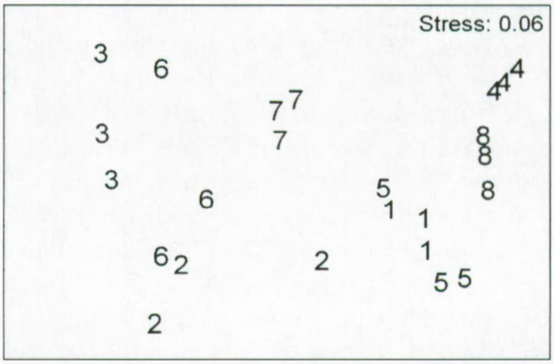


Figure 9. non-Metric Multidimensional Scaling based on Euclidean distances from √√ biomass data. 1: December 2003, 2: April 2004, 3: July 2004, 4: October 2004, 5: March 2005, 6: June 2005, 7: August 2005, 8: October 2005.

Table 1. Non-parametric multivariate analysis (NPMANOVA, based on Bray-Curtis dissimilarity) on √√ abundance data of the Kilmore shipwreck. Date was a fixed factor with 8 levels (N=3).

Source	df	SS	MS	F	P
Date	7	19343.1	2763.3	6.959	0.001
Residual	16	6353.7	397.1		
Total	23	25696.8			

The ordination plot for biomass data isolated the spring and summer samples from the autumn and winter ones (Figure 9). However, the distance between each date was superior to the abundance pattern, individualizing the dates more clearly.

The results from the non-metric multivariate analysis of variance from abundance data are presented on tables 1 and 2. It confirms the results from the ordination plot. The fall and winter samples are different from the spring and summer samples for their abundance and biomass pattern. However, for the biomass data, the analysis of variance does less clearly isolates the different dates that what could be observed on the ordination plot. With no transformation, only the samples from October 2004 and 2005 were different from those of December 2003. Putting more weight on the less represented species, more differences between dates appeared but there was no clear pattern in these differences.

Seasonal characteristic species

The number of species which were indicator of the Kilmore shipwreck was relatively high (16 species with IndVal>75; table 3). The best represented group were the crustaceans with decapods and amphipods. *Mytilus edulis* was invariably found as juveniles (<1 cm) while all the other species had adults in their representatives. The indicator species by season are presented on table 4. Except for *Liocarcinus* sp. in winter, the IndVal were low and there was a low number of species which were significantly indicator of a season with certitude. In winter, several polychaete and crustacean species had an IndVal around 50. The cnidarian *Alcyonium digitatum* was the second indicator species. This species was only found as juveniles composed of a few polyps which were not found afterwards. *Monocorophium sextonae*, although not significantly, was again more characteristic of the winter period. In spring, two sponge species (*Esperiopsis fucorum* and *Halichondria* cf *panicea*) were ubiquitous together with the pioneer polychaete *Pomatoceros triqueter* and juveniles of *Aequipecten opercularis*. The only significant species was the bryozoan *Scrupocellaria scruposa* which was developing on the perisarc of *T. indivisa*. During summer, four species of polychaetes (*Eusyllis blomstrandi*, *Phyllodoce mucosa*, *Lanice conchilega* and *Harmothoe* sp.) were indicator of the assemblages. Not indicator but potentially important because of their predatory behaviour on *T. indivisa*, the nudibranch *Dendronotus frondosus*, the syllid *Procerastea halleziana* and the pycnogonid *Achelia* sp. were abundant in summer. The amphipod *Stenothoe monoculoides* together with *M. edulis* and *J. herdmani*

Table 2. Pair-wise comparison of macrofauna assemblages from the Kilmore shipwreck on different dates using non-parametric multivariate analysis of variance (NPMANOVA, based on Bray-Curtis dissimilarity for abundance data and Euclidean distance for biomass data). Raw data were subjected to a set of transformation prior to analysis. P values estimated through asymptotic Monte-Carlo sampling. NS: not significant, * p<0.05, ** p<0.01, *** p<0.001.

Date	Abundance						Biomass					
	No trans.		√√		Presence/ absence		No trans.		√√		Ln (x+1)	
	t	P	t	P	t	P	t	P	t	P	t	P
12/2003-04/2004	19.4	NS	19.7	*	20.5	*	1.7	NS	1.1	NS	1.0	NS
07/2004	36.0	**	30.7	**	28.8	*	1.7	NS	1.5	NS	2.0	*
10/2004	25.1	*	34.3	**	37.7	**	2.8	*	5.1	**	8.6	***
03/2005	13.98	NS	16.8	NS	16.4	NS	2.1	NS	1.1	NS	0.6	NS
06/2005	37.7	**	37.2	**	36.3	**	1.9	NS	1.3	NS	1.2	NS
08/2005	42.2	**	37.9	**	38.6	**	1.6	NS	1.1	NS	1.6	NS
10/2005	20.4	*	31.9	**	34.5	**	2.7	*	3.4	**	3.0	*
04/2004-07/2004	14.5	NS	20.0	*	19.4	*	0.6	NS	0.3	NS	0.8	NS
10/2004	31.3	**	33.1	**	30.9	*	1.4	NS	2.2	*	3.2	**
03/2005	16.7	NS	15.6	NS	13.4	NS	0.7	NS	0.4	NS	0.8	NS
06/2005	11.9	NS	23.9	*	20.5	*	0.9	NS	0.7	NS	0.6	NS
08/2005	14.5	NS	25.1	*	25.0	*	1.2	NS	0.8	NS	0.7	NS
10/2005	23.6	*	30.0	**	28.2	*	1.4	NS	2.0	*	2.2	*
07/2004-10/2004	66.9	***	45.4	**	34.4	**	1.7	NS	3.0	**	5.9	***
03/2005	24.8	*	19.3	NS	15.4	NS	0.8	NS	0.6	NS	1.1	NS
06/2005	32.8	*	24.6	*	22.3	*	1.4	NS	0.8	NS	0.9	NS
08/2005	14.4	NS	24.7	*	24.3	*	1.4	NS	1.1	NS	1.1	NS
10/2005	39.1	**	40.4	**	34.4	**	1.5	NS	2.4	*	2.9	*
10/2004-03/2005	18.3	NS	20.0	NS	21.5	*	1.3	NS	2.3	*	3.2	**
06/2005	95.3	***	53.6	***	42.9	**	1.4	NS	1.7	NS	2.1	NS
08/2005	133.3	***	54.2	**	44.9	**	1.1	NS	3.8	**	6.3	***
10/2005	27.6	**	40.9	**	48.2	**	0.9	NS	1.8	NS	2.4	*
03/2005-06/2005	25.0	*	19.4	NS	17.0	NS	1.2	NS	0.7	NS	0.9	NS
08/2005	26.9	*	19.5	NS	18.2	NS	1.0	NS	0.7	NS	0.8	NS
10/2005	11.8	NS	16.4	NS	17.0	NS	1.2	NS	2.0	*	2.1	*
06/2005-08/2005	49.5	**	36.0	**	36.6	**	1.2	NS	0.9	NS	0.9	NS
10/2005	42.1	**	41.8	**	38.0	**	1.7	NS	1.7	NS	1.8	NS
08/2005-10/2005	46.1	**	43.6	**	44.2	**	1.3	NS	2.8	*	2.9	*

Table 3. Indicator species of the temporal series from the Kilmore shipwreck. The indicator values (IndVal) were calculated from √√ transformed abundance data. Only the species with indicator values above 75 are presented. CNI: Cnidaria, CRU: Crustacea, ECH: Echinodermata, MOL: Mollusca, POL: Polychaeta, TUN: Tunicata.

Species		IndVal	Species		IndVal
1. Actiniaria	CNI	100	9. *Mytilus edulis*	MOL	95.2
2. *Jassa herdmani*	CRU	100	10. *Pilumnus hirtellus*	CRU	95.2
3. *Oerstedia dorsalis*	NEM	100	11. *Phtisica marina*	CRU	90.5
4. *Ophiothrix fragilis*	ECH	100	12. *Caprella tuberculata*	CRU	85.7
5. *Pisidia longicornis*	CRU	100	13. *Diplosoma* sp.	TUN	85.7
6. *Tubularia indivisa*	CNI	100	14. *Harmothoe* sp.	POL	85.7
7. *Amphipholis squamata*	ECH	95.2	15. *Lepidonotus squamatus*	POL	81.0
8. *Monocorophium sextonae*	CRU	95.2	16. *Stenothoe monoculoides*	CRU	81.0

were also characteristics of the assemblage. In fall, cnidarians (*Obelia* sp. and *clytia hemisphaerica*) and the polychaete *Eumida* sp. were indicator species.

3.3 Value of *T. indivisa* as microhabitat

A significant positive correlation ($p<0.05$) between the biomass of *T. indivisa* and the abundance of species was observed for 24 species. The strongest correlations were noted for *Mytilus edulis*, *Jassa herdmani*, *Ophiothrix fragilis*, *Harmothoe* sp., *Amphipholis squamata*, *Caprella tuberculata* and *Lepidonotus squamatus* (Spearman $R^2 > 0.69$, $R^2 < 0.001$; table 5). The biomass of *T. indivisa* was also positively correlated with the species richness of the samples ($R^2=0.562$, $p<0.008$; figure 10). The relation was not strictly linear and was flattening off when *T. indivisa* biomass was above 200 $g.m^{-2}$. *T. indivisa* biomass was also negatively correlated with the Shannon-Wiener index ($R=-0.677$, $p<0.001$) and the Simpson index ($R=-0.650$, $p<0.002$) but was not correlated with the taxonomic distinctiveness and variation in taxonomic distinctiveness.

The number of species which were associated with *T. indivisa* (meaning living attached on or invariably found on *T. indivisa*) was generally superior to 55% of the species richness of the samples (Figure 9). Only the sample of October 2004 had 46% of its species depending on *T. indivisa.* This set of species accounted for 86% (December 2003) or more of the total density of individuals in the samples (Figure 9). However, there was no systematic trend in the association (both in species number and density) with the period of the year.

4. DISCUSSION

4.1 Abiotic environment

Around the Kilmore shipwrecks, several abiotic parameters showed a variation at the scale of the year. First of these is the water temperature which ranged from 7°C to 19°C. The temperature minima, maxima and mean by month are slightly different between years and could induce differential recruitment and growth between years.

The Kilmore lies outside the high turbidity zone that is located in the Belgian-Dutch coastal zone (Fettweis & Van den Eynde, 2003). Its mean value for total suspended matter is 6.2 $mg.l^{-1}$ but shows monthly variability. Higher total suspended matter occurred during autumn and winter than

Table 4. Indicator species by season on the Kilmore shipwreck. The indicator values (IndVal) were calculated from √√ transformed abundance data. Maximal IndVal were bolded. Only the species with IndVal above the last significant IndVal were included. ** Significant at $p < 0.05$ level for the two randomization tests. * Significant at $p < 0.05$ level for only one of the two randomization test. NS: not significant.

Species		IndVal	Sign.
WINTER			
Liocarcinus sp.	CRU	**100.0**	**
Alcyonium digitatum	CNI	**68.6**	**
Polyclinum aurantium	TUN	**56.9**	*
Macropodia parva	CRU	**56.1**	*
Rissoidae	MOL	**56.0**	**
Sabellaria spinulosa	POL	**53.8**	*
Cumacea sp.	CRU	**50.0**	*
Epitonium clathratulum	MOL	**50.0**	*
Eunicidae	POL	**50.0**	*
Euspira pulchella	MOL	**50.0**	*
Phyllodoce mucosa	POL	**50.0**	*
Polycirrus sp.	POL	**50.0**	*
Sthenelais boa	POL	**50.0**	*
Thelepus setosus	POL	**50.0**	*
Thoralus cranchii	CRU	**50.0**	*
Tubulanus sp.	NEM	**50.0**	*
Stenothoe marina	CRU	43.5	NS
Bicellariella ciliata	BRY	**37.5**	NS
Nassarius incrassatus	MOL	**37.0**	NS
Monocorophium sextonae	CRU	32.8	NS
Oerstedia dorsalis	NEM	31.4	**
SPRING			
Esperiopsis fucorum	POR	43.2	NS
Scrupocellaria scruposa	BRY	**43.1**	*
Halichondria cf *panicea*	POR	39.0	NS
Pomatoceros triqueter	POL	38.5	NS
Aequipecten opercularis	MOL	35.3	NS
Jassa herdmani	CRU	42.4	**
SUMMER			
Eusyllis blomstrandi	POL	**55.6**	*
Phyllodoce mucosa	POL	53.9	**
Lanice conchilega	POL	**51.9**	**
Stenothoe monoculoides	CRU	50.4	**
Psammechinus miliaris	ECH	46.5	NS
Eulalia viridis	POL	45.2	NS
Procerastea halleziana	POL	**44.4**	NS
Asterias rubens	ECH	**44.4**	NS
Mytilus edulis	MOL	43.0	**
Jassa herdmani	CRU	42.4	**
Caprella tuberculata	CRU	41.4	NS
Sycon ciliatum	POR	38.3	NS
Harmothoe sp.	POL	36.2	*
FALL			
Clytia hemisphaerica	CNI	**50.0**	**
Eumida sp.	POL	**50.0**	**
Obelia sp.	CNI	**50.0**	**

during spring and summer. The origin of this variation is not biological (i.e. plankton production) but abiotic. The greater number of storm events during the autumn and winter period probably generate an increased re-suspension of the finer sediments. Another source is the river particulate matter inputs from the Scheldt estuary which show seasonal variations. Values are in the North Sea. These are high values compared to the central North Sea but are in agreement with what is found on the coastal region of the Southern North Sea. This concentration of suspended matter certainly explains why no algae species were found on shipwrecks (Zintzen *et al.* submitted). The quantity of light reaching shipwrecks should be near or below the photosynthesis compensation point hence insufficient for algae growth.

The Kilmore is exposed permanently to strong tidal currents all the year round. Currents intensity and direction on the bottom layers did not change with season but followed daily and lunar cyclical variations. The fraction of calm periods (current speed < 0.10 m.s^{-1}) was very low (less than 0.2 % of the time) and currents above 0.75 m.s^{-1} occurred during each spring tide. This highly hydrodynamic environment will select a set of species adapted to settle, feed and reproduce in such conditions. It is also possible that different microhabitats will be created within the shipwreck since there is a prevailing current direction that will create zone of differing turbulence and shear stress. Since the shipwreck is oriented along the prevailing water currents, relatively protected surface should be found on the inside part of the hull.

4.2 Structural effect *Tubularia indivisa* on community.

The *Tubularia indivisa* community developing on the North Sea shipwrecks showed large monthly variation of its biomass. The largest part of this variation was due to the hydroid itself with biomass ranging from 5 g AFDW.m^{-2} (October) to 912 g AFDW.m^{-2} (July). These values and their ratio to the total biomass of the community which ranged from 59 to 82 % are particularly high. Gili & Hughes (1995) noticed that the contribution of biomass from communities dominated by hydroids in shallow water may reach 15 to 20 % of the total biomass, but was generally far under these values. Hughes (1983) studied the life history of *T. indivisa* and confirmed the large settlement of actinula larvae on the perisarc of the adults in spring, followed by their rapid growth. Afterwards, the settlement of larvae was probably precluded by the development of the other epibionts and the increased density of predators like the nudibranch *Dendronotus frondosus*,

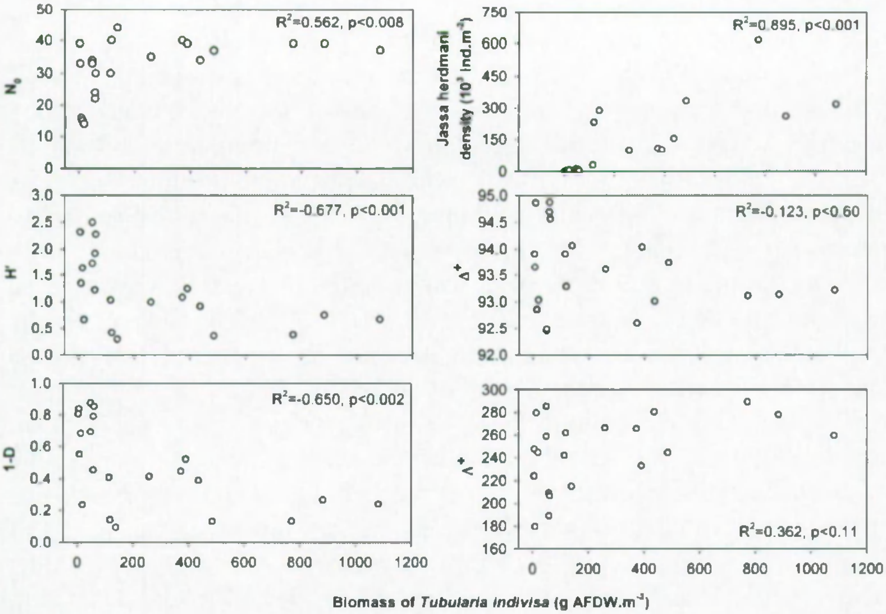


Figure 10. Spearman rank order correlation between standing biomass of *Tubularia indivisa* and univariate measures of diversity. N_0 is the species richness, H' is the Shannon-wiener index (natural log), 1-D is the Simpson index, Δ^+ is the taxonomic distinctiveness, Λ^+ is the variation in taxonomic distinctiveness.

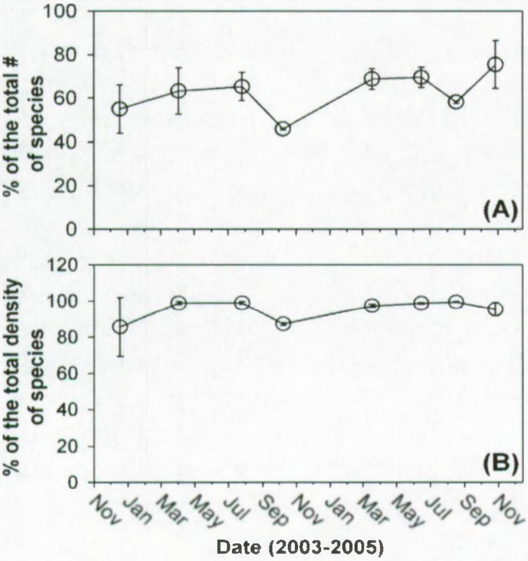


Figure 11. Temporal variation of the % of total number (A) and density (B) of species which are associated with *Tubularia indivisa.*

the syllid *Procerastea halleziana* and pycnogonids (*Achelia* sp., probably *Achelia echinata*). *Procerastea halleziana* (Genzano & San Martin, 2002) and other species of pycnogonids (Genzano, 2002) were known to feed on *Tubularia crocea* by piercing their perisarc. Among the epibionts potentially decreasing the settlement of actinula larvae from *T. indivisa*, the bryozoan *Electra pilosa* played certainly a role by its large incrustation of the perisarc, especially at the end of the summer period. In spring the activity of the large density of filter feeders, like the amphipod *Jassa herdmani* or caprellid species could significantly prey upon the actinulae. Obviously, the simple physical presence of the tube construction gathered by *J. herdmani* could explain a further difficulty for actinulae to settle. In late summer and autumn, a drastic decrease of *T. indivisa* biomass occurred, probably as a result of the predatory behaviour of epibenthic species and the lack of recruits from the summer period. During winter, some of the hydrocauli must be able to regenerate hydrants producing a winter cohort as observed on the East coast of Britain (Hughes, 1983) and biomass could already start to increase. The possibility for individuals to regenerate after being predated upon should be necessary if we consider the propagules which are responsible for the dissemination of *T. indivisa*. Actually, the actinula larvae of tubulariids directly produced by fixed gonophores are non feeding (Boero & Bouillon, 1993). It is usually accepted in the literature that the actinula larvae from hydroids have a very short dispersal capacity because they tend to sink and most of the time, they will settle not far from their parents (Pyefinch & Downing, 1949). These authors further suggested that the release of actinulae from *Tubularia larynx* was markedly reduced at current speed above 0.03 $m.s^{-1}$, implying that the release of actinulae should concentrate around the slack-water period of the tidal cycle. This could limit the dispersal by currents. Consequently, the rapid increase of biomass after autumn should have its origin on individuals already living on the shipwreck. However, Pyefinch & Downing (1949) measured a sinking rate for *T. larynx* of 1 $mm.s^{-1}$. If we consider the height at which the actinulae are released (usually at least 10 cm from the colonies in North Sea shipwrecks) and the velocity of the currents around shipwrecks (only 1.7 % of the tidal cycle with current speed under 0.10 $m.s^{-1}$), even at the slack-water period, it is highly probable that the actinulae could be transported far from the parents. Furthermore, Yamashita *et al.* (2003) could keep the actinulae of *Tubularia mesembryanthemum* (= *T. crocea*) alive and able to settle for more than two weeks in laboratory experiments. It is also frequently found on plankton samples (Schuchert, pers. com.). It is then estimated that the

Table 5. Spearman rank correlation between the biomass of *Tubularia indivisa* and the abundance of species in the samples (N=21). Only the species with $p<0.05$ are shown.

Species		**R^2**	**P value**
Mytilus edulis	MOL	0,891	0,000
Jassa herdmani	CRU	0,870	0,000
Ophiothrix fragilis	ECH	0,834	0,000
Harmothoe sp.	POL	0,794	0,000
Amphipholis squamata	ECH	0,760	0,000
Caprella tuberculata	CRU	0,747	0,000
Lepidonotus squamatus	POL	0,697	0,000
Nereis pelagica	POL	0,662	0,001
Lanice conchilega	POL	0,655	0,001
Stenothoe monoculoides	CRU	0,626	0,002
Sycon ciliatum	POR	0,611	0,003
Asterias rubens	ECH	0,608	0,003
Phtisica marina	CRU	0,603	0,004
Pilumnus hirtellus	CRU	0,578	0,006
Eulalia viridis	POL	0,549	0,010
Psammechinus miliaris	ECH	0,510	0,018
Dendronotus frondosus	MOL	0,507	0,019
Phyllodoce mucosa	POL	0,501	0,021
Actiniaria	CNI	0,487	0,025
Baseodiscus delineatus	NEM	0,467	0,032
Cuthona sp.	MOL	0,462	0,035
Eusyllis blomstrandi	POL	0,450	0,040
Stenothoe sp.	CRU	0,449	0,041
Pisidia longicornis	CRU	0,448	0,050

dispersal of actinula larvae from *T. indivisa* could be frequently realized at the scale of one shipwreck (100 m) and certainly between these spots of hard substrates (1-10 km). Another sign of the large dispersal capacity of this species lies in its frequent observation on buoys and mooring lines at great distance from any other source of hard substrates (Hughes, pers. com.). It is interesting to note that on a larger temporal scale, Cornelius (1981) found that two thirds of the widely distributed hydroids in the cooler part of the northern hemisphere lacked a medusa stage. Boero & Bouillon (1983) noted that the possession of theoretically more or less efficient means of dispersal seems not to be so important for the distribution of the species. They range should finally be a function of their environmental tolerance.

To our knowledge, shipwrecks on the Belgian waters are the only known location where *T. indivisa* is the yearly dominant feature of a subtidal community. The Kilmore is under water since 1906 and all recreational diver records on this site confirmed its dominance. Its success in this particular environment is difficult to explain. On natural grounds, *T. indivisa* is present but never dominating. The inspection of the fouling community of North Sea offshore platforms during 11 years revealed that after a period of dominance of a few years (3-6 years), the hydroid community was gradually replaced by the sea anemone *Metridium senile*. This last species was only found dominating the shipwreck of the Belgian waters close to the coast (Zintzen *et al.* submitted). The environment created by shipwrecks could be responsible for a particular current pattern which would be favourable to the settlement, recruitment and/or growth of this species. On experimental panels set up to alter both shear stress and turbulence independently, Mullineaux & Garland (1993) observed a preferential settlement of *T. crocea* on region with high turbulence and high shear stress. This observation was supported by Lemire & Bourget (1996) who noticed that *T. crocea* larvae densities were higher on the most exposed surfaces of complex panels. The shipwrecks offer a large area of exposed surface to currents. Baynes & Szmant (1989) analyzed the pattern of moving water around a shipwreck and showed differential water turbulence and pressure with location on the structure. Current eddies were also detected around shipwrecks (Lindquist & Pietrafesa, 1989). A more thorough analysis of *T. indivisa* cover and biomass on the different structure of the shipwreck would help understand if this species respond differentially to water motion. Another factor that could explain the yearly success of *T. indivisa* is the attraction by conspecifics. Aggregation among hydroids is a frequent phenomenon (Boero, 1984) and experiments on *T. larynx* suggested that settlement could be enhanced by adult extracts (Nellis & Bourget, 1996). Since individuals were present all year round on shipwrecks, the actinulae could use adults as settlement cues.

Besides the action of competition for space, the temperature regime of the Belgian waters certainly plays a significant role. The regression of coenosarc can occur when hydroids are placed in cold water, and the resulting dormant stage regenerates when placed in warmer water (Calder, 1990). Temperature has been proved to influence the seasonal abundance of several species of hydroids (see references in Gili & Hughes, 1995). Hughes (1983) measured that the growth of *T. indivisa* was almost ten times higher in July than during winter.

4.3 Epibiont community on *Tubularia indivisa*

Dean (1981) already showed that motile species responded positively to the structure supplied by sessile species. A positive correlation exists in our study between species richness of motile and sessile species and the biomass of *Tubularia indivisa*. However, the relation was not linear but showed a plateau at biomass of *T. indivisa* above 200 $g.m^{-2}$. Interestingly, the number of species that the hydroid could sustain was limited, even if its abundance increased. Certainly, the hydroid offered a limit number of microhabitats that were available beyond a critical amount of individuals.

Tubularia indivisa also offered a support for a diversified set of species. An inverse relation exists with diversity indices (Shanonn-Wiener and Simpson) because of the strong dominance of a few species. This pattern was also observed on intertidal colonies of *T. crocea* (Genzano, 2001). Half of the species, representing the major fraction of the total density of individuals, were directly associated (i.e. attached) with the hydroid. It is plausible that proteinaceous and/or polysaccharidic compounds in the perisarc of the hydroid would be responsible for the attraction of a set of species. This has been demonstrated for scallops with *T. larynx* (Harvey *et al.*, 1995b). Schmidt (1983) also explained that the presence of *T. larynx* on experimental panels was favouring the settlement and subsequent rapid domination of ascidian species (*Ciona instestinalis* and *Ascidiella aspersa*). However, Bourget & Harvey (1998) observed on *T. larynx* that various species of juveniles were found at densities up to twenty times more than on other substrata. Following this observation, they showed that the recruitment pattern at scale larger than 3 cm on plastic arborescent structures designed to mimic the hydroid could be explained by passive settlement processes only. It is only at small scale (*ca* 1 mm) that active selection was detected. Consequently, the settlement of species on the shipwreck tubulariids could be the result of the passive flux of larvae from the surrounding water masses, but the acceptation/rejection of the site would be an active mechanism. Describing the associated fauna of intertidal *T. crocea*, Genzano (2001) noticed that crustaceans (mostly *Jassa falcata* and *Caprella* sp.) were the most abundant species. Although not restricted to living in association with hydroids, it seems that these species find an environment particularly suitable for their growth as observed in our results. It may be possible that species of the genus *Jassa* gets no particular positive effect from tubulariids besides an increased surface available for colonization. For example, *Jassa herdmani* is found in high densities on any submerged artificial structure on the BPNS (buoys, vessel, harbour wall,...) (Kerckhof, pers.com.) and does not require the presence of any hydroid species. This genus is generally found among algae, sponges, hydroids ad bryozoans of rocky shores as well as on newly available substrates and harbour walls (Conlan, 1989). Caprellid species are known to prey upon other small crustaceans and seems to be immune to nematocysts. *Pseudoprotella phasma* was known to adopt a clepto-commensalist behaviour by stealing captured preys by the hydrant of *Eudendrium glomeratum* (Bavestrello *et al.*, 1996). The caprellid species on shipwrecks could well benefit from the large population of *J. herdmani* which is available throughout the year, stealing them from the tentacles of *T. indivisa* or directly preying upon them. *Phtisica marina*, one of the abundant species on shipwrecks, seems to be able to switch between a predatory and filter feeding behaviour following its posture (Guerra-Garcia *et al.*, 2002). For the second important caprellid species (*Caprella tuberculata*), our under water observations go in the same direction: this species holds an 'up-right' posture like *P. marina*, probably leading to the same feeding strategy (see Takeuchi & Hirano (1995) for review of caprellids clinging behaviour). We also observed that this species was often found in the close vicinity of the hydrant of *T. indivisa*, which lets us assume a direct relation of the caprellids with its host. Although not observed during diving, mutualistic interactions between caprellids and hydrozoans exist. Caine (1998) observed a striking behaviour of *Paracaprella tenuis* when a nudibranch predator of its host, a hydrozoan, was approaching. This resulted in the deterring of the predator. It is certainly difficult for a caprellid to deter large adults of *Dendronotus frondosus* which are the primary consumer of *T. indivisa* on shipwrecks, but they could have an effect on juveniles and other smaller nudibranch species encountered on shipwrecks (*Cuthona* sp. and *Eubranchus* sp.). We also identified three stenothoid amphipods with relatively high densities: *Stenothoe marina*, *S. valida* and *S. monoculoides* (respective maximal densities: 2,300, 1,500 and 6,100 ind.m^{-2}). The Stenothoidae are often found on hydroids and seems to be immune to nematocysts (Gili & Hughes, 1995). The anomuran decapod *Pisidia longicornis* was also found at densities (315 ind.m^{-2} in October to 5,400 ind.m^{-2} in August) far beyond what is usually described in the literature. This species is very abundant on the eastern English Channel where it lives on pebbly bottoms (Carpentier *et al.*, 2005) but sampling method prevents analytical comparisons. In Ireland, Robinson & Tully (2000) found that the highest densities of this species were recorded in early September (640 ind.m^{-2}).

There was a large number of winter characteristic species, when the density of the dominant species was lower. In spring, the bryozoan *Scrupocellaria scruposa* rapidly developed at the base of *T. indivisa*. This genus seems to be frequent on temperate artificial structures (Sconfietti & Marino, 1989; Mallinson *et al.*, 1999; Moreno, 2000; Ardizzone *et al.*, 2000; Relini, 2000; Collins *et al.*, 2002; Watson & Barnes, 2004) and *S. scruposa* is found as one of the first settler on artificial panels (Lindsay *et al.*, 2006). In summer, the large density of *J. herdmani* made it characteristics together with a set of annelid species which could largely prey upon the *J. herdmani* stock. In fall, two species of hydroids, *Obelia* sp. and *clytia hemisphaerica*, were characteristics of the assemblage probably because of the degradation of *T. indivisa* which allowed them to develop.

The set of epibionts associated with the hydroid displayed an apparent regularity from year to year. However, the species richness showed a decrease during the fall-winter period in our results. During this period, a number of species are either absent from the shipwrecks or present under a form that was not accessible with our sampling technique (e.g. encystment or regression stage with size under the mm). A question that remains open is the origin of the species on shipwrecks which are found at several km from each other and the interaction these metapopulations may have with each other. With the high current speed observed on the BPNS region, it is reasonable to think that these sites are probably not strongly isolated but interconnected by dispersal of propagules. These propagules could either be planktonic stages, juveniles for species with direct development (like all the abundant amphipod species found in our study) or even adults with relatively small body size. However, it may be that the colonization of shipwrecks is achieved by only a few propagules. In this case, shipwrecks may have self-sustaining populations of non-planktonic species, while the offspring of planktonic developers do not remain in the area to maintain a sustainable population (Johnannesson, 1988). The answer to these questions could be found in genetic and dispersal model analysis.

ACKNOWLEDGMENTS

The authors wish to thank the crews of the RV Zeeleeuw and RV Belgica for their help during the sampling campaigns and to Céline Delforge for the great help during the sorting process. It's also our pleasure to thank all the people who helped collecting the samples: Drs Y. Laitat, A. Simon, D. Delbare, E. Vanden Bergh, T. Schils, Mss C. Delforge and R. Gyssens and Mrs P.B. Demoulin, G. Rooms, D. Marsham, F. Cray, M. Van Espen, Y. Verkemping, M. Backx, J.P. De Blauwe, J. Haelters, F. Hernandez, F. Darchambeau, G. Van Hoydonck, A. Vanhaelen, R. Knuts & P. Van de Steen. UGent (G. de Smet and M. Steyaert) helped for the pigment analysis. This study has been financially supported by a 'plan Action II' grant (contract N° WI/36/C04) from the Belgian Science Policy. The second author is grateful to MUMM BMDC for data, REMSEM group for the availability of satellite data and Model groups for model results availability. His participation to this study has been funded by BEWREMABI project (Belgian Science Policy).

REFERENCES

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**: 32-46.

Anderson, M. J. & Robinson, J. 2003. Generalised discriminant analysis based on distances. *Australian and New Zealand Journal of Statistics*, **45**: 301-318.

Ardizzone, G. D., Somaschini, A. & Belluscio, A. 2000. Prediction of benthic and fish colonization on the Fregene and other Mediterranean artificial reefs. pp 113-128. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Bavestrello, G., Cerrano, C., Cattaneo-Vietti, R. & Sara, M. 1996. Relations between *Eudendrium glomeratum* (Cnidaria, Hydromedusae) and its associated vagile fauna. *Scientia Marina*, **60**: 137-143.

Baynes, T. W. & Szmant, A. M. 1989. Effects of current on the sessile benthic community structure of an artificial reef. *Bulletin of Marine Science*, **44**: 545-566.

Boero, F. 1984. The ecology of marine hydroids and effects of environmental factors: a review. *Marine Ecology*, **5**: 93-118.

Boero, F. C. & Bouillon, J. 1993. Zoogeography and life cycle patterns of Mediterranean hydromedusae (Cnidaria). *Biological Journal of the Linnean Society*, **48**: 29-266.

Bourget, E. & Harvey, M. 1998. Spatial analysis of recruitment of marine invertebrates on arborescent substrata. *Biofouling*, **12**: 45-55.

Bray, J. R. & Curtis, J. T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs*, **27**: 325-349.

Brey, T. 1986. Formalin and formaldehyde-depot chemicals: effects on dry weight and ash free dry weight of two marine bivalve species. *Meeresforschung - Reports on Marine Research*, **31**: 52-57.

Bulloch, D. K. 1965. The development of the wreck *Pinta* as a marine habitat. *Underwater Naturalist*, **31**: 17-32.

Caine, E.A. 1987. Potential effect of floating dock communities on a South Carolina estuary. *Journal of Experimental Marine Biology and Ecology*, **108**: 83-91.

Caine, E. A. 1998. First case of caprellid amphipod-hydrozoan mutualism. *Journal of Crustacean Biology*, **18**: 317-320.

Calder, D. R. 1990. Seasonal cycles of activity and inactivity in some hydroids from Virginia and South Carolina. *Canadian Journal of Zoology*, **68**: 442-450.

Carpentier, A., Vaz, S., Martin, C. S., Coppin, F., Dauvin, J.-C., Desroy, N., Dewarumez, J. M., Eastwood, P. D., Ernande, B., Harrop, S., Kemp, Z., Koubbi, P., Leader-Williams, N., Lefèbvre, A., Lemoine, N., Loots, C., Meaden, G. J., Ryan, N. & Walkey, M. 2005. Eastern Channel habitat atlas for marine resource management (CHARM). Interreg IIIA, 225 pp.

Claereboudt, M.R., Bureau, D., Cote, J. & Himmelman, J.H. 1994. Fouling development and its effect on the growth of juvenile giant scallops (*Placopecten magellanicus*) in suspended culture. *Aquaculture*, **121**: 327-342.

Clarke, K.R. 1999. Nonmetric multivariate analysis in community-level ecotoxicology. *Environmental Toxicology and Chemistry*, **18**: 118-127.

Clarke, K. R. & Warwick, R. M. 1998. A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, **35**: 523-531.

Clarke, K.R. & Warwick, R.M. 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology-Progress Series*, **216**: 265-278.

Collins, K.J., Jensen, A.C., Mallinson, J.J., Roenelle, V. & Smith, I.P. 2002. Environmental impact assessment of a scrap tyre artificial reef. *ICES Journal of Marine Science*, **59**: S243-S249.

Conlan, K. E. 1989. Delayed reproduction and adult dimorphism in males of the amphipod genus *Jassa* (Corophioidea: Ischyroceridae): an explanation for systematic confusion. *Journal of Crustacean Biology*, **9**: 601-625.

Connor, D. W., Allen, J. H., Golding, N., Howell, K. L., Lieberknecht, L. M., Northen, K. O. & Reker, J. B. 2004. The marine habitat classification for Britain and Ireland, Version 04.05, Circalittoral rock section. Joint Nature Conservation Commitee, Peterborough, UK, 127 pp.

Cornelius, P. F. S. 1981. Life cycle, dispersal and distribution among the Hydroida. *Porcupine Newsletter*, **2**: 47-50.

Costello, M. J., Emblow, C. S. & White, R. 2001. European Register of Marine Species. A check-list of the marine species in Europe and a bibliography of guides to their identification. *Patrimoines naturels*, **50**: 1-463.

Cusson, M. & Bourget, E. 2005. Global pattern of macroinvertebrate production in marine benthic habitat. *Marine Ecology-Progress Series*, **297**: 1-14.

Dean, T. A. 1981. Structural aspect of sessile invertebrates as organizing forces in an estuarine fouling community. *Journal of Experimental Marine Biology and Ecology*, **53**: 163-180.

Dean, T. A. & Hurd, L. E. 1980. Development in an estuarine fouling community: the influence of early colonists on later arrivals. *Oecologia*, **46**: 295-301.

Degraer, S., Vincx, M., Meire, P. & Offringa, H. 1999. The macrozoobenthos of an important wintering area of the common scoter (*Melanitta nigra*). *Journal of the Marine Biological Association of the UK*, **79**: 243-251.

Doody, J. P., Johnston, C. & Smith, B. 1993. Directory of the North Sea coastal margin. Joint Nature Conservation Committee, Peterborough, UK, 262 pp.

Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**: 345-366.

Fettweis, M. & Van den Eynde, D. 2003. The mud deposits and the high turbidity in the Belgian-Dutch coastal zone, southern bight of the North Sea. *Continental Shelf Research*, **23**: 669-691.

Forteath, G. N. R., Picken, G. B., Ralph, R. & Williams, J. 1982. Marine growth studies on the North Sea oil platform Montrose Alpha. *Marine Ecology-Progress Series*, **8**: 61-68.

Gaston, G.R., Bartlett, J.H.W., McAllister, A.P. & Heard, R.W. 1996. Biomass variations of estuarine macrobenthos preserved in ethanol and formalin. *Estuaries*, **19**: 674-679.

Genzano, G.N. 1998. Hydroid epizoites on *Tubularia crocea* and *Sertularella mediterranea* from the intertidal of Mar del Plata, Argentina. *Biologiya Morya (Vladivostok)*, **24**: 126-129.

Genzano, G.N. 2002. Associations between pycnogonids and hydroids from the Buenos Aires littoral zone, with observations on the semi-parasitic life cycle of *Tanystylum orbiculare* (Ammotheiidae). *Scientia Marina*, **66**: 83-92.

Genzano, G.N. & San Martin, G. 2002. Association between the polychaete *Procerastea halleziana* (Polychaeta: Syllidae: Autolytinae) and the hydroid *Tubularia crocea* (Cnidaria: Hydrozoa) from the Mar del Plata intertidal zone, Argentina. *Cahiers de Biologie Marine*, **43**: 165-170.

Genzano, G.N. 2001. Associated fauna and sediment trapped by colonies of *Tubularia crocea* (Cnidaria, Hydrozoa) from the rocky intertidal of Mar del Plata, Argentina. *Biociencias*, **9**: 105-119.

Gili, J.M. & Hughes, R.G. 1995. The ecology of marine benthic hydroids. *Oceanography and Marine Biology: an Annual Review*, **33**: 351-426.

Goss-Cusard, S., Jones, J., Kitching, J. A. & Norton, T. A. 1979. Tide Pools of Carrigathorna and Barloge Creek. *Philosophical Transaction of the Royal Society (Series B)*, **287**: 1-44.

Guerra-Garcia, J.M., Corzo, J. & Garcia-Gomez, J.C. 2002. Clinging behaviour of the Caprellidea (Amphipoda) from the Strait of Gibraltar. *Crustaceana*, **75**: 41-50.

Harvey, M., Bourget, E. & Gagne, N. 1997. Spat settlement of the giant scallop, *Placopecten magellanicus* (Gmelin, 1791), and other bivalve species on artificial filamentous collectors coated with chitinous material. *Aquaculture*, **148**: 277-298.

Harvey, M., Bourget, E., Legault, C. & Ingram, R.G. 1995a. Short-term variations in settlement and early spat mortality of Iceland scallop, *Chlamys islandica* (O.F. Müller). *Journal of Experimental Marine Biology and Ecology*, **194**: 167-187.

Harvey, M., Bourget, E. & Miron, G. 1993. Settlement of Iceland Scallop *Chlamys islandica* Spat in Response to Hydroids and Filamentous Red Algae - Field Observations and Laboratory Experiments. *Marine Ecology-Progress Series*, **99**: 283-292.

Harvey, M., Miron, G. & Bourget, E. 1995b. Resettlement of Iceland scallop (*Chlamys islandica*) spat on dead hydroids: Response to chemical cues from the protein-chitinous perisarc and associated microbial film. *Journal of Shellfish Research*, **14**: 383-388.

Hughes, R.G. 1983. The life-history of *Tubularia indivisa* (Hydrozoa: Tubulariidae) with observations on the status of *T. ceratogyne*. *Journal of the Marine Biological Association of the UK*, **63**: 467-479.

Jensen, A., Collins, K. J. & Smith, P. 2000. The Poole Bay artificial reef project. pp 263-287. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Johannesson, K. 1988. The paradox of Rockall: why is a brodding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*). *Marine Biology*, **99**: 507-513.

Kaandorp, J. A. 1982. Rocky substrate communities of the infralittoral fringe of the Boulonnais coast, NW France: a quantitative survey. *Marine Biology*, **92**: 255-265.

Kruskal, J. B. & Wish, M. 1978. Multidimensional scaling. Sage University Paper series on Quantitative Applications in the Social Sciences n°11. Sage Publications, Beverly Hills and London., 86 pp.

Lanckneus, J., van Lancker, V., Moerkerke, G., Van den Eynde, D., Fettweis, M., de Batist, M. & Jacobs, P. 2001. Investigation of the natural sand transport on the Belgian continental shelf (BUDGET). Final report. Federal Office for Scientific, Technical and Cultural Affairs (OSTC), 104 pp.

Leewis, R. J. & Hallie, F. 2000. An artificial reef experiment off the Dutch Coast. pp 289-306. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Leewis, R. J., van Moorsel, G. W. N. M. & Waardenburg, H. W. 2000. Shipwrecks on the Dutch Continental Shelf as artificial reefs. pp 419-434. *In* Jensen, A. C, Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publishers, Dordrecht.

Lemire, M. & Bourget, E. 1996. Substratum heterogeneity and complexity influence micro-habitat selection of *Balanus sp* and *Tubularia crocea* larvae. *Marine Ecology-Progress Series*, **135**: 77-87.

Leonhard, S. B., Pedersen, J. & Moeslund, B. 2004. Hard bottom substrate monitoring. Horns Rev Offshore Wind Farm. Annual status report 2003. Bio/consult as, Copenhague, Denmark, 62p.

Lindquist, D.G. & Pietrafesa, L.J. 1989. Current vortices and fish aggregations - the current field and associated fishes around a tugboat wreck in Onslow Bay, North-Carolina. *Bulletin of Marine Science*, **44**: 533-544.

Lindsay, H., Todd, C., Fernandes, T. & Huxham, M. 2006. Recruitment in epifaunal communities: an experimental test of the effects of species composition and age. *Marine Ecology-Progress Series*, **307**: 49-57.

Luyten, P. J., Jones, J. E., Proctor, R., Tabor, A., Tette, P. & Wild-Allen, K. 1999. COHERENS – A coupled Hydrodynamic-Ecological model for regional and shelf seas. Users documentation. Report, Management Unit of the Mathematical Models of the North Sea, Brussels, 914 pp.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Science Ltd, Oxford, UK, 256 pp.

Mallinson, J. J., Collins, K. J. & Jensen, A. C. 1999. Species recorded on artificial and natural reefs, Poole Bay, 1989-1996. *Dorset Proceedings*, **121**: 113-122.

MarBEF 2004. European Marine Biodiversity Datasets. Available online at http://www.marbef.org/data/dataset.php. Accessed on 24-8-2006.

Moreno, I. 2000. Artificial reef programme in the Balearic Islands: Western Mediterranean Sea. pp 219-233. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Mullineaux, L.S. & Garland, E.D. 1993. Larval recruitment in response to manipulated field flows. *Marine Biology*, **116**: 667-683.

Nechad, B., De Cauwer, V., Park, Y. & Ruddick, K. 2003. Suspended Particulate Matter (SPM) mapping from MERIS imagery. Calibration of a regional algorithm for the Belgian coastal waters. MERIS user workshop, 10-13th November 2003 . (Frascati). European Space Agency SP549.

Nellis, P. & Bourget, E. 1996. Influence of physical and chemical factors on settlement and recruitment of the hydroid *Tubularia larynx*. *Marine Ecology-Progress Series*, **140**: 123-139.

Pakhomov, E.A. 2003. Correction of zooplankton and benthos biomass under-estimations from formaldehyde-preserved samples. *Archive of Fishery and Marine Research*, **50**: 141-148.

Pison, V. & Ozer, J. 2003. Operational products and services for the Belgian coastal waters. pp 503-509. *In* Dalhin, H., Flemings, N. C., Nittis, K., and Petersson, S. E. (eds), Building the European capacity in operational oceanography. Proceedings of the Third International Conference on EuroGOOS, Elsevier Oceanography, series 69.

Pyefinch, K. A. & Downing, F. S. 1949. Notes on the general biology of *Tubularia larynx* Ellis & Solander. *Journal of the Marine Biological Association of the UK*, **28**: 21-44.

Relini, G. 2000. Coal ash for artificial habitats in Italy. pp 343-364. *In* Jensen, A., Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publisher, Dordrecht.

Robinson, M. & Tully, O. 2000. Dynamics of a subtidal population of the porcellanid crab *Pisidia longicornis* (Decapoda: Crustacea). *Journal of the Marine Biological Association of the UK*, **80**: 75-83.

Rumohr, H., Brey, T. & Ankar, S. 1987. A compilation of biometric conversion factor for benthic invertebrates of Baltic Sea. *Baltic Marine Biology Publications*, **9**: 1-56.

Sampaolo, A. & Relini, G. 1994. Coal ash for artificial habitats in Italy. *Bulletin of Marine Science*, **55**: 1277-1294.

Schmidt, G. H. 1983. The hydroid *Tubularia larynx* causing 'bloom' of the ascidians *Ciona intestinalis* and *Ascidiella aspersa*. *Marine Ecology-Progress Series*, **12**: 103-105.

Sconfietti, R. & Marino, R. 1989. Patterns of zonation of sessile macrobenthos in a lagoon estuary (northern Adriatic Sea). *Scientia Marina*, **53**: 655-661.

Shapiro, S. S. & Wilk, M. B. 1965. An analysis of variance test for normality (complete samples). *Biometrika*, **52**: 591-611.

Takeuchi, I. & Hirano, R. 1995. Clinging behaviour of the epifaunal caprellids (Amphipoda) inhabiting the *Sargassum* zone on the Pacific coast of Japan, with its evolutionary implications. *Journal of Crustacean Biology*, **15**: 481-492.

Walters, L.J. & Wethey, D.S. 1996. Settlement and early post settlement survival of sessile marine invertebrates on topographically complex surfaces: The importance of refuge dimensions and adult morphology. *Marine Ecology-Progress Series*, **137**: 161-171.

Watson, D.I. & Barnes, D.K.A. 2004. Temporal and spatial components of variability in benthic recruitment, a 5-year temperate example. *Marine Biology*, **145**: 201-214.

Wetzel, M.A., Leuchs, H. & Koop, J.H.E. 2005. Preservation effects on wet weight, dry weight, and ash-free dry weight biomass estimates of four common estuarine macro-invertebrates: no difference between ethanol and formalin. Helgolander Meeresuntersuchungen, 59: 206-213.

Whomersley, P. & Picken, G. B. 2003. Long-term dynamics of fouling communities found on offshore installations in the North Sea. Journal of the Marine Biological Association of the UK, 83: 897-901.

Woodhead, P. M. J. & Jacobson, M. E. 1985. Epifaunal settlement, the processes of community development and succession over two years on an artificial reef in the New York Bight. Bulletin of Marine Science, 37: 364-376.

Yamashita, K., Kawaii, S., Nakai, M. & Fusetani, N. 2003. Larval behavioral, morphological changes, and nematocyte dynamics during settlement of actinulae of Tubularia mesembryanthemum, Allman 1871 (Hydrozoa : Tubulariidae). Biological Bulletin, 204: 256-269.

Zintzen, V., Massin, Cl., Norro, A. & Mallefet, J. 2006. Epifaunal inventory of two shipwrecks from the Belgian Continental Shelf. Hydrobiologia, 555: 207-219.

Zintzen, V., Norro, A., Massin, C. & Mallefet, J. Submitted. Spatial variability of epifaunal communities from an artificial habitat on a highly hydrodynamic environment. Marine Ecology-Progress Series.

Chapter VI - Shipwrecks and ecosystem functioning

Parablennius gattorugine on the Kilmore shipwreck.

ARTICLE 6: MACROBENTHOS OF SHIPWRECKS WITHIN AND AROUND THE BELGIAN WATERS AS A POTENTIAL FOOD RESOURCE FOR FISH POPULATIONS

The literature review of the thesis introduced the reader to the extended range of papers which concentrated their effort on artificial reefs dedicated to fisheries management. Most of theses papers dealt with artificial reefs which were planned, but the power of other structures like offshore platforms to attract fish was also highlighted. Indeed, shipwrecks also attract fish. As soon as we could enjoy correct visibility on Belgian shipwrecks, it appeared evident that a large amount of fish were attracted by every site we investigated. The most obvious species was *Trispoterus luscus* (pouting), but other commercially important species were frequently observed: *Pollachius pollachius*, *Pollachius virens*, *Gadus morhua* (cod) and D*icentrarchus labrax* (seabass). Other species typical of hard substrates were also censused by the divers, like *Parablennius gattorugine* or apparently *Crenilabrus melops*. There is no doubt that such species as *P. gattorugine* would not be present without the presence of shipwrecks because they are restricted to live on hard bottoms. In this case, the shipwrecks supply the essential habitat for a species to survive and help to produce more fish biomass. However, other species like the Gadidae mentioned above are not restricted to hard bottoms and are thus attracted by shipwrecks. We do not know why these fish are found so frequently and abundantly around reefs. What is an important question is to know if these species are just attracted without any other effect, or if they find in these places some advantage over living far from any reef. In other words, it would be interesting to know if shipwrecks allow producing more fish biomass. This would be an important discovery for fisheries management on Belgian waters.

These questions are not easily answered because they need a global approach on the fish stocks in the area.

One of the advantages that commercially important species could find living around Belgian shipwrecks, would be to feed on the large amount of biomass which develop on these sites. We decided to investigate the diet of *Gadus morhua* and *Dicentrarchus labrax* that were caught on shipwreck sites. This was achieved by following recreational fishermen who specifically go fishing on North Sea shipwrecks because of higher expected catches. An agreement was found to collect the stomachs of the catches.

We acknowledge that the following study has several weak points: (1) the number of collected samples is relatively low, (2) due to fishing regulations, only specimens above 30 cm could be collected; thus not results for juveniles/subadults are available, (3) it does not give take into account other factors than shipwreck species in attracting fish populations (like the provision of shelter).

However, the results will unambiguously show that at least *G. morhua* is using shipwreck fauna as food source.

MACROBENTHOS OF SHIPWRECKS WITHIN AND AROUND THE BELGIAN WATERS AS A POTENTIAL FOOD RESOURCE FOR FISH POPULATIONS

Oliver T. Crawford[1], Steven Degraer[2], Jérôme Mallefet[3], Vincent Zintzen[3,4,*]

[1] Environment Agency, Anglian Regional Office, Kingfisher House, Goldhay Way, Orton Goldhay, Peterborough, Cambridgeshire, PE2 5ZR, UK.
[2] University of Ghent, Department of Biology, Marine Biology Section, K.L. Ledeganckstraat 35, B9000 Gent, Belgium.
[3] University of Louvain, Biology Laboratory, Kellner Building, place Croix du Sud 3, B-1348 Louvain-la-Neuve, Belgium.
[4] Royal Belgian Institute of Natural Sciences, Rue Vautier 29, B-1000 Brussel, Belgium.
*Email of corresponding author: vincent.zintzen@naturalsciences.be

Keywords: Stomach content analysis, shipwrecks, artificial reefs, *Dicentrarchus labrax*, *Gadus morhua*, feeding strategy.

1. INTRODUCTION

Shipwrecks of the Belgian and neighbouring waters attract fish species, in particular *Dicentrarchus labrax* (Linnaeus, 1758) (seabass) and *Gadus morhua* (Linnaeus, 1758) (cod). These two species, as well as Pollack, *Pollachius pollachius* (Linnaeus, 1758) and Pouting, *Trisopterus luscus* (Linnaeus, 1758), are targeted by sport fishermen whom specifically seek shipwrecks knowing that the aggregation of these fish yields better catches. The reasons why fish are attracted by shipwrecks are that they provide shelter from currents and predators (Danner *et al.*, 1994;Barshaw & Spanier, 1994), are possible recruitment sites (Bull & Kendall, 1994) and potentially harbour favoured prey (Pike & Lindquist, 1994). If any of these effects truly occur, it is likely that the biomass production of these species will be enhanced, either through better growth, improved gamete production or increased recruitment.

Recent biological surveys of shipwrecks in Belgian (Massin *et al.*, 2002; Zintzen *et al.*, 2006) and Dutch (Leewis *et al.*, 2000) waters have documented far greater macrobenthos biodiversity and biomass compared with the surrounding soft sediments (Van Hoey *et al.*, 2004). Not only is the biomass greater per unit area but the fauna is significantly different, most belonging to the sessile and slow moving fauna (Zintzen *et al.*, in prep.). Whether this fauna is a key factor for the attraction of fish is still poorly documented.

An investigation was carried out to discern whether the epifauna of shipwrecks was a key constituent of fish diet caught in the vicinity of these sites and if, as a consequence, these species are using the shipwreck environment as a feeding ground. Two commercially important fish species, cod and seabass, were targeted. The rejection of this hypothesis would allow concluding that fish are attracted by shipwrecks for other reasons that the increased biomass of hard substrate preys.

2. MATERIAL AND METHOD

The most direct way to investigate the importance of a potential food source is to study its status within the diet via stomach content analysis. Stomachs of *Dicentrarchus labrax* and *Gadus morhua* were sampled between 30th September 2004 and 30th March 2005 by accompanying sport fishing excursions specifically visiting shipwrecks. Sites were located between 30 and 55 km from the coast, on Belgian, French (distance from Belgian waters <10 km) and Dutch (distance from Belgian waters< 45 km) waters. 71 stomachs were collected; 26 from seabass and 45 from cod. The size of seabass and cod ranged from 30 to 60 cm and from 30 to 90 cm, respectively. Smaller stomachs could not be collected because the legislation in place did not allow for fishing specimens under 30 cm and results will apply to adult populations. Stomachs were kept in buffered formalin (final concentration: 4 %, pH 8.2-8.4) for 24-48h and then transferred to buffered alcohol. Prey items were sorted and identified under binocular microscope to the lowest taxonomic level possible to facilitate comparisons with the fauna of shipwrecks. Where possible, prey fish had their stomach contents identified also. After deducting empty stomachs there were 18 seabass and 40 cod samples available for analysis.

Dry weights of all food items were measured to the nearest mg after drying at 80°C until constant weight. Traditional methods, frequency of occurrence (%O) and the percentage weight (%W) (Hyslop, 1980), and multivariate methods, % Principal Component Analysis (%PCA; De Billy *et al.*, 2000) of dietary analysis were used to assess the feeding strategy and importance of prey items in the diets. All calculations for the %PCA were made with the software package ADE-4 (Thioulouse *et al.*, 1997). A similarity matrix of stomach samples was constructed using the Bray-Curtis similarity coefficient (Bray & Curtis, 1957). This was then subjected to one-way analysis of similarity (ANOSIM) tests to ascertain whether there were significant differences between the stomach content of the two species (Clarke & Warwick, 2001). Similarity percentages (SIMPER) tests were carried out to identify the prey items which contributed most to similarity and dissimilarity between fish species (Clarke & Warwick, 2001). All the results were compared with an extensive faunal list of shipwrecks macrobenthos from Belgian waters created during several campaigns (see Massin *et al.*, 2002 and Zintzen *et al.*, 2006), as well as with species list of soft sediment species collected in the framework of several projects (see Van Hoey *et al.*, 2004). The community of all these shipwrecks will be dominated by the hydrozoan *Tubularia indivisa* which allow for the development of a diversified epibenthic community. A species was considered being typical of shipwrecks if it was found in more than 10% of the samples taken from shipwrecks and found in less than 3% of the soft sediment samples. A species was deemed typical of soft sediment if it was present in more than 10% of the soft samples and less than 3% of shipwreck samples. When species occurred frequently (>10% of the samples) on soft sediment and shipwrecks, the species was considered identified on wrecks, but not exclusive to hard substrates.

3. RESULTS

The seabass diet was dominated by fish, accounting for 95% of the weight (Table 1). The majority of individuals specialised on it. *Trachurus trachurus* was the only identified species. The other food items were soft bottom invertebrates which contributed minimally to the diet (Figure 1).

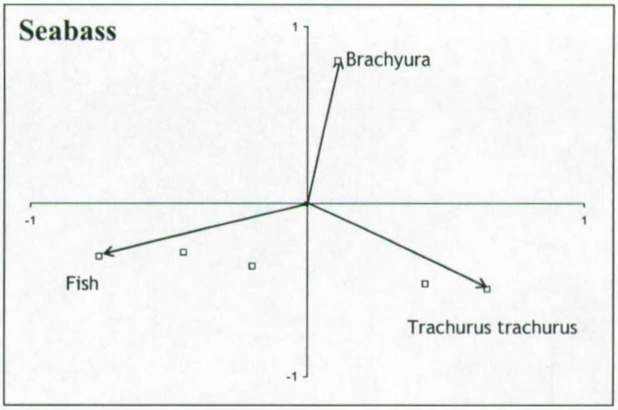
The cod diet was far more diverse. Of the 47 food items identified 24 had been identified on shipwrecks. Fish (Clupeidae and *Limanda limanda*) dominated by weight, followed by species identified on shipwrecks, among which some species restricted in their distribution to shipwrecks, such as *Necora puber*, *Ophiothrix fragilis*, *Pisidia longicornis* and *Pilumnus hirtellus* (Table 1). The most frequently occurring food items after fish were *Tubularia indivisa* and *Jassa herdmani*, two species which characterise shipwreck communities. *P. longicornis* and *O. fragilis* occurred in large numbers in some stomachs: three stomachs included 91, 63 and 49 individuals of *Pisidia longicornis*, a species repeatedly taken with *P. hirtellus* or *Liocarcinus holsatus*; one stomach contained solely *O. fragilis* with a total of 89 individuals. The most important food items to cod were fish, *N. puber*, *B. undatum*, *O. fragilis* and *P. longicornis* (Figure 1 and Table 1).

The one-way ANOSIM showed that the seabass and cod stomach samples did not actually significantly differ from each other. However, the significance level was low at 10.8% with an R-value of 0.068. A SIMPER test revealed that the average similarity for seabass was 35.88% and 17.36%

Table 1. Frequency of occurrence (%O), dry weight (DW) and percentage of dry weight (%DW) of prey items found in the stomachs of Seabass (*Dicentrarchus labrax*, N=18) and Cod (*Gadus morhua*, N=40) taken on shipwrecks from Belgian waters. * Taxa identified on wrecks or found exclusively on hard substrates. ** Taxa identified on wrecks, but not exclusive to hard substrates. na: not applicable.

PREY CATEGORY	**COD**			**SEABASS**		
	% O	**DW (g)**	**% DW**	**% O**	**DW (g)**	**% DW**
PISCES						
Unidentifed sp.	55	170.894	58.706	66.67	27.538	64.38
Trachurus trachurus (Linnaeus, 1758)	-	-	-	38.89	13.243	30.96
Limanda limanda (Linnaeus, 1758)	5.0	60.021	20.619	-	-	-
Clupeidae sp.	2.5	7.009	2.408	-	-	-
Congridae sp.	2.5	0.021	0.007	-	-	-
CRUSTACEA						
Unidentified sp.	5	0.331	0.114	-	-	-
DECAPODA						
Necora puber (Linnaeus, 1767)*	12.5	10.824	3.718	-	-	-
Unidentified Brachyura sp.	17.5	5.79	1.989	11.11	0.862	2.02
Pisidia longicornis (Linneaus, 1767)*	22.5	4.233	1.454	-	-	-
Pilumnus hirtellus (Linnaeus, 1761)*	7.5	3.933	1.351	-	-	-
Liocarcinus holsatus (Fabricius, 1798)**	7.5	2.002	0.688	-	-	-
Liocarcinus sp.**	5	1.414	0.486	-	-	-
Paguridae sp.**	7.5	0.697	0.239	-	-	-
Crangon crangon (Linnaeus, 1758)	10	0.368	0.126	-	-	-
Anomura sp.	2.5	0.244	0.084	-	-	-
Pagurus bernhardus (Linnaeus, 1758)**	2.5	0.168	0.058	5.56	0.371	0.87
Portunidae sp.**	2.5	0.145	0.05	-	-	-
Unidentified Decapoda sp.	5	0.07	0.024	-	-	-
Unidentified Natantia sp.	10	0.028	0.01	-	-	-
Galathea intermedia Lilljeborg, 1851	2.5	0.016	0.005	-	-	-
AMPHIPODA						
Jassa herdmani (Walker, 1893)*	25	0.283	0.097	-	-	-
Caprella linearis (Linnaeus, 1767)*	2.5	0.02	0.007	-	-	-
Unidentified Amphipoda sp.	12.5	0.016	0.005	-	-	-
Caprella tuberculata Guérin, 1836*	5	0.005	0.002	-	-	-
Phtisica marina Slabber, 1769*	2.5	<0.001	<0.001	-	-	-
Stenothoe marina (Bate, 1856)**	2.5	<0.001	<0.001	-	-	-
Corophiidae sp.	2.5	<0.001	<0.001	-	-	-
ANNELIDA						
Arenicola marina (Linnaeus, 1758)	5	1.487	0.511	-	-	-
Unidentified Polychaeta sp.	2.5	0.085	0.029	-	-	-
Sabellaria spinulosa Leuckart, 1849*	5	0.024	0.008	-	-	-
Nephtyidae sp.	2.5	0.015	0.005	-	-	-
ECHINODERMATA						
Ophiothrix fragilis (Abildgaard,1789)*	10	5.972	2.052	-	-	-
Unidentified Ophiuroidea sp.	2.5	0.055	0.019	-	-	-
Echinocardium cordatum (Pennant, 1777)	2.5	0.005	0.002	-	-	-

PREY CATEGORY	**COD**			**SEABASS**		
	% O	**DW (g)**	**% DW**	**% O**	**DW (g)**	**% DW**
CNIDARIA	15	3.071	1.055	-	-	-
Tubularia indivisa Linnaeus, 1758*	22.5	0.017	0.006	-	-	-
Tubularia sp.*	2.5	0.011	0.004	-	-	-
Plumulariidae sp.	2.5	<0.001	<0.001	-	-	-
Sertularia sp.**	10	<0.001	<0.001	-	-	-
Unidentified Hydrozoa sp.	2.5	0.111	0.038	-	-	-
Actiniaria sp.**						
MOLLUSCA	-	-	-	5.56	0.643	1.5
Unidentified Prosobranchia	5	6.178	2.122	-	-	-
Buccinum undatum Linnaeus, 1758	2.5	0.167	0.057	-	-	-
Nassarius incrassatus (Ström, 1768)*	2.5	0.023	0.008	-	-	-
Euspira pulchella (Risso, 1826)**						
BIVALVIA	12.5	1.41	0.484	5.56	0.116	0.27
Shell fragments	5	0.756	0.26	-	-	-
Aequipecten opercularis (Linnaeus, 1758)*	2.5	0.097	0.033	-	-	-
Pectinidae sp.**						
TUNICATA	2.5	0.001	<0.001	-	-	-
Diplosoma sp.*						
OTHER	32.5	3.082	1.059	-	-	-
Unidentified fragments						
NON FOOD ITEMS	5	na	na	-	-	-
Fibre	15	na	na	5.56	na	na
Rock	10	na	na	-	-	-
Sand	2.5	na	na	-	-	-
Wood	7.5	na	na	5.56	na	na
Pomatoceros triqueter (Linnaeus, 1758) tubes	12.5	na	na	-	-	-
Sabellaria spinulosa tubes						



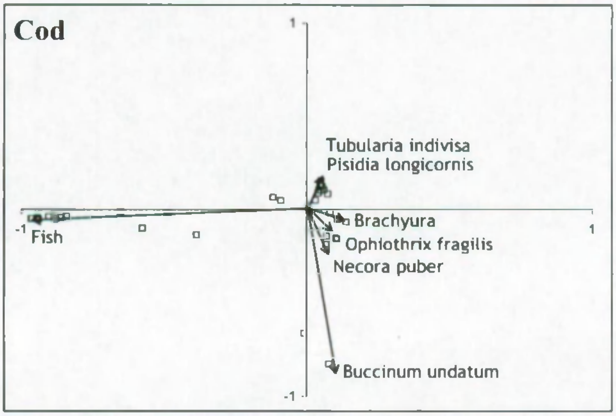


Figure 1. After row percentage transformation principal component analysis (%PCA) of the stomach contents (expressed as dry weight of prey items) from *Dicentrarchus labrax* (Seabass) and *Gadus morhua* (Cod) taken on Belgian shipwrecks. □ indicates one stomach. Only the important variables (prey items) are projected. Seabass: axes 1 and 2 projected (70.6% and 29.16% of the total variation respectively). Cod: axes 1 and 5 (38.83% and 6.15% of the total variation).

for cod with unidentified fish contributing the most to the similarity within each group.
Only 9 *T. trachurus*, 3 unidentified fish and the 1 Clupeid had reached a low enough level of digestion to extract the content of their stomachs. The lengths of the *T. trachurus* ranged from 8.2 cm to 10.2 cm. The unidentified fish and clupeid were of similar size and maturity. The amphipod *Atylus swammerdami* (Milne-Edward, 1830) was identified in the *T. trachurus* stomachs. Species of the genus *Bathyporeia* were identified from the unidentified fish. These are amphipods which also inhabit fine sediment of low mud content. Finally, the mysid *Schistomysis spiritus* (Norman, 1860) was identified from the Clupeid stomach.

4. DISCUSSION

The largest part of the diet for seabass was composed of fish and Brachyura. The unidentified fish are most probably *Trachurus trachurus*. The *T. trachurus* identified in the seabass stomachs were probably members of the stock abundant in the Southern North Sea during autumn (Pawson, 1995). It seems that the seabass temporarily specialised on the stock at that time. The fat and energy content of adult *T. trachurus* is highest in autumn (Abaunza *et al.*, 2003) which would make them more appealing to the seabass. Interestingly, Kelly (Kelley, 1987) did not observe *T. trachurus* in the seabass he sampled around the southern and western coast of the UK. The question of whether seabass prey on *T. trachurus* at the shipwreck location is not easily answered. *Trachurus trachurus* has been identified as a resident (at least temporarily) of shipwrecks (Massin *et al.*, 2002) and the specimens from the seabass stomachs were easily identifiable suggesting they were taken in the habitat they were caught in, i.e. the shipwrecks. However, seabass are a highly mobile fish making it possible that food, although still being quiet fresh when collected near shipwrecks, was swallowed in a different habitat. The lengths of the *T. trachurus* ranged from 8.2 cm to 10.2 cm, which classes them as juvenile (Knijn *et al.*, 1993). The stomach content of *T. trachurus* specimens suggested they spend time foraging in a habitat of fine sand. Thus it is most probable that *T. trachurus* forage at soft sediments surrounding the shipwrecks. Therefore seabass either prey on *T. trachurus* at the soft sediments or at the shipwrecks when *T. trachurus* return for shelter. In consequence, it is probably the presence of *T. trachurus* in the close vicinity of shipwrecks which attracts seabass. The attraction of *T. trachurus* could be linked to the shelter from currents and predators provided by the structure of shipwreck.

Essentially, the prey items found to be most important to the cod were fauna which grow largest (Fish, *Necora puber* or *Buccinum undatum*) or form dense aggregations on shipwrecks (*Tubularia* sp, *Jassa herdmani*, *Pisidia longicornis* and *Ophiothrix fragilis*, see Zintzen *et al.*, 2006). This is probably because food selection by cod is primarily governed by the size of the food items in relation to their own size (Daan, 1973). The cod's diet gradually shifts from crustaceans to fish with increasing size because for small cod, fish are towards the upper limit of prey size whereas they can easily find crustaceans of an appropriate size. In contrast, crustaceans would be below the appropriate size for larger cod (Daan, 1973). If prey size is important to cod then it is hard to see why these fish would consume *Tubularia sp.*, *Jassa herdmani* and the other amphipods and cnidarians identified on shipwrecks. Given their size they are unlikely to be important. Therefore given the very small quantities yet relatively high occurrence in stomachs, in conjunction with their vast coverage on shipwrecks, it is most probable that *Tubularia* sp., *J. herdmani*, *P. longicornis* and *O. fragilis* were consumed accidentally whilst cod preyed on Brachyura for example. Their presence within the stomach of cod, can thus be considered to be a marker of the feeding ground, rather than a selected food item for cod. The occurrence of the other amphipods and hydrozoans in the stomachs may be due to the fact that the species diversity is very high in the *T. indivisa* community found on the shipwrecks (Zintzen *et al.*, 2006). However, a number of individuals had no *Tubularia sp.* in their stomach while a high number of the small decapod *P. longicornis* and the ophiuroid *O. fragilis* were found. It suggests that these cod were specifically targeting these two species because they are closely associated with *Tubularia sp* which acts as a support for other species on shipwrecks.

In conclusion, although cod and seabass are often found together in large shoals surrounding shipwrecks, different reasons might explain why these fish aggregate there. Stomach content analysis suggests that these species might have different predation strategies: while cod appears to prey on organisms coming to feed on wreck epifauna, seabass are more likely to feed on other fish species seeking shelter or attracted by other parameters resulting from the presence of the wreck.

Shipwrecks of the Belgian and neighbouring waters attract fish species, in particular *Dicentrarchus labrax* (Linnaeus, 1758) (seabass) and *Gadus morhua* (Linnaeus, 1758) (cod). These two species, as well as Pollack, *Pollachius pollachius* (Linnaeus, 1758) and Pouting, *Trisopterus luscus* (Linnaeus, 1758), are targeted by sport fishermen whom specifically seek shipwrecks knowing that the aggregation of these fish yields better catches.

ACKNOWLEDGEMENT

We thank Dr Claude Massin for his suggestions and careful revision of the manuscript. This study has been supported by a 'plan Action II' grant attributed to Mr Vincent Zintzen from the Federal Office for Scientific, Technical and Cultural Affairs (OSTC).

REFERENCES

Abaunza, P., Gordo, L., Karlou-Riga, A., Murta, A., Eltink, A. T. G. W., Garcia Santamaria, M. T., Zimmerman, C., Hammer, C., Lucio, P., Iversen, S. A., Molloy, J. & Gallo, E. 2003. Growth and reproduction of horse mackerel, *Trachurus trachurus* (Carangidae). *Reviews in Fish Biology and Fisheries*, **13**: 27-61.

Barshaw, D. & Spanier, E. 1994. Anti-predator behaviors of the Mediterranean slipper lobster, *Scyllarides latus*. *Bulletin of Marine Science*, **55**: 375-382.

Bray, J. R. & Curtis, J. T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs*, **27**: 325-349.

Bull, A. & Kendall, J. 1994. An indication of the process - offshore platforms as artificial reefs in the Gulf of Mexico. *Bulletin of Marine Science*, **55**: 1086-1098.

Clarke, K. R. & Warwick, R. M. 2001. Change in marine communities: an approach to statistical analysis and interpretation. 2nd edition. PRIMER-E, Plymouth, UK, 172 pp.

Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod. *Journal of Sea Research*, **6**: 479-517.

Danner, E. M., Wilson, T. C. & Schlotterbeck, R. E. 1994. Comparison of rockfish recruitment of neashore artificial and natural reefs off the coast of central California. *Bulletin of Marine Science*, **55**: 333-343.

De Billy, V. D., Doledec, S. & Chessel, D. 2000. Biplot presentation of diet composition data: an alternative for fish stomach contents analysis. *Journal of Fish Biology*, **56**: 961-973.

Hyslop, E. J. 1980. Stomach content analysis - a review of methods and their application. *Journal of Fish Biology*, **17**: 411-429.

Kelley, D. F. 1987. Food of bass in UK waters. *Journal of the Marine Biological Association of the UK*, **67**: 275-286.

Knijn, R. J., Boon, T. W., Heessen, H. J. L. & Hislop, J. R. G. 1993. Atlas of North Sea fishes. Based on bottom-trawl survey data for the years 1985-1987. ICES Cooperative Research Report, No.194.

Leewis, R. J., van Moorsel, G. W. N. M. & Waardenburg, H. W. 2000. Shipwrecks on the Dutch Continental Shelf as artificial reefs. pp 419-434. *In* Jensen, A. C, Collins, K. J, and Lockwood, A. P. M. (eds), Artificial reefs in European Seas, Kluwer Academic Publishers, Dordrecht.

Massin, Cl., Norro, A. & Mallefet, J. 2002. Biodiversity of a wreck from the Belgian Continental Shelf: monitoring using scientific diving. Preliminay results. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **72**: 67-72.

Pawson, M. G. 1995. Biogeographical identification of English Channel fish and shellfish stocks. Fisheries Research Technical Report Number 99, Ministry of Agriculture, Fisheries and Food Directorate of Fisheries Research, UK.

Pike, L. & Lindquist, D. 1994. Feeding ecology of spottail pinfish (*Diplodus holbrooki*) from an artificial and natural reef in Onslow Bay, North Carolina. *Bulletin of Marine Science*, **55**: 363-374.

Thioulouse, J., Chessel, D., Dolédec, S. & Oliver, J. M. 1997. ADE-4: a multivariate analysis and graphical display software. *Statistics and computing*, **7**: 75-83.

Van Hoey, G., Degraer, S. & Vincx, M. 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuarine, Coastal and Shelf Science*, **59**: 599-613.

Zintzen, V., Massin, Cl., Norro, A. & Mallefet, J. 2006. Epifaunal inventory of two shipwrecks from the Belgian Continental Shelf. *Hydrobiologia*, **555**: 207-219.

ARTICLE 7: THE SPONGE INHABITING BARNACLE *ACASTA SPONGITES* (POLI, 1795) (CRUSTACEA, CIRRIPEDIA), A NEW RECORD FOR THE SOUTHERN NORTH SEA: HOW ARTIFICIAL HABITATS MAY INCREASE THE RANGE OF A SPECIES.

It was already stressed that shipwrecks in the Southern Bight of the North Sea are patches of hard substrates in a seabed dominated by soft sediments. The species list of the article 2 revealed that a large number of species were new for the Belgian fauna and that among these, some were southern species whose records on shipwrecks extend their previous distribution further to the north. The barnacle *Acasta spongites* is one of these species. This short paper takes the example of this sponge inhabiting barnacle to illustrate the potential role of artificial habitats for the dissemination of species. In the context of global warming, shipwrecks may have an important role to play in order to facilitate the spreading of species to the north. Indeed, artificial habitats created by man activities may act as stepping stones. However, this paper is naturally no proof that *A. spongites* is extending to the north because of global warming. It may be that this species was never found on the Southern Bight of the North Sea simply because we never searched for it at the right place before. However, what may be the cause, it is clear that shipwrecks provide the habitat for a set of species typically associated with hard substrates and extend the distribution of some.

THE SPONGE INHABITING BARNACLE *ACASTA SPONGITES* (POLI, 1795) (CRUSTACEA, CIRRIPEDIA), A NEW RECORD FOR THE SOUTHERN NORTH SEA: HOW ARTIFICIAL HABITATS MAY INCREASE THE RANGE OF A SPECIES.

Vincent Zintzen[1,2] and Francis Kerckhof[3]

[1] Royal Belgian Institute of Natural Sciences, Malacology Section, Rue Vautier 29, B-1000 Brussels, Belgium.
[2] University of Louvain, Biology Laboratory, Kellner Building, place Croix du Sud 3, B-1348 Louvain-la-Neuve, Belgium.
[3] Royal Belgian Institute of Natural Sciences, Marine Environmental Management Section, 3e en 23e Linieregimentsplein, B-8400 Oostende, Belgium.

1. INTRODUCTION

Barnacle species of the genus *Acasta* Leach, 1818 are obligate symbionts of Demospongiae (Choristida, Axinellida, Poecilosclerida, Haplosclerida and Dictyoceratida) (Zullo & Standing, 1983; Kolbasov, 1993) although some species are found in Anthozoa (Alcyoniaria, Octocorallia and Antipatharia) (Kolbasov, 1993; Van Syoc & Winther, 1999). Twenty seven species belonging to this genus were described (Kolbasov, 1993), most of them distributed in tropical, subtropical and warm temperate regions of the world. *Acasta spongites* (Poli, 1795) is the only known member of the genus occurring in North-East Atlantic waters.

The known geographic occurrence of *A. spongites* ranges from the British Isles (Pilsbry, 1916; Moyse, 1961; Bassindale, 1964) to the Mediterranean (Pilsbry, 1916; Relini, 1980; Koukouras & Matsa, 1998) through the Atlantic coast of France (Bocquet-Védrine, 1966; du Boullay *et al.*, 2002). However, we have no knowledge of the presence of *A. spongites* along the Spanish and Portuguese Atlantic coast. The species is apparently not reported from the West African coasts (Stubbings, 1967) and from the North Sea (Nilsson-Cantell, 1978). It is also mentioned in the Red Sea, Japan and South Africa (Newman & Ross, 1976) but these records may need confirmation. The occurrence around the British Islands is restricted to the south and south-west coasts only (MarBEF-EurOBIS, 2004) and it is also noted on the south coast of Ireland (MarBEF-EurOBIS, 2004). Overall, the number of recent records stays very limited. The earlier presence of the species in the English Channel is documented in by the Plymouth marine fauna (Marine Biological

Association, 1957) and the species list of Glaçon (Glaçon, 1971). However, if recent records are rather scarce, the species is not uncommon in suitable habitats of the western Channel (own observations).

A. spongites is a sublittoral species living embedded in various species of Demospongiae (Darwin, 1854; Relini, 1980). In north-western European waters, *A. spongites* is invariably found associated with the sponge *Dysidea fragilis* (Montagu, 1818) (Crisp & Southward, 1961; Moyse, 1961; Bassindale, 1964; Hayward & Ryland, 2000). The sponge and its host need hard substrates for their establishment which is obviously a limiting factor for the spreading of both species.

2. MATERIAL AND METHOD

The Belgian Continental Shelf consists mostly of sandy sediments with some patches of pebbles in gullies between sandbanks (Lanckneus *et al.*, 2001; Kerckhof & Houziaux, 2003). However, typical epifaunal species are present on the large number of shipwrecks that can be found in the Belgian marine waters (Zintzen *et al.*, 2006). Until recently, these offshore hard substrates received little attention and their biota remained largely unknown. A recent investigation which studied the epifauna of four shipwrecks in Belgian marine waters was performed between 2003 and 2005 and revealed the presence of *A. spongites* on one of the sites. This shipwreck, the Kilmore, sank in 1906 and lays south-west of the Westhinder sandbank, 32 km offshore (N051°23'.730 - E002°29'.790; WGS84) at a depth of 30 m (LMWS). Sixty three quantitative samples (frames of 25x25 cm) were scraped from the surface of the shipwreck.

3. RESULTS AND DISCUSSION

Two of these samples revealed the presence of in total three specimens of *A. spongites* in samples taken at five meters above the bottom. The first specimen was found in March 2005. It measured 8.6 mm (basal diameter), by 9.2 mm (height from base to summit of the carina). The size of the two specimens found in August 2005 was 3.9 x 3.6 mm and 3.0 x 3.2 mm, respectively. Mature size given for this species in the literature is about 8 mm in basal diameter (Bassindale, 1964; Relini, 1980) indicating that at least the specimens from March can be considered as adults. They were all associated with the sponge *D. fragilis*. This sponge was identified on 13% of all the samples from the Kilmore and on 10% of all the samples from prospected Belgian shipwrecks (N=192). The fouling community of the Kilmore was dominated by the hydrozoan *Tubularia indivisa* Linnaeus, 1758 which covered most of the shipwreck surface. A more detailed description of the epifaunal communities on shipwrecks can be found elsewhere (Massin *et al.*, 2002; Zintzen *et al.*, 2006). Other barnacles found during the study of Belgian shipwrecks included *Verruca stroemia* O.F. Müller, 1776 and *Balanus crenatus* Bruguiére, 1789.

This is the first record of *A. spongites* for Belgium and for the Southern Bight of the North Sea. It has not been found on other shipwrecks yet, but it is reasonable to think that a more intensive sampling effort would bring new records from other sites in natural and artificial hard substrates. Furthermore, *D. fragilis* was identified on other shipwrecks. Since *A. spongites* is living in a sponge which is largely covering the barnacle, its presence may remain unnoticed to the unskilled observer.

Recently, other barnacle species with warm water affinities such as *Balanus perforatus* Bruguiére, 1789 and *Balanus amphitrite* Darwin, 1854 as well as more exotic species have been discovered in the waters off the Southern North Sea (Kerckhof, 2002) and Kerckhof unpublished records) and in the English Channel (Southward, 1995). It indicates that certain barnacle species are spreading to the north or establishing themselves as a response to recent climate changes which are predicted to result in broad planktonic, pelagic and benthic community changes (Southward *et al.*, 1995; Hiscock *et al.*, 2003; Hawkins *et al.*, 2003; Southward *et al.*, 2005; Mieszkowska *et al.*, 2006). However, certain particular habitats were not thoroughly sampled in the past, so it is difficult to assess if the presence of a certain species with southern affinities might be the result of a range extension, due to the recent warming up, or if it was present over a longer period of time and overlooked/neglected in the past.

The fauna of the eastern part of the English Channel can be considered as an impoverished version of the western part. Many species present in the western English Channel are apparently absent in the eastern part while all species present in the east are generally present in the west (Crisp & Southward, 1958). This distribution pattern of species is thought to be mostly a result of a temperature gradient with warmer and less fluctuating temperatures in the western English Channel than in the eastern part. However, the absence of suitable habitat may also prevent the larvae of some species which need hard substrates to survive long enough to find an appropriate settling place. Hard substrates are indeed available for the settlement of epifaunal species around the Dover Strait because of the strong currents which prevent sedimentation in this particular area (Davoult & Richard, 1988; Davoult *et al.*, 1988; Davoult & Richard, 1990; Migne &

Davoult, 1997). However in the areas immediately adjacent to the Dover Strait, only isolated patches of natural hard substrates remain. This strongly limits the probability for larvae of epifaunal species to find a suitable settling place. Our finding is an illustration of the fact that so-called southern epifaunal species can penetrate into the Southern North Sea and survive, provided that a suitable habitat is present, for example shipwrecks.

Until recently, hard substrates in Belgian marine waters received little attention due to their limited presence and the practical problems to sample them. Nonetheless, our findings support the view that certain particular and rare/uncommon habitats such as hard substrates whether artificial or not, might act as stepping stones and thus enhance the further spreading of certain warm water species limited to hard substrates further into the North Sea. It has to be noticed that the sponge itself, *D. fragilis*, has only been recently recognized as occurring in the Southern North Sea (Zintzen *et al.*, 2006).

In Belgian marine waters, *A. spongites* lives under the influence of Atlantic water masses which pass through the English Channel. Generally, the residual current is running from south-west to north-east (Pingree & Maddock, 1977). This ensures a high salinity and a steady supply of larvae. In the region of the Hinderbanks, other species with southern affinities (molluscs, bryozoans) have recently been found and were previously unknown to the Southern North Sea (Houziaux; Kerckhof; Zintzen unpublished data). Further to the north, in the Dutch and German part of the North Sea, similar regions occur with patches of natural hard substrate and shipwrecks that might be suitable for the establishment of a whole suite of epifouling species with southern affinities. However, all these particular habitats were and still are incompletely known which hampers the ongoing discussion on the possible effects of climate change.

REFERENCE LIST

Bassindale, R. 1964. British barnacles, with keys and notes for the identification of the species. Synopses of the British fauna n°14, Linnean Society of London, 68 pp.

Bocquet-Védrine, J. 1966. Structure et croissance du test calcaire chez le cirripède operculé *Acasta spongites* (Poli). *Archives de Zoologie Expérimentale et Générale*, **107**: 693-702.

Crisp, D. J. & Southward, A. J. 1958. The distribution of intertidal organisms along the coast of the English Channel. *Journal of the Marine Biological Association of the UK*, **37**: 157-208.

Crisp, D. J. & Southward, A. J. 1961. Different types of cirral activity of barnacles. *Philos.T.Roy.Soc.B*, **705**: 271-308.

Darwin, C. 1854. A monograph on the subclass Cirripedia, with figures of all the species. The Balanidae, (or sessile cirripedes); the Verrucidae, etc. The Ray Society, London, 684 pp.

Davoult, D., Dewarumez, J. M., Prygiel, J. & Richard, A. 1988. Carte des peuplements benthiques de la partie française de la Mer du Nord. *Comptes Rendus de l'Académie des Sciences, Série III*, **306**: 5-10.

Davoult, D. & Richard, A. 1988. Les ridens, haut-fond rocheux isolé du Pas de Calais: un peuplement remarquable. *Cahiers de Biologie Marine*, **29**: 93-108.

Davoult, D. & Richard, A. 1990. Etude expérimentale du recrutement du peuplement sessile des fonds caillouteux du Pas-de-Calais (France). *Cahiers de Biologie Marine*, **31**: 181-200.

du Boullay, H., Davoult, D., Delpech, J.-P., Dorobisz, L., Lampert, L., Maheux, F., Richard, I. & Rumebe, M. 2002. Surveillance écologique et halieutique du site Electronucléaire de Paluel. Rapp. IFREMER RST.DEL/PB/01.04, 128 pp.

Glaçon, R. 1971. Faune et flore du littoral Boulonnais. Institut de Biologie maritime et régionale de Wimereux, Wimereux, 38 pp.

Hawkins, S. J., Southward, A. J. & Genner, M. J. 2003. Detection of environmental change in a marine ecosystem - evidence from the western English Channel. *Science of the Total Environment*, **319**: 245-256.

Hayward, P. J. & Ryland, J. S. 2000. Handbook of the marine fauna of North-West Europe. Oxford University Press, New-York, 800 pp.

Hiscock, K., Southward, A., Tittley, I. & Hawkins, S. 2003. Effects of changing temperature on benthic marine life in Britain and Irelands. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **14**: 333-362.

Kerckhof, F. 2002. Barnacles (Cirripedie, Balanomorpha) in Belgian waters, an overview of the species and recent evolutions, with emphasis on exotic species. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **72**: 93-104.

Kerckhof, F. & Houziaux, J.-S. 2003. Biodiversity of the Belgian marine areas. pp 350-389. *In* Peeters, M., Franklin, A., and Van Goethem, J. L. (eds), Biodiversity in Belgium, Royal Belgian Institute of Natural Sciences, Brussels.

Kolbasov, G. A. 1993. Revision of the genus *Acasta* Leach (Cirripedia: Balanoidea). *Zoological Journal of the Linnean Society*, **109**: 395-427.

Koukouras, A. & Matsa, A. 1998. The Thoracican Cirriped fauna of the Aegean Sea: new information, check list of the Mediterranean species, faunal comparisons. *Senckenbergiana maritima*, **28**: 133-142.

Lanckneus, J., van Lancker, V., Moerkerke, G., Van den Eynde, D., Fettweis, M., de Batist, M. & Jacobs, P. 2001. Investigation of the natural sand transport on the Belgian continental shelf (BUDGET). Final report. Federal Office for Scientific, Technical and Cultural Affairs (OSTC), 104 pp.

MarBEF-EurOBIS 2004. European node of the Ocean Biogeographic Information System. Available online at http://www.marbef.org/data/eurobis.php. Accessed on 6-7-2006.

Marine Biological Association 1957. Plymouth Marine Fauna 3rd ed. Plymouth.

Massin, Cl., Norro, A. & Mallefet, J. 2002. Biodiversity of a wreck from the Belgian Continental Shelf: monitoring using scientific diving. Preliminay results. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **72**: 67-72.

Mieszkowska, N., Kendall, M.A., Hawkins, S.J., Leaper, R., Williamson, P., Hardman-Mountford, N.J. & Southward, A.J. 2006. Changes in the range of some common rocky shore species in Britain - a response to climate change? *Hydrobiologia*, **555**: 241-251.

Migne, A. & Davoult, D. 1997. Quantitative distribution of benthic macrofauna of the Dover Strait pebble community (Eastern English channel, France). *Oceanologica acta*, **20**: 453-460.

Moyse, J. 1961. The larval stages of *Acasta spongites* and *Pyrgoma anglicum* (Cirripedia). *Proceedings of the Zoological Society of London*, **137**: 371-392.

Newman, W. A. & Ross, A. 1976. Revision of the balanomorph barnacles; including a catalog of the species. *San Diego Society of Natural History*, **Memoir 9**: 1-109.

Nilsson-Cantell, C. A. 1978. Cirripedia Thoracica and Acrothoracica. *Marine Invertebrates of Scandinavia*, **5**: 1-113.

Pilsbry, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. *Bulletin of the Natural History Museum*, **93**: 1-366.

Pingree, R. D. & Maddock, L. 1977. Tide residuals in the English Channel. *Journal of the Marine Biological Association of the UK*, **57**: 339-354.

Relini, G. 1980. 'Cirripedi Toracici'. Guide per il risonoscimento delle specie animali acque lagunari e costiere italiane. Consiglio Nazionale delle Recherche, Genova, 120 pp.

Southward, A.J. 1995. Occurrence in the English-Channel of a warm-water Cirripede, *Solidobalanus fallax*. *Journal of the Marine Biological Association of the UK*, **75**: 199-210.

Southward, A.J., Hawkins, S.J. & Burrows, M.T. 1995. 70 years observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English-Channel in relation to rising sea temperature. *Journal of Thermal Biology*, **20**: 127-155.

Southward, A.J., Langmead, O., Hardman-Mountford, N.J., Aiken, J., Boalch, G.T., Dando, P.R., Genner, M.J., Joint, I., Kendall, M.A., Halliday, N.C., Harris, R.P., Leaper, R., Mieszkowska, N., Pingree, R.D., Richardson, A.J., Sims, D.W., Smith, T., Walne, A.W. & Hawkins, S.J. 2005. Long-term oceanographic and ecological research in the western English Channel. *Advances in Marine Biology*, **47**: 1-105.

Stubbings, H. G. 1967. The cirriped fauna of tropical West Africa. *Bulletin of the British Museum of Natural History, Zoology*, **15**: 229-319.

Van Syoc, R. J. & Winther, R. 1999. Sponge-inhabiting barnacles of the Americas: a new species of *Acasta* (Cirripedia, Archaeobalanidae), first record from the Eastern Pacific, including discussion of the evolution of cirral morphology. *Crustaceana: International Journal of Crustacean Research*, **72**: 467-486.

Zintzen, V., Massin, Cl., Norro, A. & Mallefet, J. 2006. Epifaunal inventory of two shipwrecks from the Belgian Continental Shelf. *Hydrobiologia*, **555**: 207-219.

Zullo, V. A. & Standing, J. D. 1983. Sponges-inhabiting barnacles (Cirripedia: Archeobalanidae) of the Carolinian province, Southeastern United States, with the description of a new species of *Membranobalanus* Pilsbry. *Proceedings of the Biological Society of Washington*, **31**: 468-477.

Chapter VII - General discussion and perspectives

Asterias rubens on the Kilmore shipwreck.

Cancer pagurus on a bed of *Tubularia indivisa* (Kilmore shipwreck).

1. GENERAL DISCUSSION

1.1 The presence of artificial reefs on the Belgian waters

The first part of this thesis introduced the reader to the idea that artificial reefs represent a popular and accessible technology for modifying aquatic ecosystems. Their deployment, mainly in coastal waters has increased significantly over the past two decades (Seaman, 2000). Originally, artificial reefs were built for the interests of a variety of commercial, recreational, conservation and management sectors. However, not every artificial reef is supported by an original goal, either because their planning is poorly designed or more simply because a wealth of hard structures are spread over the sea bottom for a diversified set of reasons implying the presence of man at sea. Shipwrecks on the Belgian Part of the North Sea (BPNS) can be considered as such unplanned artificial reefs. They were not purposely sunk, but still, they inevitably act as artificial reefs. Another example for the Belgian waters is the future implantation of windmill fields which will add a significant new amount of hard substrates to the seabed. In a context of growing manipulation of our coastal environment, the subtidal positioning and large repartition of shipwrecks allow them to be interesting models for the evaluation of artificial hard substrate impacts at sea.

1.1.1 Occurrence and repartition

Up to now, 231 obstruction points, most of them being shipwrecks, are officially recognised by the Administration for Navigation and Coast of Belgium (Zintzen *et al.*, submitted$_a$). This figure represents a significant number of artificial reefs on the BPNS. 19% of the shipwrecks lay under navigation routes and 23% at less than two nautical miles from harbours. 83% of the shipwrecks are at less than 30 km from the coast. It means that generally, a wreck can be found at each node of a grid of 3.87 km side, but on the coastal zone, this grid would have a size of 3.01 km and offshore a size of 6.64 km. They totalise an area lying between 0.85 km^2 and 1.49 km^2. These estimations represent 0.025% and 0.043% of the surface of the BPNS which is relatively low. However, if taking into account the biomass from shipwrecks epifauna compared to the biomass on soft sediment, this percentage may increase to 4% for the BPNS (see below). The frequency and repartition of shipwrecks for the neighbouring countries are in the same range. It points out to a discrete but extended network of artificial hard substrates created by shipwrecks. Up to now, one never considered that these shipwrecks may constitute a true network of hard substrates. The seabed of the Southern Bight of the North Sea was considered as mostly soft sedimented with some rare, localized and poorly studied gravely areas.

1.1.2 General condition of the shipwrecks

The older site made of steel on the BPNS is the Kilmore which sunk in 1906. World War I and II are responsible for a large part of the ship wreckages (26%). Other sinkings were caused by collisions and storm events. Divers observed that coastal shipwrecks which are always in shallow waters (<20 m) are generally in poor conditions, often buried in sand and largely broken into small pieces, while further offshore, they are still well preserved. For example, the Kilmore is underwater for 100 years and most of its structures are still clearly identifiable. On relatively protected conditions, the life span of shipwrecks is potentially long and further enhanced by the presence of fouling organisms which prevent the direct exposure of steel to sea water (Gabriele *et al.*, 1999; Sun *et al.*, 2003). This is particularly true for organisms strongly attached to the surface by calcification such as barnacles or serpulid polychaetes (Ma, 1989). These organisms were abundant on the studied shipwrecks. The evolution of their structural complexity with time is susceptible to affect their habitat value especially for fishery resources (Steimle & Zetlin, 2000).

Although outside the scope of this study, it should be noted that the value of shipwrecks does not only rely on their biological colonization but also on their archaeological heritage. We are at the premise of this work and a lot of information has still to be collected on our maritime history (Pieters, 2006).

1.1.3 Linking shipwreck habitat to species richness

The MacArthur & Wilson's (1967) equilibrium model of species-area relationships on islands can be easily transferred to shipwrecks. Following this theory, species richness of an island is dependant on its size and distance to mainland. However, other factors can explain variation in species richness. An important one is the diversity of habitats and it is often difficult to discern this effect from the area effect (Blondel, 1995). If an area is constituted of more habitats, it will inevitably contain more species. It is difficult to say if different shipwrecks represent different types of habitats. Indeed, each shipwreck is particular in having a particular structure which depends on the type of boat, age, orientation to prevailing currents, distance to the coast... but it seems feasible to find sites with close structural characteristics but located at varying distance from a source populations (e.g. at increasing distance from the Dover Strait). The number of sites we investigated is not large enough to have such panel of site coherences. What

we observed, is that for the four investigated sites located at an approximately equal distance from the coast, we could not discern pattern of species richness, even if some sites were smaller compared to others (Zintzen *et al.* submitted$_c$). This conclusion is nevertheless biased by the method used to estimate species richness (only based on the number of species present on the community dominated by *Tubularia indivisa* while the diversity of the whole habitat should have been estimated).
It stays that shipwrecks offer a nice model to test for hypothesis related to degree of isolation and species richness.

1.1.4 Abiotic environment

In the region, maximum depth is about 40 m and tides highly influence the distribution of sediments and their benthic communities (Larsonneur *et al.*, 1982). Mean spring tide amplitudes are around 4 m. East of the Dover Strait, current velocities decrease as a result of the increasing opening between continental Europe and UK after the Dover Strait, allowing for the sedimentation of finer particles. Soft sediments dominate the seabed of the Belgian part of the North Sea (BPNS). As a general rule, offshore shipwrecks are located in deeper waters while coastal sites are shallower.
On the basis of temperature, salinity, turbidity and currents information, we could discern three zones (Zintzen *et al.*, submitted$_b$). (1) A coastal zone with periodic salinity decreases (from 35.1 psu down to 28.1 psu), large seasonal temperature fluctuation (0.4-21.9°C), high total suspended matter load (mean monthly value up to 20.9 $mg.l^{-1}$) and reduced current velocity, (2) An offshore zone with more stable temperature (4.7-20.3°C) and salinity (33.8-35.3 psu) environment, less turbid waters (up to 6.2 $mg.l^{-1}$) and high current speed, (3) An intermediate zone with intermediate results for the abiotic parameters and fast current velocities. These differences are the result of stronger influence offshore of the Channel waters from the Atlantic and influence of freshwater input from the Scheldt – Rhine estuary inshore. These three zones were already defined by Govaere *et al.* (1980), based on the macrobenthos of soft sediments, by M'harzi *et al.* (1998) based on phyto- and zooplankton communities and by Dewick *et al.* (2003) based on hyperbenthos.
The monthly variation of abiotic parameters for an intermediate site (Kilmore) showed the following conclusions (Zintzen *et al.*, submitted$_c$): (1) the water temperature varied between 4.2°C in March and 20.3°C in August, (2) salinity showed few variations around 33.9 psu, (3) bottom tidal currents followed a semi-diurnal cycle and were preferentially NE oriented with 84%

of them in the range 0.25-0.75 $m.s^{-1}$, (4) mean value for total suspended matter was 6.2 $mg.l^{-1}$ with large variations at a monthly scale.

Information about the abiotic parameters on different part of one shipwreck is missing. The orientation of shipwrecks with the prevailing water direction must have an influence on the distribution of species on the shipwrecks as it has already been shown on tropical waters (Baynes & Szmant, 1989). Some part on the shipwrecks may be more protected/exposed than others. This differential exposition could result in discrepancies in the epifauna species that will preferentially develop. Further research on the local variation (at the scale of one shipwreck) of abiotic parameters would be needed to solve this question.

1.2 The fauna of shipwrecks in a context of soft-sedimented continental shelf

The current pooled species richness for Belgian shipwrecks is 224 sp. Among these taxa, 22 were observed *in situ* or after examination of digital picture while the other were directly collected and preserved in the Royal Belgian Institute of natural Sciences (IG number: 29462). Many of them are new for the Belgian fauna (Zintzen *et al.*, 2006, Zintzen, in prep.). The sessile and vagile species represented 23% and 77% of the species, respectively. In this order, the Annelida, Arthropoda, Mollusca, Cnidaria and Bryozoa were the most species rich phyla (Zintzen, in prep.).

Shipwrecks from Belgian waters are patches of hard substrate in sea beds dominated by soft sediments. Species, trophic and biomass analysis of this study showed that soft sediments and artificial hard substrates (shipwrecks) are distinct habitats. The presence of these hard substrate patches in a soft sediment dominated sea bed increased the structural (new species) as well as functional diversity (different abundance and biomass patterns, different trophic structure) of the Belgian waters.

1.2.1 Species life history

The life history of many benthic marine animals includes a planktonic larval stage that can last for weeks to month, perhaps even years, leading to potential large dispersal capabilities (Levin & Bridges, 1995). One of the predicted consequences of larval development is larger geographical ranges (Hohenlohe, 2004). While data have generally supported this hypothesis, the trends may be reversed in some cases. For example, the geographical range of non-planktonic species may be larger than those of related planktonic developers when rare dispersal by rafting or drifting of adults establishes new populations in isolated habitats (see the introduction of the thesis and Johannesson, 1988). These habitats then may have self-sustaining populations of non-planktonic species, while the offspring of planktonic developers do not remain in the area to maintain a sustainable population.

It is interesting to note that on shipwrecks, the most abundant species on offshore and intermediate sites, the hydroid *Tubularia indivisa*, has no pelagic development stage. Furthermore, the most dominant species (in terms of densities) are amphipods (*Jassa herdmani*, *Caprella tuberculata*, *Phtisica marina*, *Stenothoe* spp., *Monocorophium* spp.). All of them are characterized by a direct development which produces small replicates of adults and have no defined pelagic stage. The dominance of these species may be explained by their faculty to limit the dispersal capacity for most of the individuals, and hence, settle close to their parents, on the same wreck. However, many species commonly found on our shipwreck sites possess a planktotrophic larva (*Ophiothrix fraglis*, *Pisidia longicornis*, *Psammechinus miliaris*, *Electra pilosa*) or lecithotrophic larva (*Alcyonium digitatum*). Shipwrecks are consequently either in the range of a natural source of propagules (i.e. most probably the Dover Strait area) or interconnected between themselves. It is interesting to note that these last species with a planktonic phase are common on the Dover Strait, while species with no pelagic phase are less common.

These different strategies should have consequences on gene flow between populations of the same species. If we consider that the transfer of a specimen with direct development to another shipwreck (through rafting or drifting) is an occasional event with a low probability of occurrence, we can consider that these populations are partially closed. Most genetic studies for benthic marine invertebrates conforms to the expectation that (1) planktonic larval transport confers migration and genetic cohesion between populations and (2) that species with non-pelagic development show marked interpopultion heterogeneity (Todd *et al.*, 1998). It would be interesting to investigate the exchange between these populations through genetic analysis and model simulations, as suggested further in the perspectives of this chapter. It would give valuable insights on the true state of isolation that shipwrecks may have and hence, on dispersal capacity of different larval types.

1.2.2 Species patterns

The results indicate that few species are shared by soft sedimented and shipwreck habitats (9.6%) and that their faunal assemblages are distinct (Zintzen *et al.*, submitted$_a$). There is a shift from a habitat dominated by bivalves and polychaetes on soft sediments to shipwrecks dominated by crustaceans, polychaetes and cnidarians. Diversity indices show that shipwrecks are more species rich and that their taxonomic diversity is also higher than on soft sediments. Shipwrecks are strongly dominated by suspension feeders and have consequently a distinct and less diversified trophic structure than what is found on the surrounding sediments.

The comparison with natural hard substrate communities from Belgian water is still limited because little data are available up to now. From a first analysis, we note that many species are shared by both habitats, but that contrary to shipwrecks, natural assemblages were not dominated by a single species (Zintzen, in prep.).

A large area where natural hard substrate occurs exists around the Dover Strait where the distance between France and UK is the smallest and tidal currents the highest. The fauna of the pebble community from the Dover Strait has been better documented and it appears that, although sharing 18% of its species with shipwrecks, the dominating sessile species were not the same. In the pebbles of the Dover Strait, the sessile fauna was mostly dominated by bryozoan species and the octocoralian *Alcyonium digitatum*, while the largest fraction of the sessile epifauna of wrecks belonged to the hydrozoans and actiniarians (*Tubularia* spp. and *Metridium senile*) (Zintzen *et al.*, 2006).

Different hypotheses can be raised to explain these differences. First, since shipwrecks offer a structure which protrudes from several meters above the seabed, they could well provide a habitat more protected to sand abrasion than pebbles. The strong hydrodynamics in the area, combined with the presence of sand can have an abrasive effect on species. This is highlighted by the presence of species adapted to sand abrasion like the tube annelid *Sabellaria spinulosa* in the Dover Strait (Davoult & Clabaut, 1988). However, *S. spinulosa* was also identified on shipwrecks, showing that shipwrecks are not entirely protected from sand abrasion. Secondly, the stability of both substrates is different. Particularly strong currents or storm events might have a more profound effect on pebbles than on the rigid and large structure of shipwrecks (Posey *et al.*, 1996). Under the effect of these events, pebbles can be moved and the epifauna damaged or covered by sand transport. On shipwrecks, important storm events can lead to the collapsing of a part of the superstructure but frequent small scale perturbation events are unlikely to occur. Thirdly, passive suspension feeding seems to be the privileged mode of nutrition on both habitats. The rate of particles filtered by an organism is a function of particle density and current velocity. This last parameter could be enhanced on shipwrecks because current speed is higher at increasing distance from the bottom and when it encounters an obstacle. Finally, human activities like fisheries are more intense on natural grounds like pebbles than on shipwrecks and might also lead to more frequent perturbations on pebbles. This can have strong effects on the development of epibenthic species (Engel & Kvitek, 1998; Fraschetti *et al.*, 2001). To test this last hypothesis, the present assemblages of shipwrecks should be compared with a reference collection of natural hard substrate communities before they suffer from high fishery pressure. The collection of Gilson held at the Royal Belgian Institute of natural Sciences is currently the best available baseline resource to produce such an analysis. He thoroughly sampled the Belgian continental shelf in the beginning of the XXth century, including gravely areas.

1.2.3 Nutrition and biomass

There was a strong dominance of suspension feeders on shipwrecks compared to the feeding habits in the surrounding soft sediments (Zintzen *et al.*, submitted). In this respect, shipwreck communities have a clear affinity with the 'pebbles with epifauna' community described on the Dover Strait (Prygiel *et al.*, 1988; Davoult, 1990; Migne & Davoult, 1997; Foveau, 2005; Alizier, 2005). Flow velocity has a marked effect on structuring benthic community. Flach *et al.* (1998) noted that an increased density of suspension feeders was observed where flow velocity increased. Sessile suspension feeders rely on the movement of water to fulfil their food requirement. The potential food available to the taxa is a function of particle concentration and rate at which particle can be delivered. When suspension feeders are active on or near the almost smooth and featureless sea bed, they have to feed on the boundary layer. The presence of other substrata such as shipwrecks modifies the pattern of moving waters, thereby altering the selection of fauna according to their feeding type (Baynes & Szmant, 1989; Leichter & Witman, 1997). Varying obstacles ranging from hydroids to seamounts can induce an increased productivity at their peaks/tops due to current acceleration (Hughes, 1975; Genin *et al.*, 1986; Leichter & Witman, 1997).

The biomass on Belgian shipwrecks has a mean value of about 628 g Ash Free Dry Weight.m^{-2} with maximal value peaking at 3,148 g AFDW.m^{-2} (Zintzen *et al.*, submitted$_a$). The biomass on hard substrates is on average 85 times larger than on soft sediments from the coastal area. When combining the ratio of biomass on hard substrates and soft sediments with the occurrence of hard substrate, the biomass on artificial structures represents about 4 % of the total biomass from the BPNS. This is a gross estimation but nevertheless it proves that the species from artificial habitats can represent a significant part of the biomass in coastal systems.

The general food web organization for shipwrecks and for the surrounding soft-sediments could be quite different. Both entirely depend on exogenous food source but the bioaccumulation of organic matter on soft sediments is partly realized by surface and sub-surface deposit feeder. This step is virtually inexistent on shipwrecks certainly because water movement and turbulence do not favour the deposition of particles (Davoult & Gounin, 1995).

1.3 Structure of shipwreck communities

Historically, the term community has often denoted associations of plants or animals occurring in a particular locality and dominated by one or more prominent species or by some physical characteristic (Ricklefs & Miller, 2000). However, the limits of a community may not all the time be carefully delineated, their limit being arbitrary with respect to the geographic and ecological distributions of their component species. Generally speaking, communities are not discrete units separated by abrupt transitions in species composition. Species tend to be distributed over ecological gradients of conditions independently of the distribution of other species.

The case of shipwreck is special because each site has clear and unambiguous boundary with soft sediment communities, but still shipwreck sites are found on a gradient of different environmental parameters like depth, current, turbidity, salinity and temperature over the Belgian continental shelf. Our results indicate that communities on shipwrecks can best be described by dominant species. However, if we would have based our definition of communities on the concept of association of animals in a particular locality, the component species of this community would have been different since we observed different assemblages of organisms at the same place (i.e. *Tubularia indivisa* and *Metridium senile* on intermediate sites). Like Van Hoey *et al.* (2004) who defined several communities for the Belgian continental shelf, we will define several communities for artificial hard substrates.

All shipwreck sites are strongly dominated by cnidarians in terms of biomass and by amphipods in terms of abundances (Zintzen *et al.* submitted$_{a,b,c}$).

Three groups of shipwrecks could be determined at varying distance from the coast. These groups are in agreement with the observed abiotic environment described above. The anthozoan *Metridium senile* dominates a species poor community of the coastal sites in association with a more diversified hydroid community dominated by *Tubularia larynx*. This later community has a lower biomass value (102 g AFDW.m^{-2}) and significantly lower species richness compared to the other sites. *Tubularia indivisa* dominates the community of the sites located offshore, with an average biomass of 229 g AFDW.m^{-2}. Intermediate sites are also dominated by *T. indivisa*, but a higher biomass (424 g AFDW.m^{-2}) is observed.

Generally, the percentage of shipwreck surface not covered by epifauna is 30%. Cover is on average high for the sites at an intermediate distance from the coast, medium to high for offshore sites and low for sites close to the coast, probably because of a higher sedimentation rate.

Similar onshore-offshore gradient for the Belgian continental shelf has already been reported for other benthic assemblages (meio-, macro-, epi-, hyperbenthos) (Govaere *et al.*, 1980; Cattrijsse & Vincx, 2001; Dewicke *et al.*, 2003; Van Hoey *et al*, 2004). The decrease of the coastal influence seems to be a common structuring factor in benthic communities. However, it is still unknown which environmental gradient(s) in particular is (are) the most important in explaining communities structure. Dewick *et al.* (2003) stated that the merohypernethos of the Belgian area was more abundant in a transitional area between coastal and offshore zone because of a flood-dominated current offshore and ebb-dominated current onshore which create a zone of passive accumulation. This could also lead to an improved supply of larvae to shipwreck sites.

The reasons why the *Metridium senile* community is better thriving in shallower waters may be because either (1) these waters are more productive or (2) because they have a hydrodynamic regime or physical characteristics which favours *M. senile* or (3) because shallow-water gives it an adaptive advantage to its direct competitor which are *Tubularia* spp. The combined effect of increased effect of storms and commonness of *Balanus crenatus* in coastal waters could lead to an increased rate of winter mortality for *T. indivisa* by dislodgment (Hughes, 1983). The openings created may be easily colonized by *M. senile* because its asexual reproduction by pedal laceration and its capability of oriented locomotion make it a very strong competitor for space (Anthony & Svane, 1995). Further, the gamete production of *T. indivisa* in winter is very low and not susceptible to colonize quickly empty spaces (Hughes, 1983).

The community dominated by *T. indivisa* has a high species richness and abundance of organisms. Its species richness varies from 15 in October to 42 in August with a mean value of 33 species per sample (Zintzen *et al.*,

submitted$_c$). Diversity indices are higher during autumn and winter because of the strong dominance of a few crustacean species. The total density is very high and ranges from 6,500 ind.m^{-2} in October to 445,800 ind.m^{-2} in July, a major part of these individuals being due to the amphipod *Jassa herdmani*. The biomass of the community shows large monthly variation that could result from both biotic and abiotic factors. It varies from 9 g AFDW.m^{-2} in October to 1,106 g AFDW.m^{-2} in July, with *T. indivisa* itself constituting between 59 and 82% of the total biomass. These values are particularly high. Gili & Hughes (1995) noticed that the contribution of biomass from community dominated by hydroids in shallow water may reach 15 to 20 % of the total biomass, but was generally far under.
T. indivisa also offer a support for a diversified set of species. Half of the species, representing the major fraction of the total density of individuals, were directly associated (i.e. attached) with the hydroid. This pattern was also observed on intertidal colonies of *Tubularia crocea* (Genzano, 2001). Proteinaceous and/or polysaccharidic compounds in the perisarc of the hydroid may be responsible for the attraction of a set of species. This has already been demonstrated for scallops with *T. larynx* (Harvey *et al.*, 1995b). Schmidt (1983) also explained that the presence of *T. larynx* on experimental panels was favouring the settlement and subsequent rapid domination of ascidian species (*Ciona instestinalis* and *Ascidiella aspersa*). However, Bourget & Harvey (1998) observed on *T. larynx* that various species of juveniles were found at densities up to twenty times more than on other substrata. Following this observation, they showed that the recruitment pattern at scale larger than 3 cm on plastic arborescent structures designed to mimic the hydroid could be explained by passive settlement processes only. It is only at small scale (*ca* 1 mm) that active selection was detected. Consequently, the settlement of species on the shipwreck tubulariids could be the result of the passive flux of larvae from the surrounding water masses, but the acceptation/rejection of the site would be an active mechanism.

We believe that *T. indivisa* is a key species for the epifaunal communities of Belgian shipwrecks because it allows for the development of many other species by providing attachment surface and protection from currents. Another species, the amphipod *J. herdmani* is strongly dependent on the amount of *T. indivisa* which is available. Together, these two species can transfer a large amount of organic and inorganic material from the pelagic compartment to the benthos and consequently be the source of a complex food web on shipwrecks.

1.4 Shipwrecks in the North Sea ecosystem

1.4.1 Impact on halieutic resource

Like other artificial structures at sea, shipwrecks of the Belgian and neighbouring waters attract fish species, potentially because (i) they provide shelters from currents and predators (Barshaw & Spanier, 1994; Danner *et al.*, 1994), (ii) are possible recruitment sites (Bull & Kendall, 1994) and (iii) potentially harbour favoured prey (Pike & Lindquist, 1994). Two commercially important fish species, cod (*Gadus morhua*) and seabass (*Dicentrarchus labrax*), were studied to see if they were using the shipwrecks as feeding grounds (Crawford *et al.*, submitted). Stomach content analysis showed that if both species are often found together in large shoals surrounding shipwrecks, different reasons might explain why these fish aggregate there. These species might have different predation strategies: while cod appears to prey on organisms coming to feed on wreck epifauna, seabass are more likely to feed on other fish species seeking shelter or attracted around shipwrecks by other parameters resulting from its presence. Recently, Rostad *et al.* (2006) showed that fish were attracted by vessels and that could simply be due to the noise that boats are producing. Currents striking an artificial reef create vortices which can produce noise frequencies audible for fish species (Lindquist & Pietrafesa, 1989). Nevertheless, the reason why fish may be attracted by noise is currently unknown.

1.4.2 Impact on species distribution

The presence of shipwrecks might also have an impact on the distribution of species. A barnacle, *Acasta spongites*, which lives embedded in the sponge *Dysidea fragilis* was found for the first time in the Southern Bight of the North Sea on several shipwreck samples (Zintzen & Kerckhof, submitted). Other species, like the sea anemone *Actinothoe sphyrodeta* have apparently their first records in the Southern Bight in this study. This finding is an illustration of the fact that so-called southern epifaunal species can penetrate into the Southern North Sea and survive, provided that a suitable habitat is present, for example shipwrecks. It supports the view that certain particular and rare/uncommon habitats such as hard substrates whether artificial or not, might act as stepping stones and thus enhance the further spreading of certain warm water species limited to hard substrates further into the North Sea. It may naturally impact the repartition of species but also their genetic diversity by allowing an easier transfer of allele from normally unconnected populations.

To the north, in the Dutch and German part of the North Sea, similar regions occur with patches of natural hard substrates and shipwrecks that might be suitable for the establishment of a whole suite of epifouling species with southern affinities. However, all these particular habitats were and still are incompletely studied. In this context, the implication of global warming in the spreading of southern species is difficult to estimate.

2. PERSPECTIVES

This work aimed at describing epifaunal communities developing on artificial hard substrates in the particular environment of the North Sea. It was the first of this type on shipwrecks for the region. As such, the first step to apprehend a new habitat imposes a comprehensive descriptive work to encompass globally the structure of the communities and search for the right question to be answered. With the results of this study, it is now possible to move from a descriptive framework to an experimental design which will allow for hypotheses testing. We have highlighted a number of questions of interest which could and should be developed in the future.

2.1 Species and community ecology

The persistence of the communities dominated by *Metridium senile* and *Tubularia indivisa* deserves further attention. First, the dominance of each of these communities at varying distance from the coast still needs to be explained. Transplantation studies are feasible to see if environmental conditions are responsible for the observed patterns, or if the source of variation has to be explained by other factors, like for example in the competitive behaviour of both species.

Furthermore, a set of close associations between the hydrozoan *T. indivisa* and a number of amphipods has been observed. The type of associations in question would need to be analyzed. Particularly, the amphipods *Jassa herdmani*, *Stenothoe* spp., *Caprella tuberculata* and *Phtisica marina* are found in such large densities that they deserve special attention. It would be interesting to test if the accumulation of these species follows a passive or active model for site selection as well as studying their trophic status in the *T. indivisa* community.

The trophic ecology of *T. indivisa* itself should be studied since they account for the major proportion of the Belgian shipwrecks epifaunal biomass. It may directly use the large amount of juvenile *J. herdmani* which are available. The feeding status of other tubulariids species has already been studied (Gili *et al.*, 1996; Genzano, 2005) and the importance of hydroids for bentho-pelagic coupling stressed (Gili & Hughes, 1995; Gili *et al.*, 1998).

Tributyltin (TBT) paints are used to prevent fouling on ship hauls. Its use has been banned for ships under 25 m since 1990 (Vyncke & Devolder, 1994). In 2001, an international convention on TBT banning was signed and has been effective since 2003. It is interesting to note that caprellid species accumulate and are very sensitive to TBT (Ohji *et al.*, 2003a; Ohji *et al.*, 2003b; Ohji *et al.*, 2004). Since these species have a rapid turn-over, they could be punctual (both temporal and spatial) markers of TBT levels in our waters. This would allow following the decline of these substances independently from the high levels often described in sediments.

2.2 Shipwrecks as stepping stones for the dispersal of species

The extent and repartition of natural hard substrates in the Southern North Sea is still poorly documented and if their existence is certain, their spreading is patchy. Furthermore, it is highly probable that even if affinities will be high, the communities developing on natural and artificial hard substrate will differ. In this context, shipwrecks could act as stepping stones for the dissemination of a set of species. This could have impacts for the dissemination of some warm water species to the North during the next decades. It could also lead to a decrease in genetic diversity of some species by allowing allele transfer between populations which should not be into contact otherwise. Another exciting issue is related to population ecology. We do not know how the populations on different shipwrecks are connected to each other or if they function like relatively isolated entities. Shipwrecks may effectively be considered as the habitat for metapopulations. The genetic structure of the metapopulation might be studied in the light of the life history of species, especially their development type (i.e. with or without a planktonic larval stage).

The difference between natural and artificial substrates as a source of propagules could be tested through experimental panel studies. These could be placed close to shipwrecks and natural pebble fields. The colonization would be followed by regularly collecting these panels.

J. herdmani could be a very nice model to study for its dissemination capacity. Actually, this species has a direct development (embryos develop into small adults without planktonic stages) but is very abundant on shipwrecks and all kind of artificial substrate in the Southern North Sea. We suspect the juveniles to be the vector of this species, but it still needs to be formally tested. Again, experimental panels could be used to study the dissemination of this species.

A genetic analysis of *J. herdmani* populations found along the Atlantic coast would help understand global dispersion pattern for this species, as well as resolving a number of supposed incorrect records in past and present studies. A more precise analysis with short-term markers could also be made on the different metapopulation from Belgian shipwrecks. Actually, part of the material to realize these analyses have already been collected.

Hydrodynamic models coupled to meteorological data would also be tools of interest to estimate the dispersal of species between shipwreck sites. These models could be coupled to biotic models for selected species. Preliminary studies have been realized in collaboration with the MUMM for *J. herdmani* but since this model considered propagules as passive, it could be potentially applied to any species with dispersal capacity mainly driven by passive phenomenon. We studied the survival time of *J. herdmani* in laboratory conditions. At 5°C, their median survival time (survival of 50% of the individuals) was 18 days, and their maximal survival time was 39 days. At 13°C, these figures dropped to 14 and 29 days, respectively. Based on the scraped samples we made on the Bourrasque, Kilmore and Birkenfels shipwrecks and the respective area of this shipwrecks, we estimated a number of individuals that could leave the sites. It was assumed that 5% of all individuals were taken by currents. The results for the three sites are presented on the figures 1, 3 and 5 for August 2002 and on figures 2, 4 and 6 for August 2004. We can see that the results largely differ for the two dates. This is due to varying meteorological conditions at the respective dates. In some cases, individuals from one site can arrive to another, but it is not systematically occurring. Simulation like these, in conjunction with DNA analysis could certainly bring interesting results on the mid-range dispersal of that species.

2.3 Halieutic resources around shipwrecks

The amount of fish around shipwrecks was particularly important and rises a number of questions. The reasons why artificial hard substrates, such as shipwrecks and other man-made marine structures, attract fish still remain mostly unanswered. They are certainly mainly behavioural. It is possible that shipwrecks (i) provide shelter from currents or predators, (ii) are possible sites for reproduction and/or recruitment and (iii) potentially harbour favoured prey. These functions must have implications on the fitness of species aggregating around these shipwrecks, but have to date not been addressed. These shipwrecks may have a nursery effect on certain species. The large number of potential prey and increased biomass compared to the surrounding soft sediments may attract and give a source of food for young specimens. This may result in a higher survival and growth rate of juveniles, with an enhancement of production of exploitable fish populations. The young fish assemblage on a shipwreck could be investigated by the use of a light trap (in combination with remote sensing) and some small tangle nets around the site. The basic use of shipwrecks by fish deserves further attention. Our first study on stomach content of cod and seabass suggested that fish utilize this habitat differentially. Shipwrecks may also lead to shift in fish behaviour (diet shifts, diurnal and migrating behaviour). In order to determine the space and food resources utilisation and the activity pattern of targeted species, an acoustic telemetry study could be conducted.

Biotelemetry allows remote sensing of the positions, movements or behavioural variable of pelagic fish species inside their environment. To investigate these diet shifts, samples taken from fishing could be dissected and investigated for stomach content. Behaviour could finally be studied *in-situ* by mean of remotely operated cameras.

These questions are important because shipwrecks may produce more fish and/or offer an alternative to conventional fishery practices like trawling which have a profound impact on the marine environment (Bergman & Hup, 1992; Morton, 1996; Kaiser *et al.*, 1998; Engel & Kvitek, 1998; Schwinghamer *et al.*, 1998; Pranovi *et al.*, 2000; Schratzberger *et al.*, 2002; Widdicombe *et al.*, 2004; De Biasi, 2004; Freese *et al.*, 2005).

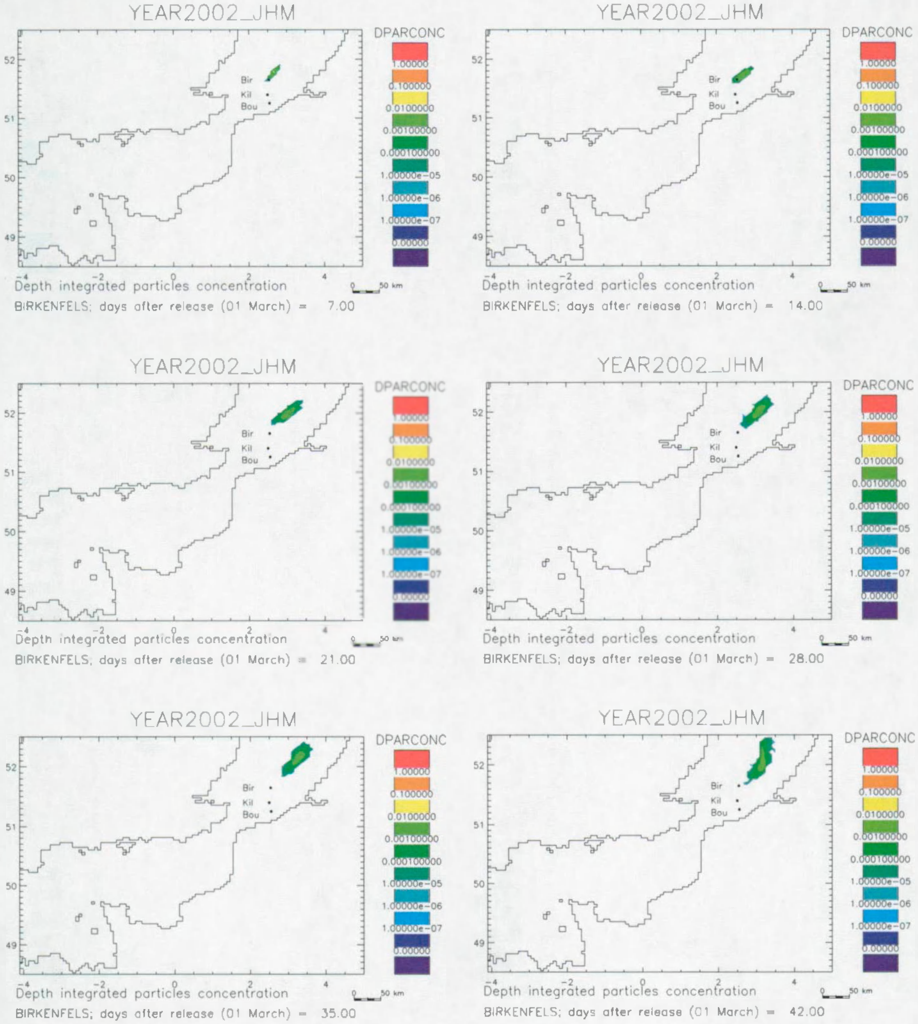


Figure 1. Spatial distribution of depth integrated concentration of particles (juveniles of *Jassa herdmani*) for each week. The particles were released on 1 August 2002 from the Birkenfels. Initial number of particles: 24,000,000.

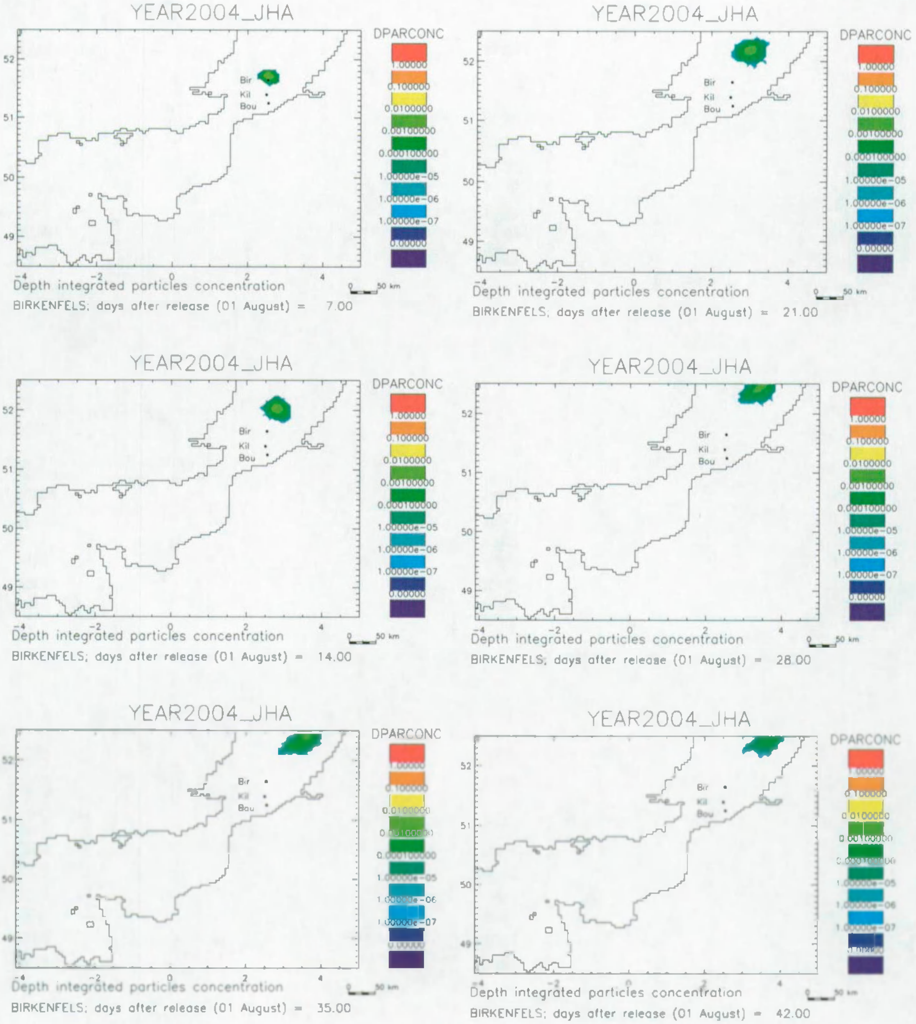


Figure 2. Spatial distribution of depth integrated concentration of particles (juveniles of *Jassa herdmani*) for each week. The particles were released on 1 August 2004 from the Birkenfels. Initial number of particles: 24,000,000.

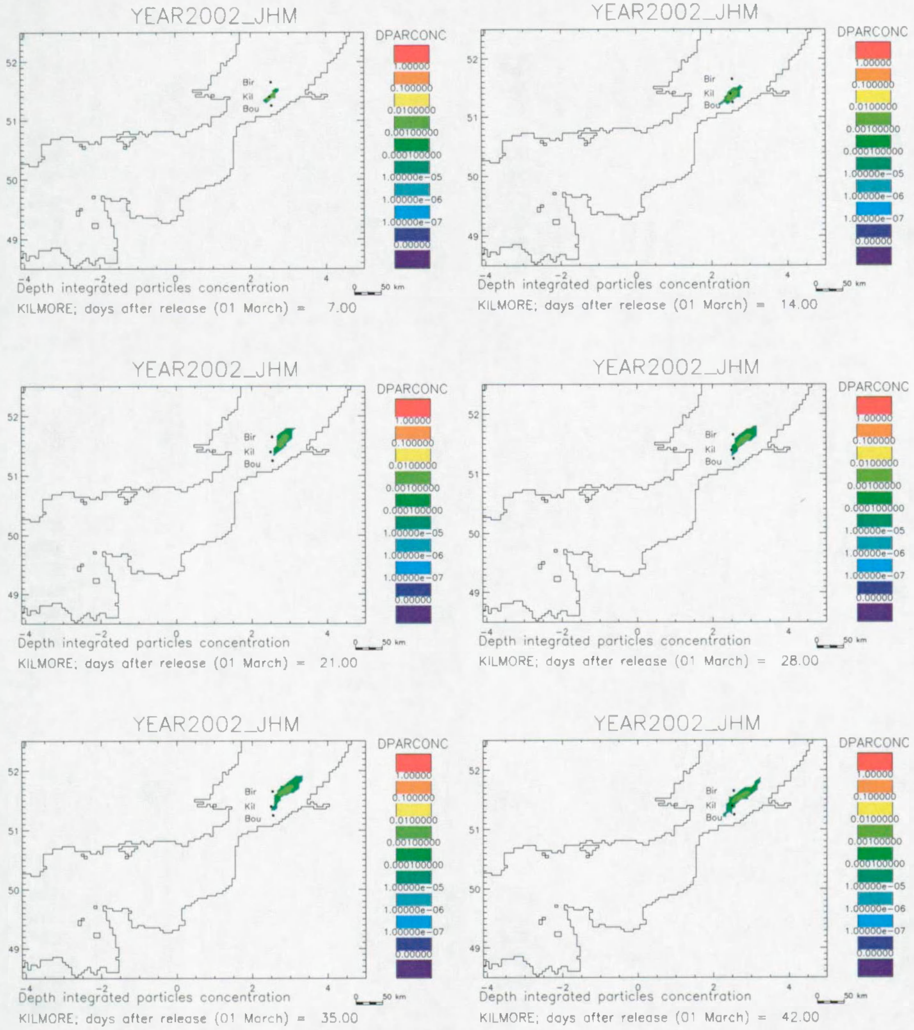


Figure 3. Spatial distribution of depth integrated concentration of particles (juveniles of *Jassa herdmani*) for each week. The particles were released on 1 August 2002 from the Kilmore. Initial number of particles: 19,700,000.

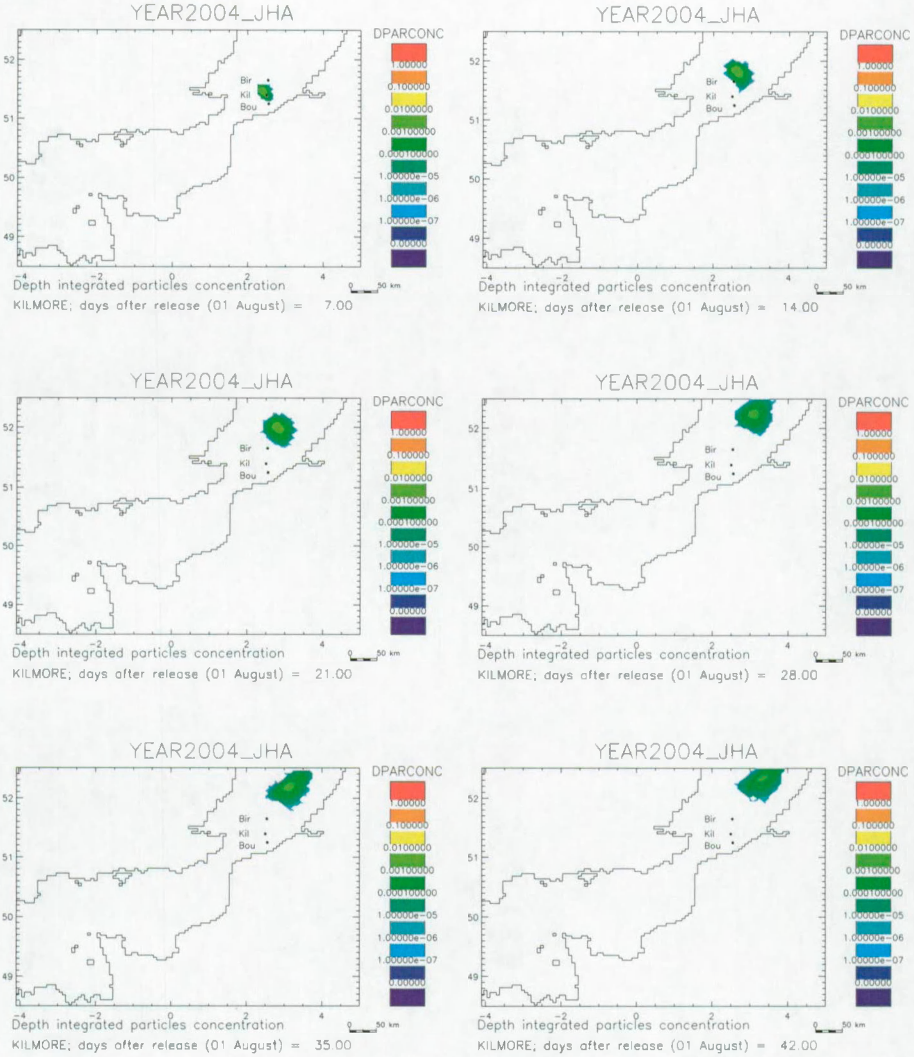


Figure 4. Spatial distribution of depth integrated concentration of particles (juveniles of *Jassa herdmani*) for each week. The particles were released on 1 August 2004 from the <u>Kilmore</u>. Initial number of particles: 19,700,000.

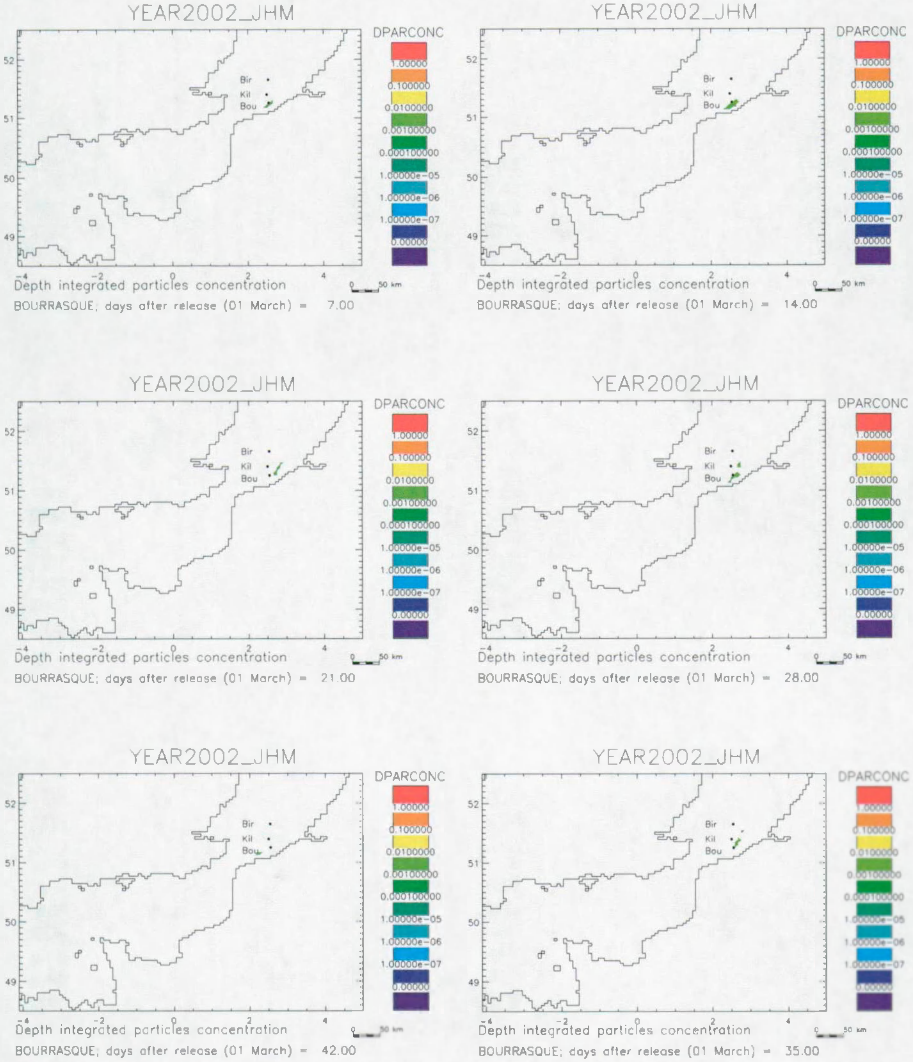


Figure 5. Spatial distribution of depth integrated concentration of particles (juveniles of *Jassa herdmani*) for each week. The particles were released on 1 August 2002 from the Bourrasque. Initial number of particles: 6,200,000.

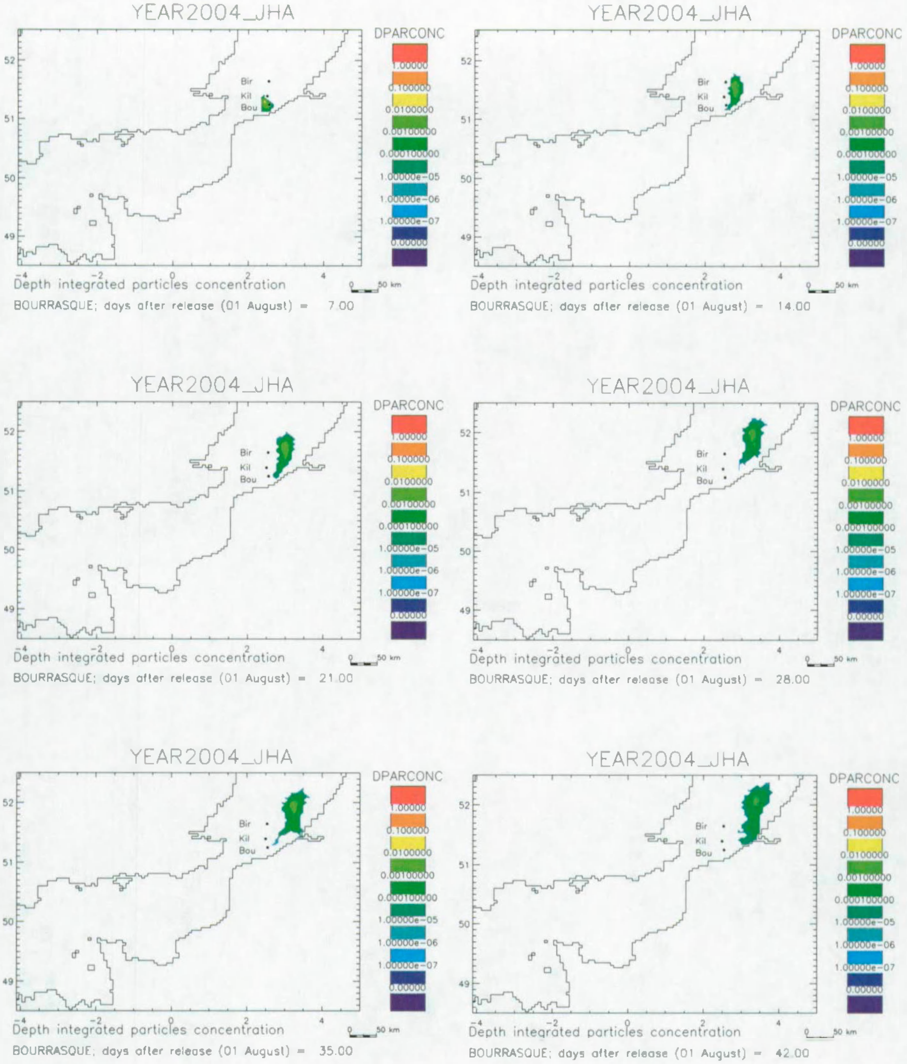


Figure 6. Spatial distribution of depth integrated concentration of particles (juveniles of *Jassa herdmani*) for each week. The particles were released on 1 August 2004 from the Bourrasque. Initial number of particles: 6,200,000.

References

Alizier, S. 2005. Evolution spatio-temporelle de l'épifaune vagile et de l'endofaune du peuplement des cailloutis à épibiose sessile dans le Détroit du Pas de Calais. Rapport de Diplôme Superieur de Recherche, Océanologie biologique, Station Marine de Wimereux, 78 pp.

Anthony, K. R. N. & Svane, Ib. 1995. Effects of substratum instability on locomotion and pedal laceration in *Metridium senile* (Anthozoa: Actiniaria). *Marine Ecology-Progress Series*, **124**: 171-180.

Barshaw, D. & Spanier, E. 1994. Anti-predator behaviors of the Mediterranean slipper lobster, *Scyllarides latus*. *Bulletin of Marine Science*, **55**: 375-382.

Baynes, T. W. & Szmant, A. M. 1989. Effects of current on the sessile benthic community structure of an artificial reef. *Bulletin of Marine Science*, **44**: 545-566.

Bergman, M. J. N. & Hup, M. 1992. Direct effects of beamtrawling on macrofauna in a sandy sediment in the southern North Sea. *ICES Journal of Marine Research*, **49**: 5-11.

Blondel, J. 1995. Biogéographie. Approche écologique et évolutive. Collection d'écologie N°27, Masson, Paris, 297 pp.

Bull, A. & Kendall, J. 1994. An indication of the process - offshore platforms as artificial reefs in the Gulf of Mexico. *Bulletin of Marine Science*, **55**: 1086-1098.

Cattrijsse, A. & Vincx, M. 2001. Sustainable management of the North Sea: Biodiversity of the benthos and the avifauna of the belgian coastal waters. Federal Office for Scientific, Technical and Cultural Affairs, Brussels, 48 pp.

Crawford, O., Degraer, S., Mallefet, J. & Zintzen, V. Submitted. Macrobenthos of shipwrecks within and around the Belgian waters as a potential food resource for fish populations. *Belgian Journal of Zoology*.

Danner, E. M., Wilson, T. C. & Schlotterbeck, R. E. 1994. Comparison of rockfish recruitment of neashore artificial and natural reefs off the coast of central California. *Bulletin of Marine Science*, **55**: 333-343.

Davoult, D. 1990. Biofaciès et structure trophique du peuplement des cailloutis du Pas-de-Calais (France). *Oceanologica acta*, **13**: 335-348.

Davoult, D. & Clabaut, P. 1988. Le passage des fonds sableux de la baie de Wissant aux fonds caillouteux du large et les peuplements benthiques associées. *Journal de la Recherche Océanographique*, **1-2**: 32-35.

Davoult, D. & Gounin, F. 1995. Suspension-feeding activity of a dense *Ophiothrix fragilis* (Abildgaard) population at the water-sediment interface: time coupling of food availability and feeding behaviour of the species. *Oceanologica acta*, **41**: 567-577.

De Biasi, A.M. 2004. Impact of experimental trawling on the benthic assemblage along the Tuscany coast (north Tyrrhenian Sea, Italy). *ICES Journal of Marine Science*, **61**: 1260-1266.

Dewicke, A., Cattrijsse, A., Mees, J. & Vincx, M. 2003. Spatial patterns of the hyperbenthos of subtidal sandbanks in the southern North Sea. Journal of Sea Research, 49: 27-46.

Engel, J. & Kvitek, R. 1998. Effects of otter trawling on a benthic community in monterey bay national marine sanctuary. *Conservation Biology*, **12**: 1204-1214.

Flach, E., Lavaleye, M., de Stigter, H. & Thomsen, L. 1998. Feeding types of the benthic community and particle transport across the slope of the NW European Continental Margin (Goban Spur). *Progress in Oceanography*, **42**: 209-231.

Foveau, A. 2005. Evolution des fonds à *Modiolus modiolus* dans le détroit du Pas de Calais. Rapport de stage d'un Master Recherche 2 EDEL, La Rochelle, Station Marine de Wimereux, 45 pp.

Freese, L., Auster, P. J., Heifetz, J. & Wing, B. L. 2005. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. *Marine Ecology-Progress Series*, **182**: 119-126.

Gabriele, M., Bellot, A., Gallotti, D. & Brunetti, R. 1999. Sublittoral hard substrate communities of the northern Adriatic Sea. *Cahiers de Biologie Marine*, **40**: 65-76.

Genin, A., Dayton, P. K., Londsale, P. F. & Spiess, F. N. 1986. Coral on seamount peaks provide evidence of current acceleration over deep topography. *Nature*, **322**: 59-61.

Genzano, G.N. 2005. Trophic ecology of a benthic intertidal hydroid, *Tubularia crocea*, at Mar del Plata, Argentina. *Journal of the Marine Biological Association of the UK*, **85**: 307-312.

Gili, J. M., Alva, R., Coma, R., Orejas, C., Pagès, F., Ribes, M., Zabala, M., Arntz, W., Buillon, J., Boero, F. & Hugues, R. G. 1998. The impact of small benthic passive suspension feeders in shallow marine ecosystems: the hydroids as an example. *Zoologische Verhandelingen*, **323**: 99-105.

Gili, J.M. & Hughes, R.G. 1995. The ecology of marine benthic hydroids. *Oceanography and Marine Biology - An Annual Review*, **33**: 351-426.

Gili, J.M., Hughes, R.G. & Alva, V. 1996. A quantitative study of feeding by the hydroid *Tubularia larynx* Ellis and Solander, 1786. *Scientia Marina*, **60**: 43-54.

Govaere, J. C. R., Van Damme, D., Heip, C. & De Coninck, L. A. P. 1980. Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring. Helgolander Wissenschaftliche Meeresuntersuchungen, **33**: 507-521.

Hohenlohe, P.A. 2004. Limits to gene flow in marine animals with planktonic larvae: models of Littorina species around Point Conception, California. Biological Journal of the Linnean Society, **82**: 169-187.

Hughes, R. G. 1975. The distribution of epizoites on the hydroid *Nemertesia antennina* (L.). *Journal of the Marine Biological Association of the UK*, **55**: 275-294.

Hughes, R.G. 1983. The life-history of *Tubularia indivisa* (Hydrozoa: Tubulariidae) with observations on the status of *T. ceratogyne*. *Journal of the Marine Biological Association of the UK*, **63**: 467-479.

Johannesson, K. 1988. The paradox of Rockall: why is a brodding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*). *Marine Biology*, **99**: 507-513.

Kaiser, M.J., Edwards, D.B., Armstrong, P.J., Radford, K., Lough, N.E.L., Flatt, R.P. & Jones, H.D. 1998. Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES Journal of Marine Research*, **55**: 353-361.

Larsonneur, C., Bouysse, P. & Auffret, J.-P. 1982. The superficial sediments of the English Channel and its Western Approaches. *Sedimentology*, **29**: 851-864.

Leichter, J.J. & Witman, J.D. 1997. Water flow over subtidal rock walls: Relation to distributions and growth rates of sessile suspension feeders in the Gulf of Maine - Water flow and growth rates. *Journal of Experimental Marine Biology and Ecology*, **209**: 293-307.

Levin, L. A. & Bridges, T. S. 1995. Pattern and diversity in production and development. pp 1-48. *In* McEdwards, L. (ed), Ecology of marine invertebrates larvae, CRC Press, Boca Raton, FL.

Lindquist, D.G. & Pietrafesa, L.J. 1989. Current vortices and fish aggregations - the current field and associated fishes around a tugboat wreck in Onslow Bay, North-Carolina. *Bulletin of Marine Science*, **44**: 533-544.

M'harzi, A., Tackx, M., Daro, M. H., Kesaulia, I., Caturao, R. & Podoor, N. 1998. Winter distribution of phytoplankton and zooplankton around some sandbanks of the Belgian coastal zone. *Journal of Plankton Research*, **20**: 2031-2052.

Mac Arthur, R. H. & Wilson, E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ, 203 pp.

Ma, S. D. 1989. The corrosive effect of barnacles on low alloy steels. *Chinese Journal of Oceanology and Limnology*, **7**: 31-33.

Migne, A. & Davoult, D. 1997. Quantitative distribution of benthic macrofauna of the Dover Strait pebble community (Eastern English channel, France). *Oceanologica acta*, **20**: 453-460.

Morton, B. 1996. The subsidiary impacts of dredging (and trawling) on a subtidal benthic molluscan community in the southern waters of Hong Kong. *Marine Pollution Bulletin*, **32**: 701-710.

Ohji, M., Arai, T. & Miyazaki, N. 2003a. Biological effects of tributyltin exposure on the caprellid amphipod, *Caprella danilevskii*. *Journal of the Marine Biological Association of the UK*, **83**: 111-117.

Ohji, M., Arai, T. & Miyazaki, N. 2003b. Timing of sex disturbance caused by tributyltin exposure during the embryonic stage in the caprellid amphipod, *Caprella danilevskii*. *Journal of the Marine Biological Association of the UK*, **83**: 943-944.

Ohji, M., Aral, T. & Miyazaki, N. 2004. Effects of tributyltin on the survival in the caprellid amphipod *Caprella danilevskii*. *Journal of the Marine Biological Association of the UK*, **84**: 345-349.

Pieters, M. 2006. Les épaves, un voyage dans le temps: mythe archéologique ou réalité. Journée d'étude: les épaves, éternelles ou perdues à jamais, 20/06/2006, Ostende.

Pike, L. & Lindquist, D. 1994. Feeding ecology of spottail pinfish (*Diplodus holbrooki*) from an artificial and natural reef in Onslow Bay, North Carolina. *Bulletin of Marine Science*, **55**: 363-374.

Pranovi, F., Raicevich, S., Franceschini, G., Farrace, M.G. & Giovanardi, O. 2000. Rapido trawling in the northern Adriatic Sea: effects on benthic communities in an experimental area. *ICES Journal of Marine Research*, **57**: 517-524.

Prygiel, J., Davoult, D., Dewarumez, J. M., Glaçon, R. & Richard, A. 1988. Description et richesse des peuplements benthiques de la partie française de la Mer du Nord. *Comptes Rendus de l'Académie des Sciences, Série III*, **306**: 5-10.

Ricklefs, R. E. & Miller, G. L. 2000. Ecology. Fourth Edition. W.H. Freeman and Company, USA, 822 pp.

Rostad, A., Kaartvedt, S., Klevjer, T. A. & Melle, W. 2006. Fish are attracted to vessels. *ICES Journal of Marine Science*, **63**: 1431-1437.

Schratzberger, M., Dinmore, T.A. & Jennings, S. 2002. Impacts of trawling on the diversity, biomass and structure of meiofauna assemblages. *Marine Biology*, **140**: 83-93.

Schwinghamer, P., Gordon, D.C., Rowell, T.W., Prena, J., McKeown, D.L., Sonnichsen, G. & Guigne, J.Y. 1998. Effects of experimental otter trawling on surficial sediment properties of a sandy-bottom ecosystem on the Grand Banks of Newfoundland. *Conservation Biology*, **12**: 1215-1222.

Seaman, W. 2000. Artificial reef evaluation with application to natural marine habitats. CRC Press, Boca Raton, 246 pp.

Steimle, F. W. & Zetlin, C. 2000. Reef habitats in the middle Atlantic Bight: abundance, distribution, associated biological communities, and fishery resource use. *Marine Fisheries Review*, **62**: 24-42.

Sun, H.Y., Ma, S.D., Hou, B.R., Zhang, J.L., Huang, G.Q. & Zhu, X.R. 2003. Mathematical analysis of long term fouling corrosion in sea water. *Corrosion Engineering, Science and Technology*, **38**: 223-227.

Todd, C.D., Lambert, W.J. & Thorpe, J.P. 1998. The genetic structure of intertidal populations of two species of nudibranch molluscs with planktotrophic and pelagic lecithotrophic larval stages: are pelagic larvae "for" dispersal? *Journal of Experimental Marine Biology and Ecology*, **228**: 1-28.

Van Hoey, G., Degraer, S. & Vincx, M. 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. Estuarine, Coastal and Shelf Science, 59: 599-613.

Vyncke, W. & Devolder, M. 1994. Tributyltin in de belgische kustwateren en -havens. *Water*, **74**: 10-13.

Widdicombe, S., Austen, M.C., Kendall, M.A., Olsgard, F., Schaanning, M.T., Dashfield, S.L. & Needham, H.R. 2004. Importance of bioturbators for biodiversity maintenance: indirect effects of fishing disturbance. *Marine Ecology-Progress Series*, **275**: 1-10.

Zintzen, V. In prep. Species inventory of shipwrecks from the Belgian part of the North Sea: a comparison with the epifauna on adjacent natural substrates. Intended for *Bulletin de l'Institut royal des Sciences natuelles de Belgique.*

Zintzen, V., Degraer, S., Massin, Cl., & Mallefet, J. Submitted$_a$. Shipwrecks increase structural and functional biodiversity in soft sediment sea beds. *Journal of Sea Research.*

Zintzen, V. & Kerckhof, F. Submitted to *Belgian Journal of Zoology.*

Zintzen, V., Massin, Cl., Norro, A. & Mallefet, J. 2006. Epifaunal inventory of two shipwrecks from the Belgian Continental Shelf. *Hydrobiologia*, **555**: 207-219.

Zintzen, V., Norro, A., Massin, Cl., & Mallefet, J. Submitted$_b$. Spatial variability of epifaunal communities from artificial habitat: shipwrecks in the Southern Bight of the North Sea. *Marine Ecology – Progress series.*

Zintzen, V., Norro, A., Massin, Cl., & Mallefet, J. Submitted$_c$. The hydroid *Tubularia indivisa* (Cnidaria, Tubulariidae) plays a structural role on artificial habitat communities. *Journal of Sea Research.*

Acknowledgements

I believe that few PhD projects were supported by such a large number of people from all different kind of horizons. And in which conditions! The North Sea conditions, naturally. A glimpse of what it truly means…
First, it starts with a 'GO' the day before made by Claude or myself. It tries to be confident although the weather conditions look quiet limit to dive tomorrow. But we have to try. Then, prepare all your stuff carefully, doubled check your material, everything must work smoothly when entering the water. It's 4.00 AM, wake up, the tide does not wait for us. Travel 120 km or more to get to our ship. A coffee will be welcome, if you do not suffer from see sickness, the wind blows at 5 beaufort today, it's 7.00 AM and the ship is leaving. After the briefing where some crazy scientist will ask you to do some stupid work underwater, you have some spare time to rest, or to arrange some problem with your or our material. But still, we will wait to be onsite to see if the dive is feasible. Maybe we do not show it, but me or Alain, take the stress through the window: dive or not, safe or not? Today, we will go for it. The crew finds the wreck quiet easily this time. Right, we are still on time with the scheduled planning and the tide. Water temperature is around 10°C, not too bad, and visibility should be averaged (i.e. 3 m). You are lucky, you will do safety first and dance on the zodiac still more or less dry, waiting for your buddies which will be scraping underwater. They make surface, visibility ok, but still some current, you will have to hang on and creep onto the rope to get down and try finding a protected place to work. It's now 1.00 PM, everybody is back to the boat and we have four good samples. Refilling the tank, the batteries of the torch and the bodies, we still need you for the second dive. Take some rest. 6 hours later and the boat is moving, but not for the second dive, we go back to the coast. Wind is now blowing 6-7 beaufort and turned, to the north. Not a single sandbank to protect us now. Diving would be too dangerous. At least, you will be a little bit earlier at home.
Many of yours know this day schema by heart (it's still a nice one), and even if these times were among the most exhausting I ever knew, I am sure that, like me, you found something very exciting in all this agitation. Thanks to all of you, all this study was made feasible. Thanks also to Alain N. which filled me in with its knowledge on this very particular and difficult environment. I learned a lot.

Not easy to be promoter, especially when the topic goes out of its direct sphere of knowledge. But Claude and Jérôme, you did it for a best and were always available at the right time. I am also particularly grateful for your tenacity, together with Alain, in first developing a shipwreck program for the

North Sea. No an easy task. Thanks to that, I had the opportunity to join the ride. Claude, I will never forget the care you took correcting my reference lists. This is crazy! You did also a outstanding job for the Belgian fauna after the pre-defense. And Jérôme, I never made such a mess underwater than with you in Banyuls. Hopefully, the coraligene will survive! You filled me in with your knowledge. Thanks a lot for that.

Yves, Claudine, Rose, Marc, and all the lab fellows, for your support divers et varié during these 4 long years.

Thanks to Charlotte H. and Oliver C. for their assiduity during their final project on shipwrecks. Thanks also to Dr Titine for the great time preparing the field course of Wimereux and during the ophiurid collection in Banyuls.

Thank you to the VLIZ and Belgica for ship time support.

Thank you to Mr. J. Van Goethem for welcoming my presence on its department.

And a special consideration to all the people who could help me forgetting about this project when I was out of the office. Let's hope we will still do a lot more together in the near future.

Oh, and yes, I could not forget Anne-lise, Raymond and Rex, my aquarium fish who also supported me all the way through.

Posters and oral presentations

POSTERS

Importance of wrecks for the biodiversity of the Belgian Continental Shelf

V. Zintzen, Cl. Massin, A. Norro & J. Mallefet.

Poster presented at the 38th European Marine Biology Symposium (6-13 septembre 2003), Aveiro, Portugal.

The Southern North Sea is mainly characterised by numerous subtidal sandbanks that have been thoroughly studied during last decades. As a consequence the marine biodiversity of the Belgian continental shelf is well known for the infauna of its soft sediment. However the fauna of hard substrates, mainly represented by wrecks, has been poorly documented. In fact the techniques used for sampling soft sediments are not adequate for complex structures like wrecks. The only suitable technique to learn more about epibenthic communities of our coast is diving. Three wrecks on a south-North axe are studied by the means of three complementary techniques: direct observation, photography and sampling by scratching of the wreck surface. The first results reveal an extremely rich sessile and slow moving fauna. In the first wreck investigated 52 species were identified after only three dives. The second wreck shows similar results but with a different species structure. This number of species is much higher than that found in the surrounding sediments. Many species encountered are considered as rare and some are new for the Belgian fauna. Striking differences between horizontal and vertical surfaces have been observed in terms of species assemblage. These are only preliminary results but this study will lead to a better comprehension of the structural and functional biodiversity of the Belgian continental shelf hard substrates.

Shipwrecks: hotspot for biodiversity.

V. Zintzen, Cl. Massin, A. Norro, A. Cattrijsse, E. Vanden Berghe, S. Degraer, M. Steyaert, M. Vincx & J. Mallefet. 2004. Poster presented at the VLIZ young scientist day, Friday 5 March 2004, Brugge, Belgium. VLIZ Special Publication, 17, page 85.

Hard bottom substrates at sea allow the development of communities that are often rich in terms of species diversity. Non-biogenic structures such as shipwrecks are an integral part of these substrates, even if they have an anthropogenic origin and the species assemblages they harbour could be for that reason qualified as 'exotic'. There are 200 recent shipwrecks on the Belgian Continental Shelf (BCS) and thus represent a large fraction of the hard substrate available locally; their presence has an additional interest if we know that the major part of the English Channel and Southern Bight of the North Sea consists almost exclusively of soft sediments. Five shipwrecks on the BCS will be studied in order to assess the meio- and macrofaunal diversity using direct observations and scuba sampling techniques. The soft sediments close to shipwrecks will also be studied to serve as model for area relatively undisturbed by fisheries (untrawled). Added to this, the influence of shipwrecks on local hydrodynamics and sediment transport will favour the colonization by fragile epibenthic species and as a consequence increase habitat complexity. For each site, standard abiotic parameters and current vector will be measured and modelled. The information will be centralized in a database and diffused through a web site devoted to the biodiversity of the BCS. The results will be relevant to the management of the BCS; the anthropogenic hard substrates of shipwrecks can serve as a model for what will happen with the installation of offshore windmills. A brochure will increase public awareness about the importance of marine diversity, and increase public support for marine protected areas.

Subtidal amphipod communities associated with artificial hard substrate on the Belgian continental shelf.

V. Zintzen, Cl. Massin, & J. Mallefet

Poster presented at the VLIZ young scientist day, Friday 25 February 2005, Brugge, Belgium. VLIZ Special publication, 20, pp 71.

The amount of artificial habitats in the marine environment has been continuously increasing during the last decades. Shipwrecks, among others, belong to the unplanned category of artificial habitat. Only a few studies described their epibenthic communities and their ecological impacts have been barely addressed. Further, the diversity pattern of different faunal groups for the Belgian continental Shelf (mainly macrobenthos and nematodes of soft sediments) has often only been discussed in relation to the type of sediment encountered. The epibenthic assemblages which are characteristics of shipwrecks offer the opportunity to look for a hypothetic onshore-offshore gradient with a relative independence of the sediment type. The abundance of 16 species of amphipoda from four shipwrecks located at increasing distance from the coast were analysed with multivariate techniques. Four communities of amphipod were isolated each of them characteristic of a single shipwreck. More, the two species of the Genus *Monocorophium* (*M. sextonae* and *M. acherusicum*) showed a remarkable pattern with *M. sextonae* being absent from the coastal zone and further increasing in abundance offshore. *M. acherusicum* showed an exactly opposite pattern and is consequently not found offshore.

Unplanned artificial reefs in the Southern Bight of the North Sea: Shipwrecks as new habitats for epifaunal communities.

V. Zintzen, Cl. Massin & J. Mallefet

Poster presented at the 40th European Marine Biology Symposium, 21-25th of August 2005, Vienna, Austria. Proceedings of the 40th European Marine Biology Symposium, 21-25th of August 2005, Vienna, Austria, page 77.

The amount of artificial habitats in the marine environment has been continuously increasing during the last decades. Within this framework, the 3-dimensional hard structure provided by shipwrecks represents a very special habitat. This is especially true for the Southern Bight of the North Sea where shipwrecks are widely distributed in flat and soft sediment dominated bottoms. The Belgian waters harbour an official total number of 231 obstructions (mainly shipwrecks) for navigation or fisheries. It means that an obstruction could be found at each node of a grid of 4 by 4 km. The conditions in the Southern Bight of the North Sea (strong tidal currents, poor visibility, harsh weather, and cold) combined with the unusable traditional sampling techniques make the exploration of shipwrecks a challenging work for scientific divers. Investigations on 4 shipwrecks at varying distance from the coast reveal that most of the 190 taxa found on a total scraped surface of 6 m^2 are not usual inhabitants of the surrounding sediments. Biomass exhibit values a hundred times higher than those of the surrounding sediments (mean around 650 g/m^2). Cnidaria associated with tube-building amphipods are the dominant communities. The action of man has added a significant amount of hard substrate available for colonization by diversified epifauna communities. This increases locally the species richness with the possible consequences of the dissemination of unwanted species and the mixing of the genetic information of naturally distant populations. Furthermore, sediments around shipwrecks could act as models for undisturbed habitat. The shipwrecks prevent soft-substrate ecosystems from being trawled by beam trawl fisheries as well as alter the local hydrodynamic and sedimentology. The absence of beam trawling will directly allow soft-substrate epifauna to fully develop. Finally, this added habitat provides refuge for commercially important species such as fish or crayfish.

ORAL PRESENTATIONS

Faunal diversity on wrecks, first results for the Belgian Continental Shelf.

V. Zintzen, Cl. Massin, A. Norro & J. Mallefet.

Oral presentation at 10th Benelux Congress of Zoology, 2004, Leiden University, the Netherlands. Proceedings of the 10th Benelux Congress of Zoology, Leiden University, the Netherlands, page 152.

The Southern North Sea is mainly characterised by numerous subtidal sandbanks that have been thoroughly studied during last decades. As a consequence the marine biodiversity of the Belgian continental shelf is well known for the infauna of its soft sediment. However the fauna of hard substrates, mainly represented by wrecks, has been poorly documented. In fact the techniques used for sampling soft sediments are not adequate for complex structures like wrecks. The only suitable technique to learn more about epibenthic communities of the Belgian coast is diving.

Three wrecks on a south-north axe are studied by the means of three complementary techniques: direct observation, photography and sampling by scratching of the wreck surface.

The first results reveal an extremely rich sessile and slow moving fauna. In the first wreck investigated 52 species were identified after only three dives. The second wreck shows similar results but with a different species structure. This number of species is much higher than that found in the surrounding sediments. Many species encountered are considered as rare and some are new for the Belgian fauna. Striking differences between horizontal and vertical surfaces have been observed in terms of species assemblage.

These are only preliminary results but this study will lead to a better comprehension of the structural and functional biodiversity of the Belgian continental shelf hard substrates.

La mer du Nord comme vous ne l'avez jamais vue: aperçu de la biodiversité du plateau continental belge.

V. Zintzen

Séminaires du centre de recherché sur la biodiversité, session 2004, BDIV, Université catholique de Louvain, Belgique.

Description and implications of unplanned artificial reefs: shipwrecks in the Southern Bight of the North Sea (Belgium)

V. Zintzen, Cl. Massin, A. Norro & J. Mallefet.

Oral presentation at the 8th International Conference on Artificial Reefs and Artificial Habitats, 10-14th of April 2005, Biloxi, USA. Proceedings of the 8th International Conference on Artificial Reefs and Artificial Habitats, 10-14th of April 2005, Biloxi, USA, page 80.

The Southern part of the North Sea is characterized by a small average depth, high productivity and turbidity, strong tidal currents, dominance of soft sediments and is heavily navigated. These features associated with the two World War events produce a very special environment where shipwrecks can be considered as islands of hard substrates in a sea of sandy sediments. The Belgian waters harbour an official total number of 231 wrecks for a total surface of about 3600 km^2 and a coastline of 66 km. As a result, a wreck could be found at each node of a 4 by 4 km grid. The first step in the understanding of the possible role of these added hard substrates is the description of their communities. The macrofauna of 4 shipwrecks, along a north-south transect from the coastline, has been investigated using scuba techniques. We identified 201 taxa out of 99 samples. Results indicate a dominance of a few amphipod species but the communities are strongly structured by two cnidarian species. The density of fish around the structures, although not quantified, was important, including some commercial species. The taxonomic diversity (Taxonomic distinctness) of these epibenthic communities is compared with the surrounding sediments and with natural hard substrates (gravels/pebbles) found further south in France. This puts in light how unplanned artificial reefs can sustain functional diversity compared to natural habitats, a prerequisite to their potential use as surrogate for natural substrates.

Faunal diversity on wrecks: first results for the Belgian continental shelf.

Zintzen V.

Oral presentation on the PhD Student day, 2nd of June 2005, University of Louvain, Belgium.

Importance des épaves pour la biodiversité des eaux marines belges.

V. Zintzen

Journée d'étude: les épaves, éternelles ou perdues à jamais? 20 juin 2006. Ostende, Belgique.

Les eaux belges occupent la baie sud de la Mer du Nord. Les fonds marins de celle-ci sont dominés par des sédiments dits meubles (sables et vases) et qui sont opposés à des sédiments de type durs (zone rocheuse, blocs de différente taille). Les zones importantes de substrats durs les plus proches des eaux belges se trouvent au niveau de la Manche Orientale, dans le détroit de Douvres. Là, le rétrécissement de la distance entre la France et le Royaume-Uni entraîne une accélération des courants avec comme conséquence directe l'impossibilité pour des particules fines (comme du sable ou de la vase) de sédimenter. A cet endroit, on observe donc de larges zones où la roche affleure ou encore la présence de champs de blocs. Au-delà de cette zone, en Belgique, la vitesse des courants diminue fortement et l'on trouve principalement sables et vases. Les substrats durs d'origine naturelle se font rares.

La faune associée aux substrats durs et meubles est totalement différente. Dans les substrats meubles, la majorité des animaux vivent enfouis (on parlera d'endofaune) et seules quelques espèces vivent à la surface du sédiment. Ces animaux peuvent se répartir dans les trois composantes de l'espace. Sur les substrats durs, les animaux n'ont pas la possibilité de s'enfouir car le substrat n'est pas friable et ils ne peuvent ainsi pas jouir d'une troisième dimension pour leur répartition dans l'espace. Ils doivent vivre à la surface du substrat qui leur est offert (on parlera d'épifaune).

Si les substrats durs d'origine naturelle sont rares en Belgique, il existe tout un tas d'objets sur le fond de la Mer du Nord provenant des activités de l'Homme et qui peuvent faire office de récif artificiel. L'exemple le plus frappant est celui des épaves. Plus de 230 objets (dont la plupart sont des épaves) sont parsemées sur les 3600 km^2 de nos eaux territoriales, soit une épave tous les 4 km si elles étaient réparties de manière uniforme. En pratique, on les trouve surtout proche de la côte et aux alentours des routes de navigation.

Une faune particulière et composée d'espèces typiques de fonds durs va se développer sur ces structures. A ce jour, 230 espèces ont été identifiées (invertébrés et poissons confondus). Une diversité bien supérieure à ce que l'on trouve dans les sédiments environnants. Plusieurs de ces espèces n'avaient jamais été mentionnées dans les eaux belges auparavant. La prospection de plusieurs sites localisés à des distances variables de la côte a montré que chaque épave possède sa faune distincte. On appelle communauté un ensemble d'espèces vivant ensemble. Il existe une différence très nette entre la communauté dominante sur les épaves proches de la côte et celle sur les sites plus éloignés. Proche de la côte, une anémone de mer (l'œillet de mer, *Metridium senile*) forme une couverture dense et exclut la plupart des autres espèces. Plus au large, un hydrozoaire (la tubulaire, *Tubularia indivisa*), c'est-à-dire un proche cousin des anémones est l'élément de base de la communauté dominante sur ces sites. A l'opposé de l'œillet de mer, la tubulaire permet le développement d'une communauté diversifiée car elle offre un support colonisable par de nombreuses autres espèces.

North Sea wrecks: hotspots for biodiversity

Zintzen, V., Vanden Berghe, E., Degraer, S., Norro, A. & Mallefet, J.

Oral presentation (not speaker) in the colloquium: To sea or not to sea - 2nd international colloquium on maritime and fluvial archaeology in the Southern North Sea area, , 21-23 September 2006, Brugge, Belgium. VLIZ Special Publication, 32: pages 39-40.

The amount of artificial habitats in the marine environment has been continuously increasing during the last decades. Besides planned artificial reefs mainly devoted to fisheries enhancement, lost cargo, fishing nets and shipwrecks belong to the category of accidental submerged structures. These 3-dimensional structures represent a very special habitat especially when they are widely distributed in flat and sand or mud dominated area as it is the case in the Belgian waters. These waters are one of the most heavily navigated areas in the world and combined with the consequences of World War I & II, the number of obstructions, most of them being shipwrecks is not anecdotic. The Belgian waters harbour an official total number of 231 obstructions for navigation or fisheries. As a consequence, shipwrecks create a network of hard substrate in a sea of sand. Even if scientific publications about the topic are scarce, there is a general agreement that these sites harbour a large amount of all kind of living organisms. This is particularly striking when artificial substrates are lying on soft sediments where they look like an oasis of live. Actually, the presence of shipwrecks implies that many organisms are found in the area because they need to live on a firm substrate. This substrate could not be found anywhere else... At the moment, we collected and identified on Belgian shipwrecks more than 200 species. The consequence is an increased biodiversity for the Belgian waters. It also creates a habitat that is targeted by different fish species, some of them being commercially important like the Cod and Seabass. We observed that the concentration of these species around shipwrecks is high and we have clues that some of them are eating the fauna living on shipwrecks or using it as a hunting ground. There is still much work to understand the role of shipwrecks in our waters!

Annex

Annex 1. Description of the samples used during the thesis. QT: quantitative sample (25x25 cm), QL: qualitative sample, H: horizontal, V: vertical, O: oblique. Depth is not corrected for tide. The number of specimens and species richness are given for quantitative samples.

SHIPWRECK	COORDINATES (WGS84)	DATE	REFERENCE	TYPE	DEPTH (M)	ORIENTATION	NUMBER OF SPECIMENS	SPECIES RICHNESS
Birkenfels	N051°38',990 E002°32',268	11/07/2001	BRK-20010711-1	QT	22	H	4794	31
Birkenfels	N051°38',990 E002°32',268	11/07/2001	BRK-20010711-2	QT	27	H	244	24
Birkenfels	N051°38',990 E002°32',268	11/07/2001	BRK-20010711-3	QT	29	H	805	17
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-1	QT	23	V	505	27
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-10	QT	27	H	154	16
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-11	QL	20	V	-	-
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-12	QT	19	H	415	21
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-13	QT	21	V	521	16
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-2	QT	23	V	268	24
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-3	QT	23	V	256	27
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-4	QT	23	H	536	22
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-5	QT	23	V	665	36
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-7	QT	27	V	1	1
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-8	QT	25	V	2219	37
Birkenfels	N051°38',990 E002°32',268	4/09/2002	BRK-20020904-9	QL	25	V	-	-
Birkenfels	N051°38',990 E002°32',268	5/09/2002	BRK-20020905-1	QL	27	-	-	-
Birkenfels	N051°38',990 E002°32',268	5/09/2002	BRK-20020905-3	QT	27	H	249	24
Birkenfels	N051°38',990 E002°32',268	5/09/2002	BRK-20020905-5	QT	23	H	2842	41
Birkenfels	N051°38',990 E002°32',268	5/09/2002	BRK-20020905-6	QT	30	V	78	12
Birkenfels	N051°38',990 E002°32',268	5/09/2002	BRK-20020905-7	QT	30	V	2518	50
Birkenfels	N051°38',990 E002°32',268	5/09/2002	BRK-20020905-8	QL	-	-	-	-
Birkenfels	N051°38',990 E002°32',268	5/09/2002	BRK-20020905-9	QL	-	-	-	-
Birkenfels	N051°38',990 E002°32',268	21/10/2003	BRK-20031021-1	QT	23	H	1178	23
Birkenfels	N051°38',990 E002°32',268	21/10/2003	BRK-20031021-2	QT	24	V	1699	26
Birkenfels	N051°38',990 E002°32',268	21/10/2003	BRK-20031021-3	QL	24	H	-	-
Birkenfels	N051°38',990 E002°32',268	21/10/2003	BRK-20031021-4	QT	20	V	284	11
Birkenfels	N051°38',990 E002°32',268	22/10/2003	BRK-20031022-1	QT	23	H	835	18

Shipwreck	Coordinates (WGS84)	Date	Reference	Type	Depth (m)	Orientation	Number of specimens	Species richness
Birkenfels	N051°38',990 E002°32',268	22/10/2003	BRK-20031022-2	QT	23	V	727	20
Birkenfels	N051°38',990 E002°32',268	22/10/2003	BRK-20031022-3	QT	23	H	283	14
Birkenfels	N051°38',990 E002°32',268	22/10/2003	BRK-20031022-4	QT	23	V	678	20
Birkenfels	N051°38',990 E002°32',268	16/09/2004	BRK-20040916-1	QT	22	H	309	16
Birkenfels	N051°38',990 E002°32',268	16/09/2004	BRK-20040916-2	QT	22	H	682	18
Birkenfels	N051°38',990 E002°32',268	16/09/2004	BRK-20040916-3	QT	21	V	4274	23
Birkenfels	N051°38',990 E002°32',268	16/09/2004	BRK-20040916-4	QT	22	H	593	21
Birkenfels	N051°38',990 E002°32',268	16/09/2004	BRK-20040916-5	QL	22	H	-	-
Birkenfels	N051°38',990 E002°32',268	16/09/2004	BRK-20040916-6	QT	25	V	2256	27
Birkenfels	N051°38',990 E002°32',268	18/05/2005	BRK-20050518-1	QT	27	V	11757	24
Birkenfels	N051°38',990 E002°32',268	18/05/2005	BRK-20050518-2	QT	27	V	2141	32
Birkenfels	N051°38',990 E002°32',268	18/05/2005	BRK-20050518-3	QT	27	V	766	30
Bourrasque	N051°14',964 E002°33',026	4/07/2002	BRQ-20020704-3	QT	17	H	205	11
Bourrasque	N051°14',964 E002°33',026	4/07/2002	BRQ-20020704-4	QT	17	V	125	13
Bourrasque	N051°14',964 E002°33',026	5/07/2002	BRQ-20020705-5	QT	20	V	171	14
Bourrasque	N051°14',964 E002°33',026	5/07/2002	BRQ-20020705-6	QT	18	H	170	23
Bourrasque	N051°14',964 E002°33',026	5/07/2002	BRQ-20020705-7	QT	20	V	7598	40
Bourrasque	N051°14',964 E002°33',026	5/07/2002	BRQ-20020705-8	QT	18	H	204	21
Bourrasque	N051°14',964 E002°33',026	5/07/2002	BRQ-20020705-9	QT	20	H	751	20
Bourrasque	N051°14',964 E002°33',026	18/03/2003	BRQ-20030318-1	QT	18	H	42	10
Bourrasque	N051°14',964 E002°33',026	18/03/2003	BRQ-20030318-2	QT	18	H	13	1
Bourrasque	N051°14',964 E002°33',026	18/03/2003	BRQ-20030318-3	QT	18	V	93	13
Bourrasque	N051°14',964 E002°33',026	18/03/2003	BRQ-20030318-4	QT	18	V	181	11
Bourrasque	N051°14',964 E002°33',026	27/05/2004	BRQ-20040527-1	QT	18	H	196	8
Bourrasque	N051°14',964 E002°33',026	27/05/2004	BRQ-20040527-2	QT	20	V	288	8
Bourrasque	N051°14',964 E002°33',026	27/05/2004	BRQ-20040527-3	QT	18	H	54	2
Bourrasque	N051°14',964 E002°33',026	27/05/2004	BRQ-20040527-4	QT	19	V	91	1
Bourrasque	N051°14',964 E002°33',026	27/05/2004	BRQ-20040527-5	QT	17	H	77	3
Bourrasque	N051°14',964 E002°33',026	27/05/2004	BRQ-20040527-6	QT	18.4	O	107	2
Bourrasque	N051°14',964 E002°33',026	10/08/2004	BRQ-20040810-1	QT	17	H	424	16

Shipwreck	Coordinates (WGS84)	Date	Reference	Type	Depth (m)	Orientation	Number of specimens	Species richness
Bourrasque	N051°14',964 E002°33',026	10/08/2004	BRQ-20040810-2	QT	18	V	100	1
Bourrasque	N051°14',964 E002°33',026	10/08/2004	BRQ-20040810-3	QT	17	H	190	21
Bourrasque	N051°14',964 E002°33',026	8/10/2004	BRQ-20041008-1	QT	20	V	533	14
Bourrasque	N051°14',964 E002°33',026	8/10/2004	BRQ-20041008-2	QT	20	H	491	20
Bourrasque	N051°14',964 E002°33',026	8/10/2004	BRQ-20041008-5	QT	18	H	668	13
Bourrasque	N051°14',964 E002°33',026	8/10/2004	BRQ-20041008-7	QT	18	V	908	19
Bourrasque	N051°14',964 E002°33',026	8/10/2004	BRQ-20041008-8	QT	18	V	147	5
Bourrasque	N051°14',964 E002°33',026	4/05/2005	BRQ-20050504-1	QT	18	V	152	20
Bourrasque	N051°14',964 E002°33',026	4/05/2005	BRQ-20050504-2	QT	18	V	229	13
Bourrasque	N051°14',964 E002°33',026	4/05/2005	BRQ-20050504-3	QT	18	V	168	21
Callisto	N051°41',939 E002°37',305	27/05/2004	CAL-20040527-1	QT	25	H	10224	31
Callisto	N051°41',939 E002°37',305	27/05/2004	CAL-20040527-2	QT	26	V	7755	22
Callisto	N051°41',939 E002°37',305	27/05/2004	CAL-20040527-3	QT	27	V	4074	44
Callisto	N051°41',939 E002°37',305	27/05/2004	CAL-20040527-4	QT	27	H	1440	23
Callisto	N051°41',939 E002°37',305	27/05/2004	CAL-20040527-5	QT	24	V	15539	24
Callisto	N051°41',939 E002°37',305	17/06/2005	CAL-20050617-2	QT	30	V	2169	35
Callisto	N051°41',939 E002°37',305	17/06/2005	CAL-20050617-3	QT	30	V	4119	41
Callisto	N051°41',939 E002°37',305	17/06/2005	CAL-20050617-6	QL	30	V	-	-
Duc de Normandie	N051°25',517 E002°36',339	3/06/2005	DUC-20050603-2	QT	30.5	V	5836	30
Duc de Normandie	N051°25',517 E002°36',339	3/06/2005	DUC-20050603-3	QT	32	V	775	34
Duc de Normandie	N051°25',517 E002°36',339	3/06/2005	DUC-20050603-8	QT	32	V	638	33
Garden City	N051°29',141 E002°18',321	27/06/2005	GAR-20050627-1	QT	29	V	8704	32
Garden City	N051°29',141 E002°18',321	27/06/2005	GAR-20050627-3	QT	29	V	3023	29
Garden City	N051°29',141 E002°18',321	27/06/2005	GAR-20050627-4	QT	28	V	5747	36
John Mahn	N051°28',937 E002°41',339	29/06/2005	JON-20050629-4	QT	29	V	7726	36
John Mahn	N051°28',937 E002°41',339	29/06/2005	JON-20050629-5	QT	29	V	4290	33
John Mahn	N051°28',937 E002°41',339	29/06/2005	JON-20050629-6	QT	29	V	1837	24
Kilmore	N051°23',730 E002°29',790	18/03/2003	KLM-20030318-1	QT	32	H	1190	50
Kilmore	N051°23',730 E002°29',790	12/06/2003	KLM-20030612-1	QT	30	H	7756	55
Kilmore	N051°23',730 E002°29',790	12/06/2003	KLM-20030612-2	QT	30	H	10367	53

SHIPWRECK	COORDINATES (WGS84)	DATE	REFERENCE	TYPE	DEPTH (M)	ORIENTATION	NUMBER OF SPECIMENS	SPECIES RICHNESS
Kilmore	N051°23',730 E002°29',790	12/06/2003	KLM-20030612-3	QT	31	V	12718	44
Kilmore	N051°23',730 E002°29',790	12/06/2003	KLM-20030612-4	QT	30	H	15428	40
Kilmore	N051°23',730 E002°29',790	12/06/2003	KLM-20030612-5	QT	32	V	12603	55
Kilmore	N051°23',730 E002°29',790	12/06/2003	KLM-20030612-6	QL	-	-	-	-
Kilmore	N051°23',730 E002°29',790	12/06/2003	KLM-20030612-7	QL	-	-	-	-
Kilmore	N051°23',730 E002°29',790	18/12/2003	KLM-20031218-1	QT	32	H	889	34
Kilmore	N051°23',730 E002°29',790	18/12/2003	KLM-20031218-3	QT	32	V	1457	34
Kilmore	N051°23',730 E002°29',790	18/12/2003	KLM-20031218-4	QL	-	-	-	-
Kilmore	N051°23',730 E002°29',790	2/04/2004	KLM-20040402-1	QT	30	H	592	24
Kilmore	N051°23',730 E002°29',790	2/04/2004	KLM-20040402-10	QL	-	-	-	-
Kilmore	N051°23',730 E002°29',790	2/04/2004	KLM-20040402-2	QT	31	V	22391	38
Kilmore	N051°23',730 E002°29',790	2/04/2004	KLM-20040402-3	QT	30	H	16	7
Kilmore	N051°23',730 E002°29',790	2/04/2004	KLM-20040402-4	QT	30	V	9060	41
Kilmore	N051°23',730 E002°29',790	2/04/2004	KLM-20040402-5	QT	30	H	4090	43
Kilmore	N051°23',730 E002°29',790	2/04/2004	KLM-20040402-6	QT	30	H	6868	22
Kilmore	N051°23',730 E002°29',790	2/04/2004	KLM-20040402-7	QT	30	V	5699	25
Kilmore	N051°23',730 E002°29',790	2/04/2004	KLM-20040402-8	QT	30	O	4329	39
Kilmore	N051°23',730 E002°29',790	2/04/2004	KLM-20040402-9	QT	31	V	2417	31
Kilmore	N051°23',730 E002°29',790	26/07/2004	KLM-20040726-1	QT	32	V	22844	38
Kilmore	N051°23',730 E002°29',790	26/07/2004	KLM-20040726-2	QT	26	H	12148	28
Kilmore	N051°23',730 E002°29',790	26/07/2004	KLM-20040726-3	QL	26	H	-	-
Kilmore	N051°23',730 E002°29',790	26/07/2004	KLM-20040726-4	QT	33	V	19149	40
Kilmore	N051°23',730 E002°29',790	26/07/2004	KLM-20040726-5	QT	25	H	18003	28
Kilmore	N051°23',730 E002°29',790	26/07/2004	KLM-20040726-6	QT	29	H	7263	36
Kilmore	N051°23',730 E002°29',790	8/10/2004	KLM-20041008-2	QT	34	H	294	18
Kilmore	N051°23',730 E002°29',790	8/10/2004	KLM-20041008-3	QT	34	V	395	33
Kilmore	N051°23',730 E002°29',790	8/10/2004	KLM-20041008-4	QT	34	H	402	39
Kilmore	N051°23',730 E002°29',790	18/03/2005	KLM-20050318-1	QT	30	V	585	25
Kilmore	N051°23',730 E002°29',790	18/03/2005	KLM-20050318-2	QT	32	V	471	31
Kilmore	N051°23',730 E002°29',790	18/03/2005	KLM-20050318-3	QT	31	V	586	23

Shipwreck	Coordinates (WGS84)	Date	Reference	Type	Depth (m)	Orientation	Number of specimens	Species richness
Kilmore	N051°23',730 E002°29',790	18/03/2005	KLM-20050318-4	QT	31	V	1480	31
Kilmore	N051°23',730 E002°29',790	15/06/2005	KLM-20050615-1	QT	28	V	12483	35
Kilmore	N051°23',730 E002°29',790	15/06/2005	KLM-20050615-2	QT	28	V	9340	40
Kilmore	N051°23',730 E002°29',790	15/06/2005	KLM-20050615-3	QT	28	V	8079	36
Kilmore	N051°23',730 E002°29',790	17/08/2005	KLM-20050817-2	QT	30	V	15666	41
Kilmore	N051°23',730 E002°29',790	17/08/2005	KLM-20050817-3	QT	30	V	18968	45
Kilmore	N051°23',730 E002°29',790	17/08/2005	KLM-20050817-6	QT	30	H	1940	25
Kilmore	N051°23',730 E002°29',790	17/08/2005	KLM-20050817-7	QT	30	H	2187	26
Kilmore	N051°23',730 E002°29',790	17/08/2005	KLM-20050817-8	QT	30	H	4438	28
Kilmore	N051°23',730 E002°29',790	27/10/2005	KLM-20051027-1	QT	28	V	320	17
Kilmore	N051°23',730 E002°29',790	27/10/2005	KLM-20051027-2	QT	28	V	200	16
Kilmore	N051°23',730 E002°29',790	27/10/2005	KLM-20051027-3	QT	28	V	490	15
LCT 457	N051°24',671 E002°43',710	29/06/2005	LCT-20050629-4	QT	20	V	4539	26
LCT 457	N051°24',671 E002°43',710	29/06/2005	LCT-20050629-5	QT	20	V	5222	32
LCT 457	N051°24',671 E002°43',710	29/06/2005	LCT-20050629-6	QT	20	V	12239	36
LST 420	N051°15',460 E002°40',756	3/06/2005	LST-20050603-3	QT	13	V	7771	22
LST 420	N051°15',460 E002°40',756	3/06/2005	LST-20050603-4	QT	13	V	1426	22
LST 420	N051°15',460 E002°40',756	3/06/2005	LST-20050603-8	QT	12	V	713	20
Sperrbrecher 142	N051°16',644 E002°49',791	26/07/2004	SPR-20040726-2	QT	10	H	87	3
Sperrbrecher 142	N051°16',644 E002°49',791	26/07/2004	SPR-20040726-3	QT	11	V	2938	16
Sperrbrecher 142	N051°16',644 E002°49',791	26/07/2004	SPR-20040726-4	QL	-	-	-	-
Sperrbrecher 142	N051°16',644 E002°49',791	26/07/2004	SPR-20040726-5	QT	11	H	340	10
Sperrbrecher 142	N051°16',644 E002°49',791	26/07/2004	SPR-20040726-6	QT	13	V	29	1
Sperrbrecher 142	N051°16',644 E002°49',791	26/07/2004	SPR-20040726-7	QT	12	H	51	1
Sperrbrecher 142	N051°16',644 E002°49',791	11/08/2004	SPR-20040811-1	QT	10	H	53	1
Sperrbrecher 142	N051°16',644 E002°49',791	11/08/2004	SPR-20040811-4	QT	14	V	855	11

Achevé d'imprimer sur les presses de l'imprimerie CIACO
(Louvain-la-Neuve, Belgique, tél +32.10.47.55.35)
Février 2007

Université catholique de Louvain
Faculté des sciences
Département de biologie
Unité de Biologie animale, laboratoire de Biologie Marine
Croix du Sud 3, boîte 4 1348 Louvain-la-Neuve
Tél. 32 (0) 10 47 87 50 – fax 32 (0) 10 47 34 76
Email Mallefet@bani.ucl.ac.be
http://www.biol.acl.ac.be/bmar

Institut royal des Sciences naturelles de Belgique
Département de Malacologie
Rue Vautier, 29, 1000 Bruxelles
Tél. 32 (0) 2 627 43 47
Email: claude.massin@sciencesnaturelles.be
http://www.naturalsciences.be

The seabed of the Southern Bight of the North Sea is mostly composed of sandy soft sediments. Natural hard substrates like pebbles are rare and only occur locally. Lost cargos or shipwrecks lie on the seabed as results of unintentional processes, but because of their inherent structure, they effectively act as artificial reefs deprived of an *a priori* defined set of functions. On Belgian waters, 231 shipwrecks and other artificial hard structures are dispersed on the continental shelf. Together with the sunken vessels of the neighbouring countries, they create a network of individually isolated hard substrates available for the colonization of the epifauna. The faunal diversity of these shipwrecks has never been studied before.

This thesis analyzed the diversity as well as spatial and temporal variation in community structure of ten Belgian shipwreck sites.

A total of 224 macrospecies have been identified, with at least 50 species new or rare for the Belgian fauna and Southern North Sea. All shipwrecks are strongly dominated by cnidarians in terms of biomass and by amphipods in terms of abundances. The artificial hard substrate communities isolate strongly from the surrounding soft sediment communities by sharing few species, being dominated by different faunal groups and having a distinct trophic organization. Looking at a cross-shore gradient of sites, three groups of shipwrecks could be determined. *Metridium senile*, a sea anemone, dominates a species poor community of the coastal sites. Channel water masses influence the offshore sites causing a more stable abiotic environment. The hydrozoan *Tubularia indivisa* dominates this community. Intermediate sites are also dominated by *T. indivisa*, but a higher biomass is here observed.

It also appears that this *T. indivisa* is a key species allowing for the settlement of a large set of secondary epibionts.

The shipwreck network is further discussed in the context of the regional diversity, dispersal of species and fisheries based applications.

Vincent Zintzen
Né à Verviers (1977)
Ingénieur Agronome (UCL, 2000)

museum