



# Spatial variability of epifaunal communities from artificial habitat: Shipwrecks in the Southern Bight of the North Sea

Vincent Zintzen<sup>a,b,\*</sup>, Alain Norro<sup>c</sup>, Claude Massin<sup>a</sup>, Jérôme Mallefet<sup>b</sup>

<sup>a</sup> Royal Belgian Institute of Natural Sciences, Rue Vautier 29, B-1000 Brussels, Belgium

<sup>b</sup> University of Louvain, Biology Laboratory, Kellner Building, place Croix du Sud 3, B-1348 Louvain-la-Neuve, Belgium

<sup>c</sup> Royal Belgian Institute of Natural Sciences, Management Unit of the North Sea Mathematical Models, 100 Gulledele, 1200 Brussels, Belgium

Received 23 April 2007; accepted 11 July 2007

Available online 4 September 2007

## Abstract

We investigated the cover, community structure and abiotic environment of nine shipwrecks lying at increasing distance 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 their epifaunal composition, three groups of shipwrecks could be determined. *Metridium senile* dominated a species poor community of the coastal sites. On the same sites, a *Tubularia larynx* community with a more species-rich assemblage was also developing. The *T. larynx* community had a lower biomass value (102 g AFDW m<sup>-2</sup>) and significantly lower species richness compared to the other sites. The coastal 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<sup>-2</sup>. Intermediate sites were also dominated by *T. indivisa*, but a higher biomass (424 g AFDW m<sup>-2</sup>) 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.

© 2007 Elsevier Ltd. All rights reserved.

**Keywords:** artificial substrata; epizoots; population density; biomass; *Tubularia*; *Metridium senile*; North Sea

## 1. Introduction

Artificial hard substrata have increasingly occurred at sea since man started using the sea and its resources (Connell and Glasby, 1999). Certainly, the most profound and visible effect of this action are coastal constructions that dramatically changed the nature and extent of hard substrata both in shallow-water and intertidal areas (Glasby and Connell, 1999; Bacchiocchi and Aioldi, 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 and Kendall, 1994; Relini et al., 1998; Stanley and Wilson, 2000; Fabi et al., 2004; Love, 2005 and see references in Jensen et al. (2000) and Jensen (2002)). Lost cargos or shipwrecks form a less conspicuous range of artificial hard substrata that lie on the seabed as results of unintentional processes (Bullock, 1965; Hiscock, 1980; Leewis et al., 2000; Steimle and Zetlin, 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 the resulting communities are distinct from those maturing on natural grounds surrounding them (Carr and Hixon, 1997; Glasby, 2001; Badalamenti et al., 2002; Smith and Rule, 2002;

\* Corresponding author. Royal Belgian Institute of natural Sciences, Rue Vautier, 29, 1000 Brussels, Belgium.

E-mail address: [vincent.zintzen@naturalsciences.be](mailto:vincent.zintzen@naturalsciences.be) (V. Zintzen).

Knott et al., 2004). Not only new hard substratum may be added to the sea but novel habitats are created, distinct from those naturally occurring in the area (Connell, 2000; Connell, 2001; Holloway and Connell, 2002).

In areas dominated by soft sediments, shipwrecks form a patchy network of hard substrata (Zintzen et al., 2006) whose interconnections are unknown (Bacchiocchi and Aioldi, 2003). Transfer must occur between the local populations of shipwrecks 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. This work will also help to better predict how the hard substrata that will be likely added by energy generation devices in the area (wind and wave power generation) may be colonized.

## 2. Materials and methods

### 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 (Larsonneur et al., 1982) and their benthic communities. 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 substrata like pebbles are rare and only occur locally in the swales between sandbanks (Lanckneus et al., 2001).

On the 3640 km<sup>2</sup> 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 sunk 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. The selected shipwrecks of Table 1 sank between 1940 and 1969, measure between 46 and 156 m in length and have structures emerging from 3 to 22 m above the seabed. Their location in the BPNS (distance from the coast: 8–29 nautical miles) is positively correlated to their depth (8–37 m – MLLWS – Mean Lower Low Water Springs levels). Their orientation on the seabed is variable.

### 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 substrata.

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 × 0.5 m quadrats 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 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 not practically feasible to manually sample all the communities on shipwrecks, the 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. This assemblage is known to harbour a diverse faunal association (Zintzen et al., 2006) and was present on all investigated sites. All organisms within quadrats of 0.25 × 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<sub>2</sub> 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 and Bourget, 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 (48 h at 70 °C), re-weighted (dry weight) and then burned at 500 °C for 12 h. 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

Table 1  
Localization and basic information on the nine shipwrecks under study

Wreck	WGS-84 coordinates	Date of sunk	Distance from the coast (nautical miles)	Length $\times$ width $\times$ height <sup>a</sup> (m)	Depth (MLLWS) (m)	Orientation
A-Birkenfels	N 51°38', 989 E 02°32', 268	1966	29	156 $\times$ 18 $\times$ 22	37	174°
B-Callisto	N 51°41', 950 E 02°37', 330	1959	29	146 $\times$ 19 $\times$ 8	28	28°
C-Garden city	N 51°29', 170 E 02°18', 320	1969	25	160 $\times$ 21 $\times$ 14	26	27°
D-Kilmore	N 51°23', 730 E 02°29', 790	1906	17	87 $\times$ 13 $\times$ 8	30	46°
E-John Mahn	N 51°28', 930 E 02°41', 350	1942	17	46 $\times$ 9 $\times$ 4	29	104°
F-Duc de Normandie	N 51°25', 524 E 02°36', 345	1942	16	51 $\times$ 11 $\times$ 7	29	164°
G-LCT 457	N 51°24', 670 E 02°43', 720	1944	12	63 $\times$ 10 $\times$ ? <sup>b</sup>	21	67°
H-Bourrasque	N 51°14', 964 E 02°33', 026	1940	8	74 $\times$ 12 $\times$ 3	18	81°
I-LST 420	N 51°15', 510 E 02°40', 830	1944	6	109 $\times$ 13 $\times$ 4	8	128°

<sup>a</sup> The height was estimated from multibeam sonar images, i.e. the highest structure above the seabed level.

<sup>b</sup> ? unavailable data.

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 and Bourget (2005). This factor has to be considered as a minimum one.

### 2.3. Abiotic data

The following abiotic data were accessed: water temperature, salinity, turbidity, vertically averaged current velocity and direction, chlorophyll *a* content of water above shipwreck and chlorophyll *a* content of sediments on shipwreck.

Seawater temperature and salinity (Practical Salinity Units) 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 and 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 ( $\text{mg l}^{-1}$ ) 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 Fettweis et al. (2007), 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 and Ozer, 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 min. The runs started in august 2004, resulting in at least 230 days of data for each shipwreck site.

Water samples ( $3 \times 1$  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 and Jeffrey (1997). For water samples, the results were expressed as  $\mu\text{g}$  per litre and the sediment samples as  $\mu\text{g}$  per gram of sediments.

### 2.4. Data analysis

#### 2.4.1. Photographic quadrats

Per site, 7–13 pictures were found of a quality high to allow identification. The percentage cover of epibiota from each quadrat was estimated by identifying taxa under 196 regularly spaced points with CPCe software (Kohler and Gill, 2006). The 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-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 fourth-root transformed data and tested by an ANOSIM procedure (Clarke and Warwick, 2001b). A SIMPER breakdown was performed to determine the epibenthic categories that contribute most to the average similarity within sites (Clarke and Warwick, 2001b).

#### 2.4.2. *Tubularia* association

Species richness (S), the Simpson index (D, based on biomass values to take into account the colonial organisms) (as recommended by Magurran, 2004), the average taxonomic distinctness ( $\Delta^+$ ) and the variation in taxonomic distinctness ( $\Delta^+$ ) (Clarke and Warwick, 1998; Clarke and Warwick, 2001a) were used as univariate summary variables to characterize the biological diversity of each site. 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's 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). All 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 and Wilk, 1965).

Multivariate exploratory analysis of the scraped samples from the *Tubularia* association was conducted on biomass data. Because of the low number of replicates by site ( $N = 3$ ), the data were pooled by site (shipwreck) and square-root transformed to give more weight in the analysis to the less abundant species. Similarity between each pair of samples was then calculated with the Bray-Curtis similarity coefficient (Bray and Curtis, 1957). The resulting matrix was 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 two dimensional nMDS plot was measured using Kruskal's stress formula I (Kruskal and Wish, 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 and Warwick, 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. We retained the following abiotic 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 ( $>1$ ,  $1-0.75$ ,  $0.75-0.50$ ,  $0.50-0.25$ ,  $0.20-0.10$ ,  $<0.10 \text{ m s}^{-1}$ ) (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). Draftsman plot of environmental data was done to estimate skewness of data and transformation applied if necessary. Environmental data with strong collinearity (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 and 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 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.

### 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.

Temperature varied between 0.4 and 22.1 °C (Fig. 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



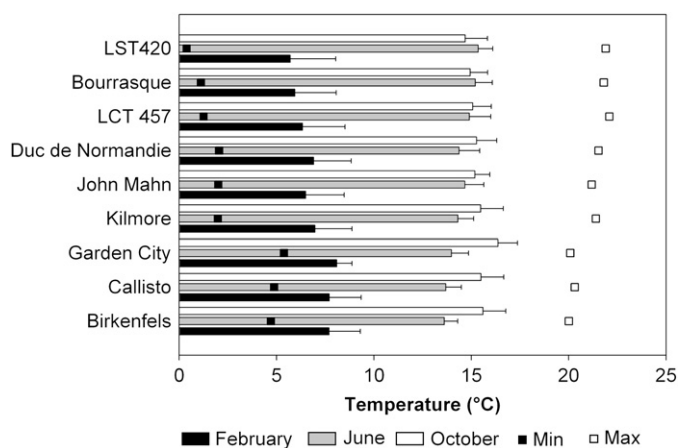


Fig. 1. Water temperature on the nine shipwrecks. The mean monthly values (+SD) for February, June and October are presented together with minimal and maximal observed temperature. Period covered: 1993–2006.

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 (Fig. 2). In February, the coastal sites showed a decreased salinity of approximately two units compared to the intermediate and offshore sites (Fig. 2A). Salinity values recorded in October showed less variation amongst the nine sites. Three groups differentiated from the minimal and maximal salinities (Fig. 2B). Lowest salinities were recorded on the LST420, Bourrasque and LCT457 as they 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. Fig. 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<sup>-1</sup>, 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<sup>-1</sup>. For all sites, the frequency of low current velocity (<0.2 m s<sup>-1</sup>) was comprised between 9.0 and 15.1% and the period of very low current velocity (calms, <0.1 m s<sup>-1</sup>) was always under 1.1% in frequency. The most frequently occurring current velocity was comprised between 0.6 and 1.0 m s<sup>-1</sup>, except for the LST420 and Bourrasque where current velocity in the range 0.4–0.8 m s<sup>-1</sup> 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<sup>-1</sup> and 15.3 mg l<sup>-1</sup>, respectively, while reaching 9.7 mg l<sup>-1</sup> at LCT457. Values for the Kilmore, Duc de Normandie and John Mahn fell between 7.3 and 7.8 mg l<sup>-1</sup>. At the Garden City, Birkenfels and Callisto, late summer TSM values of 6.1–6.2 mg l<sup>-1</sup> were found. Secchi readings confirmed TSM measurements (Fig. 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 µg l<sup>-1</sup> (Fig. 5). The sediments contained chlorophyll *a* in concentration ranging from 0.9 to 6.1 µg g<sup>-1</sup>. 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.

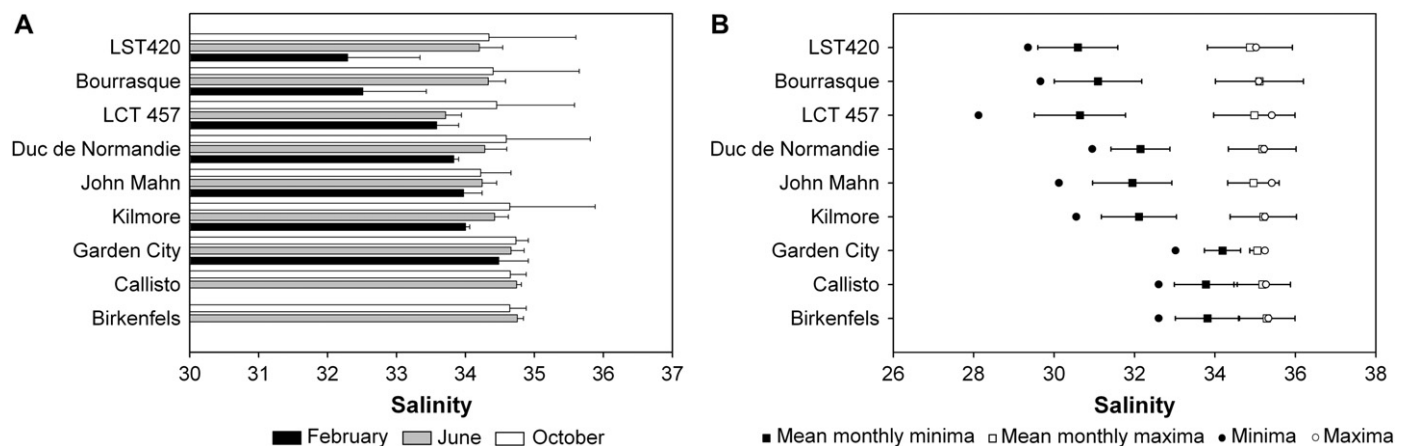


Fig. 2. Water salinity on the nine shipwrecks. (A) Mean monthly values (+SD) for February, June and October. (B) Mean (±SD) monthly minima and maxima. Period covered: 1993–2006.

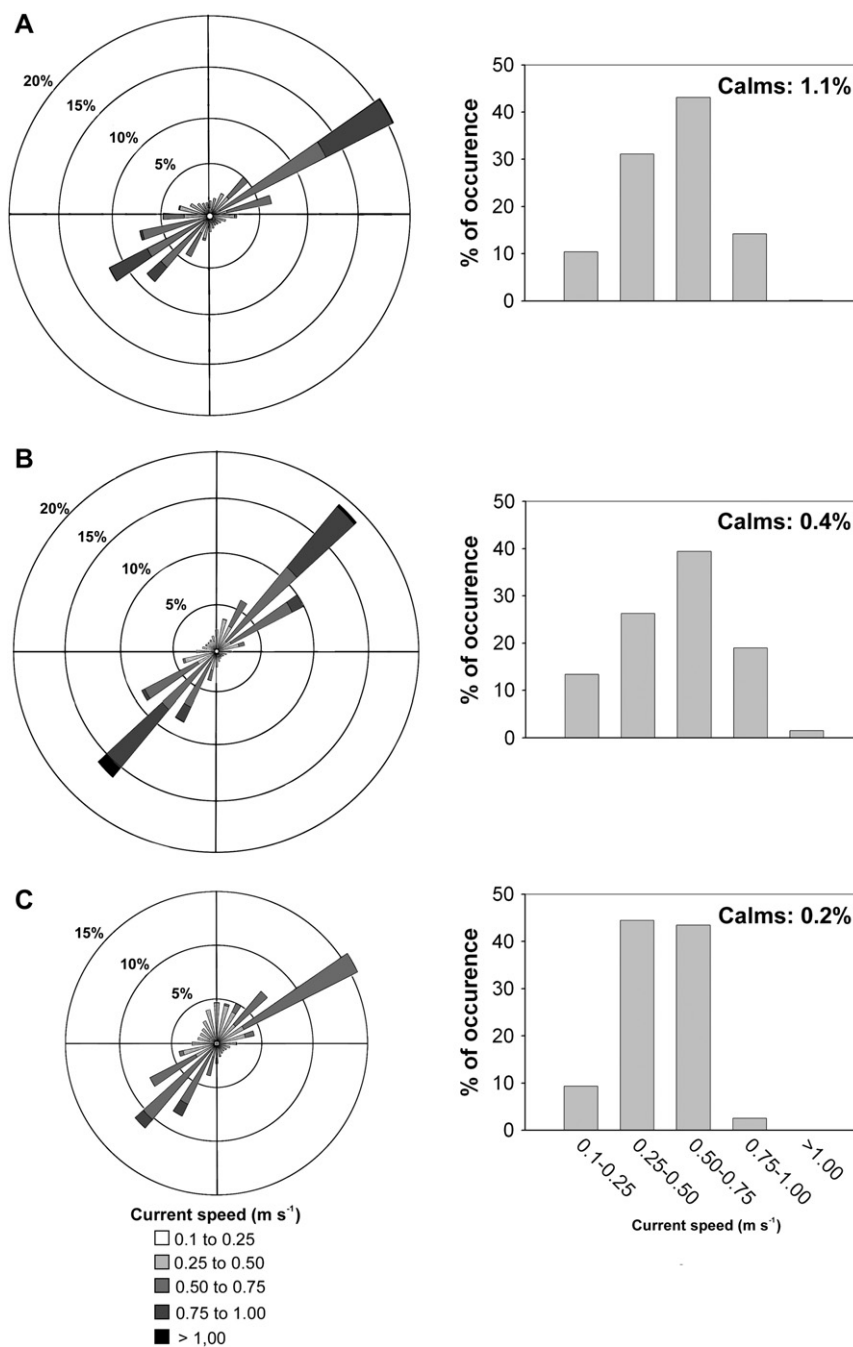


Fig. 3. Current roses and % of occurrence of currents for an offshore (Birkenfels, A), intermediate (Duc de Normandie, B) and coastal sites (LST 420, C). The currents were computed from a 3D hydrodynamic model forced by UK Met Office meteorological forecast (August 2004–July 2005, time step: 10 min).

### 3.2. 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 (Fig. 6). 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 *Tubularia indivisa* and *Tubularia larynx*) always associated with a tube building amphipod (*Jassa herdmanni*), *Sagartia* sp., *Asterias rubens*, *Metridium senile* and *Diadumene cincta* (Fig. 6). Less common taxa identified were: *Actinothoe sphyrodeta*, *Cancer pagurus*, *Dendronotus frondosus*, *Diplosoma* 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 *Metridium senile* and 29% covered by

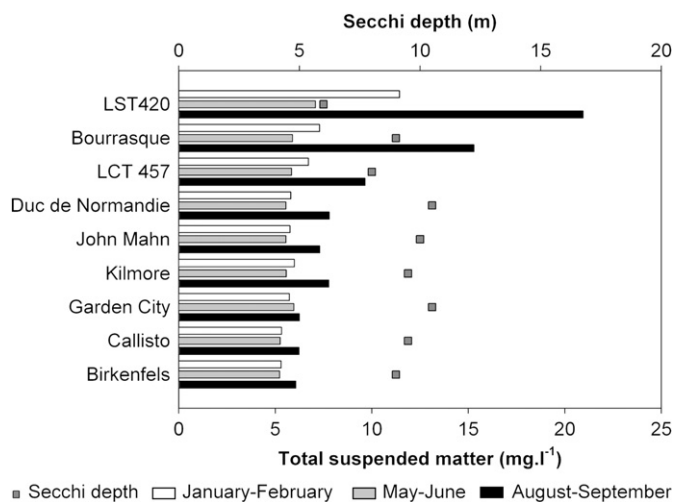


Fig. 4. Mean total suspended matter by period of the year and by site estimated from Modis satellite imagery (period covered: July 2002–October 2005) and Secchi depth taken on the sampling dates.

a mixture of *T. indivisa* – *T. larynx* – *J. herdmanni* (if excluding bare surface). The other sites were on average covered at 81% by *T. indivisa* – *J. herdmanni*.

A multivariate analysis of the data on coverage is presented in Fig. 7. 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*.

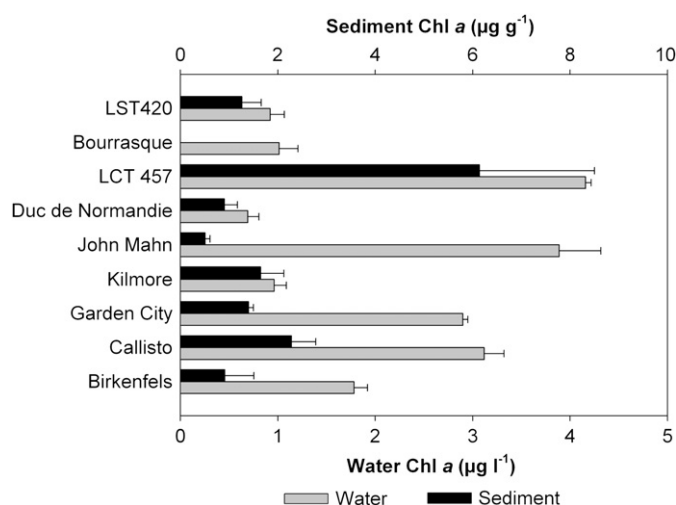


Fig. 5. Chlorophyll *a* concentration ( $N = 3$ ,  $\pm$ SD) of water and sediment samples from the shipwreck sites.

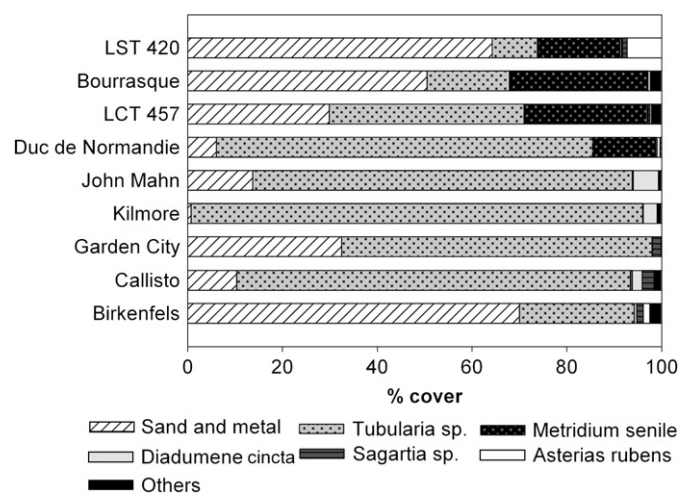


Fig. 6. Mean percentage cover of epifauna on the shipwrecks estimated from photographic quadrats. Others: *Actinothoe sphyrodeta*, *Cancer pagurus*, *Dendronotus frondosus*, *Diplosoma* sp., *Porifera*, *Haliclona* sp., *Jassa* tubes, *Nassarius* sp., *Necora puber*, *Nemertesia antennina*, *Ophiotrix fragilis*, *Paguridae*, *Pomatoceros triqueter*, *Sycon ciliatum*, *Urticina felina*, fishing lines/net and unidentified feature.

The Birkenfels was closely associated with this last group of shipwrecks even if some of the quadrats showed a very low cover of *Tubularia* spp. On the offshore sites (Garden City, Birkenfels, Callisto), *Sagartia* sp. together with *D. cincta* were well represented. The LST 420, LCT 457 and Bourrasque were less dominated by *Tubularia* spp. while *M. senile* was the dominant taxa on Bourrasque and LST 420. *Metridium senile* 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.

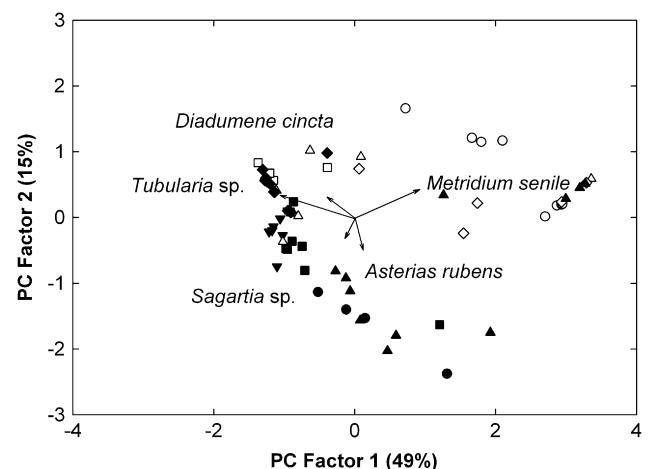


Fig. 7. Principal Composant Analysis biplot of the epifauna cover data (on covariance matrix, fourth-root-transformed data). Only the main variables and the sites with  $\sum \text{Cos}^2 \geq 0.40$  are represented. Sites symbolism: ■ Bourrasque, □ LST 420, ● John Mahn, ○ Duc de Normandie, ◆ Birkenfels, ◇ Kilmore, ▲ Callisto, △ LCT 457, × Garden City.

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. Table 2 presents the results of the BIO-ENV analysis. Depth was the best single correlated factor ( $r = 0.393$ ). However, other factors could 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  $0.75 \text{ m s}^{-1}$  and current velocity proportion between 0.50 and  $0.25 \text{ m s}^{-1}$ ). The addition of other factors only slightly improved the correlation.

### 3.3. The Tubularia community from SCUBA sampling

#### 3.3.1. Diversity and abundance of epifauna

A total of 90 species were recorded. Species richness 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 Fig. 8). The John Mahn had a significant higher Simpson index ( $D$ ) than the Birkenfels, Callisto, Duc de Normandie and Garden City (SNK,  $p < 0.05$  and Fig. 8). The average taxonomic distinctness ( $\Delta^+$ ) and the variation in taxonomic distinctness ( $\Delta^+$ ) showed little variations between sites. The following significant differences were found ( $p < 0.05$ ): Kilmore versus Bourrasque for  $\Delta^+$ , Duc de Normandie versus Bourrasque for  $\Delta^+$  and for  $\Delta^+$ .

A total of 47% of the species were present in only one (23 species) or two sites (19 species). 32% of the species were

present on 7–9 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 3). 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 ( $\pm$ SD) of  $116,997 \pm 31,700 \text{ ind m}^{-2}$  and a maximal density of  $180,000 \text{ ind m}^{-2}$  in one sample of the Kilmore shipwreck. Other amphipods (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.

#### 3.3.2. Biomass

The mean biomass recorded on the shipwrecks was  $288 \text{ g AFDW m}^{-2}$  (Fig. 9). It naturally does not include the materials from tubes built mostly by the amphipod *Jassa herdmani*. However, it is worth noting that, on average, the organic material accumulated in these tubes was equivalent to  $92 \text{ g AFDW m}^{-2}$ . The hydrozoans *Tubularia indivisa* and *Tubularia larynx* accounted for 69% of the recorded biomass. Crustaceans, mainly amphipod 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  $584 \pm 207$ ,  $474 \pm 597$  and  $471 \pm 391 \text{ g AFDW m}^{-2}$ , respectively. Lowest biomass values were found at the LST 420

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, Nemertinata; POL, Polychaeta

Species		Global mean abundance (ind $\text{m}^{-2}$ )	Dispersion (%site)	Local mean abundance (ind $\text{m}^{-2}$ )	Site of maximal mean abundance
<i>Jassa herdmani</i>	CRU	63,029	100	116,997	Kilmore
<i>Caprella tuberculata</i>	CRU	3219	78	22,677	Kilmore
<i>Phthisica marina</i>	CRU	1343	100	4315	John Mahn
<i>Stenothoe valida</i>	CRU	1253	89	4192	LCT457
<i>Pisidia longicornis</i>	CRU	950	100	1909	Callisto
<i>Ophiothrix fragilis</i>	ECH	831	100	1269	Garden City
<i>Stenothoe monoculoides</i>	CRU	823	89	3643	Kilmore
<i>Phyllodoce mucosa</i>	POL	804	89	6533	LCT457
<i>Mytilus edulis</i>	MOL	516	100	2971	Kilmore
<i>Asterias rubens</i> juv.	ECH	363	67	885	LCT457
Actiniaria	CNI	345	100	581	Duc de Normandie
<i>Stenothoe marina</i>	CRU	334	100	731	LCT457
<i>Monocorophium sextonae</i>	CRU	299	89	1435	LCT457
<i>Metopa alderi</i>	CRU	245	89	944	John Mahn
<i>Harmothoe</i> spp.	POL	152	100	427	John Mahn
<i>Oerstedia dorsalis</i>	NEM	141	100	427	LST420
<i>Sabellaria spinulosa</i>	POL	121	89	555	Callisto
<i>Amphipholis squamata</i>	ECH	107	78	624	Kilmore
<i>Eulalia viridis</i>	POL	74	78	475	LCT57
<i>Pilumnus hirtellus</i>	CRU	63	89	144	Callisto



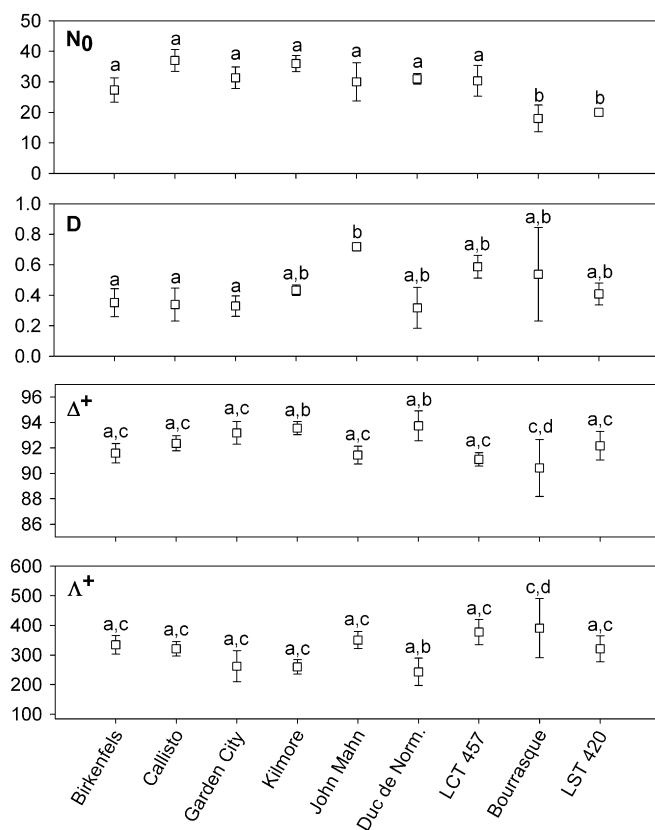


Fig. 8. Mean number of species ( $N_0$ ), Simpson index ( $D$ ), taxonomic distinctness ( $\Delta^+$ ) and variation in taxonomic distinctness ( $\Lambda^+$ ) for each shipwreck site ( $N = 3$ ,  $\pm$ SD). Sites with the same letters did not differ significantly at  $p < 0.05$  (SNK test).

and Bourrasque ( $55 \pm 73$  and  $150 \pm 65$  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.

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 ( $R$ ) based on spearman rank coefficient. Combinations 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

# var.	$R$	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%

### 3.3.3. Multivariate pattern

The Bourrasque (site H on Fig. 10) and LST 420 (site I) were found to clearly differ from the other shipwrecks in the ordination plane (Fig. 10A). Ordination and clustering identified two additional groups (Fig. 10B,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 F) 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 dominant *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.

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  $0.75 \text{ m s}^{-1}$ , current velocity proportion between  $0.50$  and  $0.25 \text{ m s}^{-1}$  and salinity for January explained almost as well the relation between biotic and abiotic data (Table 4). 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  $0.75 \text{ m s}^{-1}$ , current velocity proportion between  $0.75$  and  $0.50 \text{ m s}^{-1}$ , and angular difference between heading of the shipwreck and prevailing current direction.

### 3.3.4. Indicator species

Shipwrecks in general were represented by a large number of indicator (characteristic) species that had a high level of fidelity to that community (Table 5). 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* and *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. An identical 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 opisthobranch *Dendronotus frondosus* and the sponge *Sycon ciliatum* had their maximum indicator value at the

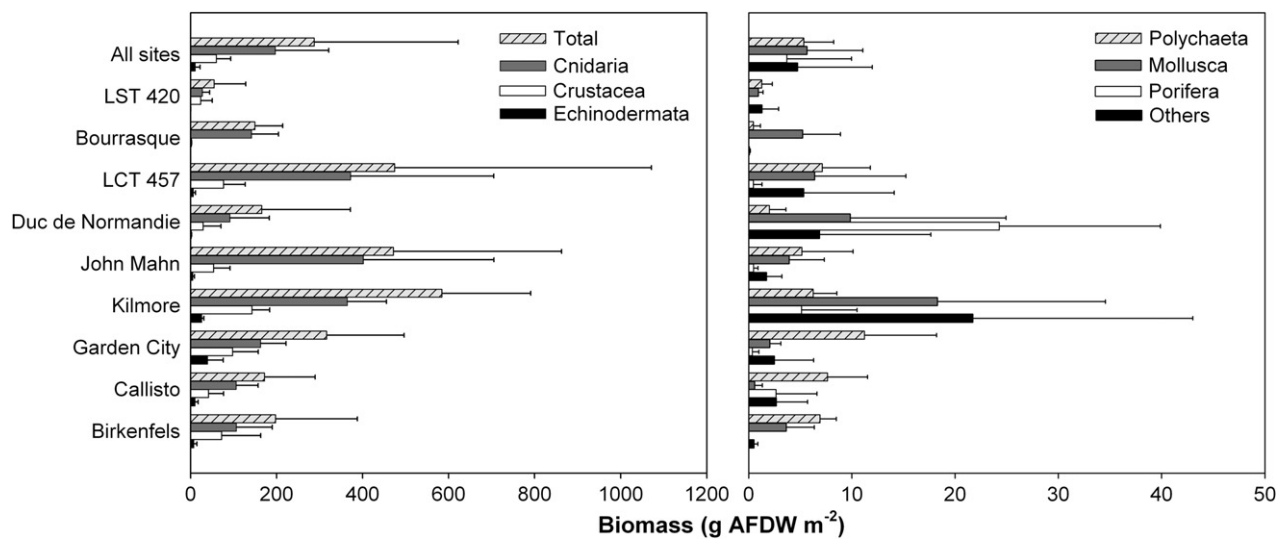


Fig. 9. Mean biomass values ( $N = 3$ ,  $+SD$ ) of shipwrecks sites for main taxonomic groups. Others: Tunicata, Nemertea, Bryozoa and Turbellaria.

intermediate site 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 Rissoiidae in the Callisto and the opisthobranch *Catriona gymnota* at the Bourrasque.

## 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 and Davoult, 1997;

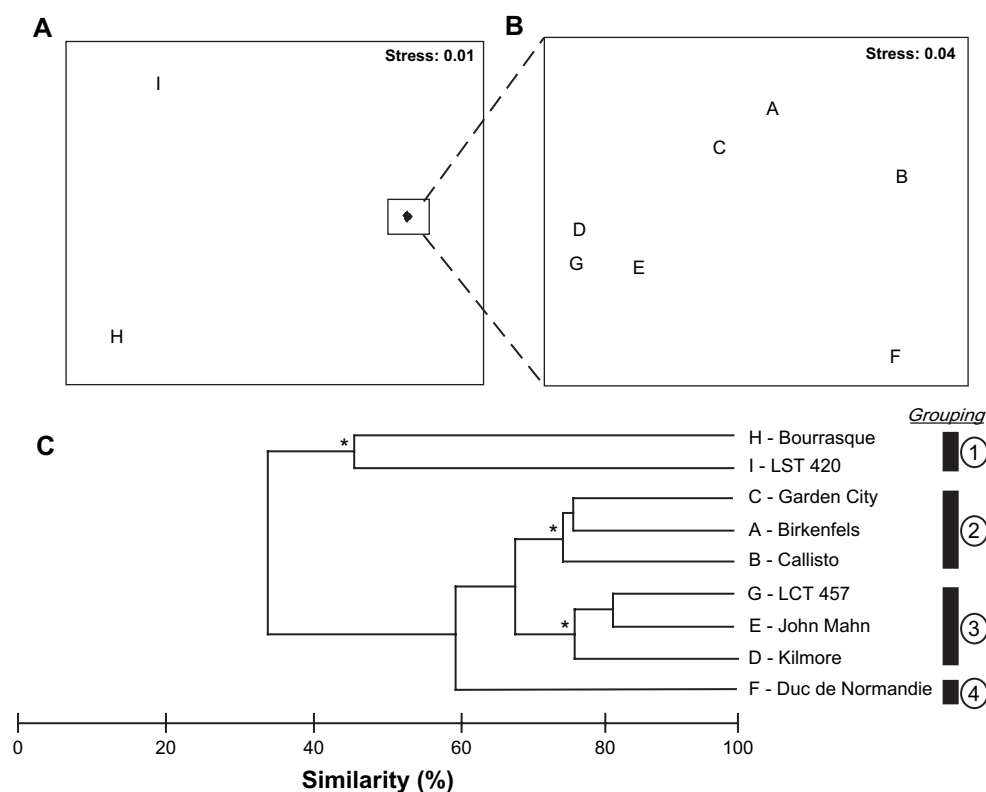


Fig. 10. Multivariate analysis of similarity between sites (Bray-Curtis coefficient on square root transformed biomass data). (A) nMDS of all sites; H: Bourrasque, I: LST 420. (B) nMDS of undiscernible sites in (A); A: Birkenfels, B: Callisto, C: Garden City, D: Kilmore, E: John Mahn, F: Duc de Normandie, G: LCT 457. (C) Clustering of sites; \* significant at  $p < 0.05$  after SIMPROF (Permutations for mean profile: 2000, Simulation permutations: 999).

Table 4

Indicator species values (IndVal), mean biomass (g AFDW m<sup>-2</sup>) 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<sup>-2</sup>, 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 test

Species	Ind-Val (%)	Birkenfels	Callisto	Garden city	Kilmore	John Mahn	Duc de Nomandie	LCT457	Bourrasque	LST420
All sites										
<i>Tubularia indivisa</i>	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
<i>Jassa herdmanni</i>	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
<i>Phtisica marina</i>	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
<i>Actiniaria</i>	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
<i>Harmothoe</i> 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
<i>Ophiorthrix fragilis</i>	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
<i>Mytilus edulis</i>	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
<i>Stenothoe marina</i>	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
<i>Monocorophium sextonae</i>	81	0.2/3	0.1/3	0/3	0/3	0.1/3		0.5/3	0/3	0/1
<i>Oerstedtia dorsalis</i>	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
<i>Pisidia longicornis</i>	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
<i>Stenothoe valida</i>	81	0.4/3	0.5/3	0.3/3	0.8/3	1.9/3	0.2/3	3.7/3	0/1	
<i>Electra pilosa</i>	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
<i>Pilumnus hirtellus</i>	77	0.3/3	1.1/2	0.7/3	1.2/3	0.7/3	0.1/3	0.5/3		0/1
<i>Lanice conchilega</i>	74	0/1	0/1	0.2/3	0.1/3	0.1/3	0.4/3	0.1/3		0.5/3
<i>Lepidonotus squamatus</i>	74	0.5/3	0/2	0.2/2	1.1/3	0.2/3	0.2/3	0.4/2		0/2
<i>Stenothoe monoculoides</i>	70	0/2	0.1/3	0.1/3	0.5/3	0.1/3	0/1	0.1/3		0/1
<i>Caprella tuberculata</i>	66	1/3	0.4/3	0.6/3	6.4/3	0/2	1/3		0/1	
<i>Metopa alderi</i>	66	0/2	0.5/3		0.1/2	0.6/3	0.4/3	0.1/3	0/1	0/1
<i>Asterias rubens</i> juv.	62		0/2		0.2/3	0.1/3	0.1/3	0.8/3		0.3/3
<i>Phyllodoce mucosa</i>	62		0/2	0/1	0.1/3	0.1/2	0.1/2	3.1/3	0.4/2	0/2
<i>Amphipholis squamata</i>	59		0/3	0.2/3	0.3/3	0/2	0/2	0/2		0/1
<i>Pomatoceros triqueter</i>	59	2.8/2	2.6/3	6.7/3	1.4/2	0.5/2	0.3/2	0.4/2		
<i>Dendronotus frondosus</i>	55			0.7/3	15.9/3	3.8/2	9.7/3	5.7/2	0/1	0.1/1
<i>Cuthona</i> sp.	51	0.2/3		0/1	0.1/3	0/2	0/2	0/1		0.4/2
<i>Eulalia viridis</i>	51	0/2	0.1/1	0.1/1	0.1/3	0/3	0/1	0.2/3		
<i>Psammecinus miliaris</i>	51	0/2	0.1/2	0.6/3	0.1/3	0/2		0/2		
<i>Sabellaria spinulosa</i>	51	0.8/2	3.6/2	0.2/2	0.2/2	0/1	0.5/3	0.1/1	0/1	
<i>Syllis gracilis</i>	51	0/2	0/2	0/2	0/2	0/1	0/2	0.2/3		
Offshore sites										
<i>Aequipecten opercularis</i>	91**	0.3/3	0.3/3	0.5/3	0.1/2	0/1			0/1	
<i>Pomatoceros triqueter</i>	76**	2.8/2	2.6/3	6.7/3	1.4/2	0.5/2	0.3/2	0.4/2		
<i>Actiniaria</i>	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
<i>Ophiorthrix fragilis</i>	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
<i>Psammecinus miliaris</i>	67*	0/2	0.1/2	0.6/3	0.1/3	0/2		0/2		
<i>Sabellaria spinulosa</i>	58*	0.8/2	3.6/2	0.2/2	0.2/2	0/1	0.5/3	0.1/1	0/1	
<i>Heteranomia squamula</i>	55**	0/2	0.1/2	0.3/2	0/3	0/1	0.1/2			
<i>Musculus</i> sp.	54**	0/2	0/1	0/2		0/1				
<i>Nereis pelagica</i>	53**	2.2/2	0.2/2	1.4/1			0/1	0.2/1		
<i>Pisidia longicornis</i>	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										
<i>Dendronotus frondosus</i>	80**			0.7/3	15.9/3	3.8/2	9.7/3	5.7/2	0/1	0.1/1
<i>Stenothoe valida</i>	80**	0.4/3	0.5/3	0.3/3	0.8/3	1.9/3	0.2/3	3.7/3	0/1	
<i>Electra pilosa</i>	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
<i>Phtisica marina</i>	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
<i>Tubularia indivisa</i>	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
<i>Phyllodoce mucosa</i>	65*		0/2	0/1	0.1/3	0.1/2	0.1/2	3.1/3	0.4/2	0/2
<i>Harmothoe</i> 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
<i>Asterias rubens</i> juv.	62**		0/2		0.2/3	0.1/3	0.1/3	0.8/3		0.3/3
<i>Stenothoe monoculoides</i>	58*	0/2	0.1/3	0.1/3	0.5/3	0.1/3	0/1	0.1/3		0/1
<i>Sycon ciliatum</i>	57**			0.1/1	4.5/3	0.1/1	6.3/2	0.4/1		
<i>Lepidonotus squamatus</i>	57*	0.5/3	0/2	0.2/2	1.1/3	0.2/3	0.2/3	0.4/2		0/2
<i>Syllis gracilis</i>	57**	0/2	0/2	0/2	0/2	0/1	0/2	0.2/3		
<i>Metopa alderi</i>	53	0/2	0.5/3		0.1/2	0.6/3	0.4/3	0.1/3	0/1	0/1
Coastal sites										
<i>Tubularia larynx</i>	97**	2.1/1						0.7/1	59.9/3	3/3
<i>M. acherusicum</i> <sup>a</sup>	83**								0/3	0.1/2

(continued on next page)

Table 4 (continued)

Species	Ind-Val (%)	Birkenfels	Callisto	Garden city	Kilmore	John Mahn	Duc de Normandie	LCT457	Bourrasque	LST420
<i>Stenothoe marina</i>	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
<i>Catriona gymnota</i>	50**								1.7/3	
<i>Metridium senile</i>	50**								59.2/2	3.6/1
<i>Obelia bidentata</i>	50**								2/2	0/1
Garden City										
<i>Psammechinus miliaris</i>	68	0/2	0.1/2	0.6/3	0.1/3	0/2		0/2		
<i>Odontosyllis fulgurans</i>	55**		0/1	0/3	0/1	0/1	0/1	0/1	0/1	
Birkenfels										
—	—	—	—	—	—	—	—	—	—	—
Callisto										
<i>Eulalia aurea</i>	70**	0/1	0.1/3		0/1					
<i>Polyclinum aurantium</i>	64*		1/2		0/1					
<i>Molgula cf occulta</i>	58*	0.1/2	0.5/2							
Kilmore										
<i>Scrupocellaria scruposa</i>	79**		0/2		0.2/3					
<i>Electra pilosa</i>	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
<i>Caprella tuberculata</i>	67**	1/3	0.4/3	0.6/3	6.4/3	0/2	1/3		0/1	
<i>Amphipholis squamata</i>	55*		0/3	0.2/3	0.3/3	0/2	0/2	0/2		0/1
<i>Stenothoe monoculoides</i>	53**	0/2	0.1/3	0.1/3	0.5/3	0.1/3	0/1	0.1/3		0/1
Duc de Normandie										
<i>Myxilla rosacea</i>	74**		0.8/1		0.6/1		4.1/3			
<i>Halichondria cf panicea</i>	54*		0.4/1				1.9/2			
John Mahn										
—	—	—	—	—	—	—	—	—	—	—
LCT 457										
<i>Phyllodoce mucosa</i>	81**		0/2	0/1	0.1/3	0.1/2	0.1/2	3.1/3	0.4/2	0/2
<i>Syllis gracilis</i>	75**	0/2	0/2	0/2	0/2	0/1	0/2	0.2/3		
<i>Nemertinata</i> sp.	58*		0/1					0.2/2		
<i>Turbellaria</i>	57*			0/1				0.1/2		
<i>Asterias rubens</i> juv.	52**		0/2		0.2/3	0.1/3	0.1/3	0.8/3		0.3/3
<i>Monocorophium sextonae</i>	50**	0.2/3	0.1/3	0/3	0/3	0.1/3		0.5/3	0/3	0/1
Bourrasque										
<i>Catriona gymnota</i>	100**								1.7/3	
<i>Tubularia larynx</i>	91**	2.1/1						0.7/1	59.9/3	3/3
<i>Balanus crenatus</i>	66*						0/1		0.5/2	
<i>Obelia bidentata</i>	65*								2/2	0/1
<i>Metridium senile</i>	62*								59.2/2	3.6/1
LST 420										
<i>Eumida</i> sp.	60**							0/1		0/3
<i>M. acherusicum</i> <sup>a</sup>	51								0/3	0.1/2

<sup>a</sup> *Monocorophium acherusicum*.

Guichard and Bourget, 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 *Pomatosceros triqueter* and the barnacle *Balanus crenatus*) and *Sabellaria spinulosa* 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

the encrusting 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 (3–5 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



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 ( $R$ ) based on spearman rank coefficient. Combinations 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

# var.	$R$	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%

load, reduced current speed and a freshwater influence; (2) a transition zone with intermediate depths, turbidity values and the strongest currents; and (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 next.

#### 4.3. The *Metridium senile* community

The *Metridium senile* community dominated in the shallower waters (LST420, Bourrasque and LCT457) 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. In Helgoland, *M. senile* together with *Pomatoceros triqueter* was largely represented on shallow natural hard substrata 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. Whomersley and Picken (2003) also pointed at the dominance of *M. senile* up to depths of 140 m on offshore platforms in the North Sea, indicating that its poor representation on deeper shipwrecks in Belgian waters may not strictly be depth dependant. In Belgian waters, *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, consequently finding 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 and Svane, 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 the coastal 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 non-exclusive hypothesis explaining the success of *Metridium 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 *Tubularia 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 and Svane, 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 *Tubularia larynx* occurred on the coastal sites. These species are common on many waters around the world (Pyefinch and Downing, 1949; Schmidt, 1983; Foster et al., 1994; Lemire and Bourget, 1996; Orlov, 1996; Steimle and Zetlin, 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 *Metridium 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. The widely contribute to the establishment of the biological diversity on shipwrecks by providing increased surface of settlement. In terms of abundance (up to 180,000 ind m<sup>-2</sup>) and biomass (173 g AFDW m<sup>-2</sup>), the amphipod *Jassa herdmani* was the most common of these epibionts. Caprellids (*Caprella tuberculata* and *Phthisica marina*) were also abundant (up to 1700 ind m<sup>-2</sup> and 9360 ind m<sup>-2</sup>, respectively). Gili et al. (1996) found that *Tubularia 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 the amphipods 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<sup>-2</sup>. On shipwrecks in the Dutch sector of the North Sea, Leewis et al. (2000) found a mean biomass value of 642 g AFDW m<sup>-2</sup>. Many of their samples were taken in a *Metridium senile* assemblage which was only one of the discerned assemblages in their study. In Leewis' study, the average biomass of that community was 1072 g AFDW m<sup>-2</sup> and it was the highest observed on Dutch shipwrecks. That value is comparable to the mean biomass value of 1243 g AFDW m<sup>-2</sup> ( $N = 14$ , unpublished data) we recorded for the *M. senile* assemblages of the coastal sites.

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<sup>-2</sup> (Leewis et al., 1994). On pebbles in the Dover Strait, Migne and Davoult (1997) estimated a mean value of 281 g AFDW m<sup>-2</sup>.

Our biomass values are among the highest recorded values for epibenthic communities in temperate waters. Kuhne and Rachor (1996) recorded 30–180 g AFDW m<sup>-2</sup> for the macrofauna of a stony sand area in the German Bight of the North Sea. The dry weight of the macrofauna of hard substrata in the Bristol Channel was found to be 24.5 g m<sup>-2</sup> (dry weight) (George and Warwick, 1985). Steimle (1985) also reported a lower (wet weight) value of 238 g m<sup>-2</sup> 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<sup>-2</sup> (Duineveld et al., 1991; Heip et al., 1992) and around 30–50 g AFDW m<sup>-2</sup> for the *Abra alba* community (Prygiel et al., 1988). Consequently, we can conclude 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.

#### 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 and the evenness and taxonomic components of diversity within the shipwreck fauna did not show any clear pattern with distance from the coast. The average taxonomic distinctness and variation in taxonomic distinctness were not able to discriminate between sites with varying environmental conditions. This failure was

already observed in other studies (Somerfield et al., 1997; Mouillot et al., 2005) and it seems that these indices could be more related to long-term structural changes in ecosystem processes than to small-scale variations (Ramos Miranda et al., 2005). 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 *Tubularia larynx* which replaced *Tubularia indivisa*. The biomass of *T. indivisa* was lower on the offshore sites than on intermediate sites. An explanation could be the lower productivity of the offshore waters linked to a decrease in suspended sediments (our results and Fettweis and Van den Eynde, 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., 1990). 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 the two areas.

One of the most ecologically important gradients is the cross-shore gradient on the coastal area where 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. *Metridium senile*).

The analysis of indicator species revealed that a large number of species were typical of shipwrecks in general. It showed up that no taxa were exclusively indicative of some of the groupings, but that some taxa were more common or had 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 and Jumars, 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*. The latter species, an anomouran, 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 the amphipod populations observed under the binocular 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 *P. triqueter* 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<sup>-2</sup>). They use the perisarc of *Tubularia* spp. as an attachment site before leaving that hard substratum to start their benthic life. Actinarians (mainly represented by *Diadumene cincta*) and *Ophiothrix fragilis* were also more abundant on offshore sites. The mean density of the ophiuroid was 900 ind m<sup>-2</sup> with a maximum value of 3650 ind m<sup>-2</sup> 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 since *O. fragilis* takes advantage of the inhalant currents created by the sponges (Turon et al., 2000). *Ophiothrix fragilis* is abundantly represented on the pebble areas of the deeper waters in the English Channel (Ellis and Rogers, 2000) where suitable hydrodynamic conditions are met for the formation of large beds (tidal currents 10–25 cm s<sup>-1</sup> and low sedimentation rates) (Davoult, 1990; Ellis and Rogers, 2000). It adopts a gregarious behaviour (Broom, 1975). Exchange with the dense population of the Dover Strait might occur as supported by simulation of larvae dispersal (Lefebvre et al., 2003). Populations of *O. fragilis* on Belgian shipwrecks may form an extension of the Dover Strait populations since 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. *Dendronotus frondosus* is a predator of *Tubularia indivisa* (Thompson and Brown, 1976; Hughes, 1983). Except for *Tubularia 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: 3219 ind m<sup>-2</sup>). However, on one site (John Mahn), it was

found in only very low abundance (21 ind m<sup>-2</sup>) 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<sup>-2</sup>. One cannot exclude that the samples were taken on these intermediate sites on locations that did not favour the development of the caprellid species. The orientation of the shipwrecks versus the dominant direction of the water current could also account for the observed pattern. 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,b, 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<sup>-1</sup>, 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 the LCT 457 and John Mahn. 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 nor distinct abiotic factors can explain the observed variation in densities. 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. It may alter the settlement, recruitment and dispersion of some species as well as the sedimentation rate and seston flux (Baynes and Szmant, 1989).

Finally, from the work achieved on UK shipwrecks (Connor et al., 2004), the European Nature Information System (EUNIS) classifies this habitat as the “*Alcyonium digitatum* and *Metridium senile* on moderately wave-exposed circalittoral steel wrecks” (Habitat code: A4.721, <http://eunis.eea.europa.eu/habitats-factsheet.jsp?tab=0&idHabitat=5539>). Around UK waters, wrecks that are subject to moderately strong to weak tidal streams are dominated by *M. senile*, *A. digitatum* and *Actinothoe sphyrodeta* while those located where tidal stream strength is elevated may be densely covered by *Tubularia indivisa*. We also observe a dominance of *T. indivisa* where the



current is the strongest and a dominance of *M. senile* on shipwrecks exposed to less strong tidal streams. However, *A. digitatum* and *A. sphyrodeta* were mostly observed on the offshore sites (strong current), not especially associated with *M. senile*. The vagile epibenthos of the UK classification share several species like the decapods *Cancer pagurus* and *Necora puber*. To our knowledge, the information concerning shipwreck fauna in the North Sea is limited to the work of Hiscock (1980) in UK waters and the paper of Leewis et al. (2000) in The Netherlands. The comparison of their faunal list with our results indicates a clear dominance of the cnidarians, mostly *Tubularia* spp. and *M. senile*, with many other epifaunal species in common like barnacles and amphipods (caprellid species and tube-building amphipods). Nonetheless, many accompanying species are typical of the local/regional species pool and are not shared between sites.

## Acknowledgements

The authors wish to thank the crews of the R.V. Zeeleeuw and R.V. 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, Ms 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). J.M. is a research associate of the FRNS. Finally, we thank two anonymous reviewers for their constructive remarks on the manuscript.

## References

- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.
- Anthony, K.R.N., Svane, I., 1995. Effects of substratum instability on locomotion and pedal laceration in *Metridium senile* (Anthozoa: Actiniaria). *Marine Ecology-Progress Series* 124, 171–180.
- Bacchiocchi, F., Airolidi, L., 2003. Distribution and dynamics of epibiota on hard structures for coastal protection. *Estuarine, Coastal and Shelf Science* 56, 1157–1166.
- 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.
- 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.
- 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* 31, 52–57.
- Broom, D.M., 1975. Aggregation behaviour of the brittle-star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the UK* 55, 191–197.
- 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.
- 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., Lefebvre, A., Lemoine, N., Loots, C., Meaden, G.J., Ryan, N., Walkey, M., 2005. Eastern Channel Habitat Atlas for Marine Resource Management (CHARM). European Program Interreg IIIA, 225 pp. Available from <http://charm.canterbury.ac.uk/>.
- Carr, M.H., Hixon, M.A., 1997. Artificial reefs: the importance of comparisons with natural reefs. *Fisheries* 22, 28–33.
- 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., 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, second ed. PRIMER-E, Plymouth, UK, 172 pp.
- 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.
- 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.
- 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. Joint Nature Conservation Committee, Peterborough, UK, ISBN 1 861 07561 8. <http://www.jncc.gov.uk/MarineHabitatClassification> (internet version).
- 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.
- Davault, D., 1990. Biofaciès et structure trophique du peuplement des cailloutis du Pas-de-Calais (France). *Oceanologica 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*). *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.
- Dufrène, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345–366.
- 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.
- Ellis, J.R., Rogers, S.I., 2000. The distribution, relative abundance and diversity of echinoderms in the eastern English Channel, Bristol Channel, and Irish Sea. *Journal of the Marine Biological Association of the UK* 80, 127–138.



- 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.
- 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.
- 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.
- Fettweis, M., Nechad, B., Van den Eynde, D., 2007. An estimate of the suspended particulate matter (SPM) transport in the southern North Sea using SeaWiFS images, in situ measurements and numerical model results. *Continental Shelf Research* 27, 1568–1583.
- Fortéath, 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.
- Galéron, J., Sibuet, M., Mahaut, M.-L., Diné, A., 2000. Variation in structure and biomass of the benthic communities at three contrasting sites in the tropical Northeast Atlantic. *Marine Ecology-Progress Series* 197, 121–137.
- 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., 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.
- George, C.L., Warwick, R.M., 1985. Annual macrofauna production in a hard-bottom reef community. *Journal of the Marine Biological Association of the UK* 65, 713–735.
- 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.
- Glasby, T.M., 2001. Development of sessile marine assemblages on fixed versus moving substrata. *Marine Ecology-Progress Series* 215, 37–47.
- Glasby, T.M., Connell, S.D., 1999. Urban structures as marine habitats. *Ambio* 28, 595–598.
- 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.
- Guichard, F., Bourget, E., 1998. Topographic heterogeneity, hydrodynamics, and benthic community structure: a scale-dependent cascade. *Marine Ecology-Progress Series* 171, 59–70.
- Heip, C., Basford, D., Craeymeersch, J.A., Dewarumez, J.M., Dorjes, J., Dewilde, P., Duineveld, G., Eleftheriou, A., Herman, P.M.J., Niemann, 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.
- Holloway, M.G., Connell, S.D., 2002. Why do floating structures create novel habitats for subtidal epibiota? *Marine Ecology-Progress Series* 235, 43–52.
- Houthuys, R., Trentesaux, A., De Wolf, P., 1994. Storm influences on a tidal sandbank's surface (Middelkerke Bank, southern North Sea). *Marine Geology* 121, 23–41.
- 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.C., 2002. Proceedings of the Seventh International Conference on Artificial Reefs and Related Habitats. *ICES Journal of Marine Research* 59, 1–362.
- Jensen, A.C., Collins, K.J., Lockwood, A.P.M., 2000. Artificial Reefs in European Seas. Kluwer Academic Publishers, Dordrecht, 508 pp.
- 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. *Helgolander Meeresuntersuchungen* 45, 317–344.
- 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.
- Kohler, N.E., Gill, S.M., 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. *Computers and Geosciences* 32, 1259–1269.
- Kruskal, J.B., Wish, M., 1978. Multidimensional Scaling. In: Sage University Paper series on Quantitative Applications in the Social Sciences n°11. Sage Publications, Beverly Hills and London, 86 pp.
- Kuhne, S., Rachor, E., 1996. The macrofauna of a stony sand area in the German Bight (North Sea). *Helgolander Meeresuntersuchungen* 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), 104 p. Available from <http://www.belspo.be/>.
- 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., Waardenburg, H.W., Vandertol, M.W.M., 1994. Biomass and standing stock on sublittoral hard substrates in the Oosterschelde estuary (SW Netherlands). *Hydrobiologia* 283, 397–412.
- Leewis, R.J., van Moorsel, G.W.N.M., Waardenburg, H.W., 2000. Shipwrecks on the Dutch Continental Shelf as artificial reefs. In: Jensen, A.C., Collins, K.J., Lockwood, A.P.M. (Eds.), *Artificial Reefs in European Seas*. Kluwer Academic Publishers, Dordrecht, pp. 419–434.
- Lefebvre, A., Ellien, C., Davout, 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.
- 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.
- Lesser, M.P., Witman, J.D., Sebens, K.P., 1994. Effects of flow and seston availability on scope for growth of benthic suspension-feeding invertebrates from the Gulf of Maine. *Biological Bulletin* 187, 319–335.
- Love, M.S., 2005. More Fun Than Working for a Living – Tales of 10 years of Research on the Fishes of California Oil Platforms. *Proceedings of Eighth International Conference on Artificial Reefs and Artificial Habitats*, Biloxi, USA, p. 3.
- 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 p. Available from <http://www.mumm.ac.be>.
- 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.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Science Ltd, Oxford, UK, 256 pp.
- Massin, C.L., Norro, A., Mallefet, J., 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* 72, 67–72.
- Migne, A., Davout, D., 1997. Quantitative distribution of benthic macrofauna of the Dover Strait pebble community (Eastern English channel, France). *Oceanologica Acta* 20, 453–460.
- Mouillot, D., Gaillard, S., Aliaume, C., Verlaque, M., Belsher, T., Troussellier, M., Do Chi, T., 2005. Ability of taxonomic diversity indices to discriminate coastal lagoon environments based on macrophyte communities. *Ecological Indicators* 5, 1–17.
- 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. In: *Rapport 91.19. Bureau Waardenburg*

- bv, Culemborg, AJ Culemborg, The Netherlands, Available from: Bureau Waardenburg bv, Postbus 365, 4100, 49 pp.
- 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., Arai, 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.
- Orlov, 1996. Biology of the White Sea hydrozoan *Tubularia indivisa* (Hydrozoa, Athecata). Zoologicheskii Zhurnal 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. Scientia Marina 59, 165–179.
- Otto, L., Zimmermann, J.T.F., Furnes, G.H., Mork, M., Saetre, R., Becker, G., 1990. Review of the physical oceanography of the North Sea. Netherlands Journal of Sea Research 26, 161–238.
- Pakhomov, E.A., 2003. Correction of zooplankton and benthos biomass underestimations from formaldehyde-preserved samples. Archive of Fishery and Marine Research 50, 141–148.
- Picken, G., 1986. Moray Firth fouling communities. Proceedings of the Royal Society of Edinburgh B 91, 213–220.
- Pison, V., Ozer, J., 2003. Operational products and services for the Belgian coastal waters. In: Dalhin, H., Flemings, N.C., Nittis, K., Petersson, S.E. (Eds.), Building the European Capacity in Operational Oceanography. Proceedings of the Third International Conference on EuroGOOS, Elsevier Oceanography, series 69, pp. 503–509.
- 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.
- 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.
- 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.
- Ramos Miranda, J., Mouillot, D., Flores Hernandez, D., Sosa Lopez, A., Do Chi, T., Ayala Perez, L., 2005. Changes in four complementary facets of fish diversity in a tropical coastal lagoon after 18 years: a functional interpretation. Marine Ecology-Progress Series 304, 1–13.
- Relini, G., Tixi, F., Relini, M., Torchia, G., 1998. The macrofouling on offshore platforms at Ravenna. International Biodeterioration and Biodegradation 41, 41–55.
- Ricciardi, A., Bourget, E., 1998. Weight-to-weight conversion factors for marine benthic macroinvertebrates. Marine Ecology-Progress Series 163, 245–251.
- 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.
- 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.
- Schmidt, G.H., 1983. The hydroid *Tubularia larynx* causing ‘bloom’ of the ascidians *Ciona intestinalis* and *Ascidia aspersa*. Marine Ecology-Progress Series 12, 103–105.
- Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika 52, 591–611.
- 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.
- Somerfield, P.J., Olsford, F., Carr, M.R., 1997. A further examination of two new taxonomic distinctness measures. Marine Ecology-Progress Series 154, 303–306.
- 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., 1985. Biomass and estimated productivity of the benthic macrofauna in the New York Bight. Estuarine, Coastal and Shelf Science 21, 539–554.
- 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.
- Thompson, T.E., Brown, G.H., 1976. British Opisthobranch Molluscs. The Linnean Society of London. In: Synopses of the British Fauna, No 8. Academic Press, London, 203 pp.
- Turon, X., Codina, M., Tarjuelo, I., Uriz, M.J., 2000. Mass recruitment of *Ophiotrix fragilis* (Ophiuroidea) on sponges: settlement patterns and post-settlement dynamics. Marine Ecology-Progress Series 2000, 201–212.
- 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 Hoey, G., Vincx, M., Degraer, S., 2005. Small- to large-scale geographical patterns within the macrobenthic *Abra alba* community. Estuarine, Coastal and Shelf Science 64, 751–763.
- 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.
- Wolff, W.J., 1973. The estuary as a habitat, an analysis of data on the soft bottom macrofauna of the estuarine area of the rivers Rhine, Meuse, Scheldt. Zoologische Verhandlungen 126, 1–242.
- Wright, S.W., Jeffrey, S.W., 1997. High-resolution HPLC system for chlorophylls and carotenoids of marine phytoplankton. In: Jeffrey, W., Mantoura, R.F.C., Wright, S.W. (Eds.), Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods. UNESCO, Paris, pp. 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.