Artificial hard substrata from the Belgian part of the North Sea and their influence on the distributional range of species

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ABSTRACT. A comprehensive list of the macrospecies recorded on ten shipwrecks from the Belgian Part of the North Sea is presented. The historical records of these species in the area are also reviewed to address the potential role of shipwrecks in providing habitats for species typically associated with hard substrata. The current pooled species richness for Belgian shipwrecks consists of 224 spp., including 12 fish species. Among these species, 46 are new records to the Belgian fauna. Species on shipwrecks fulfil a gap in the regional distribution of sessile and mobile epibenthos. The records of several species are interrupted in the Southern Bight of the North Sea, simply because their habitats, natural hard substrata, are rare in this area and poorly studied. Another consequence of the presence of hard substrata offered by artificial sources is the increase in the distributional range of several species. Due to the presence of artificial substrata, a total of 12 southern species presented an extension of their known geographical range to the North.

KEY WORDS: Epifauna, shipwreck, North Sea, distribution of species

INTRODUCTION

In the Southern Bight of the North Sea, the seabed is largely dominated by fine sediments (Houbolt, 1968). At the southern tip of this area, the seabed of the Dover Strait is the last large area comprising hard substrata (rocky outcrops, gravel and pebble fields) (Cabioch & Glaçon, 1975). North-East of the Dover Strait, the increasing opening between continental Europe and UK results in decreased current velocity, allowing sedimentation of finer particles. Consequently, soft sediments dominate the seabed of the Belgian part of the North Sea (BPNS). Natural hard substrata such as rocky bottoms are absent and pebbles are rare, only occurring locally in the swales between sandbanks (Lanckneus et al., 2001). Further to the North, areas of gravel become even smaller and more widely separated (Veenstra, 1969; Kuhne & Rachor, 1996; Lanckneus et al., 2001). A strong correlation exists between substrate type and associated taxa (Duineveld et al., 1991; Van Hoey et al., 2004; Van Hoey et al., 2005). Hard substrata favour development of assemblages dominated by large epifaunal species, which in turn allow settlement of secondary colonizers. In comparison, the third dimension offered by fine sediment substratum promotes the establishment of infaunal species (Fraschetti et al., 2003). In the BPNS lie a large number of artificial structures comprising mainly shipwrecks (Massin et al., 2002; Zintzen et al., 2006). Even if the shipwrecks were not planned as artificial reefs, they provide a habitat for species typically associated with hard substrata that may not be encountered otherwise in the area (Hiscock, 1980; Forteath et al., 1982; Picken, 1986; Leewis et al., 2000; Zintzen et al., 2007; Zintzen et al., 2008). *In fine*, they are a source of hard substrata, which facilitate the development of an epifaunal community, locally increasing the pool of species. In a context of local population of hard substrate epifaunal species that are widely and sparsely dispersed over an area such as the Southern Bight of the North Sea, the existence of shipwrecks may have important implications on the repartition, dissemination and genetic variability of these species.

In this paper, we present a comprehensive list of the macrospecies recorded on ten shipwrecks from the BPNS, complemented by a review of past records of these species in the North Sea to address the potential role of shipwrecks in providing habitat for species typically associated with hard substrata.

MATERIALS AND METHODS

Ten shipwreck sites from the BPNS (8-37m depth) were investigated between 2001 and 2005 using SCUBA divers. The ten vessels (Table 1, Fig. 1) had been sunk for at least 40 years and consequently, it was considered that their communities had reached a mature state (van Moorsel et al., 1991; Leewis et al., 2000). In total, 108 samples were collected. Quantitative sampling, during daylight, was done by scraping off all the living fauna within frames of 25x25cm on randomly selected surfaces (both vertically and horizontally orientated). On board, animals were relaxed in a 3.5% $MgCl_2$ solution during two hours and transferred to a buffered formalin solution (final concentration 4%, pH 8.2-8.4). Later, specimens were transferred to 70% buffered alcohol for permanent storage. The samples were sorted using a binocular microscope, and the macrofauna (>1mm) was identified to the lowest possible taxonomic level and counted. The material collected was deposited in the collections of the Royal Belgian Institute of Natural Sciences under the General Inventory number 29462. Most samples were taken between March and September as weather conditions during late autumn and winter generally did not

TABLE 1

Studied shipwreck sites.

SHIPWRECK SITES	WGS-84 COORDINATES	DEPTH (MLLWS) (m)	DATE OF SUNK	SAMPLING YEARS (20xx)
1 - Birkenfels	N 51°38',989 E 02°32',268	37	1966	01-02-03-04-05
2 - Callisto	N 51°41',950 E 02°37',330	28	1959	04-05
3 - Garden City	N 51°29',170 E 02°18',320	26	1969	05
4 - John Mahn	N 51°28',930 E 02°41',350	29	1942	05
5 - Duc de Normandie	N 51°25',524 E 02°36',345	29	1942	05
6 - LCT 457	N 51°24',670 E 02°43',720	21	1944	05
7 - Kilmore	N 51°23',730 E 02°29',790	30	1906	03-04-05
8 - Bourrasque	N 51°14',964 E 02°33',026	18	1940	02-03-04-05
9 - LST 420	N 51°15',510 E 02°40',830	8	1944	05
10 - Sperrbrecher	N 51°16',650 E 02°49',780	9	1942	04

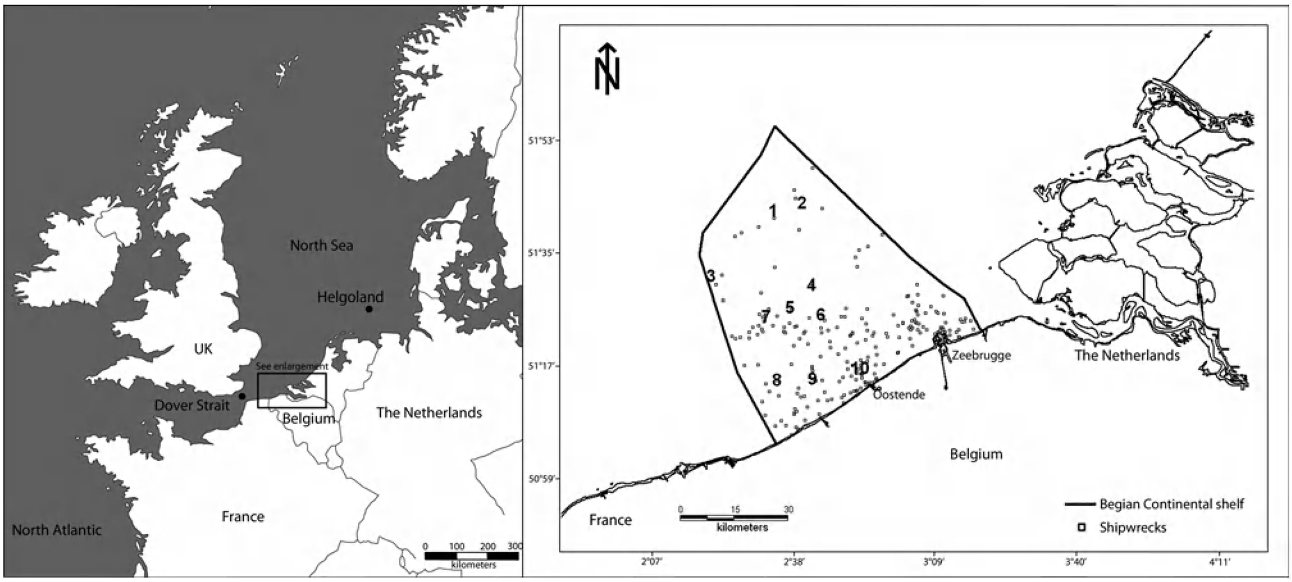

Fig. 1. – Localization of the studied shipwrecks. 1: Birkenfels, 2: Callisto, 3: Garden City, 4: John Mahn, 5: Duc de Normandie, 6: LCT 457, 7: Kilmore, 8: Bourrasque, 9: LST 420, 10: Sperrbrecher. Source: Afdeling Waterwegen Kust, Belgium.

allow sampling. Species only recorded between October and February are presented in a separate table. Some species were also recorded as *in situ* observations by divers and digital picture analysis. They are also presented in a separate table. Rare species are defined as those mentioned once or twice in past studies.

In addition, we reviewed the historical records of these species in the BPNS by screening regional faunal listings (GOVAERE, 1978; CATTRIJSSE & VINCX, 2001; DAUVIN et al., 2003; DEGRAER et al., 2006) and the Zoological Record for the last 30 years. For records considered new to the area, we went through the literature to compile distributional ranges at the scale of the North Sea and surrounding area. Species were defined either as Northern species, if their distributional range was restricted to the Northern part of the North Sea, or as Southern species if they were only recorded from the Lusitanian Province. The distributional range was further refined as 'Southern North Sea' if the species was recorded as far North as Helgoland, or 'Northern North Sea' if the range extended South to this point. Species are defined as cosmopolitan if they have been previously recorded outside the present area of study. From this information, the implications of shipwrecks from the BPNS were defined as either (1) filling a gap in the distributional range of the species if the species was recorded North and South of the BPNS or (2) permitting an extension of the distributional range to the North or to the South.

RESULTS

The species richness and average density ranges for the different shipwrecks between March and September (2001-2005) are presented in Table 2. The species richness for the period March-September totals 193 species. Another nine species were only sampled between October and February (Table 3). An additional 22 species were observed *in situ* or after examination of digital pictures (Table 4). Consequently, the pooled species richness for Belgian shipwrecks is 224 spp. Of these species, 46 can be considered new to the Belgian fauna (Table 5). Their actual distributions in the North Sea are given in this table. Most of the species mentioned in our study have been recorded from north and south of the BPNS, although ten species have a meridional distribution, with shipwrecks extending their distribution to the north (*Actinothoe sphyrodeta*, *Eulalia aurea*, *Lysidice ninetta*, *Marphysa sanguinea*, *Polydora hoplura*, *Sphaerosyllis bulbosa*, *Thelepus setosus*, *Tritonia manicata*, *Acasta spongites, Lysianassa ceratina*). Some species rare for the area have also been recorded (Table 6). Although our results are focussed on the fauna of shipwrecks, we note that no macroalgae were either seen or sampled by divers at any time.

TABLE 2

Distribution of the epifaunal species on the ten investigated shipwrecks. Only the data collected between April and September are used. Sites are ordered from offshore to coastal zone. BRK: Birkenfels (N=25 samples of 25x25cm), CAL: Callisto (N=7), GAR: Garden City (N=3), JON: John Mahn (N=3), DUC: Duc de Normandie (N=3) LCT: LCT 457 (N=3), KLM: Kilmore (N=32), BRQ: Bourrasque (N=23), LST: LST 420 (N=3), SPR: Sperrbrecher (N=6). A simplified scale of dominance was attributed to the colonial species: ● present, ●● abundant, ●●● dominant.

	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
PORIFERA										
Dysidea fragilis (Montagu, 1818)	●	●			●		●			
Esperiopsis fucorum (Esper, 1794)				●	●		●			
Halichondria cf panicea (Pallas, 1766)					●●		●			
Haliclona oculata (Pallas, 1766)					●		●			
Haliclona sp.	●						●	●		
Hymeniacidon perlevis (Montagu, 1818)		●					●			
Leucosolenia sp.		●	●	●		●	●			
Myxilla rosacea (Lieberkühn, 1859)					●●		●			
Phorbas plumosus (Montagu, 1818)							●			
Sycon ciliatum (Fabricius, 1780)	●	●●	●	●●	●●	●●	●●			
CNIDARIA										
Hydrozoa										
Bougainvillia muscus (Allman, 1863)								●		
Campanularia volubilis (Linnaeus, 1758)	●							●		
Clytia gracilis (Sars, 1850)								●		
Clytia hemisphaerica (Linnaeus, 1767)	●						●	●		
Halecium sp.							●			
Hydractinia echinata (Flemming, 1828)	●							●	●	
Hydrallmania falcata (Linnaeus, 1758)								●		
Laomedea flexuosa Alder 1857								●		
Nemertesia antennina (Linnaeus, 1758)							●	●		
Obelia bidentata Clarke, 1875	●						●	●	●	
Sarsia eximia (Allman, 1859)		●								
Sertularia cupressina Linnaeus, 1758								●●		
Tubularia indivisa Linnaeus, 1758	●●●	●●●	●●●	●●●	●●●	●●●	●●●	●●	●●●	
Tubularia larynx Ellis & Solander, 1786	●●					●●	●●	●●		
ANTHOZOA										
Actiniaria	100-1000	100-1000	100-1000	100-1000	100-1000	100-1000	100-1000	10-100	100-1000	100-1000
Alcyonium digitatum Linnaeus, 1758	0-10	0-10	10-100				10-100			
Diadumene cincta Stephenson, 1925	10-100						100-1000	100-1000		
Metridium senile (Linnaeus, 1767)	0-10						0-10	100-1000	10-100	100-1000
PLATYHELMINTHES										
Eurylepta cornuta (O.F. Müller, 1776)					0-10					
Turbellaria			0-10			10-100	0-10			
NEMERTEA										
Baseodiscus delineatus (Delle Chiaje, 1825)		10-100	0-10			10-100	10-100			
Nemertinata sp.		0-10				100-1000				
Oerstedia dorsalis (Abildgaard, 1806)	10-100	10-100	10-100	10-100	100-1000	100-1000	100-1000	10-100	100-1000	
ANNELIDA										
POLYCHAETA										
Alentia gelatinosa (M. Sars, 1835)	0-10									
Autolytus sp.	10-100	0-10		0-10			10-100	0-10		
Cirratulidae		0-10								
Cirratulus cirratus (O.F. Müller, 1776)	0-10						0-10			
Cirratulus filiformis Keferstein, 1862							0-10	0-10		
Cirratulus sp.								0-10		
Cirriformia tentaculata (Montagu, 1808)	0-10				0-10		0-10			0-10
Dipolydora coeca (Oersted, 1843)							0-10			
Eteone longa (Fabricius, 1780)							10-100			
Eteone picta Quatrefages, 1865								0-10		

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

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	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Eulalia aurea Gravier, 1896	0-10	10-100					0-10			
Eulalia sp.	0-10						0-10			
Eulalia viridis (Linnaeus, 1768)	10-100	10-100	10-100	10-100	0-10	100-1000	10-100	0-10		0-10
Eumida sp.	0-10					10-100		10-100	10-100	
Eupolymnia nebulosa (Montagu, 1818)	0-10									
Eupolymnia nesidensis (Delle Chiaje, 1828)	0-10							0-10		
Eusyllis blomstrandi Malmgren, 1867	10-100		10-100	10-100	0-10	0-10	10-100	0-10		
Gattyana cirrhosa (Pallas, 1766)								0-10		
Harmothoe sp.	10-100	10-100	100-1000	100-1000	10-100	100-1000	100-1000	100-1000	10-100	0-10
Kefersteinia cirrata (Keferstein, 1862)	10-100		10-100	10-100	10-100	10-100	10-100	0-10		
Lanice conchilega (Pallas, 1766)	10-100	10-100	10-100	10-100	10-100	10-100	10-100	10-100	100-1000	10-100
Lepidonotus squamatus (Linnaeus, 1758)	10-100	10-100	10-100	10-100	10-100	10-100	10-100		10-100	
Lumbrineris latreilli Audouin & Milne-Ed., 1834							0-10			
Lumbrineris sp.							0-10			
Marphysa sanguinea (Montagu, 1815)							0-10			
Neoamphitrite figulus (Dallyell, 1853)							0-10			
Nereimyra punctata (O.F. Müller, 1788)								0-10		
Nereis pelagica Linnaeus, 1758	10-100	10-100	10-100		0-10	0-10	0-10	10-100		10-100
Nicolea venustula (Montagu, 1818)							0-10			
Nicomache sp.								0-10		
Ophelia sp.								0-10		
Owenia fusiformis Delle Chiaje, 1842							0-10			
Pectinaria koreni (Malmgren, 1866)							10-100			
Pholoe inornata Johnston, 1839	10-100	0-10					10-100			
Phyllodoce longipes Kinberg, 1866	0-10									
Phyllodoce mucosa Oersted, 1843	100-1000	0-10	0-10	100-1000	10-100	>1000	100-1000	100-1000	100-1000	100-1000
Phyllodoce sp.							0-10	0-10		
Pista cristata (O.F. Müller, 1776)	0-10									
Poecilochaetus serpens Allen, 1904							0-10	0-10		
Polycirrus sp.							0-10			
Polydora hoplura Claparède, 1870	0-10									
Polydora sp.	0-10						0-10	0-10		
Pomatoceros triqueter (Linnaeus, 1758)	10-100	10-100	10-100	10-100	10-100	10-100	10-100	0-10		0-10
Proceraea sp.								0-10		
Procerastea halleziana Mallaquin, 1893	10-100						100-1000	0-10		
Procerastea nematodes Langerhans, 1884								0-10		
Sabellaria spinulosa Leuckart, 1849	10-100	100-1000	10-100	0-10	100-1000	10-100	10-100	0-10		
Scoloplos armiger (Allman, 1859)							0-10	0-10		
Sphaerodoropsis flavum Oersted, 1843						0-10	0-10			
Sphaerosyllis bulbosa Southern, 1914							0-10			
Sphaerosyllis sp.	0-10									
Sthenelais boa (Johnston, 1833)		0-10					0-10	0-10		
Subadyte pellucida (Ehlers, 1864)	0-10	0-10	10-100	10-100			0-10			
Syllidae	0-10									
Syllis armillaris (O.F. Müller, 1776)	10-100	0-10	10-100			0-10	10-100			0-10
Syllis gracilis Grube, 1840	10-100	10-100	10-100		10-100	100-1000	10-100	10-100		10-100
Terebellidae	10-100									
Thelepus cincinnatus (Fabricius, 1780)	10-100						0-10			
Thelepus setosus (Quatrefages, 1865)							0-10	0-10		
MOLLUSCA										
GASTROPODA										
Aeolidiidae	0-10					0-10		0-10		
Archidoris pseudoargus (Rapp, 1827)	0-10						0-10			
Catriona gymnota (Couthouy, 1838)								10-100		
Cerithiopsis tubercularis (Montagu, 1803)	0-10	0-10					0-10			
Crepidula fornicata (Linnaeus, 1758)	0-10						0-10			
Cuthona amoena (Alder & Hancock, 1845)							0-10			
Cuthona concinna (Alder & Hancock, 1843)							0-10			
Cuthona sp.	10-100	0-10	0-10	10-100	10-100	10-100	10-100	0-10	10-100	
Dendronotus frondosus (Ascanius, 1774)	0-10		10-100	10-100	10-100	10-100	10-100	0-10	0-10	

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

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	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Doto pinnatifida (Montagu, 1804)							0-10			
Epitonium clathratulum (Kanmacher, 1798)	10-100	0-10	10-100					10-100		
Eubranchus pallidus (Alder & Hancock, 1842)							0-10			
Eubranchus sp.	0-10						0-10	0-10	10-100	
Euspira pulchella (Risso, 1826)	0-10	10-100					0-10	0-10		
Facelina bostoniensis (Couthouy, 1838)	0-10					10-100	0-10	0-10		
Lamellaria latens (O.F. Müller, 1776)							0-10			
Nassarius incrassatus (Ström, 1768)	10-100	10-100	10-100		0-10		10-100			0-10
Nassarius reticulatus (Linneaus, 1758)	0-10							10-100		
Raphitoma linearis (Montagu, 1803)	0-10						0-10			
Rissoidae	10-100	10-100					10-100	0-10		
Tergipes tergipes (Forskal, 1775)							0-10			
Tritonia cf *manicata* Deshayes, 1853							0-10			
Tritonia plebeia Johnston, 1828		0-10								
Trivia monacha (da Costa, 1778)							0-10			
Bivalvia										
Aequipecten opercularis (Linnaeus, 1758)	10-100	10-100	100-1000	0-10			10-100	0-10		
Heteranomia squamula (Linnaeus, 1758)	10-100	10-100	10-100	0-10	10-100		0-10			
Musculus sp.	0-10	10-100	10-100	0-10			0-10			
Mysella bidentata (Montagu, 1803)	0-10							0-10		
Mytilus edulis Linnaeus, 1758	100-1000	100-1000	100-1000	100-1000	100-1000	100-1000	>1000	10-100	10-100	
Ostreidae							0-10			
Venerupis geographica (Gmelin, 1791)	10-100									
Venerupis sp.	100-1000	0-10					0-10	0-10		
Sipuncula										
Golfingiida							0-10			
Crustacea										
Copepoda										
Copepoda	0-10						0-10	10-100		
Cirripedia										
Acasta spongites (Poli, 1795)							0-10			
Balanus crenatus Bruguiére, 1789	10-100				10-100		0-10	100-1000		10-100
Verruca stroemia O.F. Müller, 1776							0-10			
Cumacea										
Cumacea	0-10							0-10		
Isopoda										
Janira maculosa Leach, 1814							0-10			
Pleurocrypta porcellanae Hesse, 1876							0-10			
Amphipoda										
Abludomelita obtusata (Montagu, 1813)									0-10	
Atylus swammerdami (Milne-Edwards, 1830)			0-10					0-10	0-10	
Caprella linearis (Linnaeus, 1767)	0-10							0-10		
Caprella tuberculata Guérin, 1836	100-1000	>1000	>1000	10-100	>1000		>1000	0-10		
Iphimedia nexa Myers & McGrath, 1987	0-10	0-10					0-10			
Jassa herdmani (Walker, 1893)	>1000	>1000	>1000	>1000	>1000	>1000	>1000	>1000	>1000	>1000
Lysianassa ceratina (Walker, 1889)	0-10									
Melita hergensis Reid, 1939									0-10	
Metopa alderi (Bate, 1857)	0-10	100-1000	100-1000	100-1000	100-1000	100-1000	10-100	0-10	0-10	
Monocorophium acherusicum (Costa, 1851)								100-1000	100-1000	>1000
Monocorophium sextonae (Crawford, 1937)	100-1000	10-100	100-1000	100-1000	>1000	>1000	>1000	>1000	10-100	
Pariambus typicus (Kroyer, 1844)								0-10		
Phtisica marina Slabber, 1769	10-100	100-1000	>1000	>1000	100-1000	>1000	>1000	100-1000	10-100	
Pseudoprotella phasma (Montagu, 1804)								0-10		
Stenothoe marina (Bate, 1856)	10-100	10-100	10-100	100-1000	100-1000	100-1000	100-1000	10-100	100-1000	
Stenothoe monoculoides (Montagu, 1815)	100-1000	100-1000	100-1000	100-1000	100-1000	>1000	>1000	0-10	10-100	
Stenothoe sp.	10-100	100-1000					100-1000	10-100		0-10
Stenothoe valida Dana, 1855	10-100	100-1000	100-1000	>1000	100-1000	>1000	10-100	0-10		
Decapoda										
Anapagurus chiroacanthus (Lilljeborg, 1856)	0-10									
Atelecyclus rotundatus (Olivi, 1792)	0-10									

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

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	BRK	CAL	GAR	JON	DUC	LCT	KLM	BRQ	LST	SPR
Ebalia tumefacta (Montagu, 1808)							0-10			
Hyas araneus (Linneaus, 1758)	0-10									
Inachus phalangium (Fabricius, 1775)							0-10			
Liocarcinus arcuatus (Leach, 1814)							0-10			
Liocarcinus holsatus (Fabricius, 1798)								0-10		
Liocarcinus sp.	10-100	10-100					10-100	0-10		0-10
Macropodia parva Van Noort & Adema, 1985							0-10		0-10	
Macropodia rostrata (Linnaeus, 1761)	0-10									
Macropodia sp.							0-10			
Necora puber (Linnaeus, 1767)	0-10						0-10			
Paguridae	0-10			0-10				0-10		
Pilumnus hirtellus (Linnaeus, 1761)	10-100	100-1000	10-100	10-100	10-100	10-100	100-1000	0-10	10-100	10-100
Pisidia longicornis (Linneaus, 1767)	>1000	>1000	>1000	>1000	100-1000	100-1000	>1000	100-1000	10-100	100-1000
Thoralus cranchii (Leach, 1817)							0-10			
CHELICERATA										
PYCONOGONIDA										
Achelia sp.			0-10				10-100			
Callipallene emacinata (Dohrn, 1881)							0-10			
Nymphon rubrum Hodge, 1865							0-10			
Pycnogonum littorale (Strom, 1762)			0-10					0-10		
BRYOZOA										
CYCLOSTOMATIDA										
Crisia aculeata Hassall, 1841							●			
Disporella hispida (Fleming, 1828)	●									
Plagioecia patina (Lamarck, 1816)	●						●			
CHEILOSTOMATIDA										
Bicellariella ciliata (Linnaeus, 1758)							●●			
Conopeum reticulum (Linnaeus, 1767)								0-10		
Electra pilosa (Linnaeus, 1767)	●	●●	●●	●●	●●	●●	●●	●	●	
Scruparia chelata (Linnaeus, 1758)	●									
Scrupocellaria scruposa (Linnaeus, 1758)	●	●					●●			
CTENOSTOMATIDA										
Alcyonidium hydrocoalitum Porter, 2004	●						●			
Panolicella nutans Jebram, 1985	●									
Vesicularia spinosa (Linnaeus, 1967)								0-10		
ECHINODERMATA										
ASTEROIDEA										
Asterias rubens Linnaeus, 1758	0-10	10-100			0-10		10-100	0-10	0-10	10-100
Asterias rubens juv. Linnaeus, 1758		10-100	100-1000	100-1000	100-1000	100-1000	10-100		100-1000	
ECHINOIDEA										
Euechinoidea							0-10	0-10		
Psammechinus miliaris (Gmelin, 1778)	100-1000	100-1000	10-100	10-100		10-100	10-100	0-10		
OPHIUROIDEA										
Amphipholis squamata (Delle Chiaje, 1829)	10-100	100-1000	100-1000	10-100	10-100	10-100	100-1000	0-10	0-10	
Ophiothrix fragilis (Abildgaard,1789)	100-1000	100-1000	>1000	100-1000	100-1000	100-1000	>1000	10-100	10-100	0-10
Ophiura albida Forbes, 1839	0-10									
Ophiura sp.							0-10			
CHORDATA										
TUNICATA										
Ascidiacea	0-10									
Diplosoma sp.		●	●●	●●	●●		●●			
Molgula cf *occulta* Kupffer, 1875	0-10	10-100					10-100			
Polyclinum aurantium Milne-Edwards, 1841		●●					●●			

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

TABLE 3

Distribution of the epifaunal species exclusively recorded between October and March. Sites are ordered from offshore to coastal zone. BRK: Birkenfels (N=7), KLM: Kilmore (N=14), BRQ: Bourrasque (N=12). A simplified scale of dominance was attributed to the uncountable species: •: present, ••: abundant, •••: dominant. Density never exceeded 10 individuals.m[2] (grey).

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

TABLE 4

Species observed *in situ* by divers or from digital images but not sampled.

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

TABLE 5

Species (from shipwrecks) that are new records for the Belgian fauna. SNS: Southern North Sea species, NNS: Northern North Sea species, NC: indicates the presence of the species in the neighbouring countries (fr: France, nl: The Netherlands, uk: United Kingdom). SS: Southern species, NS: Northern species, COS: cosmopolitan species, HS (Hard Substrata) CONSEQUENCES: the implication of the presence of the Belgian shipwreck for the distributional range of species. ?: information unavailable. See text for detailed explanations of the distributional ranges.

TAXON	SNS	NNS	NC	SS	NS	COS	HS CONSEQUENCES
PORIFERA							
Dysidea fragilis	+	+	fr,uk	+	+		fill in the gap
Phorbas plumosus	+	+	fr,uk				fill in the gap
CNIDARIA							
Actinothoe sphyrodeta	-	-	fr,uk	+	-		extension to the north
Diadumene cincta	+	+	fr,uk,nl			+	fill in the gap
PLATYHELMINTHES							
Eurylepta cornuata	+	+	fr,uk	+	-	+	fill in the gap
NEMERTEA							
Oerstedia dorsalis	+	+	fr,uk,nl			+	fill in the gap
POLYCHAETA							
Alentia gelatinosa	+	+	fr,uk				fill in the gap
Cirratulus cirratus	+	+	fr,uk,nl			+	fill in the gap
Cirriformia tentaculata	+	+	fr,uk			+	fill in the gap
Dipolydora coeca	+	+	fr,uk			+	fill in the gap
Eteone picta	+	-	fr,uk,nl	+	-		fill in the gap
Eulalia aurea	-	-	fr,uk	+			extension to the north
Eupolymnia nebulosa	+	+	fr,uk,nl	-	+	+	fill in the gap
Eupolymnia nesidensis	+	+	fr,uk			+	fill in the gap
Lysidice ninetta	-	-	fr,uk	+	-	+	extension to the north

TABLE 5

Species (from shipwrecks) that are new records for the Belgian fauna. SNS: Southern North Sea species. NNS: Northern North Sea species. NC: indicates the presence of the species in the neighbouring countries (fr: France. nl: The Netherlands. uk: United Kingdom). SS: Southern species. NS: Northern species. COS: cosmopolitan species. HS (Hard Substrata) Consequences: the implication of the presence of the Belgian shipwreck for the distributional range of species. ?: information unavailable. See text for detailed explanations of the distributional ranges.

Taxon	SNS	NNS	NC	SS	NS	COS	HS consequences
Marphysa sanguinea	+	-	fr,uk	+	-	+	extension to the north
Neoamphitrite figulus	+	+	fr,uk,nl			+	fill in the gap
Nereimyra punctata	+	+	fr,uk,nl	-	+		fill in the gap
Phyllodoce longipes	+	+	fr,uk			+	fill in the gap
Pista cristata	-	+	?			+	fill in the gap from the north
Polydora hoplura	+	-	fr,uk			+	extension to the north
Procerastea halleziana	-	+	fr,uk				fill in the gap
Procerastea nematodes	-	+	fr,uk	+	-		fill in the gap
Sphaerodoropsis flavum	+	+	?			+	fill in the gap
Sphaerosyllis bulbosa	+	-	fr,uk	+	-		extension to the north
Subadyte pellucida	+	+	fr,uk,nl			+	fill in the gap
Thelepus cincinnatus	+	+	fr,uk,nl			+	fill in the gap
Thelepus setosus	-	-	fr,uk	+	-	+	extension to the north
Gastropoda							
Cerithiopsis tubercularis	-	+	fr,uk				fill in the gap
Cuthona amoena	+	+	fr,uk,nl	+	-		fill in the gap
Cuthona concinna	+	+	fr,uk,nl	-	+	+	fill in the gap from the north
Raphitoma linearis	-	+	fr,uk				fill in the gap
Tritonia cf *manicata*	-	-	uk	+	-		extension to the north
Crustacea							
Acasta spongites	-	-	fr,uk	+	-		extension to the north
Caprella tuberculata	+	+	fr,uk	+	-		fill in the gap
Lysianassa ceratina	-	-	fr,uk				extension to the north
Pleurocrypta porcellanae	+	-	fr,uk,nl	+	-		fill in the gap
Pseudoprotella phasma	+	+	fr,uk				fill in the gap
Anapagurus chiroacanthus	-	+	fr,uk				fill in the gap
Macropodia parva	+	+	fr,uk,nl		+		fill in the gap
Pygnogonide							
Callipallene emacinata	-	-	fr,uk	+			?
Bryozoa							
Crisia aculeata	+	+	fr,uk,nl				fill in the gap
Alcyonidium cellarioides	+	-	fr,uk,nl	+	-		fill in the gap and in extension to the north
Nolella pusilla	+	-	fr,uk,nl	+	-		fill in the gap and in extension to north
Tunicata							
Clavelina lepadiformis	+	+	fr,uk,nl				fill in the gap
Polyclinum aurantium	+	+	fr,uk,nl				fill in the gap

TABLE 6

Species (from Belgian shipwrecks) that could be considered rare for the Belgian fauna (mentioned only one or two times in past studies).

Porifera
Hymeniacidon perlevis
Esperiopsis fucorum
Cnidaria
Sagartiogeton undatus
Crustacea
Iphimedia nexa
Atelecyclus rotundatus
Inachus phalangium
Pycnogonide
Pycnogonum littorale
Tunicata
Ascidiella scabra

DISCUSSION

The species richness of the shipwreck macrofauna from our studies is 224, including 12 fish species observed *in situ* by divers. This is in the range of the species richness observed for soft sediment macrofauna of the BPNS where Degraer et al. (2006) identified a total of 265 species from 771 Van Veen grab samples. Taking into account that we collected only one-sixth the number of samples as did Degraer et al. (2006) and that shipwrecks represent a relatively small area compared to the continental shelf, we hypothesize that these artificial hard substrata concentrate species richness. In this respect, they can be considered as hot spots of species richness.

The number of species recorded as new to the Belgian fauna is high (46 spp.). It appears that shipwrecks fulfil a gap in the regional distribution of sessile and mobile epibenthos for these species. Shipwrecks provide a habitat suitable for typically hard substrate–associated species found further South and extend the range of populations previously found restricted to the Dover Strait (DAVOULT, 1990). The distribution of several species is interrupted in the Southern Bight of the North Sea, simply because their habitat, natural hard substrata, is rare in this area and has been poorly studied. The Paguridae *Anapagurus chiroacanthus* is a nice example of such a distribution (GARCIA-GOMEZ, 1994). It is present from Norway to the Azores, but is not recorded in the Southern North Sea. Its presence on shipwrecks of the BPNS fills the gap between populations living along the coast of France and Germany. For these species, it is possible that shipwrecks favour transfer by stepping-stone effect between local populations.

Other species such as the sea anemone *Actinothoe sphyrodeta*, have their northern limit extended by shipwrecks (see WILLIAMS, 1997). The sponge-inhabiting barnacle *Acasta spongites* was also described for the first time during this study as inhabiting the Southern Bight of the North Sea (ZINTZEN & KERCKHOF, 2009). In these examples, the hard substrata offered by artificial sources extend the range of these species. Table 2 shows 12 species presenting another extension of geographical range from South to North. In this study, we did not detect any potentially invasive species, except juveniles of *Crepidula fornicata* which have been found in small densities. However, this network of artificial hard substrata may also facilitate the dispersal of invasive species that need hard substrata to complete their life cycle. In a context of global warming, the presence of artificial hard substrate spots, which include shipwrecks, may significantly reduce the physical barriers, such as large areas of soft sediments, preventing the northward spreading of warm-water species.

No algal species were identified on subtidal Belgian habitats, either on soft sediments (VAN HOEY et al., 2004) or shipwrecks. In contrast, intertidal zones in harbours and groynes host 78 macroalgae identified in a previous study (VOLCKAERT et al., 2002). The absence of Chlorophyta and Phaeophyta needing substantial light intensities may be related to the low quantity of light reaching the seabed due to the high turbidity close to the coast and the depth offshore. The absence of Rodophyta is puzzling as some of these algae are able to live with low light intensity at more than 70m depth (VERGÉS & RODRIGUEZ-PRIETO, 2006). Encrusting red algae such as *Lithotamnium* spp. are present along the Atlantic coast of France up to the Dover Strait (FOVEAU, 2005) and of England (MALLINSON et al., 1999), but they do not penetrate into the Southern Bight of the North Sea. This could be linked to turbid conditions, abrasion of sand close to the bottom or competition with fast-growing sessile invertebrates such as *Tubularia* spp. and *Metridium senile*, which are the dominant species on the shipwrecks from the BPNS (ZINTZEN et al., 2007). Any algae establishing on the shipwreck could be removed by grazing echinids (*Psammechius miliaris*) present in large number on many shipwrecks.

The fauna of shipwrecks from the BPNS has affinities with the fauna found on gravel beds of the Dover Strait area (DAVOULT & RICHARD, 1988; PRYGIEL et al., 1988; DAVOULT, 1990; DEWARUMEZ et al., 1992; MIGNÉ & DAVOULT, 1997; FOVEAU, 2005; ALIZIER, 2005). The dominant mobile species of the pebble community from the Dover Strait are *Ophiothrix fragilis* and *Pisidia longicornis*, two species also very abundant on the Belgian shipwrecks (this study and ZINTZEN et al., 2007; ZINTZEN et al., 2008). However, the dominant sessile species are different. In Dover Strait pebble beds, the sessile fauna is mostly dominated by bryozoan species, the hydrozoan *Alcyonium digitatum* and the anthozoan *Urticina felina*, while the largest fraction of the sessile epifauna of wrecks consists of cnidarians (*Tubularia* spp. and *Metridium senile*) (ZINTZEN et al., 2007; ZINTZEN et al., 2008). The causes for such a pattern could be abiotic factors that control the recruitment and development of these assemblages. Another factor that potentially separates pebble beds and shipwrecks is the stability of the substratum. Particularly strong currents or storm events may have a more profound effect on pebbles than on large rigid structures (POSEY et al., 1996). Pebbles can be moved and the epifauna damaged, promoting the dominance of species tolerant to physical disturbance. On shipwrecks, large storm events can lead to collapse of a part of the superstructure but frequent small scale perturbation events are unlikely to occur. Passive suspension feeding seems to be the dominant feeding mode on both habitats. The rate of particle filtration by a specimen is a function of particle density and current velocity. This last parameter could be enhanced on shipwrecks since current speed is higher at increasing distance from the bottom, influencing the final pattern of dominating species. Finally, human activities, such as commercial fishing, are more intense on smooth grounds such as pebbles than on shipwrecks, also leading to more frequent perturbation. These disturbances all have a strong effect on the development of epibenthic species (ENGEL & KVITEK, 1998; FRASCHETTI et al., 2001).

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