Mar Biol (2008) 153:405–420
DOI 10.1007/s00227-007-0819-5

RESEARCH ARTICLE

Temporal variation of *Tubularia indivisa* (Cnidaria, Tubulariidae) and associated epizoites on artificial habitat communities in the North Sea

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Received: 8 December 2006 / Accepted: 7 September 2007 / Published online: 28 September 2007

Abstract We have analyzed the composition, diversity, density and biomass of a temporal series of samples taken in a *Tubularia indivisa* community, which dominates a shipwreck in the North Sea waters (N 51°23′,730–E 02°29′,790, 17 nautical miles from the coast, 30 m depth). This shipwreck has structures emerging up to 8 m above the seabed. Water temperature ranged from 4.2°C in March to 20.3°C in August. Salinity showed few variations around 33.9 psu. Bottom tidal currents followed a semi-diurnal cycle and were preferentially NE oriented with 84% of them in the range 0.25–0.75 m s^{-1}. The mean value for total suspended matter was 6.2 mg l^{-1} with large variations on a monthly scale. The species richness of samples varied from 15 in October to 42 in August with a mean value of 33 species. Diversity indices were higher during autumn and winter because of the strong dominance of a few crustacean species during the warmer months. The total density of individuals ranged from 6,500 ind m^{-2} in October to 445,800 ind m^{-2} in July, most of these individuals belonging to the amphipod species *Jassa herdmani*. The biomass of the *T. indivisa* community varied from 9 g AFDW m^{-2} in October to 1,106 g AFDW m^{-2} in July, with *T. indivisa* itself constituting between 59 and 82% of the total biomass. The biomass of *T. indivisa* was positively correlated with species richness and with the density of 23% of the species identified on this community, suggesting that *T. indivisa* plays an important structural role in this habitat. This was further confirmed by the number of species associated with *T. indivisa* which was generally superior to 55% of the sorted species. Multivariate analysis indicated strong differences between spring/summer−autumn/winter assemblages mostly but not solely due to the abundance patterns of species. These findings support the conclusion that shipwrecks in Belgian waters allow the development of assemblages dominated by a high biomass of *T. indivisa* which in turn provides shelter for high densities and biomass of epizoites. These assemblages will further show large monthly variations in densities and composition due to large variation in *T. indivisa* biomass under an apparent repetitive annual cycle.

Introduction

Hard substrata in the marine environment are in nature bidimensional structures, but a third dimension generally develops through the growth of sessile species (Fraschetti et al. 2003). These structural aspects are important factors controlling the subsequent settlement and/or survivorship of species (Dean 1981). The modification of the colonization pattern following sessile species development can be influenced by an alteration of the flow characteristics

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Communicated by M. Wahl.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-007-0819-5) contains supplementary material, which is available to authorized users.

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(Baynes and Szmant 1989), the provision of additional surface area (Genzano 1998), more secure/attractive attachment surfaces (Schmidt 1983) and refuges from predation (Walters and Wethey 1996).

Hydroids in general and species of the genus *Tubularia* in particular are among the first species to colonize bare surfaces (Dean and Hurd 1980). *Tubularia* species are described as pioneer species because they are one of the first settlers on newly available hard substrata and are short-living (Hughes 1983). They are often found on recently submerged substrata (Bulloch 1965; Forteath et al. 1982; Woodhead and Jacobson 1985; Sampaolo and Relini 1994; Leewis et al. 2000; Leewis and Hallie 2000; Jensen et al. 2000; Leonhard et al. 2004). Sometimes they are only transient species being replaced by climatic species (Forteath et al. 1982; Claereboudt et al. 1994; Whomersley and Picken 2003), but in other cases, these represent permanent elements of an annual cycle and tend to dominate during specific periods of the year (Boero and Fresi 1986; Caine 1987).

Tubularia species are known to enhance the settlement of a set of other sessile and motile taxa (Caine 1987; Bourget and Harvey 1998; Genzano 1998) and their role in the settlement of commercially important scallop species has been tested (Harvey et al. 1993, 1995a, 1997). Some information is available on the epibionts of *Ectopleura crocea* (Genzano 1998) and the association of this species with a number of commensal pycnogonids and parasite polychaetes (Genzano and San Martin 2002; Genzano 2002).

Among the genus *Tubularia*, the species *T. indivisa* is typically a subtidal species although some isolated individuals can be found in the intertidal zone (Goss-Cusard et al. 1979; Kaandorp 1982). It is common along the North–East Atlantic coast and a long record history is available from natural highly turbulent and tide swept subtidal habitats around the UK and Ireland (Doody et al. 1993; Connor et al. 2004; MarBEF 2004). Hughes (1983) investigated the annual cycle of *T. indivisa* but there is currently no study analyzing the temporal variation of the assemblages associated with this species.

On shipwrecks of the Belgian part of the North Sea, it has been observed that *T. indivisa* strongly dominated the epifauna present in June (Zintzen et al. 2007). This dominance has been reported for many years by local divers. Combined to the apparent continuity of this community, the interesting particularity of these artificial hard substrata is that they are lying on a seabed dominated by soft sediments and that they are consequently located at great distance from any natural hard bottoms. In this study, we evaluated the hypothesis that *T. indivisa* is an essential species for structuring the communities of artificial habitats in the Southern Bight of the North Sea. This hypothesis was tested by analyzing the composition, diversity, density and biomass of a temporal series of samples taken within a community dominated by *Tubularia indivisa* and developing on a shipwreck from the Belgian waters. The following specific questions were brought forwards: (1) does the abundance of *T. indivisa* display a temporal pattern on artificial habitats, (2) which are the species associated with this community, how did this assemblage vary in time and what are their seasonal characteristic species, (3) to what extend can *T. indivisa* be considered as a micro-habitat for other species?

Materials and methods

General description of the study site

The Belgian part of the North Sea (BPNS) covers 3,640 km^2 and its seabed is dominated by soft sediments. It harbours a high geomorphological and sedimentological diversity because of the presence of numerous sandbanks (Degraer et al. 1999) and a large number of obstructions, most of them being shipwrecks, are widely dispersed on the bottom (Zintzen et al. 2006). Natural hard substrates such as pebbles are rare and only occur at some places in gullies between sandbanks (Lanckneus et al. 2001).

Following the Belgian Administration for Navigation and Coast, the Kilmore (WGS 84, N51°23′,730–E02°29′,790, 17 nautical miles from the coast) is the oldest shipwreck made of steel known in the Belgian waters. It measures 87 by 12 m and sunk in 1906 to a depth of 30 m (mean lower low water springs) with structures emerging up to 8 m above the seabed. Despite its relative long time of submersion, it is in very good state and the major parts of its structure can still be observed. The major part of the vessel is covered by a community dominated by the hydrozoan *T. indivisa* (identified following Petersen 1990) and all the samples were taken within this community.

Sampling and sample processing

Initially, the shipwreck had to be sampled on a seasonal scheme from December 2003 to December 2005. However, adverse weather conditions prevented sampling on many occasions and the Kilmore has been sampled on the eight following occasions: December 2003, April 2004, July 2004, October 2004, March 2005, June 2005, August 2005 and October 2005.

On each date, all the living fauna within frames of 25 × 25 cm selected at random in the *T. indivisa* community were scraped on the surface of the shipwreck using SCUBA. This was done three times on each sampling occasion and on vertically oriented surfaces. On board, animals were relaxed in a 3.5% $MgCl_2$ solution during 2 h and then transferred to a buffered formalin solution (final concentration 4%, pH 8.2–8.4). Later on, specimens were transferred to 70% buffered alcohol for permanent storage. The samples were then sorted using a binocular and macro-taxa (>1 mm) were identified to the lowest possible taxonomic level and counted. Colonial taxa were counted as one individual for quantitative analysis and were elsewhere considered as present or absent. From in situ and laboratory observations, systematically attached taxa or taxa invariably found living in association with *T. indivisa* were noted. Taxa are further in the text considered as species.

For every sample, wet weight (in alcohol) of the nine most important species in term of biomass was measured individually to the nearest mg with an OHAUS Adventurer balance. These nine most important taxa were determined from a complete weighting of the samples from June 2005. Prior to weighting, specimens were blotted on absorbent paper to remove excess alcohol. For each species, we calculated in triplicate wet weight to ash free dry weight conversion factors. 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 (AFDW) is the difference between dry weight and the weight after the burning process. Specimens were kept in preservatives which have a known effect on their biomass (Brey 1986; Rumohr et al. 1987; Gaston et al. 1996; Pakhomov 2003; Wetzel et al. 2005). The sorting and taxonomic work hampered to freeze the samples for conservation. In this case, Gaston et al. (1996) recommended to fix the animals in formalin solution prior to transfer into alcohol for sampling processing. However, there is no agreement on which factor to apply to correct weight loss. Consequently, we multiplied our results by a factor of 1.2 as suggested by Rumohr et al. (1987) and used by Cusson and Bourget (2005). This factor has to be considered as a minimum one.

Environmental data

The following abiotic data were collected to characterize the physical environment around the shipwrecks in the Southern Bight of the North Sea: temperature, salinity, current velocity-direction and turbidity.

The temperature series were obtained from permanent station of the Afdeling Waterwegen Kust (AWK) on the Westhinder sandbank which is located 3.8 nautical miles West from the Kilmore. Salinity data were provided by underway data from R/V Belgica. Data were extracted for the period 1993–2006 and for a location inside a 5 nautical miles square centred on the wreck position. Seabird SBE 21 system was used onboard. Temperature and salinity values used here are sub-surface values (at 3 m depth). As the Belgian zone is characterized by a well-mixed water column, these values can be considered as representative for the whole depth.

Turbidity estimates were obtained through satellite imagery collected between September 1997 and March 2004. For each site, the mean total suspended matter (mg l^{-1}) was calculated using the MODerate resolution Imaging Spectro-radiometer (MODIS) aboard the satellite EOS AQUA. A bio-optical model calibrated for the Belgian coastal waters, following the method described in Nechad et al. (2003), was applied to MODIS readings.

On each sampling date, water transparency was measured with a Secchi disk during slack period.

Data on the currents 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. Boundary conditions were provided by a larger scale model using the nesting method. The results of the model were available by layers of 1.6 m and we used the four bottom layers (4 × 1.6 m) to only consider the current parameters which had a direct effect on the shipwreck. Currents roses were constructed with values of the current that were computed every 10 min. The runs started in august 2004, resulting in at least 230 days of data.

Temporal pattern analysis

Species richness and diversity index

We used a series of univariate summary statistics to evaluate the different diversity components (i.e. species richness, abundance pattern and taxonomic diversity) and their variation in time. Univariate summary statistics used were the species richness (S) (here defined as the number of species by sampling unit), the Shannon–Wiener index (H', $\log_e$), the Simpson index (1-D) (Magurran 2004), the average taxonomic distinctness (Δ^+) and the variation in taxonomic distinctness (Λ^+) (Clarke and Warwick 1998, 2001). The taxonomic distances were evaluated through a taxonomic tree built on standard Linnean classification. We used the taxonomy proposed by Costello et al. (2001) from which we extracted a simplified tree: the retained taxonomic levels were species, genus, family, order, class and phylum. The default weights between step length of the Linnean tree were set to constant (i.e. weights were 16.7 for species in the same genus, 33.3 for species in different genus but the same family, 50 for species in different family but the same order, 66.7 for species in different orders but the same class, 83.3 for species in different class but the same phylum and 100 for species in different phyla). These indices were calculated using the DIVERSE procedure of the PRIMER statistical software package and compared across dates using Kruskal–Wallis non-parametric ANOVA.

Multivariate pattern

The temporal variability of the assemblages identified on the *T. indivisa* community was evaluated with multivariate techniques. Multivariate analysis of the scraped samples was conducted on abundance and biomass data, excluding *T. indivisa* from the analysis since the hydroid was here considered as the habitat. Similarity between each pair of samples was calculated with the Bray–Curtis similarity coefficient (Bray and Curtis 1957) for abundance data and Euclidean distance for the biomass data. We used untransformed and presence/absence data to discern from the differences between samples due to abundance of species or to the presence of species alone. This matrix was then used to explore the pattern of community structure among samples by means of ordination with non-metric multidimensional scaling (nMDS) (Clarke 1999). The goodness-of-fit of the resulting two-dimensional nMDS plot was measured using Kruskal's stress formula I (Kruskal and Wish 1978). Non-parametric multivariate analysis of variance was used to test for difference between dates using PERMANOVA (Anderson 2001). Significance test of pair-wise comparisons between each date could not be calculated through traditional permutation method because of the low number of replicates for each date ($N = 3$). P value was then calculated using Monte Carlo simulation (Anderson and Robinson 2003). Again, the Bray–Curtis similarity index was used for the abundance data and Euclidean distance for the biomass data.

Indicator species

The characteristic or indicator species of this temporal series of assemblages were also determined to see if indicator species varied with the period of the year. Indicator species for each season were characterized by mean of the Indicator Value (IndVal) coefficient (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 is evaluated using a randomization procedure (9,999 randomizations). A species was considered to be an indicator of a group if the results of two tests were significant at a level of 0.05: a *t* test computing the weighted distance between randomized values and the observed value, and the rank of the observed value among the decreasing ordered randomized value distribution. The calculations were made using the IndVal program.

Value of *T. indivisa* as microhabitat

To evaluate the importance of *T. indivisa* in providing a habitat for epizoites, correlation between biomass values of *T. indivisa* and univariate diversity statistics and between biomass of *T. indivisa* and abundance of species were analyzed by non-parametric methods [Spearman's rank correlation coefficient; the normality of the variables could not be obtained even after transformations (graphical examination of the residuals and Shapiro-Wilk's *W* test, Shapiro and Wilk 1965)].

Results

Environmental characterization

Temperature on the Kilmore ranged from 4.2°C (March 2006) to 20.3°C (August 2003) with an average value of 12.2°C (Fig. 1). March was the coldest month except for 2003 when temperatures exceptionally started to rise in February. The highest temperatures were observed in August except for 2005 when they were observed in September. The temperature displayed a cycle which was repeated from year to year (2001–2006) with only small variations.

The salinity was constant between months and comprised between 33.2 and 34.5 psu (Fig. 2) so that the Kilmore did not seem to suffer from periodic marked low salinity due to fresh water income from the local rivers input (Rhine–Meuse and Scheldt estuaries).

The hydrodynamic of the area was constrained by semi-diurnal tides resulting in the emergence of strong tidal currents. Minimum tidal currents occurred on the Kilmore generally three hours before and after local high tide. The

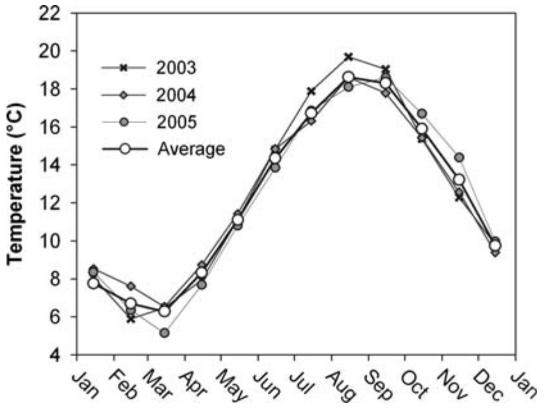


Fig. 1 Mean monthly temperature on the Westhinder station (3.8 nm from the Kilmore shipwreck) for the period June 2001 to May 2006. Data from Afdeeling Waterwegen Kust

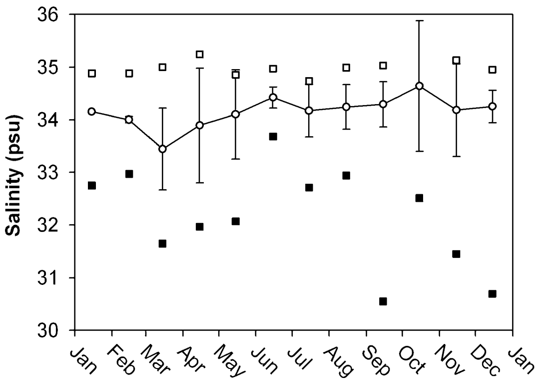


Fig. 2 Mean (±s.d.) (*open circle*), Min (*filled square*) and Max (*open square*) monthly salinity values on the Kilmore shipwreck for the period 1993–2006 extracted from the R/VBelgica underway data. Salinity measures were made at less than 5 nautical miles from the shipwreck

current roses for each month were closely similar and a typical example is presented for the month of July in Fig. 3. The current was preferentially oriented along a SW–NE axis (66% of the occurrence). It was also along these directions that currents were the strongest (up to 0.86 m s^{-1}). For other directions, the velocity of the currents did not rise above 0.50 m s^{-1}. There was no current under 0.10 m s^{-1} and the proportion of currents under 0.30 m s^{-1} was 18%. The 0.25–0.50 m s^{-1} current velocity class was the most frequent (42%), followed by the 0.50–0.75 m s^{-1} class (40%).

Mean value for total suspended matter on the Kilmore was 6.2 mg l^{-1}. Total suspended matter was clearly lower from May to September with values around 5.5 mg l^{-1} (Fig. 4). The turbidity rose from September to November and then remained constant until February at 8.0 mg l^{-1}. From February to April, the turbidity decreased sharply. The deviation around the mean values were sometimes high (March and September), indicating large monthly fluctuations of suspended matter at the monthly temporal scale.

Temporal pattern

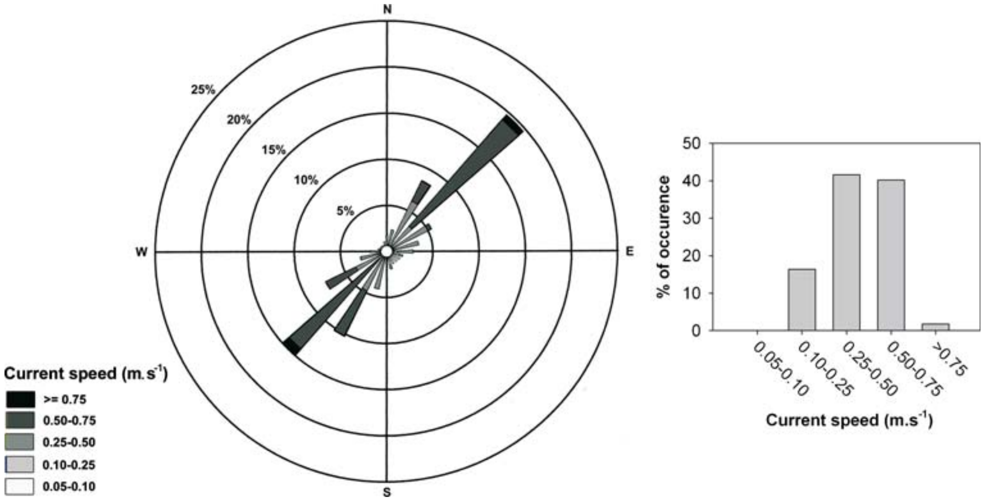
Species richness and diversity index

Univariate indices of diversity are presented in Fig. 5. The total number of species was 102 (Annexe 1). The species richness (N_0) varied from 15 in October to 42 in August with a mean value of 33 species per sample. All the other species richness values were between 30 and 40 species with the exception of the samples from March 2005 (28 sp). The result of the Kruskal–Wallis ANOVA was significant at $P < 0.03$, indicating that species richness was different from date to date. The Shannon–Wiener (H′, $\log_e$) and Simpson (1-D) indexes displayed a very similar pattern. The samples from the autumn and winter periods shared high diversity index values while spring and summer samples were strongly dominated by a few species which lowered the Shannon–Wiener and Simpson indexes. The Kruskal–Wallis ANOVA is significant at $P < 0.03$ and $P < 0.04$ for H′ and 1-D, respectively. The taxonomic distinctness (Δ^+) values had no distinct pattern linked to the time of the year. The average taxonomic distance between two species taken at random did not change with time. The variation in taxonomic distinctness (Λ^+) was also rather constant. Only two values, one at the end of 2004 and the other at the beginning of 2005 were lower, indicating a more homogeneous repartition of the species in the taxonomy of these samples.

Density and biomass

On the 1.5 m^2 surface (24 samples) scraped on the Kilmore shipwreck, a total number of 187,588 individuals were

Fig. 3 Current roses and current velocity occurrence for the Kilmore shipwreck (July 2005). MUMM operational three-dimensional model (10 min time step, 750 m grid size, UK Met Office weather forecast forcing)



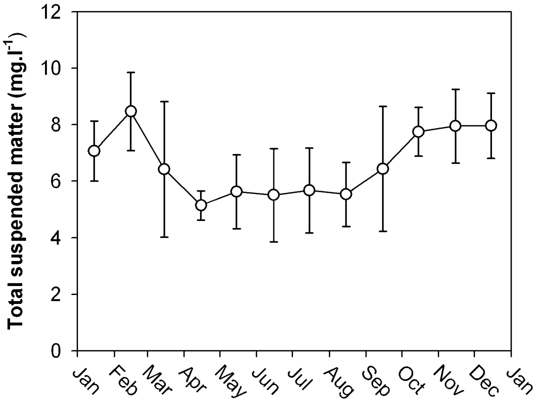


Fig. 4 Mean monthly total suspended matter (±s.d.) on the Kilmore shipwreck obtained from MODIS satellite imagery for the period July 2002 to October 2005 (number of observations = 199)

counted. The total density of the macrobenthos displayed a clear temporal variation with larger values during spring and summer periods (Fig. 6). Values ranged (mean ± s.d.) from 6,500 ± 56 ind m^{-2} in October 2004 to 445,800 ± 189,800 ind m^{-2} in July 2004. A major part of these individuals did belong to the amphipod species *Jassa herdmani* (Fig. 6). Its density ranged from 1,000 ± 385 ind m^{-2} in October 2004 to 398,500 ± 189,800 ind m^{-2} in July 2004 and closely followed the total density pattern. The abundance of Crustacea (*J. herdmani* omitted) and Echinodermata showed a peak during spring and summer months (4,600 ± 1,340 ind m^{-2} and 12,100 ± 8,120 ind m^{-2} in June 2005 and July 2004, respectively; Fig. 6). For the Crustacea, the decapod *Pisidia longicornis* and the caprellids *Phtisica marina* and *Caprella tuberculata* were the species contributing most to the observed abundances (Fig. 6). Stenothoidae were also abundant. *Ophiothrix fragilis* dominated the Echinodermata (Fig. 6). Annelida, Cnidaria and Mollusca had a very close pattern of temporal abundances. They were all more abundant in spring and summer with maximal abundances of 1,500 ind m^{-2} for Annelida, 6,100 ind m^{-2} for Cnidaria and 5,000 ind m^{-2} for Mollusca. However, some of the cnidarians species were not readily countable and were not adequately represented by abundance data. Groups with low abundance like Nemertea, Porifera, Platyhelminthes, Bryozoa and Tunicata did not show any clear temporal pattern.

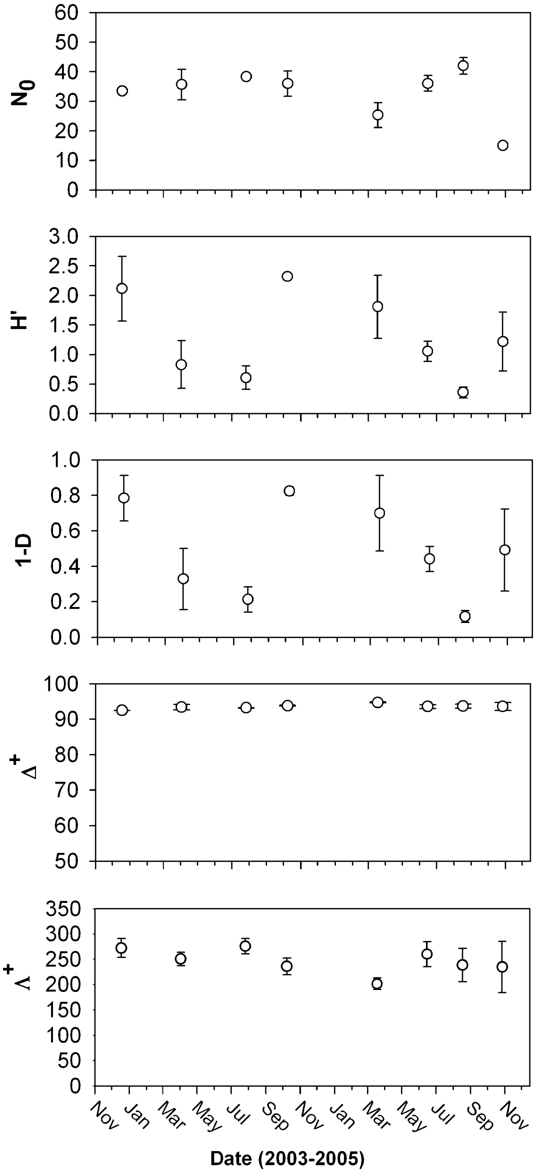


Fig. 5 Temporal variation of diversity index on the Kilmore shipwreck. Values are means ± s.d. N_0 is the species richness, *H′* is the Shannon–Wiener index (natural log), *1-D* is the Simpson index, Δ^+ is the taxonomic distinctiveness, Λ^+ is the variation in taxonomic distinctiveness

The total biomass varied from 9 g m^{-2} in October 2004 to 1,106 g m^{-2} in July 2004 (Fig. 7; all biomass values are expressed as ash-free dry weights). The variation in total biomass depended strongly on the biomass of *T. indivisa* which constituted between 59 and 82% of the total biomass (Fig. 7). Its development was already important at the end of the winter (60–324 g m^{-2}) and increased until the first part of the summer period (362–912 g m^{-2}). Afterwards, its biomass decreased until a minimum around October (5–14 g m^{-2}). The biomass of the most abundant species, *J. herdmani*, displayed the same pattern with biomasses ranging from 0.3 to 123.3 g m^{-2} (Fig. 7). The eight most abundant species have their biomass values presented in Fig. 7. For June 2005, those eight species together with *T. indivisa* and *J. herdmani* accounted for 93% of the biomass of the samples. Except the amphipod *Monocorophium sextonae* and the tunicate *Diplosoma* sp., they all had a peak of biomass at the end of spring. The last two species were more represented at the end of the winter.

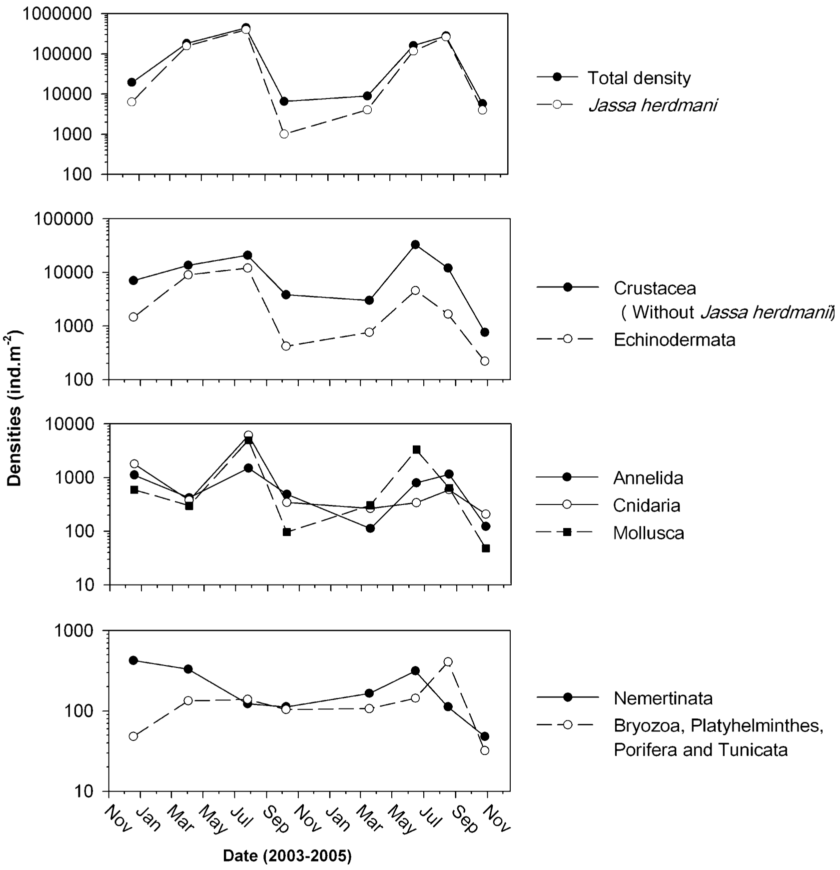


Fig. 6 Temporal variation of densities on the Kilmore shipwreck. *Y* axes are presented on a log scale

Generally, the biomass values of 2004 were higher than those of 2005. In July 2004, the biomass of *T. indivisa* was 912 g m^{-2} while we calculated 362 and 129 g m^{-2} for June and August 2005, respectively (Fig. 7).

Multivariate patterns of differences among assemblages

The non-metric multidimensional scaling ordination plot (abundance data) of the assemblages from each date showed a good consistency for the samples taken on the same dates (Fig. 8). The actual differences in abundance pattern (i.e. using untransformed data) revealed that variance was larger for the assemblages sampled during the autumn/winter than during the spring/summer period, these two groups being sharply isolated (Fig. 8a). The spring and summer samples showed stronger affinities with each other than the samples taken during autumn and winter. When looking at the species composition of the assemblages (i.e. using presence/absence data), a weaker separation of the autumn/winter *versus* spring/summer was visualized, suggesting that differences in assemblages at different times were mostly due to abundance patterns and not only to species composition (Fig. 8b).

The ordination plot for biomass data for the ten most abundant taxa isolated the spring/summer samples from the autumn/winter ones (Fig. 9). Autumn/winter samples were very similar to each other compared to spring/summer samples, suggesting larger variation of epibiont biomass during the warmer months.

The results from the non-metric multivariate analysis of variance from abundance data are presented in Tables 1 and 2 and confirmed the results from the ordination plot. Assemblage abundance pattern and biomass differed between dates (Table 1). The autumn and winter samples are different from the spring and summer samples regarding their abundance and biomass patterns (Table 2). Greater differences were detected when presence/absence data were analyzed which suggested that differences may be due to differences in the types of species that were present at different times.

Seasonal characteristic species

The number of species which were indicator of the Kilmore shipwreck was relatively high (16 species with IndVal > 75; Table 3). The best represented group was the crustaceans with decapods and amphipods. *Mytilus edulis* was invariably found as juveniles (<1 cm) while all the other species had adults in their representatives. The indicator species by season are presented in Table 4. In winter, *Liocarcinus* sp. is

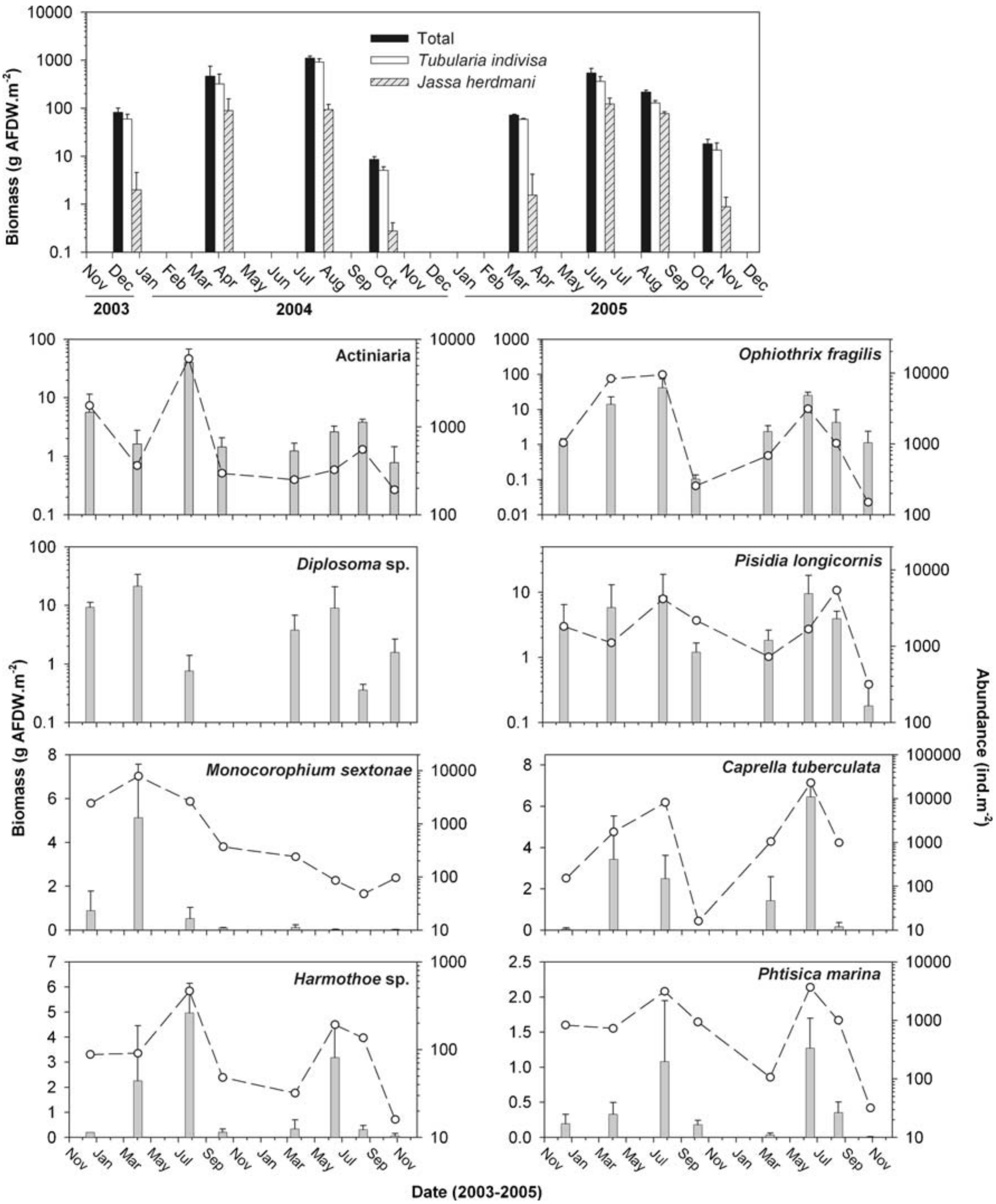


Fig. 7 Temporal variation of biomass (mean ash-free dry weights, ± s.d.) and abundance of dominant species on the Kilmore shipwreck. Abundance for *Diplosoma* sp. is not presented because this species is not countable. For readability, *Y* axes of Actinaria, *Ophiothrix fragilis*, *Diplosoma* sp. and *Pisidia longicornis* are presented on a logarithmic scale

the only species with an IndVal of 100. Rissoidae, *Sabellaria spinulosa* and *Alcyonium digitatum* had a high and significant IndVal. The cnidarian *A. digitatum* was only found as juveniles composed of a few polyps which were not found afterwards. Several polychaete and crustacean species had an IndVal around 50. *Monocorophium sextonae*, although not significant, was again more characteristic of the winter period. We did not detect indicator species for spring. During summer, a large set of species were indicator of the assemblages, including many crustaceans and polychaetes. The nudibranch *Dendronotus frondosus*, although not present as an indicator, was abundant in summer and could be potentially important because of its predatory behaviour. No species were indicator of the autumn period.

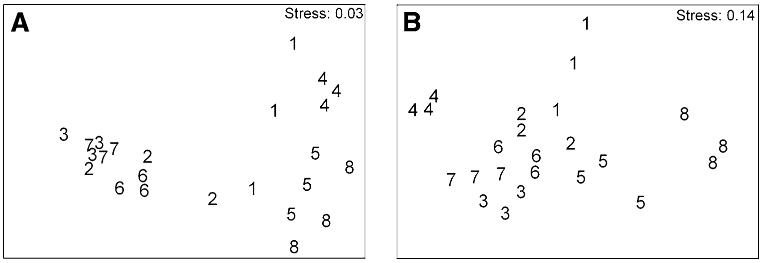


Fig. 8 Non-metric multidimensional scaling based on Bray–Curtis similarity from untransformed abundance data (**a**) and presence/absence data (**b**) on the Kilmore shipwreck. *Tubularia indivisa* was excluded from the analysis. *1* December 2003, *2* April 2004, *3* July 2004, *4* October 2004, *5* March 2005, *6* June 2005, *7* August 2005, *8* October 2005

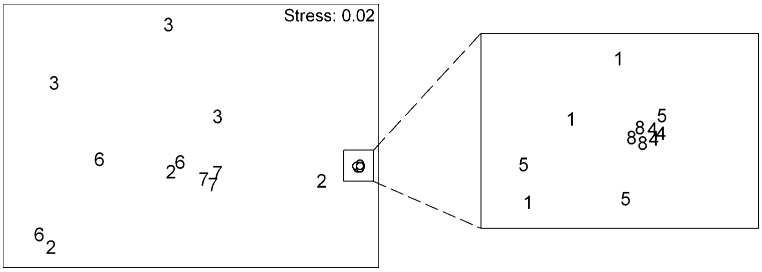


Fig. 9 Non-metric multidimensional scaling based on Euclidean distances from untransformed biomass data for the nine most important species on the Kilmore shipwreck. *Tubularia indivisa* was excluded from the analysis. *1* December 2003, *2* April 2004, *3* July 2004, *4* October 2004, *5* March 2005, *6* June 2005, *7* August 2005, *8* October 2005

Table 1 Non-parametric multivariate analysis (NPMANOVA) on abundance data (based on Bray–Curtis dissimilarity) and on biomass data (based on Euclidean distance) of the Kilmore shipwreck

Source	df	SS	MS	*F*	*P*
Abundance					
Date	7	53,552.7	7,650.4	7.394	0.001
Residual	16	16,554.4	10,34.6	3.170	0.001
Total	23	70,107.1	11,208.5		
Biomass					
Date	7	78,459.6	3,536.3		
Residual	16	56,581.3			
Total	23	135,040.9			

Date were a random factor with 8 levels ($N = 3$). *Tubularia indivisa* was excluded from the analysis

Value of *T. indivisa* as a microhabitat

A significant positive correlation ($P < 0.05$) between the biomass of *T. indivisa* and the abundance of species was observed for 24 species. The strongest correlations were noted for *M. edulis*, *J. herdmani*, *O. fragilis*, *Harmothoe* sp., *Amphipholis squamata*, *C. tuberculata* and *Lepidonotus squamatus* (Spearman $R^2 > 0.69$, $P < 0.001$; Table 5). The biomass of *T. indivisa* was also positively correlated with the species richness of the samples ($R^2 = 0.562$, $P < 0.008$; Fig. 10). The relation was not strictly linear and was flattening off when *T. indivisa* biomass was above 200 g m^{-2}. *T. indivisa* biomass was also negatively correlated with the Shannon–Wiener index ($R = -0.677$, $P < 0.001$) and the Simpson index ($R = -0.650$, $P < 0.002$) but was not correlated with the taxonomic distinctiveness nor the variation in taxonomic distinctiveness.

The number of species associated with *T. indivisa* (living attached on or invariably found on *T. indivisa*) was generally superior to 55% of the species richness of the samples (Fig. 11). The lowest percentage of association (46%) was found on October 2004. This set of species accounted for 86% (December 2003) or more of the total density of individuals in the samples (Fig. 11). However, there was no systematic trend in the association (both in species number and density) with the period of the year.

Discussion

Abiotic environment

Around the Kilmore shipwreck, several abiotic parameters showed a variation on an annual scale. First of all, the water temperature ranged from 7°C to 19°C. The temperature minima, maxima and mean by month were slightly different between years and could induce differential recruitment and growth between years.

Table 2 Pairwise comparison of macrofauna assemblages from the Kilmore shipwreck on different dates using non-parametric multivariate analysis of variance (NPMANOVA, based on Bray–Curtis dissimilarity for abundance data and Euclidian distance for biomass data)

Date	Abundance				Biomass (no trans)	
	No trans		Presence/absence			
	t	*P*	*t*	*P*	*t*	*P*
12/2003–04/2004	1.9	NS	2.1	*	1.7	NS
07/2004	3.6	**	2.9	*	2.1	*
10/2004	2.5	*	3.8	**	2.8	*
03/2005	1.4	NS	1.6	NS	1.9	NS
06/2005	3.8	**	3.6	**	2.6	*
08/2005	4.2	**	3.9	**	2.61.	*
10/2005	2.0	*	3.5	**	6	NS
04/2004–07/2004	1.5	NS	1.9	*	0.6	NS
10/2004	3.1	**	3.1	*	1.9	NS
03/2005	1.7	NS	1.3	NS	1.5	NS
06/2005	1.2	NS	2.1	*	0.9	NS
08/2005	1.5	NS	2.5	*	0.9	NS
10/2005	2.4	*	2.8	*	1.8	NS
07/2004–10/2004	6.7	***	3.4	**	2.1	*
03/2005	2.5	*	1.5	NS	1.7	NS
06/2005	3.3	*	2.3	*	1.1	NS
08/2005	1.4	NS	2.4	*	1.0	NS
10/2005	3.9	**	3.4	**	2.1	*
10/2004–03/2005	1.8	NS	2.2	*	1.0	NS
06/2005	9.5	***	4.3	**	2.8	*
08/2005	13.3	***	4.5	**	2.4	*
10/2005	2.8	**	4.8	**	1.4	NS
03/2005–06/2005	2.5	*	1.7	NS	2.4	*
08/2005	2.7	*	1.8	NS	1.9	NS
10/2005	1.2	NS	1.7	NS	1.0	NS
06/2005–08/2005	5.0	**	3.7	**	1.4	NS
10/2005	4.2	**	3.8	**	2.8	*
08/2005–10/2005	4.6	**	4.4	**	2.4	*

Tubularia indivisa was excluded from the analysis. *P* values were estimated through asymptotic Monte–Carlo sampling

NS not significant

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 3 Indicator species of the temporal series from the Kilmore shipwreck

Species		IndVal
Actiniaria	CNI	100
Jassa herdmani	CRU	100
Oerstedia dorsalis	NEM	100
Ophiothrix fragilis	ECH	100
Pisidia longicornis	CRU	100
Tubularia indivisa	CNI	100
Amphipholis squamata	ECH	95.2
Monocorophium sextonae	CRU	95.2
Mytilus edulis	MOL	95.2
Pilumnus hirtellus	CRU	95.2
Phtisica marina	CRU	90.5
Caprella tuberculata	CRU	85.7
Diplosoma sp.	TUN	85.7
Harmothoe sp.	POL	85.7
Lepidonotus squamatus	POL	81.0
Stenothoe monoculoides	CRU	81.0

The indicator values (IndVal) were calculated on abundance data. Only the species with indicator values above 75 are presented

CNI Cnidaria, *CRU* Crustacea, *ECH* Echinodermata, *MOL* Mollusca, *NEM* Nermertea, *POL* Polychaeta, *TUN* Tunicata

The Kilmore lies outside the high turbidity zone that is located in the Belgian–Dutch coastal zone (Fettweis and Van den Eynde 2003). Its mean value for total suspended matter was 6.2 mg l^{-1} but showed monthly variability. Higher total suspended matter occurred during autumn and winter than during spring and summer. The origin of this variation is not biological (i.e. plankton production) but abiotic. The greater number of storm events during the autumn and winter period probably generate an increased re-suspension of the finer sediments. Another source of suspended matter is the river particulate matter inputs from the Scheldt estuary which show seasonal variations. Values are in the range of what Eisma and Kalf (1987) described for the southern Bight of the North Sea. These are high values compared to the central North Sea but are in agreement with what is found in the coastal region of the Southern North Sea. This concentration of suspended matter certainly explains why no algae species were found on shipwrecks. The quantity of light reaching shipwrecks is near or below the photosynthesis compensation point and hence insufficient for algae growth.

The Kilmore is permanently exposed to strong tidal currents all year round. Current intensity and direction on the bottom layers did not change according to the season but followed daily and lunar cyclic variations. The fraction of calm periods (current speed < 0.10 m s^{-1}) was very low (less than 0.2% of the time) and currents above 0.75 m s^{-1} occurred during each spring tide. This highly hydrodynamic environment will select a set of species adapted to settle, feed and reproduce under such conditions. However, as there is a prevailing current direction that creates zones of different turbulence and shear stress, the possibility remains that different microhabitats are created within the shipwreck itself. Since the shipwreck is oriented along the prevailing water currents, relatively protected surface are thought to be found on the inside part of the hull.

Table 4 Indicator species by season on the Kilmore shipwreck

Species		IndVal	Sign. $P < 0.05$
Winter			
Liocarcinus sp.	CRU	**100.0**	**
Rissoidae	MOL	**88.5**	**
Sabellaria spinulosa	POL	**87.5**	**
Alcyonium digitatum	CNI	**63.2**	**
Stenothoe marina	CRU	54.9	NS
Cumacea sp.	CRU	**50.0**	*
Epitonium clathratulum	MOL	**50.0**	*
Eunicidae	POL	**50.0**	*
Euspira pulchella	MOL	**50.0**	*
Phyllodoce mucosa	POL	**50.0**	*
Polyclinum aurantium	TUN	**50.0**	*
Polycirrus sp.	POL	**50.0**	*
Sthenelais boa	POL	**50.0**	*
Thoralus cranchii	CRU	**50.0**	*
Thelepus setosus	POL	**50.0**	*
Tubulanus sp.	NEM	**50.0**	*
Spring			
–	–	–	–
Summer			
Mytilus edulis	MOL	91.7	**
Caprella tuberculata	CRU	**88.4**	**
Eulalia viridis	POL	**85.6**	**
Stenothoe monoculoides	CRU	**83.7**	**
Lanice conchilega	POL	**77.4**	**
Psammechinus miliaris	ECH	**74.4**	**
Jassa herdmani	CRU	74.3	**
Lepidonotus squamatus	POL	65.9	**
Phtisica marina	CRU	63.1	**
Harmothoe sp.	POL	62.7	**
Eusyllis blomstrandi	POL	**62.5**	**
Amphipholis squamata	ECH	59.7	*
Phyllodoce mucosa	POL	52.8	NS
Actiniaria	CNI	52.1	NS
Stenothoe valida	CRU	51.5	NS
Syllis gracilis	POL	51.1	NS
Procerastea halleziana	POL	**50.0**	**
Pisidia longicornis	CRU	48.3	NS
Dendronotus frondosus	MOL	**47.3**	NS
Ophiothrix fragilis	ECH	46.5	NS
Scrupocellaria scruposa	BRY	44.8	**
Nereis pelagica	POL	**43.5**	NS
Sycon ciliatum	POR	**43.2**	NS
Electra pilosa	BRY	43.1	*
Fall			
–	–	–	–

The indicator values (IndVal) were calculated from abundance data. Maximal IndVal were bolded. Only the species with IndVal above the last significant IndVal were included

NS not significant

* Significant at $P < 0.05$ level for only one of the two randomization tests

**Significant at $P < 0.05$ level for the two randomization tests

Table 5 Spearman's rank correlation between the biomass of *Tubularia indivisa* and the abundance of species in the samples ($N = 24$)

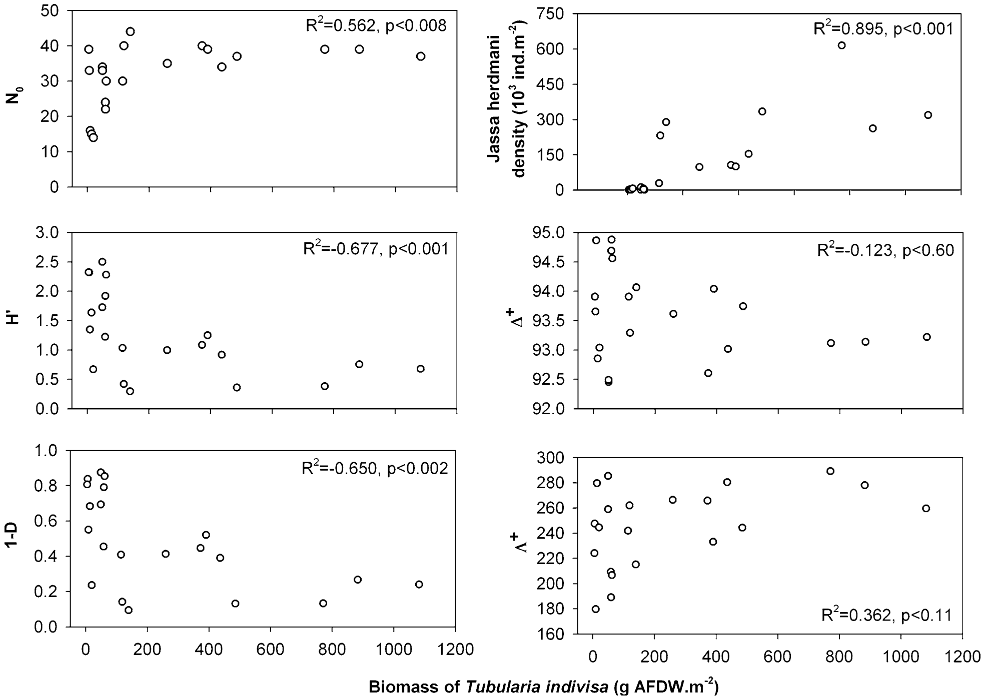
Species		R^2	P
Mytilus edulis	MOL	0.891	<0.001
Jassa herdmani	CRU	0.870	<0.001
Ophiothrix fragilis	ECH	0.834	<0.001
Harmothoe sp.	POL	0.794	<0.001
Amphipholis squamata	ECH	0.760	<0.001
Caprella tuberculata	CRU	0.747	<0.001
Lepidonotus squamatus	POL	0.697	<0.001
Nereis pelagica	POL	0.662	0.001
Lanice conchilega	POL	0.655	0.001
Stenothoe monoculoides	CRU	0.626	0.002
Sycon ciliatum	POR	0.611	0.003
Asterias rubens	ECH	0.608	0.003
Phtisica marina	CRU	0.603	0.004
Pilumnus hirtellus	CRU	0.578	0.006
Eulalia viridis	POL	0.549	0.010
Psammechinus miliaris	ECH	0.510	0.018
Dendronotus frondosus	MOL	0.507	0.019
Phyllodoce mucosa	POL	0.501	0.021
Actiniaria	CNI	0.487	0.025
Baseodiscus delineatus	NEM	0.467	0.032
Cuthona sp.	MOL	0.462	0.035
Eusyllis blomstrandi	POL	0.450	0.040
Stenothoe sp.	CRU	0.449	0.041
Pisidia longicornis	CRU	0.448	0.050

Only the species with $P < 0.05$ are shown

Temporal pattern of *T. indivisa* biomass

The *T. indivisa* community developing on the North Sea shipwrecks showed large monthly variation of its biomass, raising questions about the persistence mechanisms of this facies. The largest part of this variation was due to the hydroid itself with a biomass ranging from 5 g AFDW m^{-2} (October) to 912 g AFDW m^{-2} (July). These values and their ratio to the total biomass of the community (ranging from 59 to 82%) are particularly high. Gili and Hughes (1995) noted that the contribution of biomass from communities dominated by hydroids in shallow water may reach 15–20% of the total biomass, but was generally situated far under these values. Hughes (1983) studied the life history of *T. indivisa* and confirmed the large settlement of actinula larvae on the perisarc of the adults in spring, followed by their rapid growth. Afterwards, the settlement of larvae was probably precluded in shipwrecks from the Belgian part of the North Sea by the development of the other epibionts and the increased density of predators like the nudibranch *D. frondosus*, the syllid *Procerastea halleziana* and pycnogonids (*Achelia* sp., probably *Achelia echinata*). *Procerastea*

Fig. 10 Spearman's rank order correlation between standing biomass of *Tubularia indivisa* and univariate measures of diversity as well as between *T. indivisa* and the most abundant species on the Kilmore shipwreck, the amphipod *Jassa herdmani*. N_0 is the species richness, *H′* is the Shannon–Wiener index (natural log), *1-D* is the Simpson index, Δ^+ is the taxonomic distinctiveness, Λ^+ is the variation in taxonomic distinctiveness



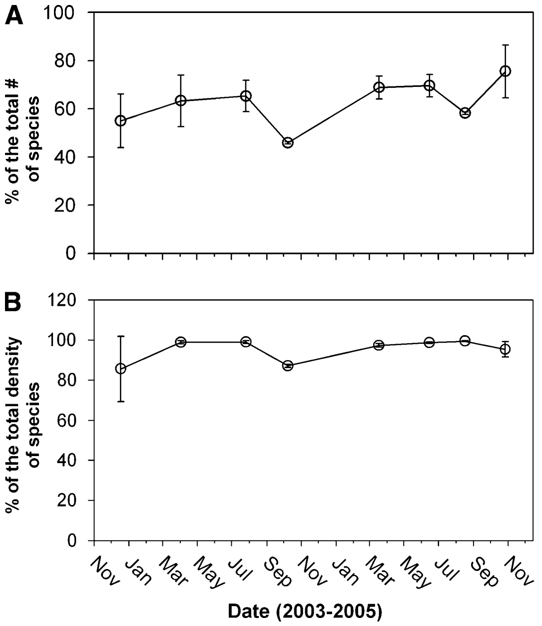


Fig. 11 Temporal variation of the % of total number (**a**) and total density (**b**) of species which are associated with *Tubularia indivisa* on the Kilmore shipwreck

halleziana (Genzano and San Martin 2002) and other species of pycnogonids (Genzano 2002) are known to feed on *E. crocea* by piercing or scraping their perisarc. Among the epibionts that potentially decrease the settlement of actinula larvae from *T. indivisa*, the bryozoan *Electra pilosa* played certainly a role by its large incrustation of the perisarc, especially at the end of the summer period in our results. In spring the activity of the large density of filter feeders, such as the amphipod *J. herdmani* or caprellid species could significantly prey upon the actinulae. A further difficulty for the actinulae is represented by the physical presence of the tube-builder *J. herdmani* who obviously hamper them to settle. In late summer and autumn, a drastic decrease of *T. indivisa* biomass occurred, probably as a result of the predatory behaviour of epibenthic species and the lack of recruits from the summer period. Dormancy through stolon and planula encystment in hydroids was already demonstrated for another sharply seasonal species (Boero et al. 1986). It is thereafter most probable that *T. indivisa* will enter this phase during the summer months. During winter, some of the hydrocauli are able to regenerate hydrants producing a winter cohort and increasing their biomass as observed on the East coast of Britain (Hughes 1983). The actinula larvae of tubulariids directly produced by fixed gonophores are non-feeding individuals (Boero and Bouillon 1993). It is usually accepted in the literature that the actinula larvae from hydroids have a very short dispersal capacity because they tend to sink; as a consequence, they will settle not far from their parents (Pyefinch and Downing 1949). These authors and Orlov (1994) further suggested that the release of actinulae from *Tubularia larynx* was markedly reduced at current speed above 0.03 m s^{-1}, implying that the release of actinulae should concentrate around the slack-water period of the tidal cycle. This could limit the dispersal by currents. Consequently, the rapid increase of biomass after autumn should have its origin on individuals already living on the shipwreck. However, Pyefinch and Downing (1949) measured a sinking rate for *T. larynx* of 1 mm s^{-1}. If we consider the height at which the actinulae are released (usually at least

10 cm from the colonies in North Sea shipwrecks) and the velocity of the currents around shipwrecks (only 1.7% of the tidal cycle with current speed under 0.10 m s^{-1}), even at the slack-water period, it is highly probable that the actinulae could be transported far from the parents. Furthermore, Yamashita et al. (2003) kept the actinulae of *Tubularia mesembryanthemum* (= *Ectopleura crocea*) alive and able to settle for more than 2 weeks in laboratory experiments. They are also frequently found on plankton samples (P. Schuchert, personal communication). Therefore, it is estimated that the dispersal of actinula larvae from *T. indivisa* can be frequently realized at the scale of one shipwreck (100 m) and certainly between these spots of hard substrata (1–10 km). Another indication of the large dispersal capacity of this species lies in its frequent presence on buoys and mooring lines located far from any other source of hard substrata (R. G. Hughes, personal communication).

Molecular analysis may be an answer to the question of the persistence and openness of shipwreck hydroid populations. If the population is open through the exchange of propagules, then there should be a low genetic variation between different shipwreck populations. If the populations is closed or receiving a low amount of propagules, the local populations should be self-sustaining and should display a low genetic diversity at the scale of one shipwreck.

It is interesting to note that on a larger temporal scale, Cornelius (1981) found that two thirds of the widely distributed hydroids in the cooler part of the northern hemisphere lacked a medusa stage. Boero and Bouillon (1993) noted that the possession of theoretically more or less efficient means of dispersal seems not to be so important for the distribution of the species. Their range should finally be a function of their environmental tolerance.

To our knowledge, shipwrecks on the Belgian waters are the only known locations where *T. indivisa* is the yearly dominant feature of a subtidal community. The Kilmore is under water since 1906 and all recreational diver records on this site confirmed its dominance. Its success in this particular environment is difficult to explain. On natural grounds, *T. indivisa* is present but never dominating. The inspection of the fouling communities on North Sea offshore platforms during 11 years revealed that after a period of dominance of a few years (3–6 years), the hydroid community was gradually replaced by the sea anemone *Metridium senile*. This last species was only found dominant on the shipwreck of the Belgian waters close to the coast (personal observation). The environment created by shipwrecks could be responsible for a particular current pattern which would be favourable to the settlement, recruitment and/or growth of this species. On experimental panels set up to alter both shear stress and turbulence independently, Mullineaux and Garland (1993) observed a preferential settlement of E. *crocea* on region with high turbulence and high shear stress. This observation was supported by Lemire and Bourget (1996) who noticed that E. *crocea* larvae densities were higher on the most exposed surfaces of complex panels. Shipwrecks offer a large area of surface exposed to currents. Baynes and Szmant (1989) analyzed the pattern of moving water around a shipwreck and showed differential water turbulence and pressure with location on the structure. Current eddies were also detected around shipwrecks (Lindquist and Pietrafesa 1989). A more thorough analysis of *T. indivisa* cover and biomass on the different structure of the shipwreck would help to understand if this species respond differentially to water motion. Another factor that could explain the yearly success of *T. indivisa* is the attraction by conspecifics. Aggregation among hydroids is a frequent phenomenon (Boero 1984) and experiments on *T. larynx* suggest that settlement is enhanced by adult extracts (Nellis and Bourget 1996). Since individuals were present all year round on the studied shipwrecks, the actinulae could use adults as settlement cues.

Besides the action of competition for space, the temperature regime of the Belgian waters certainly plays a significant role. The regression of coenosarc can occur when hydroids are placed in cold water and the resulting dormant stage regenerates when placed in warmer water (Calder 1990). Temperature has been proved to influence the seasonal abundance of several species of hydroids (see references in Gili and Hughes 1995). Hughes (1983) measured that the growth of *T. indivisa* was almost ten times higher in July than during winter.

Epibiont community on *T. indivisa*

Dean (1981) already showed that motile species respond positively to the structure supplied by sessile species. A positive correlation exists in our study between species richness of motile and sessile species and the biomass of *T. indivisa*. However, the relation was not linear but showed a plateau at a biomass of *T. indivisa* above 200 g m^{-2}. Interestingly, the number of species that the hydroid could sustain was limited, even if its abundance increased. Certainly, the hydroid offered a restricted number of microhabitats that were available beyond a critical amount of individuals.

Tubularia indivisa also offered a support for a diversified set of species. An inverse relation exists with diversity indices (Shannon-Wiener and Simpson) because of the strong dominance of a few species. This pattern was also observed on intertidal colonies of *E. crocea* (Genzano 2001). Half of the species, representing the major fraction of the total density of individuals, were directly associated (i.e. attached) with the hydroid. It is plausible that proteinaceous and/or polysaccharidic compounds in the perisarc of the hydroid may be responsible for the attraction of a set of species. This has been demonstrated for scallops with *T. larynx* (Harvey et al. 1995b; Bourget and Harvey 1998). Schmidt (1983) also explained that the presence of *T. larynx* on experimental panels favours the settlement and subsequent rapid dominance of ascidian species (*Ciona instestinalis* and *Ascidiella aspersa*). However, Bourget and Harvey (1998) showed that at scales larger than 3 cm, the recruitment pattern on plastic arborescent structures designed to mimic *T. larynx* could be explained by passive settlement processes. It is only at small scales (ca. 1 mm) that active selection was detected. Consequently, it is possible that the settlement of tubulariids species on the shipwreck results from a passive flux of larvae in the surrounding water mass and that the acceptation/rejection of the site is governed by an active mechanism.

Describing the associated fauna of intertidal *E. crocea*, Genzano (2001) noticed that crustaceans (mostly *Jassa falcata* and *Caprella* sp.) were the most abundant species. Although not restricted to living in association with hydroids, it seems that these species find an environment particularly suitable for their growth as observed in our results. It may be possible that species of the genus *Jassa* get no particular positive effect from tubulariids beside an increased surface available for colonization. *J. herdmani* is for example found in high densities on any submerged artificial structure on the BPNS (buoys, vessels, harbour walls) (F. Kerckhof, personal communication) and does not require the presence of any hydroid species. This genus is generally found among algae, sponges, hydroids ad bryozoans of rocky shores as well as on newly available substrata and harbour walls (Conlan 1989). Caprellid species are known to prey upon other small crustaceans and seems to be immune to nematocysts. The caprellid *Pseudoprotella phasma* can adopt a clepto-commensalist behaviour by stealing captured preys from the hydrant of *Eudendrium glomeratum* (Bavestrello et al. 1996). Caprellid species on shipwrecks could benefit from the large population of *J. herdmani* which is available throughout the year, stealing them from the tentacles of *T. indivisa* or directly preying upon them. *P. marina*, one of the abundant species on shipwrecks, seems to be able to switch between a predatory and filter feeding behaviour following its in situ posture (Guerra-Garcia et al. 2002). For the second most important caprellid species in our samples (*C. tuberculata*), our underwater observations go in the same direction: this species holds an ‘up-right’ posture like *P. marina*, probably leading to the same feeding strategy (see Takeuchi and Hirano 1995 for review of caprellids clinging behaviour). We also observed that this species was often found in the close vicinity of the hydrant of *T. indivisa*, which lets us assume a direct relation of the caprellid with its host. Although not observed during diving, mutualistic interactions between caprellids and hydrozoans exist. Caine (1998) observed a striking behaviour of *Paracaprella tenuis* when a nudibranch predator of its host, a hydrozoan, was approaching. This resulted in the deterring of the predator. It is certainly difficult for a caprellid to deter large adults of *D. frondosus* which are the primary consumer of *T. indivisa* on shipwrecks, but they could have an effect on juveniles and other smaller nudibranch species encountered on shipwrecks (*Cuthona* sp. and *Eubranchus* sp.). We also identified three stenothoid amphipods with relatively high densities: *Stenothoe marina*, *S. valida* and *S. monoculoides* (respective maximal densities: 2,300, 1,500 and 6,100 ind m^{-2}). The Stenothoidae are often found on hydroids and seem to be immune to nematocysts (Gili and Hughes 1995). The anomuran decapod *P. longicornis* was also found at densities (315 ind m^{-2} in October to 5,400 ind m^{-2} in August) far beyond what is usually described in the literature. This species is very abundant in the eastern English Channel where it lives on pebbly bottoms (Carpentier et al. 2005) but the different sampling method prevents analytical comparisons. In Ireland, Robinson and Tully (2000) found that the highest densities of this species were recorded in early September (640 ind m^{-2}).

The set of epibionts associated with the hydroid displayed an apparent regularity from year to year. However, in our study the species richness showed a decrease during the autumn–winter period. During this period, a number of species are either absent from the shipwreck or present under a form that was not accessible with our sampling technique (e.g. encystment or regression stage with size under one mm). A question that remains is the origin of the species on shipwrecks which are located at several km from each other as well as the interaction that these local populations may have. With the high current speed observed on the BPNS region, it is reasonable to think that these sites are probably not strongly isolated but interconnected by dispersal of propagules, although this may occur with a low exchange rate. These propagules could either be planktonic stages, juveniles of species with direct development (like all the abundant amphipod species found in our study) or even adults with relatively small body size. However, it may be hypothesised that colonization of shipwrecks is achieved by only a few propagules. In this case, shipwrecks may have self-sustaining populations of non-planktonic species, while the offspring of planktonic developers would not remain in the area, preventing these species from maintaining a sustainable population on site (Johannesson 1988). Although the large amount of amphipod species with direct development and their abundance on Belgian shipwrecks favour this hypothesis, many species with planktonic development are also common on shipwrecks. The answer to these questions could be found in genetic and dispersal model analysis.

Acknowledgments 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 is also our pleasure to thank all the people who helped collecting the samples: Drs Y. Laitat, A. Simon, D. Delbare, E. Vanden

Bergh, T. Schils, Mss C. Delforge and R. Gyssens and Mrs P.B. Demoulin, G. Rooms, D. Marsham, F. Cray, M. Van Espen, Y. Verkemping, M. Backx, J.P. De Blauwe, J. Haelters, F. Hernandez, F. Darchambeau, G. Van Hoydonck, A. Vanhaelen, R. Knuts & P. Van de Steen. Dr Christine Vanderlinden helped with the English. This study has been financially supported by a 'plan Action II' grant (contract No. 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). We also wish to thank the reviewers for their fruitful remarks which greatly improved the quality of this paper. This research was done within the laws of the country.

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