

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

Vincent Zintzen^{1,2*} & Claude Massin¹

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

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

* Corresponding author: Vincent ZINTZEN. Mail: vzintzen@yahoo.fr

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 (DUINVELD 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% MgCl₂ 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 (MLWS) (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

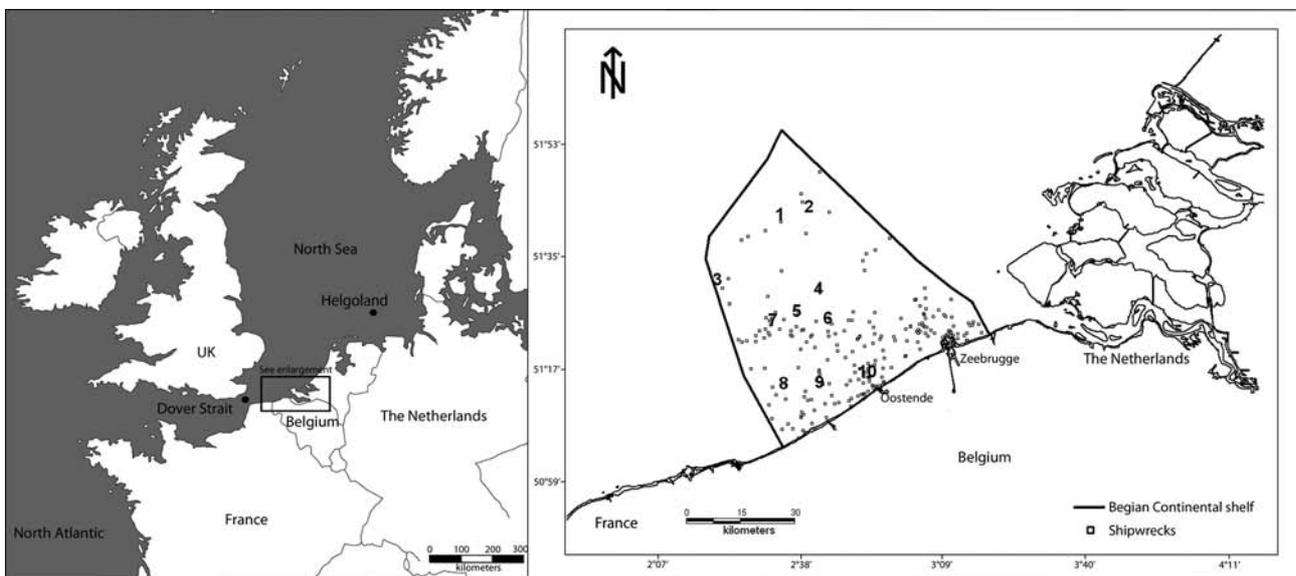


Fig. 1. – Localization of the studied shipwrecks. 1: Birkenfels, 2: Callisto, 3: Garden City, 4: John Mahn, 5: Duc de Normandie, 6: LCT 457, 7: Kilmore, 8: Bourrasque, 9: LST 420, 10: Sperrbrecher. Source: Afdeling Waterwegen Kust, Belgium.

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

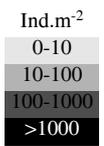


TABLE 2

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

Ind.m⁻²
 0-10
 10-100
 100-1000
 >1000

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
<i>Doto pinnatifida</i> (Montagu, 1804)							●			
<i>Epitonium clathratulum</i> (Kanmacher, 1798)	●	●	●					●		
<i>Eubranchus pallidus</i> (Alder & Hancock, 1842)							●●●			
<i>Eubranchus</i> sp.	●						●		●	
<i>Euspira pulchella</i> (Risso, 1826)	●	●						●		
<i>Facelina bostoniensis</i> (Couthouy, 1838)	●					●		●		
<i>Lamellaria latens</i> (O.F. Müller, 1776)						●		●		
<i>Nassarius incrassatus</i> (Ström, 1768)	●		●		●		●			●
<i>Nassarius reticulatus</i> (Linnaeus, 1758)	●							●		
<i>Raphitoma linearis</i> (Montagu, 1803)	●						●			
Rissoidae	●						●			
<i>Tergipes tergipes</i> (Forskål, 1775)	●						●			
<i>Tritonia cf manicata</i> Deshayes, 1853							●			
<i>Tritonia plebeia</i> Johnston, 1828		●								
<i>Trivia monacha</i> (da Costa, 1778)							●			
BIVALVIA										
<i>Aequipecten opercularis</i> (Linnaeus, 1758)	●	●	●	●			●	●		
<i>Heteranomia squamula</i> (Linnaeus, 1758)	●	●	●	●	●		●	●		
<i>Musculus</i> sp.	●	●	●	●	●		●	●		
<i>Mysella bidentata</i> (Montagu, 1803)	●	●	●	●	●		●	●		
<i>Mytilus edulis</i> Linnaeus, 1758	●●●	●●●	●●●	●●●	●●●		●●●	●●●	●●●	●●●
Ostreidae							●			
<i>Venerupis geographica</i> (Gmelin, 1791)	●									
<i>Venerupis</i> sp.	●	●								
SIPUNCULA										
Golfingiida							●			
CRUSTACEA										
COPEPODA										
Copepoda	●						●	●		
CIRRIPEDIA										
<i>Acasta spongites</i> (Poli, 1795)							●			
<i>Balanus crenatus</i> Bruguière, 1789	●				●		●	●		●
<i>Verruca stroemia</i> O.F. Müller, 1776							●			
CUMACEA										
Cumacea	●							●		
ISOPODA										
<i>Janira maculosa</i> Leach, 1814							●			
<i>Pleurocrypta porcellanae</i> Hesse, 1876							●			
AMPHIPODA										
<i>Abludomelita obtusata</i> (Montagu, 1813)								●	●	
<i>Atylus swammerdami</i> (Milne-Edwards, 1830)				●				●	●	
<i>Caprella linearis</i> (Linnaeus, 1767)	●							●	●	
<i>Caprella tuberculata</i> Guérin, 1836	●	●	●	●	●	●	●	●	●	●
<i>Iphimedia nexa</i> Myers & McGrath, 1987	●	●	●	●	●	●	●	●	●	●
<i>Jassa herdmani</i> (Walker, 1893)	●	●	●	●	●	●	●	●	●	●
<i>Lysianassa ceratina</i> (Walker, 1889)	●									
<i>Melita hergensis</i> Reid, 1939								●	●	
<i>Metopa alderi</i> (Bate, 1857)	●	●	●	●	●	●	●	●	●	●
<i>Monocorophium acherusicum</i> (Costa, 1851)	●	●	●	●	●	●	●	●	●	●
<i>Monocorophium sextonae</i> (Crawford, 1937)	●	●	●	●	●	●	●	●	●	●
<i>Pariambus typicus</i> (Kroyer, 1844)	●	●	●	●	●	●	●	●	●	●
<i>Phtisica marina</i> Slabber, 1769	●	●	●	●	●	●	●	●	●	●
<i>Pseudoprotella phasma</i> (Montagu, 1804)	●	●	●	●	●	●	●	●	●	●
<i>Stenothoe marina</i> (Bate, 1856)	●	●	●	●	●	●	●	●	●	●
<i>Stenothoe monoculoides</i> (Montagu, 1815)	●	●	●	●	●	●	●	●	●	●
<i>Stenothoe</i> sp.	●	●	●	●	●	●	●	●	●	●
<i>Stenothoe valida</i> Dana, 1855	●	●	●	●	●	●	●	●	●	●
DECAPODA										
<i>Anapagurus chiroacanthus</i> (Lilljeborg, 1856)	●									
<i>Ateleyclus rotundatus</i> (Olivier, 1792)	●									

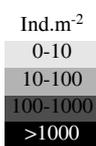


TABLE 2

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
<i>Ebalia tumefacta</i> (Montagu, 1808)							■			
<i>Hyas araneus</i> (Linnaeus, 1758)	■									
<i>Inachus phalangium</i> (Fabricius, 1775)							■			
<i>Liocarcinus arcuatus</i> (Leach, 1814)							■			
<i>Liocarcinus holsatus</i> (Fabricius, 1798)							■	■		
<i>Liocarcinus</i> sp.	■						■	■		■
<i>Macropodia parva</i> Van Noort & Adema, 1985			■				■		■	
<i>Macropodia rostrata</i> (Linnaeus, 1761)	■									
<i>Macropodia</i> sp.							■			
<i>Necora puber</i> (Linnaeus, 1767)	■						■			
Paguridae				■				■		
<i>Pilumnus hirtellus</i> (Linnaeus, 1761)	■	■	■	■	■	■	■	■	■	■
<i>Pisidia longicornis</i> (Linnaeus, 1767)	■	■	■	■	■	■	■	■	■	■
<i>Thorulus cranchii</i> (Leach, 1817)							■			
CHELICERATA										
PYCONOGONIDA										
<i>Achelia</i> sp.			■				■			
<i>Callipallene emacinata</i> (Dohrn, 1881)							■			
<i>Nymphon rubrum</i> Hodge, 1865							■			
<i>Pycnogonum littorale</i> (Strom, 1762)			■					■		
BRYOZOA										
CYCLOSTOMATIDA										
<i>Crisia aculeata</i> Hassall, 1841							●			
<i>Disporella hispida</i> (Fleming, 1828)	●									
<i>Plagioecia patina</i> (Lamarck, 1816)	●						●			
CHEILOSTOMATIDA										
<i>Bicelliariella ciliata</i> (Linnaeus, 1758)							●●			
<i>Conopeum reticulum</i> (Linnaeus, 1767)								■		
<i>Electra pilosa</i> (Linnaeus, 1767)	●	●●	●●	●●	●●	●●	●●	●	●	
<i>Scruparia chelata</i> (Linnaeus, 1758)	●									
<i>Scrupocellaria scruposa</i> (Linnaeus, 1758)	●	●					●●			
CTENOSTOMATIDA										
<i>Alcyonidium hydrocoailitum</i> Porter, 2004	●						●			
<i>Panolicella nutans</i> Jebram, 1985	●									
<i>Vesicularia spinosa</i> (Linnaeus, 1967)								■		
ECHINODERMATA										
ASTEROIDEA										
<i>Asterias rubens</i> Linnaeus, 1758	■	■			■		■	■	■	■
<i>Asterias rubens</i> juv. Linnaeus, 1758		■	■	■	■	■	■	■	■	■
ECHINOIDEA										
Euechinoidea										
<i>Psammechinus miliaris</i> (Gmelin, 1778)	■	■	■	■	■	■	■	■	■	■
OPHIUROIDEA										
<i>Amphipholis squamata</i> (Delle Chiaje, 1829)	■	■	■	■	■	■	■	■	■	■
<i>Ophiothrix fragilis</i> (Abildgaard, 1789)	■	■	■	■	■	■	■	■	■	■
<i>Ophiura albida</i> Forbes, 1839	■									
<i>Ophiura</i> sp.							■			
CHORDATA										
TUNICATA										
Ascidiacea										
<i>Diplosoma</i> sp.		●	●●	●●	●●		●●			
<i>Molgula cf occulta</i> Kupffer, 1875	■	■					■			
<i>Polyclinum aurantium</i> 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.m² (grey).

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

TABLE 4

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

CNIDARIA	
ANTHOZOA	
<i>Urticina felina</i> (Linnaeus, 1767)	
<i>Sagartia</i> sp.	
<i>Sagartiogeton undatus</i> (O.F. Müller, 1788)	
<i>Actinothoe sphyrodeta</i> (Gosse, 1858)	
CRUSTACEA	
DECAPODA	
<i>Cancer pagurus</i> Linnaeus, 1758	
MOLLUSCA	
CEPHALOPODA	
<i>Loligo vulgaris</i> Lamarck, 1798 – eggs	
<i>Acanthodoris pilosa</i> (Abildgaard in O.F. Müller, 1789)	
BRYOZOA	
CYCLOSTOMATIDA	
<i>Bugula cf turbinata</i> Alder, 1857	
CHORDATA	
TUNICATA	
<i>Asciadiella scabra</i> (O.F. Müller, 1776)	
<i>Clavelina lepadiformis</i> O.F. Müller, 1776	
PISCES	
<i>Dicentrarchus labrax</i> (Linnaeus, 1758)	
<i>Gadus morrhua</i> Linnaeus, 1758	
<i>Myoxocephalus scorpius</i> (Linnaeus, 1758)	
<i>Parablennius gattorugine</i> (Linnaeus, 1758)	
<i>Pollachius pollachius</i> (Linnaeus, 1758)	
<i>Pollachius virens</i> (Linnaeus, 1758)	
<i>Pomatoschistus</i> sp.	
<i>Scomber scombrus</i> Linnaeus, 1758	
<i>Spondyliosoma cantharus</i> (Linnaeus, 1758)	
<i>Trisopterus luscus</i> (Linnaeus, 1758)	
<i>Trisopterus minutus</i> (Linnaeus, 1758)	
<i>Trachurus trachurus</i> (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							
<i>Dysidea fragilis</i>	+	+	fr,uk	+	+		fill in the gap
<i>Phorbas plumosus</i>	+	+	fr,uk				fill in the gap
CNIDARIA							
<i>Actinothoe sphyrodeta</i>	-	-	fr,uk	+	-		extension to the north
<i>Diadumene cincta</i>	+	+	fr,uk,nl			+	fill in the gap
PLATYHELMINTHES							
<i>Eurylepta cornuata</i>	+	+	fr,uk	+	-	+	fill in the gap
NEMERTEA							
<i>Oerstedia dorsalis</i>	+	+	fr,uk,nl			+	fill in the gap
POLYCHAETA							
<i>Alentia gelatinosa</i>	+	+	fr,uk				fill in the gap
<i>Cirratulus cirratus</i>	+	+	fr,uk,nl			+	fill in the gap
<i>Cirriformia tentaculata</i>	+	+	fr,uk			+	fill in the gap
<i>Dipolydora coeca</i>	+	+	fr,uk			+	fill in the gap
<i>Eteone picta</i>	+	-	fr,uk,nl	+	-		fill in the gap
<i>Eulalia aurea</i>	-	-	fr,uk	+			extension to the north
<i>Eupolymnia nebulosa</i>	+	+	fr,uk,nl	-	+	+	fill in the gap
<i>Eupolymnia nesidensis</i>	+	+	fr,uk			+	fill in the gap
<i>Lysidice ninetta</i>	-	-	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
<i>Marphysa sanguinea</i>	+	-	fr,uk	+	-	+	extension to the north
<i>Neoamphitrite figulus</i>	+	+	fr,uk,nl			+	fill in the gap
<i>Nereimyra punctata</i>	+	+	fr,uk,nl	-	+		fill in the gap
<i>Phyllococe longipes</i>	+	+	fr,uk			+	fill in the gap
<i>Pista cristata</i>	-	+	?			+	fill in the gap from the north
<i>Polydora hoplura</i>	+	-	fr,uk			+	extension to the north
<i>Procerastea halleziana</i>	-	+	fr,uk				fill in the gap
<i>Procerastea nematodes</i>	-	+	fr,uk	+	-		fill in the gap
<i>Sphaerodoropsis flavum</i>	+	+	?			+	fill in the gap
<i>Sphaerosyllis bulbosa</i>	+	-	fr,uk	+	-		extension to the north
<i>Subadyte pellucida</i>	+	+	fr,uk,nl			+	fill in the gap
<i>Thelepus cincinnatus</i>	+	+	fr,uk,nl			+	fill in the gap
<i>Thelepus setosus</i>	-	-	fr,uk	+	-	+	extension to the north
GASTROPODA							
<i>Cerithiopsis tubercularis</i>	-	+	fr,uk				fill in the gap
<i>Cuthona amoena</i>	+	+	fr,uk,nl	+	-		fill in the gap
<i>Cuthona concinna</i>	+	+	fr,uk,nl	-	+	+	fill in the gap from the north
<i>Raphitoma linearis</i>	-	+	fr,uk				fill in the gap
<i>Tritonia cf manicata</i>	-	-	uk	+	-		extension to the north
CRUSTACEA							
<i>Acasta spongites</i>	-	-	fr,uk	+	-		extension to the north
<i>Caprella tuberculata</i>	+	+	fr,uk	+	-		fill in the gap
<i>Lysianassa ceratina</i>	-	-	fr,uk				extension to the north
<i>Pleurocrypta porcellanae</i>	+	-	fr,uk,nl	+	-		fill in the gap
<i>Pseudoprotella phasma</i>	+	+	fr,uk				fill in the gap
<i>Anapagurus chiroacanthus</i>	-	+	fr,uk				fill in the gap
<i>Macropodia parva</i>	+	+	fr,uk,nl		+		fill in the gap
PYGNOGONIDE							
<i>Callipallene emacinata</i>	-	-	fr,uk	+			?
BRYOZOA							
<i>Crisia aculeata</i>	+	+	fr,uk,nl				fill in the gap
<i>Alcyonidium cellarioides</i>	+	-	fr,uk,nl	+	-		fill in the gap and in extension to the north
<i>Nolella pusilla</i>	+	-	fr,uk,nl	+	-		fill in the gap and in extension to north
TUNICATA							
<i>Clavelina lepadiformis</i>	+	+	fr,uk,nl				fill in the gap
<i>Polyclinum aurantium</i>	+	+	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	
	<i>Hymeniacion perlevis</i>
	<i>Esperiopsis fucorum</i>
CNIDARIA	
	<i>Sagartiogeton undatus</i>
CRUSTACEA	
	<i>Iphimedia nexa</i>
	<i>Atelecyclus rotundatus</i>
	<i>Inachus phalangium</i>
PYGNOGONIDE	
	<i>Pycnogonum littorale</i>
Tunicata	
	<i>Ascidia scabra</i>

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-PIETO, 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).

ACKNOWLEDGEMENTS

The authors wish to thank the Station Marine de Wimereux for providing species list from the Dover Strait pebble community. The authors also wish to thank the crews of the RV Zeeleeuw and RV Belgica for their help during the sampling campaigns and to Céline Delforge for great help during the sorting process. It's also our pleasure to thank all the people who helped in collecting the samples: Drs J. Mallefet, A. Norro, Y. Laitat, A. Simon, D. Delbare, E. Vanden Berghe, T. Schils, Mss C. Delforge and R. Gyssens and Mrs P.B. Demoulin, G. Rooms, D. Marsham, F. Cray, M. Van Espen, Y. Verkemping, M. Backx, J. Haelters, F. Hernandez, F. Darchambeau, G. Van Hoydonck, A. Vanhaelen, R. Knuts & P. Van de Steen. We also want to thank Mr Andrew Stewart for his careful reading of the manuscript and two anonymous reviewers for critically reviewing the manuscript. This study has been financially supported by a 'plan Action II' grant (contract N° WI/36/C04) from the Belgian Science Policy and by the BEWREMABI project (Belgian Science Policy).

REFERENCES

- ALIZIER S (2005). Evolution spatio-temporelle de l'épifaune vagile et de l'endofaune du peuplement des cailloutis à épibiose sessile dans le Détroit du Pas de Calais. Rapport de Diplôme Supérieur de Recherche, Océanologie biologique, Station Marine de Wimereux: 78pp.
- CABIOCH L & GLAÇON R (1975). Distribution des peuplements benthiques en Manche Orientale, de la Baie de Somme au

- Pas-de-Calais. Comptes Rendus des Séances de l'Académie des Sciences, 280:491-494.
- CATTRISSE A & VINCX M (2001). Sustainable management of the North Sea: Biodiversity of the benthos and the avifauna of the Belgian coastal waters. Federal Office for Scientific, Technical and Cultural Affairs: 48pp.
- DAUVIN J-C, DEWARUMEZ JM & GENTIL F (2003). Liste actualisée des espèces d'Annélides Polychètes présentes en Manche. Cahiers de Biologie Marine, 44:67-95.
- DAVOULT D (1990). Biofaciès et structure trophique du peuplement des cailloutis du Pas-de-Calais (France). Oceanologica Acta, 13:335-348.
- DAVOULT D. & RICHARD A (1988). Les Ridens, haut-fond rocheux isolé du Pas-de-Calais: un peuplement remarquable. Cahiers de Biologie Marine, 29:93-107.
- DEGRAER S, WITTOECK J, APPELTANS W, COOREMAN C, DEPREZ T, HILLEWAERT H, HOSTENS K, MEES J, VANDEN BERGHE E & VINCX M (2006). The macrobenthos atlas of the Belgian Part of the North Sea, Belgian Science Policy, D/2005/1191/6, CD-ROM.
- DEWARUMEZ JM, DAVOULT D, SANVICENTE ANORVE LE & FRONTIER S (1992). Is the "muddy heterogeneous sediment assemblage" an ecotone between the pebbles community and the *Abra alba* community in the southern bight of the North Sea? Netherland Journal of Sea Research, 30:229-238.
- DUINEVELD G, KUNITZER A, NIEMANN U, DEWILDE PAWJ & GRAY JS (1991). The macrobenthos of the North Sea. Netherlands Journal of Sea Research, 28:53-65.
- ENGEL J & KVITEK R (1998). Effects of otter trawling on a benthic community in Monterey Bay national marine sanctuary. Conservation Biology, 12:1204-1214.
- FORTEATH GNR, PICKEN GB, RALPH R & WILLIAMS J (1982). Marine growth studies on the North Sea oil platform Montrose Alpha. Marine Ecology-Progress Series, 8:61-68.
- FOVEAU A (2005). Evolution des fonds à *Modiolus modiolus* dans le détroit du Pas de Calais. Rapport de stage d'un Master Recherche 2 EDEL, La Rochelle, Station Marine de Wimereux: 45pp.
- FRASCHETTI S, BIANCHI CN, TERLIZZI A, FANELLI G, MORRI C & BOERO F (2001). Spatial variability and human disturbance in shallow subtidal hard substrate assemblages: a regional approach. Marine Ecology-Progress Series, 212:1-12.
- FRASCHETTI S, GIANGRANDE A, TERLIZZI A & BOERO F (2003). Pre- and post-settlement events in benthic community dynamics. Oceanologica Acta, 25:285-296.
- GARCIA-GOMEZ J (1994). The systematics of the genus *Anapagurus* Henderson, 1886, and a new genus for *Anapagurus drachi* Forest, 1966 (Crustacea: Decapoda: Paguridae). Zoologische Verhandlungen, 295:1-131.
- GOVAERE JCR (1978). Numerieke analyse van het makrobenthos in the Southern Bight (Noordzee). Ph.D. thesis, Gent University, Belgium.
- HISCOCK K (1980). Marine life on the wreck of the M.V. 'Robert'. Report of the Lundy Field Society, 32:40-44.
- HOUBOLT JJHC (1968). Recent sediments in the Southern Bight of the North Sea. Geologie en Mijnbouw, 47:245-273.
- 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): 104pp.
- LEEWIS RJ, VAN MOORSEL GWNM & WAARDENBURG HW (2000). Shipwrecks on the Dutch Continental Shelf as artificial reefs. In: JENSEN AC, COLLINS KJ & LOCKWOOD APM (eds), Artificial reefs in European Seas, Kluwer Academic Publishers: 419-434.
- MALLINSON JJ, COLLINS KJ & JENSEN AC (1999). Species recorded on artificial and natural reefs, Poole Bay, 1989-1996. Dorset Proceedings, 121:113-122.
- MASSIN C, 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, Biologie, 72:67-72.
- MIGNÉ A & DAVOULT D (1997). Distribution quantitative de la macrofaune benthique du peuplement des cailloutis dans le détroit du Pas de Calais (manche orientale, France). Oceanologica Acta, 20:453-460.
- PICKEN G (1986). Moray Firth fouling communities. Proceedings of the Royal Society of Edinburgh B, 91:213-220.
- 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 JM, GLAÇON R & RICHARD A (1988). Distribution et richesse des peuplements benthiques de la partie française de la Mer du Nord. Compte Rendu de l'Académie des Sciences de Paris, série III, 306:5-10.
- 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.
- VAN MOORSEL GWNM, WAARDENBURG HW & VAN DER HORST J (1991). Het leven op en rond scheepswrakken en andere harde substraten in de Noordzee (1986 T/M 1990) - een synthese. Rapport 91.19, Bureau Waardenburg bv, Culemborg: 49pp.
- VEENSTRA HJ (1969). Gravels of the southern North Sea. Marine Geology, 7:449-464.
- VERGÉS A & RODRIGUEZ-PRIELO C (2006). Vegetative and reproductive morphology of *Kallymenia patens* (Kallymeniaceae, Rhodophyta) in the Mediterranean Sea. Botanica Marina, 49:310-314.
- VOLCKAERT A, ENGLEDDOW S, DEGRAER S, VINCX M, COPPEJANS E & HOFFMANN M (2002). The epilithic macrofauna and macroalgae of the hard substrates along the Belgian coast. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie, Sup. 72:13-15.
- WILLIAMS RB (1997). *Actinothoe sphyrodeta* (Cnidaria, Actinaria): the first records from Portugal and the Mediterranean Sea. Journal of the Marine Biological Association of the UK, 77:245-248.
- ZINTZEN V & KERCKHOF F (2009). The sponge-inhabiting barnacle *Acasta spongites* (Poli, 1795) (Crustacea, Cirripedia), a first record for the southern North Sea: how artificial habitats may increase the range of a species. Belgian Journal of Zoology, 139:166-168.
- ZINTZEN V, MASSIN CL, NORRO A & MALLEFET J (2006). Epifaunal inventory of two shipwrecks from the Belgian Continental Shelf. Hydrobiologia, 555:207-219.
- ZINTZEN V, NORRO A, MASSIN C & MALLEFET J (2007). Temporal variation of *Tubularia indivisa* (Cnidaria, Tubulariidae) and associated epizoites on artificial habitat communities in the North Sea. Marine Biology, 153:405-420.
- ZINTZEN V, NORRO A, MASSIN C & MALLEFET J (2008). Spatial variability of epifaunal communities from artificial habitat: Shipwrecks in the Southern Bight of the North Sea. Estuarine, Coastal and Shelf Science, 76:327-344.

Received: March 13, 2008

Accepted: November 4, 2009

Branch editor: Schön Isa/Brendonck Luc