Introduction

This volume comprises a number of the papers presented at the 44th European Marine Biology Symposium (EMBS) hosted by the University of Liverpool in September 2009. The theme of the science programme was 'Marine Biology in Time and Space'. The papers focused on describing patterns across a variety of spatial and temporal scales but with the emphasis on seeking understanding and explanations for those patterns. Time and space define the four dimensions in which scientific observations are grounded. Indeed Vito Volterra’s first model of coupled temporal interactions was developed by Umberto D’Ancona to study the interaction between fishery stocks and fishing effort, a moment considered by some to be the starting point for modern ecology (Boero 2009; Gatto 2009).

In the 21st century, new observational techniques, from DNA genetic profiling to data storage tags and remote sensing, have been developed to document these patterns, while experimental and modelling approaches are being applied to develop understanding of the factors responsible for them. The 44th EMBS therefore took as its theme ‘Marine Biology in Time and Space’ with the aim of considering recent advances in our understanding of the drivers of long term change in marine organism communities and ecosystems, the causes of spatial patterns in ecology and the consequences of catastrophic phenomena in marine systems. Papers were presented under these three main themes, though in reflection of the naturally inter-disciplinary nature of marine biology, many of them contained elements from more than one theme.

Theme 1: Long-Term Dynamics

The University of Liverpool had previously hosted the European Marine Biology Symposium (EMBS13) in 1978. At that meeting the theme was ‘Cyclic Phenomena in Marine Plants and Animals’ (Naylor & Hartnoll 1979) and temporal dynamics reappeared as one of the themes for the 44th meeting. Temporal change in marine systems occurs on long, multi-decadal, time scales. The importance of collecting and maintaining long-term data sets of the marine environment is well recognised (Ducklow et al. 2009), and several of the presented papers highlighted this (e.g. Ligas et al. 2011; Spencer et al. 2011). Indeed for the study of long-lived organisms such as cetaceans, long-term and extensive data sets are necessary to derive even the most fundamental life-history traits (Arrigoni et al. 2011).

It is clear that marine systems may be influenced by large scale environmental phenomena such as climatic variations and human activities, especially in heavily exploited areas such as the Mediterranean Sea (Ligas et al. 2011). It is also becoming increasingly clear that while we strive to understand the mechanisms controlling the dynamics of marine communities, the communities themselves, such as those around the UK are changing over time (Spencer et al. 2011). In contrast, surveys of the relatively unmodified White Sea indicate an absence of substantial change in the structure of benthic communities during the past 50 years (Solyanko et al. 2011). It is probably most important to assess the impacts of long-term change on species composition (Spencer et al. 2011) or ecosystem functioning (Neumann & Kröncke 2011). However, at a finer scale, species-specific studies indicated differential variability to different sources of anthropogenic-induced change (Ligas et al. 2011), an important consideration in the management of commercially important species. Assessment of ecosystem functioning is an increasingly important tool for a number of management purposes but, for benthic systems at least, it is essential that methodologies be consistent and consider biological traits as well as simple count and biomass metrics (Aarnio et al. 2011).

Theme 2: Spatial Patterns

An understanding of patterns of species distribution and community composition can also be gained by studies of spatial variability, and the presented papers also highlighted the importance of considering a range of scales. Designation of Marine Protected Areas (MPAs) to effectively protect vulnerable habitats from exploitative activities and preserve biodiversity should be based on knowledge of spatial factors such as distribution and dispersal (Kinlan & Gaines 2003). However MPAs will not be able to provide protection from extreme climatic events (Huete-Stauffer et al. 2011).

At a regional scale, such as in the English Channel, the trophic structure of benthic ecosystems appears to be
determined by sedimentary conditions, whatever the geographic area (Garcia et al. 2011), showing the importance of abiotic factors. It is possible to consider how species distributions are controlled by spatial factors at micro to regional scales, and their interactions, within single studies. For example, both specific frond segments and environmental factors of salinity and wave exposure are important in determining the composition of epiphyte and mobile fauna communities on habitat forming macro algae (Kersen et al. 2011). At local scales such as estuarine habitats, the coexistence of sympatric and seemingly competitor species can be explained by partitioning of resources. In the case of juvenile plaice and flounder, both flexibility and heterogeneity of diets appears to reduce niche overlap and bring order to an apparently chaotic habitat (Mariani et al. 2011). Finally, a key requirement in examining spatial effects is the establishment of discrete populations, a process which is rapidly being facilitated by molecular techniques (Luis et al. 2011).

**Theme 3: Consequences of Catastrophic Events**

Finally, both temporal and spatial factors collide when considering the impacts and influence of catastrophic events. This will become increasingly important if the incidence of these events continues to increase in frequency and/or magnitude (Cerrano & Bavestrello 2009). Mass mortality events can lead to change in ecosystem structure and function, particularly if the subjects affected are ecosystem engineers (Huete-Stauffer et al. 2011). In the case of Mediterranean corals, high temperature appeared to precipitate a mass-extinction event which was exacerbated by opportunistic bacterial infection (Huete-Stauffer et al. 2011). Catastrophic events may of course also be predictable and avoidable. On tidal mudflats, commercial dredging for cockles can cause disruption of benthic communities. However these systems can recover to their original state if dredging occurs at an appropriate intensity and frequency (Wijnhoven et al. 2011).

**Perspectives**

As ever in the study of biology, it is worth considering the work of Charles Darwin. As well as his more widely-published work, Darwin’s studies of barnacles remain authoritative (Rainbow 2011). In the bicentennial of his birth, a consideration of the influence of marine biology on the work of Darwin reveals the importance of detailed observation, critical thinking and experiments to test ideas and ultimately communicate the results (Rainbow 2011). These principles clearly continue to underpin the work of marine biologists and the work presented at the 44th European Marine Biology Symposium was a testament to this.

**References**


Life-history tables of the Mediterranean fin whale from stranding data

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Abstract

The conservation of long-lived species requires extensive, in-depth knowledge of their population structure and vital rates. In this paper we examine the structure of the Mediterranean fin whale (Balaenoptera physalus) population based on the available mortality figures from European stranding network databases compiled over the past 22 years. Such data has enabled us to lay out a first life-history (mortality) table of the population using a simple age-structured demographic model with three life-tables: calf, immature and mature. Our results reveal a high mortality rate in the first stage of life (77% per year), which decreases during the immature stage and falls further during the mature adult stage. In addition, we have calculated the corresponding life expectancies at birth (e₀), at entry in the immature stage (e₁) and at maturity (e₂) under different hypotheses on survival at the maximum age of 90 years (s₉₀) ranging between 0.1 and 3% of newborns still alive. The life expectancy at birth (e₀) at the lower bound of the chosen range (s₉₀ = 0.001) is about 6 years, entry in the immature stage (e₁) is 8.2 years, and entry in the mature stage (e₂) is about 15.6 years. This large increase is the consequence of the higher mortality in the first two stages compared with the mature one. The life expectancies are 10.1, 14.3, and 37.8 years for s₉₀ at the upper bound of the chosen range (s₉₀ = 0.03). The resulting population intrinsic growth rates (r) ranged between −1.3, and +1.7 per year. High juvenile mortality patterns imply that the stationary reproductive value (the number of female offspring produced by each female after a given age x) at the start of maturity reaches a value about seven times higher than at birth. Only optimistically high survival patterns of older individuals would allow positive intrinsic growth rates, thereby enhancing the chances of the population survival.

Introduction

Surprisingly, the fin whale (Balaenoptera physalus), which is the world’s second largest cetacean and one of its longest-lived mammals (Lockyer et al. 1977), is also one of the least-known Mysticetes in demographic terms (Notarbartolo di Sciara et al. 2003).

While some demographic studies have been conducted using industrial whaling data on Northeast Atlantic populations (Aguilar & Lockyer 1987), little is known about the demography of their counterparts in the Mediterranean, where industrial whaling has never been practised (Notarbartolo di Sciara et al. 2003). Although the data from Aguilar & Lockyer (1987) are a fundamental...
contribution to the understanding of the demography of the fin whale, no population dynamics model has ever been developed for this species. Moreover, as the Mediterranean fin whale population is genetically distinct from its Northeast Atlantic counterpart (the nearest population in geographic terms; Bérubé et al. 1998; Palsboll et al. 2004), it therefore represents a separate unit of conservation, requiring ad hoc studies.

According to the IUCN Red Data Book criteria (Reeves and Notarbartolo di Sciara, 2006), the conservation status of this Mediterranean species has been judged data deficient due to the lack of demographic information. However, a more recent assessment, still under review by the Red List Authority, has classified the Mediterranean population as vulnerable (Panigada, pers. comm.)

The survival of this population is threatened by many sources of mortality and environmental stress (Notarbartolo di Sciara & Gordon 1997; Notarbartolo di Sciara et al. 2002), the most important of which are ship collisions (Panigada et al. 2006), fishing gear entanglement, human-induced natural habitat degradation, unregulated whale-watching (Airoldi et al. 1999), and acoustic disturbance (Notarbartolo di Sciara et al. 2003; Abdulla et al. 2008). Although some ecological features, such as seasonal abundance (Forcada et al. 1996), habitat use (Panigada et al. 2005, Panigada et al. 2008; Monestiez et al. 2006; Laran & Gannier 2008), site fidelity, diving profiles (Panigada et al. 1999) and contamination by pollution (Fossi et al. 2003) have been investigated, no population dynamics study has been performed on fin whale populations to date.

Only recently have the demographic models widely used in studying other animal and plant populations (Ebert 1998; Caswell 2001; Santangelo & Bramanti 2006) been applied to the study of cetaceans (Buckland 1990; Fujiwara & Caswell 2001). Two different approaches are commonly applied in demographic studies; these are based on static or cohort life-tables. A third approach is to compile mortality tables (Caughley 1966; Caughley & Sinclair 1994; Ebert 1999), which provide precise information about size/age and sex of dead individuals. Herein we have adopted this latter approach, which to date has never been applied to cetaceans, by using stranding data. Our aim is to develop a demographic model for the Mediterranean fin whale population based on a life-history table (mortality table sensu Bergher 1990; Ricklefs and Miller 2001) built on Mediterranean stranding records.

**Material and methods**

**Stranding data**

Our demographic model has been based on all available data on fin whale strandings recorded on Mediterranean coasts between 1986 and 2007. The information on strandings along the Italian coasts has been drawn from the CSC (Cetacean Study Center) database, available online at CIBRA (2010). The Spanish and French coast stranding data have been collected respectively from the MEDACES database (2009) and the French National Stranding Network RNE (2008). Further data from Mediterranean countries without dedicated stranding databases were found in the scientific literature (Notarbartolo di Sciara et al. 2003). In our analyses we used the stranded animals’ sex and length at death. Unfortunately, the information is not uniform, as in many cases sex was not determined and exact size measurements are possible only for recently dead animals due to their rapid decomposition.

**Basic life-history data**

Fin whales are characterized by fast growth in the first part of their life, which then slows as they reach full physical maturity at about 25 years of age (Aguilar & Lockyer 1987). As a first step, we transformed the size distribution of the stranded whales into a size-stage distribution, and then into an age distribution by stage. This was carried out using the growth and reproductive parameters measured in the Northeast Atlantic population (Lockyer 1984; Aguilar & Lockyer 1987; Aguilar et al. 1988), criteria which yielded the following three age-stages: Calf (0–0.5) years, Immature (0.5–7.5) years, and Mature (7.5–90) years. The value of 90 years represents the maximum lifespan for fin whales estimated by Lockyer et al. (1977).

As a preliminary assumption we hypothesized that stranding data represent a faithful description of the real mortality by stage. This, however, holds only if the probability of stranding is equal in all life-tables. Indeed, only under such circumstances would we expect the relative distribution of stranding by stage to be the same as the true underlying distribution of deaths by stage. As precise information in this regard is lacking, such an assumption is therefore necessary to compute the mortality table.

**The mortality table**

To build up a complete mortality table for the population we used a simple demographic model based on the three above-defined life-tables, with continuous age distribution and constant mortality rates within each stage, under the assumption of population stationarity (i.e. the population is assumed to be constant in number and age structure over time).

As we assumed that no animals survive beyond the age of 90, to apply the model with constant mortality rates, it is necessary to know the fraction \( s_{90} \) of newborn individuals that survive up to the maximum age \( \omega = 90 \).
Given the lack of information on this quantity, we performed a detailed analysis of the sensitivity of the life-table to different assumptions on survival rates up to the maximum age (ranging between 0.1 and 3%). This has enabled us to compute the mortality rates (or mortality risks) \( \mu \) for each age-stage \((a_{i-1}, a_i)\) via the equation:

\[
\mu_i = \left( \frac{-1}{a_i - a_{i-1}} \right) \log \left( \frac{s(a_i)}{s(a_{i-1})} \right) \tag{1}
\]

In equation 1, the age interval \((a_{i-1}, a_i)\) denotes the \(i\)-th age-stage. Thus, as per the definitions in the previous section, the calf stage is defined by \((a_0 = 0, a_1 = 0.5\) years\), the immature stage by \((a_1 = 0.5\) years, \(a_2 = 7.5\) years\), and the difference \(h_i = a_i - a_{i-1}\) is the corresponding class length. Finally, \(s(a_i)\) denotes the fraction of newborn individuals still alive at precisely age \(a_i\) \(\text{(i.e. at the moment of transition from stage} \ i \ \text{to stage} \ (i+1))\).

The assumption of constant mortality rates within each age group implies that the corresponding survival curve has the following exponential form:

\[
s(a) = s(a_{i-1})e^{-\mu_i(a-a_{i-1})} \quad a_{i-1} \leq a < a_i \tag{2}
\]

Equation 2 means that the fraction(s) surviving at any given age \(a\) in each age group can be computed from the fraction surviving at the age of entry into the group and reducing this fraction by the mortality risk \(\mu\), which ‘accumulates’ as the individual grows older. It is worthwhile noting that equation 1 is easily derived by setting \(a = a_i\) in equation 2 and solving for \(\mu_i\).

In addition, we have calculated other standard life-table statistics, such as the life expectancy at birth \((e_0)\) and the life expectancies upon entry into subsequent stages \((e_i)\). The life expectancy at birth, which is easily computed as the area below the survival curve \(2\), represents the number of years that a newborn individual is expected to live if exposed during its lifetime to the mortality risks described by the mortality table (Keyfitz & Caswell 2007). A similar interpretation is attributed to the life expectancy at the moment of entry into the mature stage \(e_2\): this represents the number of years that an individual just entering the mature stage is expected to live if exposed during the rest of its life to the mortality risks described by the mortality table. Such measures provide a useful summary view of mortality.

Reproduction parameters

The fertility rates for females have been drawn from the literature using the standard assumption that a mature female that has not been subjected to mortality produces on average one offspring every 22–24 months (Lockyer 1984). This corresponds to an age-specific female fertility rate of about 0.25–0.28 females per year, assuming a sex ratio at birth of 1:1 (Zanardelli et al. 1999). By combining this assumption with our mortality table, we have calculated the standard reproduction measures: the net reproductive number \((R_0)\), the mean age of mothers at reproduction in the corresponding stationary population \((T)\), the population intrinsic growth rate \((r, \text{Keyfitz } & \text{Caswell 2007})\) and the reproductive value at each age in a stationary population \((\text{SRV})\). The net reproductive rate \(R_0\) represents the average number of female offspring a female expects to have during her entire life under the mortality described by the given life-table (so that the value \(R_0 = 1\) represents the threshold between population growth and decline). The stationary reproductive value \(\text{SRV}\) represents the number of female offspring remaining to be born to a female mother after any given age \(x\). Further details are reported in Appendix 1.

Results

Stranded population structure

The final dataset includes 134 individuals of known size, but whose sex was identified only in 73 cases (33 males and 40 females). The hypothesis of a balanced sex ratio in the subsample of known sex was not rejected (Chi-squared test, \(\chi^2 = 0.0833\) NS). However, given the small figures for each gender, we decided to compute a unique mortality table for the two sexes.

The time distribution of total strandings (Fig. 1) does not suggest any evident trend. Figure 2 reports the distribution of strandings by life-table in two distinct 11-year subperiods: 1986–96 and 1997–2007 and throughout the
entire period. There was a statistically significant difference in the population mortality structure between the two 11-year periods (omnibus-type likelihood ratio test on the multinomial distribution significant at 1%), suggesting that some change in mortality could have occurred in the more recent period (1997–2007). However, even though the data suggest the possibility of a change in the mortality structure, we calculated a single mortality table for the entire period to avoid the excessively small sample size that would result by splitting the data. This was supported by the lack of any evident trends in the distribution of total strandings over time (Fig. 1), as well as by some evidence of stability suggested by the monotonically decreasing structure of the normalized data (Table 1, Fig. 3).

Mortality table
As a second step we built a new mortality table (Table 1) based on the strandings according to occurrence in the three discrete life-tables into which the species life cycle has been divided (calf, immature and mature). In this perspective, the total number of strandings (134) can be interpreted as the number of newborns in a hypothetical birth cohort, of which 43 die during the calf stage, 66 during the immature stage, and the remaining 25 individuals during the mature stage (Table 1 column 5). Interpreting the data is simplified by using a hypothetical cohort of 1000 (instead of 134) recruits, as shown in Table 2, column 3: of 1000 recruits, only 679 (67.9%) enter the immature stage and only 186 enter the mature stage. Under the stationarity hypothesis, this represents the living population structure.

Clearly, the distribution of individuals by life-tables is biased by the different durations of the stages. To correct for this, we normalized the distribution to the duration of the first stage (6 months), which is the shortest (Table 1).

Using equation 1, we computed the continuous mortality rates \( \mu_1 \) inside each stage. For calves, \( \mu_1 = 0.774 \) per year, while for immature individuals, \( \mu_2 = 0.184 \) per year, less than a quarter of the calf rate. For mature whales the mortality rate ranged between 0.063 per year for \( P_{90} = 0.001 \) and 0.022 per year for \( P_{90} = 0.03 \).

Figure 3 shows the corresponding survival curves computed according to equation 2 using the values \( P_{90} = 0.001 \) and \( P_{90} = 0.03 \). The plotted survival curves differ from each other only in the third age-stage (7.5–90 years), a consequence of the different assumptions on the fraction surviving at 90 years. The curves furthermore show first an exponentially decreasing pattern within each age-stage, a result of the assumption of constant-rate mortality in each stage, and secondly a marked difference in the rate of decline in the different stages, which is consistent with the different mortality rates in the various stages.

**Table 1. Mediterranean fin whale: mortality table by life-stages.**

<table>
<thead>
<tr>
<th>Life-table</th>
<th>No. of deaths</th>
<th>Stage duration (years)</th>
<th>No. of deaths normalized by stage duration (year(^{-1}))</th>
<th>No. of survivors at onset of each stage</th>
<th>No. of survivors at onset of each stage (per 1000)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calf</td>
<td>43</td>
<td>0.5</td>
<td>86</td>
<td>134</td>
<td>1000</td>
</tr>
<tr>
<td>Immature</td>
<td>66</td>
<td>7.0</td>
<td>9.42</td>
<td>91</td>
<td>679</td>
</tr>
<tr>
<td>Mature</td>
<td>25</td>
<td>82.5</td>
<td>0.30</td>
<td>25</td>
<td>186</td>
</tr>
</tbody>
</table>
The life expectancies at the age of onset of the various stages (Fig. 4) show a marked increasing trend as a function of both the age of entry and the fraction surviving at age 90. In particular, for \( s_{90} \) at the lower bound of the chosen range (\( s_{90} = 0.001 \)), the life expectancy at birth (\( e_0 \)) is about 6 years, whereas the life expectancy upon onset of the immature stage (\( e_1 \)) is 8.2 years, and the life expectancy entering into the mature stage (\( e_2 \)) is about 15.6 years. This large increase follows from the very high mortality in the first two stages as compared with the mature stage.

At the upper bound of the chosen range (\( s_{90} = 0.03 \)) the respective life expectancies are 10.1, 14.3, and 37.8 years.

**Reproduction parameters**

By combining our set of mortality tables with fertility data we can develop scenarios of long-term population trends. The net reproductive rate \( R_0 \) ranges from a value well below one (0.73) for the \( s_{90} = 0.001 \) hypothesis, to a value considerably above unity (1.77) for \( s_{90} = 0.03 \). The mean age of mothers at reproduction correspondingly ranges between 22.8 and 36.8 years (Fig. 5). Finally, the corresponding intrinsic population growth rate \( r \) ranges between \(-1.3\%\) and \(+1.7\%\) year\(^{-1}\) (Fig. 6). Figure 7 shows the trend of the SRV with the age of the mother. In particular, the value at sexual maturity is about seven times higher than the value at birth, due to the huge mortality during pre-reproductive ages.
Discussion

This study seeks to describe the structure of the Mediterranean fin whale population by analyzing stranding records from the period 1986–2007. As the ecological characteristics of this species make data collection at sea particularly difficult (fin whales usually live far from the coast and are difficult to observe due to weather constraints and the high costs of dedicated research vessels), strandings may prove to be an alternative source of demographic data (Orsi Relini et al. 2004). This study is the first to analyze the demographic features of the Mediterranean fin whale population and, to our knowledge, the first to set out a mortality table based on cetacean stranding data.

The dataset examined does not reveal any significant divergence from a balanced sex ratio in the strandings. We are therefore unable to confirm the natural bias towards female mortality previously suggested for this species (Clark 1982; De La Mare 1985).

Our results show that the first stage of the life cycle is the most life-threatening, with a yearly risk of death of about 77%, whereas in the immature stage, death is nearly four times less likely (18%). This indicates a strong impact, natural and/or anthropogenic, on calves and immature animals, which prevents their reaching sexual maturity. On the other hand, the risk of death of mature individuals is much lower: under the most pessimistic scenario it is still only about 6.3% per year. These results confirm a pattern common to several mammals: high mortality in the youngest age classes and low ones in mature stages (Caughley 1966; Emelen 1970). Nonetheless, a very low proportion of newborns reach sexual maturity, which may represent a serious threat for the survival of this population. Indeed, even under very optimistic hypotheses on the length of the maximum lifespan and prolonged fertility, the intrinsic growth rate $r$ is likely to be positive only if the percentage of offspring surviving up to maximum age is quite high (i.e. well above 0.005).

The SRV clearly shows that the contribution to the population in terms of survival is biased toward adults: most calves and young whales do not contribute to reproduction because they will never reach sexual maturity.

In conducting this study we examined all the available data on strandings. However, these are far from representative of all Mediterranean strandings. In addition, only some of the available data were suitable for analysis, as indications on sex are lacking in about half the cases and the reported size is often approximate or even missing. To make up for this lack of data uniformity, we resorted to some necessary assumptions (population stationarity and identical stranding probabilities in each stage).

Although the proposed model is rather simple, the study nevertheless suggests that stranding data and the use of demographic models may well allow enhancing our currently limited knowledge of the demographics of this important cetacean. Future work to improve our ongoing study of fin whale populations will focus on comparing the approach applied herein with analyses of photo-identification data recorded by the Tethys Research Institute on the live population inhabiting the waters of the Pelagos Sanctuary. We also plan to investigate population dynamics under different conservation scenarios, and thereby assess its current status and risk of extinction.

At present, in spite of the existence of the Pelagos Sanctuary (Notarbartolo di Sciara et al. 2007), an MPA specifically designated to protect cetaceans and which represents the most important feeding grounds for the Mediterranean fin whale (Notarbartolo di Sciara et al. 2003), no specific regulation is currently in force for protection of this species. Regulation of naval traffic and
whale-watching activities could enhance this population’s chances of survival (Panigada et al., 2006).

Our findings suggest that mitigation measures targeted to reproductive adults, particularly addressed to increase the mean age of mothers at reproduction, are likely to be the most effective and need to be taken into account in designing proper conservation plans. The discovery of breeding grounds where calves may enjoy greater protection, could further increase survival rates. On another track, special naval traffic regulations, aimed at reducing mortality rates from ship collisions, could enhance the survival of mature females and calves. Mitigating other sources of mortality and stress, such as chemical and acoustic pollution, whale-watching activities and natural habitat degradation, could further improve the population’s chances of survival.

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References


Demography of fin whales from strandings


Appendix

We report some technical details on the various demographic measures used in the paper.

The mathematical model of the mortality table

The mortality table is based on the following piecewise constant mortality rate over the various (continuous) age-stages [a_i−1, a_i).

\[ \mu(a) = \begin{cases} \mu_1 & a_{i-1} \leq a < a_i \\ \infty & a \geq a_n = \omega \end{cases} \] (A1)

In particular, all individuals alive at the maximal age \( a_n = \omega \) are assumed to suddenly die, which amounts to assuming a mortality rate equal to infinity. In the simplified model described in the paper there are only three age-stages \( (a_0, a_1), (a_1, a_2), (a_2, a_3 = \omega) \) representing the calf, the immature, and the mature stages.

The corresponding survival function, which represents the probability that a newborn individual dies after age \( a \) (and therefore 'survives' at least until age \( a \)) and relates to the mortality rate by the general relation \( s(a) = \exp \left( - \int_0^a \mu(u)du \right) \), is given in our model by

\[ s(a) = \begin{cases} s(a_{i-1})e^{-\mu(a_{i-1})(a-a_{i-1})} & a_{i-1} \leq a < a_i \\ 0 & a \geq a_n \end{cases} \] (A2)

which defines a piecewise exponential survival function over each age-stage.

Let \( h_i = a_i - a_{i-1} \) denote the size of the \( i \)-th age-stage. The life expectancy at birth, i.e. the life expectancy at entry in the stage of calf, is given by:

\[ E[0] = \sum_{i=1}^{n} h_i \int_{a_{i-1}}^{a_i} (1 - s(a))da \]
Similarly equations can be derived for the life expectancies at the age of entry in the immature and mature stages, denoted by \( e_1, e_2 \) in the main text. For example the life expectancy at the age \( a_2 \) of entry in the mature stage is given by:

\[
e_2 = \int_{a_2}^{a_\infty} \frac{s(a)}{s(a_2)} da = \frac{1}{\mu_3} \left( 1 - e^{-\mu_3(a - a_2)} \right) \quad (A4)
\]

By combining the life-table with suitable assumptions on age-specific fertility rates of female whales (taken as given) we can compute a variety of reproduction indices. Following the assumption adopted in the text, the age-specific fertility rate is given by:

\[
m_F(a) = \begin{cases} m_F & a_2 < a < a_3 \\ 0 & \text{elsewhere} \end{cases} \quad (A5)
\]

i.e. it is unchanging over time and constant over the whole mature stage.

Therefore, it quickly follows that:

\[
R_0 = m_F s_2 e_2 \quad (A6)
\]

i.e. that the Net Reproduction Number \( R_0 \) factorises as the product of the fertility rates times the probability of surviving until the mature stage times the life expectancy in the mature stage. The corresponding mean age of mothers at the birth of their female offspring (computed with reference to the stationary population of birth density \( R_0^{-1} m(a)p(a) \)) is given by:

\[
T = \left( a_2 + \frac{1}{\mu_3} \right) - (\sigma - a_2) \frac{e^{-\mu_3(\sigma - a_2)}}{1 - e^{-\mu_3(\sigma - a_2)}} \quad (A7)
\]

The intrinsic growth rate \( r \) of the population, which represents the speed of growth or decay that the population would achieve in the long-term on the assumption that the vital rates are maintained constant over time, is given as:

\[
r = m_F p(a_2) e^{-r m_F} \left( 1 - c^{-(r + \mu_3)(a - a_2)} \right) - \mu_3 \quad (A8)\tag{m10}
\]

In the paper we also computed a quantity that we called the Stationary Reproductive Value (SRV), which represents, on the assumption that the population is stationary, the number of female calves remaining to be born to a female after any given age \( a \). This function is defined as:

\[
SRV = \int_a^{a_\infty} \frac{s(x)}{s(a)} m_F(x) dx
\]
Temporal change in UK marine communities: trends or regime shifts?


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Keywords
Abundance; population trends; principal components; regime shift detection; regime shifts; time series; UK marine ecosystems.

Abstract
A regime shift is a large, sudden, and long-lasting change in the dynamics of an ecosystem, affecting multiple trophic levels. There are a growing number of papers that report regime shifts in marine ecosystems. However, the evidence for regime shifts is equivocal, because the methods used to detect them are not yet well developed. We have collated over 300 biological time series from seven marine regions around the UK, covering the ecosystem from phytoplankton to marine mammals. Each time series consists of annual measures of abundance for a single group of organisms over several decades. We summarised the data for each region using the first principal component, weighting either each time series or each biological component (e.g. plankton, fish, benthos) equally. We then searched for regime shifts using Rodionov’s regime shift detection (RSD) method, which found regime shifts in the first principal component for all seven marine regions. However, there are consistent temporal trends in the data for six of the seven regions. Such trends violate the assumptions of RSD. Thus, the regime shifts detected by RSD in six of the seven regions are likely to be artefacts caused by temporal trends. We are therefore developing more appropriate time series models for both single populations and whole communities that will explicitly model temporal trends and should increase our ability to detect true regime shift events.

Introduction
A growing number of studies report major changes in biological systems (Reid et al. 2001; Rudnick & Davis 2003; Lees et al. 2006; Beaugrand et al. 2008; Carpenter & Lathrop 2008; Greene et al. 2008; Hagerthey et al. 2008; Heath & Beare 2008; Hemery et al. 2008; Petersen et al. 2008). These, often high profile, observations have contributed to a move towards more holistic and integrated ‘ecosystem-based’ environmental management (United
Nations 1992). Several such studies have highlighted relatively large-scale change in aspects of the system over a short period of time (e.g. Hare & Mantua 2000; Reid et al. 2001; Weijerman et al. 2003; Daskalov et al. 2007). Such phenomena have been referred to as ecological regime shifts and have been seen as evidence of non-linear interactions and feedbacks in the ecological system, with the potential for hysteresis (Beisner et al. 2003; Potts et al. 2006). A large number of such events have been documented (Folke et al. 2004). For example, the Thresholds database (accessed 27 February 2010) contains 102 instances of regime shifts in terrestrial, freshwater and marine ecosystems (Resilience Alliance, Santa Fe Institute 2004). Lees et al. (2006) provide a review of many of the ‘regime shift’ papers published prior to 2005 and emphasise that for changes actually to constitute a regime shift, the change must propagate across multiple physical and biological components of the ecosystem.

In the majority of cases where a regime shift was postulated it was attributed to changes in the climatic system (Lees et al. 2006). There is little doubt that planetary warming is occurring and the temperature records suggest that this has been most rapid in the last three decades, with a warming trend apparent in most atmospheric and sea surface temperature datasets (IPCC 2007, section 1.1). Many published analyses of biological data focus on regime shifts that may have been caused by environmental change (e.g. Reid et al. 2001; Weijerman et al. 2005; Beaugrand et al. 2008). This raises the fundamental question: do biological interactions generally result in discontinuous dynamics at the system level? The answer has profound implications for understanding and predicting the impacts of global climate change.

A number of studies have examined time series of biological and physical variables simultaneously (Hare & Mantua 2000; Weijerman et al. 2005), often by summarizing many time series using principal components. Statistical methods can then be used to look for sudden changes in the levels of the principal components. The regime shift detection (RSD) algorithm is one such method (Rodionov 2004, 2005, 2006). RSD was initially developed for climatic data such as the Pacific Decadal Oscillation (Rodionov 2004, 2005), but has subsequently been applied to biological data such as the abundances of organisms in several trophic levels in the Black Sea ecosystem (Daskalov et al. 2007), fish stocks in four marine ecosystems (Link et al. 2009) and plankton in the Northern Adriatic Sea (Kamburska & Fonda-Umani 2009).

RSD assumes that the univariate time series of interest (such as the first principal component of a multivariate dataset) is stationary in mean except at an unknown number of discrete regime shifts (Rodionov 2004). However, it seems important to evaluate whether the assumption of stationarity in mean except at discrete shift points is appropriate for a broad range of biological time series.

Here, we apply RSD to a large collection of marine biological time series from seven regions around the British Isles. We argue that many of the apparent shifts found by RSD are in fact the consequence of gradual, rather than sudden, changes over time. We think that such gradual changes are biologically interesting, and are important because they form a dynamic baseline of genuine and sometimes large changes in marine ecosystems (Hodman-Mountford et al. 2005). However, they do not fall within the usual definition of regime shifts.

Material and Methods

Data

The UK’s Marine Environmental Change Network (MECN) links research units and universities that hold long-term or historic data on aspects of UK marine ecosystems. The MECN dataset compiled for this study includes 324 biological time series of annual observations from seven marine regions (Fig. 1). The series cover five biological components (plankton, infaunal benthos, rocky shore invertebrates, fish, and marine mammals), although not all components were represented in every region. All series within a region were reduced to the length of the shortest series from that region (from 19 to 30 years, finishing in 2006: Table 1). Some components were sampled
Table 1. Summary of the number and length of time series, and the types of biological component covered by those series in each of the seven marine regions (the continuous plankton recorder areas – see Fig. 1). The last year of data used for any of the series was 2006.

<table>
<thead>
<tr>
<th>region</th>
<th>number of time series</th>
<th>length (years)</th>
<th>start year</th>
<th>biological components</th>
</tr>
</thead>
<tbody>
<tr>
<td>D2</td>
<td>35</td>
<td>30</td>
<td>1977</td>
<td>Marine mammals, fish, zooplankton, phytoplankton</td>
</tr>
<tr>
<td>C2</td>
<td>65</td>
<td>28</td>
<td>1979</td>
<td>Marine mammals, fish, infaunal benthos, zooplankton, phytoplankton</td>
</tr>
<tr>
<td>C3</td>
<td>37</td>
<td>19</td>
<td>1988</td>
<td>Fish, zooplankton, phytoplankton</td>
</tr>
<tr>
<td>C4</td>
<td>38</td>
<td>19</td>
<td>1988</td>
<td>Marine mammals, fish, zooplankton, phytoplankton</td>
</tr>
<tr>
<td>D2</td>
<td>34</td>
<td>30</td>
<td>1977</td>
<td>Marine mammals, fish, zooplankton, phytoplankton</td>
</tr>
<tr>
<td>D3</td>
<td>68</td>
<td>19</td>
<td>1988</td>
<td>Fish, rocky shore invertebrates, zooplankton, phytoplankton</td>
</tr>
<tr>
<td>D4</td>
<td>47</td>
<td>25</td>
<td>1982</td>
<td>Fish, rocky shore invertebrates, zooplankton, phytoplankton</td>
</tr>
</tbody>
</table>

more often than annually. For these, we calculated annual means. More detailed information on the variables for each component is given below.

Plankton

Continuous plankton recorder data

For every region, we obtained eight time series derived from monthly continuous plankton recorder (CPR) samples collected by the Sir Alister Hardy Foundation for Ocean Sciences (SAHFOS). These were the phytoplankton colour index (PCI), total abundances of diatoms and dinoflagellates, echinoderm and decapod larvae, and euphausiids, and abundances of the important copepods *Calanus finmarchicus* (boreal) and *Calanus helgolandicus* (temperate). The PCI is based on the ‘greenness’ of each sample, as referenced to standard colour charts, giving one of four category values per sample. These values are based on a ratio scale of acetone extracts using spectrophotometric methods, and give an indication of phytoplankton biomass (Richardson et al. 2006; section 5.1). For all other planktonic samples, the units are the number of organisms per sample where each sample represents approximately 10 nautical miles (18.5 km) of tow, which equates to 3 m$^3$ of filtered seawater (Batten et al. 2003). For all these variables, we calculated annual means from the monthly continuous plankton recorder samples. For some variables in some years, there were no individuals observed in the majority of months (Richardson et al. 2006).

English Channel zooplankton data

In region D3 (English Channel), we also obtained 22 zooplankton variables from Station L4, which is situated in the Western English Channel (50°15.00' N, 4°13.02' W) and forms part of the Western Channel Observatory run by the Plymouth Marine Laboratory working with the Marine Biological Association of the UK. The water is 50 m deep and is tidally influenced, with a 1.1-knot surface stream at mean spring tide. Typically stratification starts in early April, persists throughout the summer and is eroded by the end of October. Station L4 is strongly influenced by the Tamar Estuary, with increased nutrients and periodic incursions of fresher surface water following heavy rain (Rees et al. 2009; Smyth et al. in press). Weekly zooplankton samples have been collected at L4 since 1988, using vertical net hauls from the sea floor to the surface of a WP2 net with a mesh-size of 200 µm and a 0.5-m diameter aperture corresponding to a mouth area of 0.25 m$^2$ (UNESCO 1968; Southward et al. 2005). The 22 species and groups used cover more than 99% of the total zooplankton abundance at this site. We used the lowest taxonomic level available for each group, and no species contributed to more than one variable. Originally, the zooplankton time series contained three missing data (Eloire et al., in press). The missing data for January and February 1988 were replaced by the average value of the month over the entire time series. For August 2000, the missing data were replaced by the average value of the monthly averages of the previous and following months, and the average value for August over the entire time series. Finally, annual averages were calculated from the monthly averages.

Infaunal benthos

For region C2 (Central North Sea), we obtained infaunal macrobenthic data from the Dove M1 time series (Buchanan & Moore 1986a). These data are based on five 0.1-m$^2$ grabs collected in September each year. The Dove station M1 (55°07' N, 01°20' W) is 10.5 km off the NE English coast. It has predominantly sandy sediment, with a 20% silt-clay content and lies in 55 m of water (Frid et al. 1996, 2009). Sampling commenced in September 1972 and the dataset analysed here covers samples taken in September of each year between September 1979 and 2006. No samples were taken, due to weather or operational constraints, in September 1987, 1991 and 2002. Buchanan & Warwick (1974) and Buchanan & Moore (1986b) describe the methods of sampling in detail.

The data used in this study are total genera abundance per square metre based on at least five replicate samples (Frid et al. 2009). Analysis at the genus level avoided any
problems in identification at the species level, or changes in taxonomy leading to problems with homonyms. The full dataset included 327 genera. To extract a shorter number of macrobenthic variables, genera were ranked separately based on total abundance across all years and persistence (frequency of occurrence). The ranks were summed and the combined score used to select the top 30 species. For years where there were missing data, an interpolated value was obtained by averaging the densities of the 2 years before and the 2 years after the missing year.

Rocky shore invertebrates

Quantitative, replicated counts of abundance were made annually using replicate 50-cm² quadrats for the boreal limpet species *Patella vulgata* (Linnaeus) and the lusitanian *Patella depressa* (Pennant) in the midshore region of semi-to exposed rocky shores in regions D3 (Western English Channel: seven locations) and D4 (Celtic Sea: eight locations for *P. vulgata*, but only seven for *P. depressa*, whose numbers were not recorded at the eighth site in some years). The cosmopolitan *Patella ulyssipontensis* was also counted, but was excluded from our analyses because most counts in most years were zero.

These sites were part of a wider UK survey (Mieszkowska et al. 2006). Three surveyors (S. Hawkins, M. Burrows and N. Mieszkowska) were involved in data collection, and have undertaken multiple cross-calibration exercises to ensure continuity and standardisation in collection methodology across the time series. Not all sites were surveyed in every year and there are gaps in the time series. A least-squares fit general linear regression model with sites and years as fixed factors was fitted to the log10(x + 10)-transformed survey data to generate predicted values for combinations of sites and years for which data was missing. The complete data matrix had 435 elements for each species. Of these, 227 elements (52%) contained real data, and 208 missing elements (48%) were filled using model data. Calculated values of $R^2$ were *P. depressa* 0.84 and *P. vulgata* 0.77. We subsequently excluded *P. depressa* at Lynmouth because as a range edge location it was not recorded in all years, leading to several zero values. Although we are concerned about the number of missing data in these time series, we think it important to consider their inclusion. Without them, the rocky shore habitat, on which many studies of the effects of climate change have focused (Hawkins et al. 2009), would not be represented in our analyses.

Fish

The most extensive fish survey data used in this analysis were collected by the Centre for Environment Fisheries and Aquaculture Science (CEFAS) (Ellis et al. 2005) during five separate long-term surveys. Four surveys used otter trawls [B2, C2 and D2 (Northern, Central and Southern North Sea) and D4 (Celtic Sea)], and three used beam trawls [D3 (English Channel), D4 (Celtic Sea), and C3 (Irish Sea)]. All surveys were conducted in autumn (August–December), fish were identified to species level, and catches were standardised to catch per hour. For each of the seven SAHFOS CPR Standard Areas, we calculated the mean catch per trawl per year for all 179 species, and then identified the dominant 30 species in each area in a way that combines persistence and abundance. Species were ranked by abundance from highest (1) to lowest (0), the ranks were multiplied by the proportion of times the species appeared in hauls, and the species with the 30 highest scores were selected. Similar methods were used by Genner et al. (2004, 2010). Pelagic species (i.e. those with an adult pelagic phase) were subsequently removed because of concerns that the gear used in these surveys sampled them incidentally. Thus, some important aspects of ecosystem change such as the ratio of pelagic to demersal fish (de Leiva Moreno et al. 2000) cannot be detected by our analyses.

In region D4 (Celtic Sea) these data were supplemented by the ‘Standard Haul’ series from the Marine Biological Association’s Laboratory, Plymouth, as part of the Western Channel Observatory. Otter trawls were undertaken at 30–50 m depth over a spatial scale of 51 × 22 km off Plymouth (50°08′–50°20′ N, 03°55′–04°39′ W) during 1911, 1913–1914, 1919–1922, 1950–1958, 1967–1979, 1983–1994 and 2001–2007. The abundance of demersal fish taxa was recorded. Over the series, seven vessels have been used for sampling, ranging in overall length from 18.3 to 39.0 m. Where data are available, trawls were undertaken at the same speeds and were comparable in dimensions: headline length range, 16.2–19.8 m; ground-rod length range, 19.8–27.4 m; main net stretched mesh diameter, 75–270 mm, and all vessels used a fine-mesh cod end or a cover (Genner et al. 2010). Data included in this analysis were standardised mean catch per hour, of all hauls during the year, for 30 species, as an annual average of all trawls collected, as previous analyses of this data suggested interannual variation is much stronger than seasonal variation (Genner et al. 2010).

Marine mammals

Estimates of total grey seal (*Halichoerus grypus*) pup production were obtained at individual breeding colonies in regions B2 (Northern North Sea: Orkney), C2 (Central North Sea: Isle of May, Fast Castle, Farne Islands), D2 (Southern North Sea: Lincolnshire, Norfolk), and C4 (West Scotland: Inner and Outer Hebrides). All seal data
were derived from surveys either conducted or reported by the Sea Mammal Research Unit (Duck & Mackey 2008; Duck et al. 2008). There are no reliable data on total population size. Pup production at a fixed set of sites can be measured reliably, although its relationship to population size is complicated by density dependence in some cases. Pup production in B2, C2 (apart from the Farne Islands), and C4 was estimated from repeated aerial surveys during the breeding season using maximum likelihood methods (Duck & Mackey 2008). C4 data were combined estimates of production from 11 colonies in the Inner Hebrides and 15 in the Outer Hebrides from 1984 onwards. Prior to 1983, data are for colonies in the Outer Hebrides only. B2 data are from up to 26 colonies in Orkney. C2 data were from two colonies in the Firth of Forth, of which only one (a new colony) was included in 1997. No aerial survey data were available in 1983 for most colonies. Where necessary, we used the mean of the values from 1982 and 1984 as an estimate of 1983 pup production for B2 and C2 (we did not need to interpolate for C4 because the starting year for this region was 1988). Pup production for the Farne Islands (C2) is the cumulative total from repeated ground counts carried out by National Trust staff. Data for the southern North Sea (D2) are from three relatively recently established colonies that are similarly ground-counted by staff from Lincolnshire Wildlife Trust, the National Trust and Natural England.

Statistical methods

The RSD algorithm is designed to detect changes in univariate time series (Rodionov 2004). We therefore used the first principal component of the data for each region as a univariate summary of the major patterns of community change. Data for each time series were natural log (x + 1)-transformed because we expect a positive relationship between level and variability (we added 1 to each observation because some time series contained zeros). We then centred and scaled the log-transformed data so that each series had mean 0 and standard deviation 1. We calculated principal components of the centred and scaled data for each region, treating each year as an observation and each time series as a variable. Because the data are time series, observations in successive years are not independent. However, such dependencies are not a serious problem when the principal components are used as descriptions of data (Jolliffe 2002; section 12.1). Maximum autocorrelation factor analysis (MAFA: Solow 1994) is an alternative technique for extracting components that describe changes in multivariate time series which explicitly deals with autocorrelation. It differs from principal components analysis in that it extracts orthogonal components with the maximum possible autocorrelation, rather than variance. This is useful for identifying smooth trends in time series. However, sudden changes such as regime shifts do not necessarily result in strong autocorrelations and might not be extracted by MAFA. As we want to determine whether changes are sudden or gradual, we think that principal components are more appropriate than MAFA for our purposes.

The time series in each region were grouped into biological components (Table 1). We are interested in regime shifts that affect multiple categories. However, the unweighted principal component analysis gives equal weight to each time series. Categories for which many time series are available may therefore dominate the first principal component. This may be undesirable because the number of time series in a category reflects only the availability and taxonomic resolution of data. We therefore also calculated weighted principal components, in which we gave equal weight to each category rather than each time series. To do this, we found the principal components of the transformed variables

$$z_{ijk} = \frac{x_{ijk} - \mu_{ik}}{\sqrt{n_j \sigma^2_{ik}}}
$$

where $x_{ijk}$ is the value of the $i$th observation from variable $j$, which is in category $k$, $\mu_{ik}$ is the sample mean for the $j$th variable, $\sigma^2_{ik}$ is the sample variance for the $j$th variable, and $n_j$ is the number of variables in the $k$th category (Deville & Malinvaud 1983; Jolliffe 2002, section 14.2.1).

The RSD algorithm is designed to detect changes at discrete times in an otherwise-stationary time series (Rodionov 2004). If there are temporal trends in populations, the original variables will not be stationary in mean, and it is unlikely that the first principal component will be stationary in mean. However, if the population is growing at a constant average rate, the first differences (the difference between the value in a given year and the value in the previous year) of the log-transformed observations will be stationary in mean. We therefore also analysed the first principal component of the first differences of log-transformed data, using both the unweighted and weighted approaches described above. When this is done, the events that RSD is searching for will be changes in the average rate of change of the first principal component, rather than changes in the level of the first principal component. Such changes are of biological interest, and correspond to changes in a weighted sum of population growth rates, but they are not always included in definitions of regime shift (reviewed by Lees et al. 2006).

We used Version 2.1 of the MATLAB implementation of the RSD software (downloaded 21 December 2009).
from http://www.climatologic.com/stars.html). RSD (Rodionov 2004) searches for shifts in the level of a stationary time series by performing \( t \)-tests on individual observations, with the null hypothesis that the \( n \)th observation is drawn from the same population as the preceding sequence of observations. If the null hypothesis of no shift is initially rejected, follow-up tests are performed on a specified number of subsequent observations. The null hypothesis may not be finally rejected if these subsequent observations do not appear consistent with the proposed shift. All analyses were done with default parameters \( I \) (cutoff length) = 10, \( \alpha \) (nominal size of test) = 0.05, \( h \) (Huber weight parameter) = 1). We have not used any correction for multiple testing among regions because we see RSD mainly as an exploratory tool, and its statistical properties are not well enough known to undertake an appropriate correction. Within any single time series, tests at each time point have nominal size \( \alpha \). However, the statistical properties of the follow-up tests have not been examined in detail. The null hypothesis is finally not rejected if any of these follow-up tests does not provide strong enough evidence against it. The overall size of the test at any time point is therefore not well defined but is certainly less than \( \alpha \). There is no correction in regime shift detection for multiple testing within a single time series, which further complicates the issue.

All analyses were done using MATLAB R2009b for Linux (The Mathworks, Inc., Natick, MA, USA). Because of concerns about gear changes and other sampling artefacts in the fish data, we repeated all the analyses without the fish. Similarly, we repeated all the analyses without the limpets, for which many observations were interpolated using a linear model.

### Results

A fairly large number of principal components are needed to account for most of the variability in the data (Fig. 2: weighted principal components gave similar results, not shown). Over all transformations, principal component methods, and regions, the first principal component explained between 16 and 47% of the variability in the data (Table 2). Thus, although the first principal component is capturing a substantial amount of variability, there are important features of the data that are not readily summarised in one dimension.

When applied to the first principal component (whether unweighted or weighted) of the log-transformed data, regime shift detection (Figs 3-9) found one regime shift in each of the regions C3 (Irish Sea, Fig. 5A,C), C4 (West Scotland, Fig. 6A,C), and D3 (English Channel, Fig. 8A,C), and two regime shifts in each of the regions B2 (Northern North Sea, Fig. 3A,C), C2 (Central North Sea, Fig. 4A,C) (the last regime shift here for the unweighted analysis was in 2006, the final year of the series), D2 (Southern North

![Fig. 2.](image-url) Scree plots for unweighted principal components analysis of the natural log \((\ln + 1)\)-transformed data for each region. Components are arranged on the horizontal axis in descending order of the amount of variance they account for. The vertical axis (eigenvalue) is the variance of each component.
Table 2. Percentage variation explained by two different forms of first principal component (unweighted and weighted) applied to two different transformations [natural log (x + 1) and first differences of natural log (x + 1)] of the data for each region.

<table>
<thead>
<tr>
<th>region</th>
<th>unweighted log</th>
<th>unweighted first difference</th>
<th>weighted log</th>
<th>weighted first difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>B2</td>
<td>27</td>
<td>16</td>
<td>44</td>
<td>28</td>
</tr>
<tr>
<td>C2</td>
<td>39</td>
<td>19</td>
<td>36</td>
<td>17</td>
</tr>
<tr>
<td>C3</td>
<td>32</td>
<td>24</td>
<td>23</td>
<td>30</td>
</tr>
<tr>
<td>C4</td>
<td>31</td>
<td>17</td>
<td>47</td>
<td>38</td>
</tr>
<tr>
<td>D2</td>
<td>37</td>
<td>16</td>
<td>45</td>
<td>33</td>
</tr>
<tr>
<td>D3</td>
<td>21</td>
<td>20</td>
<td>24</td>
<td>26</td>
</tr>
<tr>
<td>D4</td>
<td>36</td>
<td>18</td>
<td>29</td>
<td>18</td>
</tr>
</tbody>
</table>

Sea, Fig. 7A,C), and D4 (Celtic Sea, Fig. 9A,C). However, in all regions other than C2 (Central North Sea), the log-transformed data do not appear stationary in mean except at the shift points. Thus, except in C2, the apparent regime shifts found by the regime shift detection algorithm may be more appropriately described as trends.

The unweighted first principal component of the log-transformed data for C2 shows a strong step in 1995 between two apparently stationary regimes (Fig. 4A). Superficially, this is the pattern expected from a genuine regime shift. However, the step is absent from the weighted first principal component (Fig. 4C). Separate analyses of the unweighted first principal component of the log-transformed data for each category (Fig. 10) show that the step is present only in the infaunal benthos (Fig. 10B). Because the infaunal benthos make up 30 of 65 time series for C2, they dominate the overall pattern when equal weight is given to each series, but not when equal weight is given to each category. The absence of the step in other categories suggests that whatever change occurred in the seabed community was not transmitted to the other categories included in this study, and is therefore not a regime shift in the usual sense of the term.

Excluding either fish or limpets did not change the overall qualitative pattern, except that without fish there was no evidence of either trends or step changes in C3 (Irish Sea, neither unweighted nor weighted: results not shown). Thus, the trend in C3 (Fig. 5A,C) is largely driven by changes in the fish data, whether real or artefactual.

Fig. 3. Regime shift detection applied to region B2 (Northern North Sea), using two different forms of principal component (unweighted and weighted) and two different transformations [natural log (x + 1) and first differences of natural log (x + 1)]. (A) Unweighted first principal component of the natural log (x + 1)-transformed data. (B) Unweighted first principal component of the first differences of natural log (x + 1)-transformed data. (C) Weighted first principal component of the natural log (x + 1)-transformed data. (D) Weighted first principal component of the first differences of natural log (x + 1)-transformed data. In each panel, time in years is on the horizontal axis, the vertical axis is the value of the first principal component, the solid lines are the observed values, and the dashed lines are the regime means found by regime shift detection with default parameters [f (cut-off length) = 10, s (nominal size of test) = 0.05, h (Huber weight parameter) = 1].
The first principal components of the first differences of the log-transformed data (Figs 3–9B,D) are approximately stationary in mean. In all but three cases (C2 unweighted, Fig. 4B; D3 unweighted, Fig. 8B; D4 weighted, Fig. 9D), no regime shifts were detected in the principal components of first differences. In these three exceptional cases, the detected shifts were trivial (very small and in the final observation point). Thus, overall, there is little evidence for consistent changes in population growth rates. In all but two cases (Table 2), the first principal component explained more of the variability in the log-transformed data than in the first differences of log-transformed data. This is consistent with the idea that the dominant pattern in the log data is a temporal trend, which is relatively easy to capture in one dimension.

**Discussion**

There have been many reports of responses to climate change in marine species from the seas around the UK.
Over the past few decades poleward shifts in biogeographic boundaries have been recorded for plankton (Beaugrand & Reid 2003), intertidal rocky benthos (Mieszkowska et al. 2006), subtidal benthos (Hinz et al. in review) and fish (Perry et al. 2005). Changes in phenology are also widespread and important in marine systems. For example, the advancement of spring and summer events has occurred more slowly in secondary consumers than primary producers or primary consumers, and this mismatch has the potential to disrupt ecosystem function (Thackeray et al. 2010). Trends in abundance have also been documented, including increases in population abundances of benthic and pelagic species with warm water affinities close to northern range limits and cold water species close to southern range limits (Beaugrand 2003; Beaugrand & Ibanez 2004; Mieszkowska et al. 2005,
Overall, changes in UK marine communities appear to be dominated by gradual trends over the last two to three decades, rather than sudden shifts that affect many components of the community at the same time. Trends instead of sudden shifts seem plausible ecologically for this area of the world given that physical conditions are largely being driven by the gradual response to climatic trends such as changing sea temperature (Southward et al. 2005). There is evidence of multiple equilibria in a wide range of mathematical models for ecosystems including North African vegetation (Higgins et al. 2002), coral reefs (Mumby et al. 2007; Vance 2005; Rees et al. 2006; Callaway et al. 2007; Hiddink & ter Hofstede 2008; Genner et al. 2010; Eloire et al. in press; Widdicombe et al. in press). However, long-term assessments that cover a combination of time series observations representing a wider range of ecosystems components are limited in UK waters (Southward et al. 2005).
Temporal change in UK marine communities

Spencer, Birchenough, Mieszkowska, Robinson, Simpson, Frid et al.

Fig. 10. Unweighted first principal component of natural log (x + 1)-transformed data for region C2 (Central North Sea), separated into biological categories [A: marine mammals (two time series), B: infaunal benthos (30 time series), C: fish (25 time series), D: phytoplankton (three time series), E: zooplankton (five time series)]. In each panel, time in years is on the horizontal axis, the vertical axis is the value of the first principal component, the solid lines are the observed values, and the dashed lines are the regime means found by regime shift detection.

2007) and lakes (Carpenter 2005). In such models, gradual changes in physical conditions, or large enough disturbances to state variables such as the abundances of organisms, can lead to sudden changes in ecosystem state (Beisner et al. 2003). There is no doubt that regime shifts can occur, and have important socioeconomic consequences (Folke et al. 2004). However, we do not see compelling evidence for such sudden changes in our data.

The same may be true of other ecosystems to which regime shift detection has been applied. For example, the changes in six time series from the Black Sea interpreted as regime shifts by Daskalov et al. (2007, their Figure 1) could be interpreted as noisy trends rather than discrete changes in level. The same is true of the changes in phytoplankton and zooplankton in the Northern Adriatic (Kamburska & Fonda-Umani 2009; their Figure 13) and in the first principal component of a set of 114 physicochemical and biological variables from the North Sea (Kenny et al. 2009; their Figure 11). However, distinguishing between these alternatives statistically requires more sophisticated time series models that are currently in development. In the meantime, we should not too readily accept the idea of step-like regime shifts when trends appear plausible. This conclusion is consistent with some other, smaller-scale statistical analyses of UK marine time series. For example, Solow & Beet (2005) found that although there were substantial changes in the abundances of phytoplankton, copepods, cod, haddock and herring in the North Sea between 1963 and 1997, there was little evidence for a discrete regime shift between two locally stable states. In contrast, Beaugrand & Reid (2003) report multiple temporal discontinuities in North Sea biological time series. However, the events they are detecting are of a different type, because they analysed one taxon (e.g. euphausiids, copepods) at a time, and looked at a small number of taxa over a longer time period than that of our data. They calculated the principal components of spatiotemporal data for each taxon, and used a method which will detect adjacent 6-year blocks with significantly different mean values. Thus, the events they detect are relatively short-term changes in the abundances of individual taxa. However, they noted that long-term trends were the dominant pattern in their data, which is consistent with our results.

Our analyses do suggest that there was a potential regime shift in region C2 (Central North Sea) around 1995 driven primarily by the infaunal benthos. The infaunal benthic time series has been previously analysed in isolation in a more extensive form. Among the 89 dominant genera, there are a series of sudden changes in species composition at 5–10-year intervals between 1972 and 2005 (Frid et al. 2009). Despite these changes, higher-level properties such as total abundance and genera richness remained roughly constant. The most marked changes in species composition identified in the 33-year series were in the early 1980s and early 1990s. In the shorter time series analysed using RSD here, the 1980s shift may not have been detected because it was too close...
to the start of the dataset. The 1995 shift we detected may correspond to the early 1990s shift found by Frid et al. (2009). Thus, the RSD analysis is consistent with previous reports of roughly decadal shifts in species composition in the Central North Sea. However, these shifts did not propagate to the other components of the ecosystem analysed here for this region (plankton, fish, and marine mammals). There are three possible (and not mutually exclusive) explanations. First, the replacement of one polychaete-dominated assemblage by another may have little impact on other trophic levels. This could occur if many of the polychaete species are similarly suitable food items for consumers such as fish, and consume resources at similar rates. Secondly, if stocks of many fish species in the region were reduced as a result of exploitation (FAO 2009, p. 196), there may have been little scope for a response to changes in prey abundance. Thirdly, the benthic data were from a single location, and we do not know the geographical extent of the changes in species composition. Local changes may have had little effect on wide-ranging consumers, or on samples taken from other locations.

Distinguishing gradual from sudden change is important for ecosystem-based management. Thrush & Dayton (2010) discuss several examples of ‘ecological ratchets’, in which a sustained fishing impact pushes an ecosystem into a new state from which recovery to the original state is difficult. In such cases, removing the impact will not restore the system. In contrast, the lack of strong evidence for widespread regime shifts in our data suggests that most components of UK marine ecosystems might return to states observed in previous decades if both abiotic variables and human impacts were returned to their 1970s levels. This does not imply that irreversible changes did not occur before the start of our data, and may tell us little about the risk of future regime shifts (Thrush et al. 2009).

Information on the responses of multiple trophic levels to climate change is required to feed into national and international legislation (e.g. UK Marine & Coastal Access Bill, UK Climate Change Act, EU Habitats Directive and EU Marine Strategy Framework Directive). Furthermore, the Common Fisheries Policy review recognises the need for anthropogenic impacts on marine ecosystems and species to be viewed in the context of pervasive climate change (Commission of the European Communities 2008a,b, 2009). The effects of climate change on marine ecosystems are important both economically and ecologically, whether they are gradual or sudden. For example, climate-driven changes in plankton may be an important determinant of cod recruitment in the North Atlantic (Beaugrand & Kirby 2010), and declines in the abundance and distribution of kelps are likely to be decreasing available nursery grounds for juvenile fish (Mieszkowska et al. 2005). Thus, management strategies need to consider the entire ecosystem, including abiotic components, rather than focusing only on one ecosystem component alone. Furthermore, the integration of direct human effects on exploited species with direct or indirect climatic effects is needed for a realistic perspective on ecosystem responses. Our analyses have highlighted multi-decadal trends across a broad range of ecosystem components, but further analyses will be required to examine the likely drivers of the trends observed.

Although across a range of ecosystem components, our analysis has concentrated on changes in species abundances. Ecosystem approaches to management also consider ecosystem functions and services. Biological traits analysis (Bremner et al. 2006) assumes that ecosystem functions are linearly related to species abundances. If this is true, then our results imply gradual changes in ecosystem function for most biological components of most UK marine ecosystems. However, at least some ecosystem services (such as coastal protection provided by marshes, mangroves, seagrasses, and coral reefs) are nonlinearly related to species abundances (Koch et al. 2009). In such cases, there may be utility thresholds (Samhouri et al. 2010), such that management actions produce much greater responses for some ecosystem states than others, even in the absence of regime shifts. This is another area in which models with broader scope are needed.

Conclusions

Overall, change in UK marine communities may be better described as temporal trends than as abrupt regime shifts, although abrupt shifts may have occurred in some regions. Future analyses of change in UK marine communities should therefore be based on statistical models that explicitly include trends, but also allow the possibility of abrupt shifts. One promising approach is to use state-space models (Durbin & Koopman 2001), which are much more general and flexible than many other approaches to time-series analysis, and which can be applied easily to non-stationary time series.

Looking at large numbers of time series across an entire region complements the analysis of individual time series, and broadens our ability to describe and understand regime shifts and other ecosystem changes. We have shown that getting meaningful results from such an approach requires not only collaboration between large numbers of data providers, but also the critical evaluation of statistical methods.

Acknowledgements

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References


Temporal change in UK marine communities


Trends in population dynamics and fishery of *Parapenaeus longirostris* and *Nephrops norvegicus* in the Tyrrhenian Sea (NW Mediterranean): the relative importance of fishery and environmental variables

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**Abstract**

Temporal variation in the population abundance of the deep-water rose shrimp, *Parapenaeus longirostris* (Lucas, 1846) (Decapoda, Penaeidae), and the Norway lobster, *Nephrops norvegicus* (Linnaeus, 1758) (Decapoda, Nephropidae), in the Tyrrhenian Sea (NW Mediterranean), were evaluated using time-series data (1994–2008) from experimental trawl surveys and commercial landings. The influence of several environmental variables (sea surface temperature, wind-mixing index and NAO index) and fishing effort indices (number of days at sea per month and mean engine power of the trawl fleet) were investigated. The time series were analysed by means of min/max auto-correlation factor analysis (MAFA) and dynamic factor analysis (DFA). The abundance of *P. longirostris* showed a clear increasing trend, significantly correlated with the fishing effort index (number of days at sea per month), the sea surface temperature and the wind-mixing index. The temporal variations in the stock of *P. longirostris*, which has a preference for warm waters, were positively correlated with the rise of the sea surface temperature and the decrease of wind circulation. For *N. norvegicus*, an increasing trend of landings per unit of effort and recruitment index contrasted with a decreasing trend of relative population abundance (biomass and density indices).

**Introduction**

Understanding the causes and mechanisms of change in the abundance of species over time is a crucial issue in marine ecology. Fishing exploitation is considered to be one of the main factors determining the dynamics of marine populations and ecosystems (Baum et al. 2003; Morato et al. 2006; Cianelli et al. 2008; Pauly 2009). These effects include: changes in predator–prey relationships that lead to shifts in food-web structure (Cartes et al. 2001), effects on abundance and body-size distributions that can result in fauna dominated by small-size individuals (Jennings et al. 2001), genetic selection for different physical characteristics and reproductive traits (e.g. higher growth rate, earlier age-at-maturity) (Fromentin & Fonteneau 2001), effects on the populations of non-target species (e.g. cetaceans, sea birds, sea turtles) resulting from by-catch (Kaiser & De Groot 2000), suspension of superficial sediments (Smith et al. 2003), and a reduction of habitat complexity and alteration of benthic community structure (Kaiser et al. 2000).

Large-scale changes in climate and oceanographic conditions are also known to influence the dynamics of marine populations (Gislason et al. 2000; Lloret et al. 2001; Rothchild et al. 2005). For example, the influence of global warming in the 20th century on long-term changes in phytoplankton concentration in the North Atlantic has been demonstrated (Reid et al. 2001). In the
Mediterranean Sea, enrichment of nutrients in surface waters has been shown to affect pelagic food-web dynamics and fishery productivity (Molinero et al. 2008). This in turn can affect deep-sea necto-benthic communities which are known to depend on the downward flux of organic matter from the surface layers (Company et al. 2008). Additionally, changes in river discharge and surface production can alter trophic webs and assemblage compositions in deep Mediterranean waters (Cartes et al. 2009). Company et al. (2008) described how climate-driven cascading dense shelf water influences the ecology of deep-sea populations on a decadal timescale. Bartolino et al. (2008) linked the wind circulation to the recruitment of the European hake, Merluccius merluccius, one of the most important demersal species in Mediterranean waters. Many other studies have highlighted significant relationships between large-scale atmospheric variables (such as the North Atlantic Oscillation index, NAO, which is traditionally defined as the normalised pressure difference between Azores and Iceland) or local scale (surface temperature, wind circulation, etc.) atmospheric variables and demersal populations (Lloret et al. 2001; Fariña & González Herráiz 2003; Zuur et al. 2003a,b; Zuur & Pierce 2004; Erzini 2005; Maynou 2008; Cartes et al. 2009; González Herráiz et al. 2009).

Since the 1950s, a warming process has occurred in the Western Mediterranean basin. This is demonstrated by both environmental changes (e.g. surface temperature increase; see Vargas-Yánez et al. 2009) and biological changes (e.g. northward advance of thermophilic species; see CIESM 2008). In addition to environmental changes, Italian fishing grounds, similar to those of other Mediterranean countries, have been affected by a decrease of fishing effort, mainly due to the EU Common Fishery Policy, which promotes the reduction of fishing effort through incentives to decommission.

To analyse the effects of environmental and anthropogenic factors on demersal communities, two species which display different life cycles and behavioural strategies were selected: the deep-water rose shrimp, Parapenaeus longirostris (Lucas, 1846) and the Norway lobster Nephrops norvegicus (Linnaeus, 1758). Parapenaeus longirostris is a fast-growing, short-lived species with thermophilic preference (Abelló et al. 2002), inhabiting the water column layers close to the seabed. Nephrops norvegicus is a long-lived decapod, typical of temperate and cold waters, which dwells in burrows and exerts territorial behaviour (Aguzzi et al. 2003). It was hypothesised that, due to these contrasting characteristics, the two species would show different behaviours in relation to changes in environmental and anthropogenic factors. From the results, we suggest a mechanism and cause–effect relationships linking the atmospheric and environmental variables with changes in the abundance of both species.

Study area

The study area covered part of the continental shelf and the upper and middle slope off the western coasts of Italy (Central-northern Tyrrhenian Sea, Fig. 1). The Tyrrhenian Sea is semi-enclosed between islands (Corsica, Sardinia and Elba) and the mainland (Italy), and is separated from the rest of the western basin by a channel of moderate depth. It can therefore be considered a distinct entity within the Central-western Mediterranean basin (Artale et al. 1994; Gasparini et al. 2005). The circulation in the Tyrrhenian

![Fig. 1. Study area; the main isobaths are shown, as well as the sampling stations investigated during the experimental trawl survey Medits 2008. The black triangles show the three points at which satellite data were collected (42°30' N, 11°00' E; 42°00' N, 12°00' E; and 41°00' N, 13°00' E).](image-url)
Sea is organised in a series of cyclonic (anti-clockwise) and anticyclonic (clockwise) gyres determined by the wind (Artale et al. 1994). Three main cold water gyres, two cyclonic and one anticyclonic, have been detected. They undergo significant seasonal change, particularly the central anticyclonic gyre that spreads over most of the basin in spring and summer and almost disappears in autumn and winter. The intermediate (LIW) and deep waters have a constant temperature (12.8–13.0 °C). Mixing of surface and deep layers by wind-driven turbulence enriches the upper layer with nutrients (Nezlin et al. 2004), giving the Tyrrhenian Sea a relatively high concentration of nutrients within the Mediterranean basin.

**Material and methods**

From 1994 to 2008, landing data were collected monthly over 3–5 days of observation at the auction of Porto Santo Stefano, one of the most important fishing harbours of the area. The exploitation of *Parapenaeus longirostris* takes place in the fishing grounds between 200 and 400 m depth, while catches of *Nephrops norvegicus* are obtained from a greater depth range (200–600 m) (Sbrana et al. 2003). The number of trawlers habitually targeting the two species decreased during the investigated period: from 30 vessels in 1994 to 12 in 2008 (Sbrana et al. 2006). Data on specific composition of the landing (total weight by species or commercial category) and fishing effort (number of fishing days) were collected for each vessel. The landing rates (landing per unit of effort, LPUE) were calculated by taking into account the fishing day as a unit of effort (kg per day per vessel). In addition, two indices of fishing activity and capacity were computed: (i) the total number of days at sea performed by the fleet per month, and (ii) the mean engine power (kW) of the fleet per month.

During the investigated period (1994–2008), two experimental trawl surveys per year were carried out under the framework of the International bottom trawl survey in the Mediterranean (Medits) and the Italian demersal resources program (Grund). According to the sampling protocols (see Relini 1998 and Bertrand et al. 2002), the Medits survey was performed in spring and the Grund survey in autumn. The two surveys were carried out according to a depth-stratified sampling design with randomly allocated hauls within each stratum. In addition, the number of hauls in each stratum was proportional to the surface of the stratum itself. The haul position of the Medits trawl survey 2008 is shown in Fig. 1.

Mean biomass (kg km⁻²) and abundance (N km⁻²) indices were calculated for both species to obtain time series composed of two observations per year, for a total of 30 observations. A recruitment index (number of recruits per square kilometre, no. recruits km⁻²) was also computed. Following Mori et al. (2000) and Orsi Relini et al. (1998), specimens under the size of 20 mm CL (carapace length) were considered recruits. The indices of *N. norvegicus* were computed taking into account only the hauls carried out in the 200–800 m depth stratum.

To investigate the effect of hydrological conditions, mean monthly values of satellite-derived (1994–2008) sea surface temperature (SST, °C) and wind speed (W, m s⁻¹) were gathered from the Physical Oceanography Distributed Active Archive Centre (PO.DAAC: http://pod-aac.jpl.nasa.gov/index.html). Data taken from three locations (42°30′ N–11°00′ E; 42°00′ N–12°00′ E and 41°00′ N–13°00′ E; see Fig. 1) in the Tyrrhenian Sea were used to compute a mean monthly value. A wind-mixing index was calculated as the cube of the wind speed according to Bartolino et al. (2008). Monthly data of the NAO from 1994 to 2008 were obtained from the Pacific Fisheries Environmental Laboratory (PFEL: http://las.pfeg.noaa.gov/).

The time series were explored by means of auto- and cross-correlation functions. The auto-correlation function gives an indication of the amount of association between variables Y₁ and Y₁₋k, where the time lag k takes the values 1, 2, 3, etc. (Zuur et al. 2007). Thus it is used to highlight the presence of cyclic patterns in time series. Formulated differently, the auto-correlation with a time lag of k years represents the overall association between values that are separated by k time points.

The cross-correlation function shows the relationship between Y₁ and X₁₋k. Therefore this tool can be used to explore whether there is a (linear) relationship between two variables (Zuur et al. 2007, 2009). In time series analysis, the use of significantly cross-correlated variables should be avoided. The confidence intervals of the auto-correlation were obtained from ±2/√n, where n is the length of the time series.

To analyse the long-term changes of the variables, cyclical patterns were removed from the data obtained by the seasonal decomposition by Loess smoothing (Zuur et al. 2007). The data were then analysed by means of multivariate time series analysis techniques: min/max auto-correlation factor analysis (MAFA) and dynamic factor analysis (DFA) to estimate common trends. These tools were used to estimate common underlying trends from the multiple time series dataset, and to evaluate the correlations with species abundance and environmental and fishery factors. For this purpose, the time series of LPUE and of biomass and density indices were used as response variables and the environmental and fishing effort factors as explanatory variables. All analyses were performed using the software BRODGAR 2.6.6 (http://www.brodgar.com).
MAFA can be described in various ways: a type of principal component analysis especially for (short) time series; a method for extracting trends from multiple time series; a method for estimating index functions from time series; a smoothing method; or a signal extraction procedure. The underlying idea is that a trend is associated with high auto-correlation at time lag 1. Therefore, the first MAFA axis represents the trend, or the main underlying pattern in the data. This axis can also be seen as an index function or smoothing curve. Cross-correlations (canonical correlations) between the variables (both response and explanatory variables) and the trends were computed to evaluate the significance of the relationship between the variables and the trends (Erzini et al. 2005; Zuur et al. 2007). The mathematics behind MAFA are described in Solow (1994). The underlying formula is similar to principal component analysis. The MAFA calculations involve a principal component analysis on centred data, followed by a first-differencing on the principal components, and a second principal component analysis on these differenced components. As a result, the MAFA axes are mutually uncorrelated with unit variance, and the MAFA axes have decreasing auto-correlation with time lag 1 (Zuur et al. 2007).

The DFA is a method to estimate common trends, effects of explanatory variables and interactions between the response variables in a multivariate time series dataset. Statistical details and applications of DFA are given in Zuur et al. (2003a,b) and Zuur & Pierce (2004). DFA applies a dimension reduction to the N time series. The dynamic factor model, in words, is given by N Time series = linear combination of M common trends + explanatory variables + noise.

DFA models with one common trend and a symmetric, non-diagonal covariance matrix were used to analyse the datasets. A series of models were fitted, ranging from the simplest, with only one explanatory variable, to the most complex, with all the explanatory variables. Akaike’s information criterion (AIC) was used as a measure of goodness-of-fit and to compare models (Zuur et al. 2003b), with the best model having the smallest AIC. Factor loadings were used to make inferences regarding the importance of particular trends, representing underlying common patterns over time, both to specific response variables and to different groups of response variables (Erzini 2005; Erzini et al. 2005; Zuur et al. 2007).

**Results**

The analysis of the time series dataset by means of cross-correlation functions allows us to identify significant relationships between the response variables. For both species, time series of landings and trawl surveys data were significantly correlated. In the case of *Parapenaeus longirostris*, LPUE time series were positively correlated to experimental trawl survey time series (biomass and density indices) (Table 1a), suggesting a good match between fishery-dependent and fishery-independent data. The recruitment index was significantly correlated to the biomass and density indices, and the maximum cross-correlations were at time lags 0 and 2, respectively (Table 1b). This means that a peak of recruitment was directly reflected in a peak of density, while the peak of biomass followed with a time lag 2, which corresponds to 1 year. The correlations between the landing and survey time series of *Nephrops norvegicus* were significant, but negative, suggesting an inverse relationship between the two variables. However, the recruitment index was positively correlated to the LPUE, with the maximum correlation corresponding to a time lag 3. This suggests that a peak in recruitment was followed by a peak in LPUE after a time lag of more than 1 year.

The analysis of cross-correlations among the explanatory variables also provided significant results (Table 2).

**Table 1.** Response variables. (a) Cross-correlations. L = landing per unit of effort (kg per day per vessel); B = biomass index (kg km$^{-2}$); D = density index (ind km$^{-2}$); R = recruitment index (no. recruits km$^{-2}$). (b) Maximum cross-correlations: the time lags corresponding to the maximum cross-correlations are shown in the grey part of the table.

<table>
<thead>
<tr>
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<th><em>Parapenaeus longirostris</em></th>
<th><em>Nephrops norvegicus</em></th>
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Significance level for correlations: ± 0.37; significant correlations are highlighted in bold.
Table 2. Explanatory variables: cross-correlations.

<table>
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<tr>
<th></th>
<th>SST</th>
<th>$W^3$</th>
<th>NAO</th>
<th>Days</th>
<th>kW</th>
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<tr>
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<td>0.41</td>
<td>1.00</td>
</tr>
</tbody>
</table>

SST = Sea Surface Temperature (°C); $W^3$ = wind-mixing index (m$^3$·s$^{-3}$); NAO = North Atlantic Oscillation index; Days = days at sea per month; kW = mean engine power (kW). Significance level for correlations: ± 0.37. Significant correlations are highlighted in bold.

Sea surface temperature (SST) and wind-mixing index ($W^3$) were negatively correlated. SST showed an increasing trend, whereas the $W^3$ series followed a decreasing pattern. For the fishing efforts parameters, a positive correlation was found between days at sea and mean engine power.

According to the results obtained by means of cross-correlations, it was decided to use the LPUE of $P. longirostris$ and $N. norvegicus$ only as response variables for the analyses of time series. Among the explanatory variables, the wind-mixing index, the NAO index and the days at sea per month were used.

The LPUE time series of $P. longirostris$ and $N. norvegicus$ were characterized by wide fluctuations, making it impossible to identify any clear trend (Fig. 2). Both time series showed peaks in late spring (April–June), when it is known that the catch of the two species is higher. The presence of a seasonal pattern was confirmed by the auto-correlation function: significant correlations were identified at time lags of 12 and 24 months (Fig. 3). Some examples of the time series of the explanatory variables are shown in Fig. 4. The time series of days at sea per month was characterised by a clear decreasing trend (Fig. 4A). Figure 4B and C show fluctuations over time of sea surface temperature and wind speed. Sea surface temperature peaked in summer, when the wind speed was lower. These trends explain the significant, but negative, cross-correlation between the two variables. To remove the seasonal patterns, the explanatory variables were also smoothed by means of the seasonal decomposition by Loess smoothing (see Fig. 5).

The results obtained by means of MAFA described a clear scenario in the case of $P. longirostris$. The estimated trend showed an increasing pattern, although characterized by fluctuations (Fig. 6). High and positive correlations between the trend and the LPUE time series of the two species were identified (Table 3). While for $P. longirostris$ all the response variables considered (LPUE,
According to the factor loadings, only *P. longirostris* was correlated to the trend computed by means of DFA (0.223 for *P. longirostris*, and 0.006 for *N. norvegicus*). The estimated trend (Fig. 7) was similar to that obtained using MAFA, with a general increasing pattern and two main peaks in 2001 and 2006. However, this model, which was characterized by the lowest AIC value (Table 4), suggested no significant relationship with fishing effort, as it was correlated only to the monthly time series of wind-mixing index ($W^3$) and the NAO index. In fact, the estimated $t$-values for the regressions for individual species with $W^3$ and NAO were relatively large.

### Table 3. Canonical correlations between the common trend obtained through MAFA and, respectively, the response variables (landing per unit of effort time series of *Parapenaeus longirostris* and *Nephrops norvegicus*), and the explanatory variables ($W^3$ = wind-mixing index; NAO = North Atlantic Oscillation index; Days = number of days at sea per month, days).

<table>
<thead>
<tr>
<th>Response variables</th>
<th>$r$</th>
<th>Explanatory variables</th>
<th>$t$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. longirostris</em></td>
<td>0.97</td>
<td>$W^3$</td>
<td>-0.45</td>
</tr>
<tr>
<td><em>N. norvegicus</em></td>
<td>0.35</td>
<td>NAO</td>
<td>-0.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Days</td>
<td>-0.31</td>
</tr>
</tbody>
</table>

Significance level for correlations: $\pm 0.15$. Significant values are highlighted in bold.

Biomass, density and recruitment indices were correlated with the estimated trend, in the case of *N. norvegicus*, two contrasting scenarios emerged from the results: an increase in terms of LPUE and recruitment indices, and a decrease in terms of density and biomass indices.

### Table 4. Values of Akaike’s information criterion (AIC) for DFA models with one common trend and different sets of explanatory variables ($W^3$ = wind-mixing index; NAO = North Atlantic Oscillation index; Days = number of days at sea per month), based on diagonal and symmetric matrices.

<table>
<thead>
<tr>
<th>Model</th>
<th>Matrix</th>
<th>Explanatory variables</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Diagonal</td>
<td>$W^3$, NAO, Days</td>
<td>319.7</td>
</tr>
<tr>
<td>2</td>
<td>Diagonal</td>
<td>$W^3$, NAO</td>
<td>298.4</td>
</tr>
<tr>
<td>3</td>
<td>Diagonal</td>
<td>$W^3$, Days</td>
<td>307.5</td>
</tr>
<tr>
<td>4</td>
<td>Diagonal</td>
<td>NAO, Days</td>
<td>178.2</td>
</tr>
<tr>
<td>5</td>
<td>Diagonal</td>
<td>$W^3$</td>
<td>291.5</td>
</tr>
<tr>
<td>6</td>
<td>Diagonal</td>
<td>NAO</td>
<td>388.3</td>
</tr>
<tr>
<td>7</td>
<td>Diagonal</td>
<td>Days</td>
<td>248.5</td>
</tr>
<tr>
<td>8</td>
<td>Diagonal</td>
<td>–</td>
<td>258.0</td>
</tr>
<tr>
<td>9</td>
<td>Symmetric</td>
<td>$W^3$, NAO, Days</td>
<td>296.3</td>
</tr>
<tr>
<td>10</td>
<td>Symmetric</td>
<td>$W^3$, NAO</td>
<td>159.0</td>
</tr>
<tr>
<td>11</td>
<td>Symmetric</td>
<td>$W^3$, Days</td>
<td>348.5</td>
</tr>
<tr>
<td>12</td>
<td>Symmetric</td>
<td>NAO, Days</td>
<td>279.8</td>
</tr>
<tr>
<td>13</td>
<td>Symmetric</td>
<td>$W^3$</td>
<td>379.9</td>
</tr>
<tr>
<td>14</td>
<td>Symmetric</td>
<td>NAO</td>
<td>406.9</td>
</tr>
<tr>
<td>15</td>
<td>Symmetric</td>
<td>Days</td>
<td>369.7</td>
</tr>
<tr>
<td>16</td>
<td>Symmetric</td>
<td>–</td>
<td>372.1</td>
</tr>
</tbody>
</table>

The lowest AIC value is highlighted in bold.
for *N. norvegicus*, indicating strong relationships (Table 5). However, a large diagonal element of the error covariance matrix (R > 0.74) was obtained for *N. norvegicus*, confirming that these variables did not fit well to the model.

### Discussion

The present study aimed to understand the change over time of two demersal stocks in relation to environmental and anthropogenic factors, using analysis of a relatively long and complete time series of stock abundance data. In the Atlantic Ocean and North Sea, data have been collected since at least the 1950s (e.g. for many fish stocks in the North Atlantic; Rijnsdorp et al. 2006). In contrast, in the Mediterranean Sea, time series of fisheries data usually only cover the last few decades. Therefore, the availability of 15 years of fisheries data from two of the most abundant decapods of the demersal communities of Mediterranean waters, both important target species (Aguzzi et al. 2004; Sobrino et al. 2005; Guijarro et al. 2009; Morello et al. 2009), should be regarded as an unique opportunity.

The results clearly showed an increasing trend in the abundance of the stock of *P. longirostris* and a more heterogeneous scenario for *N. norvegicus* in the Tyrrhenian Sea during the investigated period. In addition, our results strongly suggest that temporal variations in the abundance of the two species were correlated with both environmental and fishing activity variables.

### Environmental effects

Atmospheric and surface water environmental variables were investigated in this study. Although these variables have been used in several studies which highlighted significant correlations with demersal and deep-sea communities (Lloret et al. 2001; Farina & González Herráiz 2003; Zuur et al. 2003a,b; Zuur & Pierce 2004; Erzini 2005; Maynou 2008; Cartes et al. 2009; González Herráiz et al. 2009), very few attempts to explain the mechanisms involved in linking upper layers and benthic habitats have been made (Company et al. 2008; Cartes et al. 2009). Many other environmental and oceanographic variables, such as primary production, chlorophyll and nutrient concentrations, salinity, upwelling, currents, and river discharge, have been shown to be influential in the life cycles and dynamics of marine ecosystems (Bahamón & Cruzado 2003; Erzini 2005; Erzini et al. 2005; Rothschild et al. 2005; Company et al. 2008; Cury et al. 2008; Cartes et al. 2009; Sardà et al. 2009). In the Tyrrhenian Sea, oceanographic parameters are poorly and irregularly considered. The value of using SST, wind circulation and the NAO index was the availability of an extensive and complete dataset covering the time span of the available fisheries data. This enabled a thorough investigation to be made into their influence over the course of 15 years.

Among the environmental variables used, only SST and the wind-mixing index (*W*<sup>3</sup>) were clearly related to the trend showed by *P. longirostris* and *N. norvegicus*, whereas the NAO index was not significantly associated with either. *Parapenaeus longirostris* is considered to be a species with a preference for warm waters, being more abundant in the Southeastern Mediterranean than in the Northwestern basin (Abello et al. 2002). The current warming of the upper and intermediate water layers of the Western Mediterranean (Vargas-Yáñez et al. 2009), reflected in the observed increase in SST and decrease in wind circulation (*W*<sup>3</sup>), could have had a positive effect on the life cycle and abundance of this species in the Tyrrhenian Sea. A possible explanation for this phenomenon is provided by Cartes et al. (2009). They hypothesised an association between high temperatures, low rainfall regimes and river discharges and a reduction in the flux of organic matter that maintain deep-water benthic communities off the Catalanian coasts. These environmental conditions resulted in a higher abundance of zooplankton and increased production of suprabenthos (Cartes et al. 2009). Although *P. longirostris* displays a wide range of prey items, its diet is mainly based on suprabenthic crustaceans, such as mysids (especially *Lophogaster typicus*) (Sobrino et al. 2005). Therefore, the warming phase observed in recent years could have favoured the *P. longirostris* population in the Tyrrhenian Sea. In addition to this, Bartolino et al. (2008) found a positive correlation between the recruitment of the European hake, *Merluccius merluccius*, and wind circulation in the Tyrrhenian Sea: high recruitment rates were associated with strong water and wind circulation. The recruitment of the two species, *M. merluccius* and *P. longirostris*, takes place in the same area, at a bottom depth of 100–150 m (Colloca et al. 2004). European hake juveniles are known to prey on crustaceans, such as the juveniles of *P. longirostris* (Carpentieri et al. 2005b). The environmental conditions which

### Table 5. Estimated t-values for regressions between the response variables (LPUE time series of *Parapenaeus longirostris* and *Nephrops norvegicus*) and the explanatory variables (*W*<sup>3</sup> = wind-mixing index; NAO = North Atlantic Oscillation index).

<table>
<thead>
<tr>
<th></th>
<th><em>W</em>&lt;sup&gt;3&lt;/sup&gt;</th>
<th>NAO</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. longirostris</em></td>
<td>1.26</td>
<td>1.23</td>
</tr>
<tr>
<td><em>N. norvegicus</em></td>
<td>-4.82</td>
<td>-3.11</td>
</tr>
</tbody>
</table>

Significant values are highlighted in bold.
positively affect *P. longirostris*, such as high temperatures and low wind circulation, are the same as those that negatively affect the recruitment of *M. merluccius* (Bartolino et al. 2008). The resulting lower predation pressure could have further enhanced the recruitment success of the deep-water rose shrimp.

In contrast, *N. norvegicus*, which showed a negative trend in terms of density and biomass indices, was negatively correlated with the NAO and the wind-mixing index. Again this may be related to mechanisms linking the productivity in the upper layers with the structure of demersal communities, as proposed by Cartes et al. (2009). While phases of warmer and dryer atmospheric conditions favour planktonic/suprabenthic feeders, benthic feeders and predators such as *N. norvegicus* (Aguzzi et al. 2009) are disadvantaged by the reduction of the organic matter flux resulting from the decreased rainfall and river discharge. Similar responses to atmospheric warming processes by *N. norvegicus* have been observed in other areas. In the context of only minor changes in fishing pressure, Farina & González Herráiz (2003) and González Herráiz et al. (2009) showed a decline in the population abundance of *N. norvegicus* in the Atlantic. This decline was associated with the positive phase of the NAO index, which determines warmer temperatures in Northern Europe (Halliday & Pinhorn 2009).

**Fishing activity effects**

The fishing effort is a complex variable that is difficult to quantify because it is influenced by many different factors, such as increasing catch efficiency and changes in fleet characteristics. Increasing catch efficiency of the fleet (also known as ‘technological creep’) is usually related positively to an increase in skipper skills, investments in auxiliary equipment, more efficient gear and materials, replacement of old vessels with new ones and, to a lesser extent, upgraded engines (Rijnsdorp et al. 2006). During the investigated period, a decrease in the number of vessels occurred: the fleets of Porto Santo Stefano and adjacent ports decreased by about 50%, producing an almost proportional decrease in fishing effort.

In the case of *N. norvegicus* the data showed two contrasting trends: an increase of landings per unit of effort and recruitment index, and a decrease of relative population abundance. The daily activity of *N. norvegicus* could help explain these divergent trends. Light intensity influences how organisms perceive their environment, modulating their inter- and intra-specific interactions. Demersal communities exposed to light intensity variations are expected to react to them, producing changes in species composition and density. Therefore, the diurnal activity cycles of demersal species may consistently bias demographic evaluation by bottom trawl sampling. Commercial fishing often operates on a 24-h basis, whereas experimental trawl surveys are usually carried out in the daytime. Trawl fleets exploiting the Tyrrhenian Sea often perform 2–3 days of fishing operations, carrying out hauls during both the day and night (Sbrana et al. 2003). Although diurnal versus nocturnal bias in sampling has been found to be moderate when trawl catches are performed on fishing grounds on the continental slope (Aguzzi & Bahamón 2009; Bahamón et al. 2009), the fact that *N. norvegicus* is a predominantly nocturnal species (Aguzzi & Sardá 2008) may help explain the differences observed between commercial and experimental survey data. *Nephrops norvegicus* spend most of the time within or at the entrance of their burrows and are caught by trawling only when they emerge. Emergence varies with time of day, season, animal size, food presence, hunger state, sex and reproductive status. Thus the fisheries exploit the population selectively and in a different manner with respect to males and females (Aguzzi et al. 2003; Aguzzi & Sardá 2008; Aguzzi & Bahamón 2009). In particular, egg-bearing females spend most of their time in their burrows during the entire egg-incubation period, which lasts for 4–6 months in the Mediterranean Sea (Aguzzi et al. 2003). Furthermore, juveniles rarely leave their burrows. These factors, related to the biology of the species, therefore, strongly contribute to protection of the *N. norvegicus* life-stages that are perceived as sensitive to trawling exploitation.

*Parapenaeus longirostris* also shows variations in density and depth distribution according to daytime rhythms and photoperiod length. Carpentieri et al. (2005a) observed higher catch rates of *P. longirostris* at night in the shelf-break in the Tyrrhenian Sea. In addition, they found the highest density index during late winter–spring, which corresponds to the spawning peak (Ardizzone et al. 1990). As most larvae occur around the 100-m isobath, adults could displace during the spawning period to shallower depths (Sobrino et al. 2005).

It is worth highlighting that the trend of *P. longirostris* was characterized by huge interannual fluctuations. Apart from environmental conditions and fishing activity, this interannual variability was probably related to the short life-span and fast growth rates of this species (Abelló et al. 2002). A similar pattern, characterized by a biomass peak in 2001, was observed in other areas of the Western Mediterranean, such as in the Balearic sub-basin (Guijarro et al. 2009).

**Conclusions**

Long-term changes in the abundance of two important demersal species in the Tyrrhenian Sea, the deep-water
rose shrimp (Parapenaeus longirostris) and the Norway lobster (Nephrops norvegicus), were found to correlate significantly with identified environmental and anthropogenic factors. While the increasing abundance of *P. longirostris* was correlated to a rise of sea surface temperature, a corresponding decrease of wind circulation and to the reduction of fishing effort, a corresponding trend for *N. norvegicus* was not evident. On one hand, the population abundance of *N. norvegicus* was negatively correlated with environmental variations, while on the other hand, it did not show any association with the general decrease of fishing effort in the area. However, the recruitment index, as calculated in the study, could be used as a proxy for change in stock abundance.

Some mechanisms have been proposed to link atmospheric conditions (sea surface temperature, wind circulation and the NAO) to the trophic webs and community structure in the deep-water benthic habitats. However, these models need to be improved to achieve a deeper and more accurate understanding of the mechanisms linking these ecosystems. Further analyses are required to better understand the relationships between variations in the abundance of demersal species and environmental and anthropogenic factors. The availability of suitable information on environmental characteristics, such as appropriate sea-floor topography, sediment composition, hydrographical characteristics, and trophic webs (prey availability, presence and abundance of predator species) is necessary to better understand the temporal change in species abundance, distribution and biology.

**Acknowledgements**

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**References**


Biomass, commonly occurring and dominant species of macrobenthos in Onega Bay (White Sea, Russia): data from three different decades

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Keywords
Anthropogenic impact; biomass; decadal variation; European seas; macrobenthos.

Abstract
Onega Bay is the largest bay in the White Sea, characterised by shallow depth, a range of sediment types and strong tidal currents. All these factors provide conditions for high species richness and biomass. This study reviews data from three surveys of sublittoral macrobenthos undertaken by Russian institutes: the benthic survey covering the entire Onega Bay in 1952; the survey performed in the northern part of the area in 1981/90, and a study carried out in 2006 in the eastern part of the bay. In total, data from 107 stations were analysed. The data in different surveys were collected by different grab types. The datasets of both 1981/90 and 2006 overlap the 1952 survey area. The pattern of biomass distribution was consistent between the years of survey and was characterised by the low biomass at the northern periphery of the bay and the highest biomass observed in the coastal waters of the Solovetsky Islands. Bivalves and cirripeds (mostly Modiolus modiolus, Arctica islandica, Balanus balanus and Verucca stroemia) dominated in biomass. Neither the biomass share of dominant species nor the frequency of occurrence of several common species in these groups changed markedly between 1952 and 1981/90. Although the results of the 2006 survey appear somewhat different from the patterns of previous years, this does not indicate major changes in the benthic communities, because the survey in 2006 was designed in a different way and its overlap with the 1952 survey was minimal. However, the dominant species (by biomass) – A. islandica, M. modiolus and V. stroemia – held their leading positions. Results of the multidimensional scaling analysis based on the biomass data for all taxa encountered in the 1952 survey indicate considerable mixing of the samples from all surveys. This may be interpreted as the absence of major shifts in the sublittoral communities of the macrobenthos of Onega Bay at decadal scale. This kind of stability may be explained by an oceanographical regime resilient to climate variation and a relatively low anthropogenic environmental impact when compared to other shallow European seas.

Introduction
Studies conducted in most European seas have shown that the composition of macrobenthic communities, species frequency of occurrence, population density and biomass often show considerable changes over time. Sometimes sudden inter-annual changes are detected, but changes are more likely across decades. Drastic shifts in
species composition and structure of communities detected in the Black Sea were found to be due to eutrophication, fishing and the introduction of alien species (Chikina & Kucheruk 2005). Reduced biomass and number of species was found in the Kattegat and Skagerrak due to direct effects of trawling, long-term temperature fluctuations and eutrophication of the area (Pearson et al. 1985; Rosenberg et al. 1987). Considerable changes in benthic communities were detected in the North Sea and the Irish Sea due to eutrophication, bottom trawling, dredging, oil drilling operations and climate variation (Frid et al. 1999, 2002; Wiekking & Krönke 2003; Krönke et al. 2004). In the Barents Sea, changes were associated with bottom trawling pressure and climate variation (Galkin 1998; Brown et al. 2005; Denisenko 2008; Carroll et al. 2008). These studies indicate the role of anthropogenic effects on the composition of macrobenthic communities.

In the White Sea, the ‘youngest’ sea of Europe (existing only since the beginning of the Holocene), belonging to both the Northeast Atlantic and Arctic realms and characterised by a very peculiar oceanographical regime (Berger & Naumov 2001; Filatov et al. 2005a,b), there has been no attempt to analyse historical datasets on subtidal benthic communities. The emphasis of previous studies has been on identifying spatial patterns (Derjugin 1928; Kudersky 1966; Beklemishev et al. 1980; Golikov et al. 1985; Lukarin et al. 1995; Berger & Naumov 2001); long-term temporal trends in benthic communities have received relatively little attention. Nevertheless, there has been a long tradition of benthic research associated with marine biological stations (Kudersky 1966; Fokin et al. 2006; Naumov 2006). The main objective of the present study was to analyse data from three different decades with regard to the composition, occurrence and biomass of dominant and common macrobenthic species and discuss if any temporal pattern is revealed by these historical datasets.

**Study area**

Onega Bay is the largest bay in the White Sea, with an area of 12,800 km². The depth of the bay is generally <50 m, with the exception of northern parts, where depths can reach 87 m. The bottom relief is uneven, especially along the coastline. Particularly complex bathymetry is observed along the bay’s western coast, where numerous islands are concentrated. A broad range of sediment types characterises Onega Bay, but coarse and hard sediments with a small percentage of silt are the dominant substrata (Berger & Naumov 2001). Onega Bay is connected to the central part of the sea by the Western and the Eastern Solovetsky Salmas, or strait (Fig. 1). Deep waters of the Salmas enable large volumes of water to enter the bay, generating strong tidal currents exacerbated by the shallow depths in the Bay. The maximum speed of a spring tide is 1.5–2.0 m·s⁻¹ in the Eastern Salma, and 1.5–1.7 m·s⁻¹ in the Western Salma (Babkov 1998; Filatov et al. 2005a). Strong tidal currents increase the turbidity of the water, leading to vertical homothermy and homohalinity in many parts of the bay. A developed thermocline is largely absent in most areas of the Northern and

![Fig. 1. Location of benthic sampling stations of surveys of Onega Bay in 1952, 1981/90 and 2006 showing overlapping station boundaries.](image-url)
Central Onega Bay (personal observations in July 2006 and June 2010). Onega Bay is the most species-rich area of the entire White Sea, with around 500 species of invertebrates and a high benthic biomass (Golikov et al. 1985; Lukanin et al. 1995). The area may be regarded as being exposed to lower anthropogenic impacts than many other Northeast Atlantic seas, as the industrial activity in the area has never been particularly high and has decreased recently (Terzhevik et al. 2005).

Methods

This study is based on the data from three benthic surveys conducted respectively in 1952, 1981/90 and 2006 (Fig. 1, Table 1). The data in the different surveys were collected using a Petersen (0.1 m²), a Petersen Ocean-50 (0.25 m²) and a Van Veen (0.1 m²) grab. Table 1 shows the dates of the surveys, vessels, number of stations, samples at a station, depth of sampling, and on-deck processing protocol.

The 1952 survey data pooled with other material collected in Onega Bay were described by Ivanova (1957) and Kudersky (1966), but our re-analysis of these data is based on the original protocols of sample examination. The 1952 survey was processed incompletely: Mollusca, Cirripedia, Brachiopoda, Echinodermata and other taxa were identified to species level by S. S. Ivanova and L. A. Kudersky. Other groups were recorded as higher taxa and the total abundance and biomass of Porifera, Hydrozoa, Polychaeta, Pontostracanida, and several orders of Crustacea, i.e. Amphipoda, Cumacea and My- sidaea, were calculated. The original station data and the protocols for processing the benthic collections by the White Sea Biological Station of the Karelian–Finnish Branch of the Academy of Sciences of USSR (WSBS KFB) are deposited in the Archive of the Karelian Science Centre of the Russian Academy of Sciences (KSC RAS) in Petrozavodsk (Anonymous 1952a,b). They were digitised in Microsoft EXCEL format suitable for further use in electronic databases. Material on Porifera, Hydrozoa, Polychaeta, Pontostracae and Bryozoa from this survey was transferred to the Zoological Institute of the then Academy of Sciences of USSR (now Russian Academy of Sciences) in Leningrad, now St. Petersburg (ZIN RAN) (Ivanova 1957). The fate of the material on other groups remains unknown.

Material from the 1981/90 surveys was identified mostly to species level, with the exception of Nemertini, Oligochaeta and some families of Porifera, Hydrozoa and Bryozoa, which were identified by A. D. Naumov, V. V. Fedyaev and V. V. Lukanin in consultation with specialists at ZISP on some faunal groups. The data are maintained in the information system 'Benthos of the White Sea' implemented in CLIPPER 5.0 algorithmic language (Naumov 2006).

Benthic collections from the 2006 survey were processed with methods and taxonomic resolution similar to the one used in 1981/90. Most of the identification was done by A. Rogacheva and K. Solyanko in consultation with other specialists. The material is stored in the Zoological Museum of the Moscow University. Due to the unclear status of the taxon usually identified as Hiatella arctica (L., 1867), namely, the possible presence of another, yet unidentified species of the genus (Naumov 2006), the bivalve was listed as Hiatella sp. for all surveys.

Table 1. Basic data for surveys in Onega Bay used in the study.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Survey</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dates</td>
<td>KFB</td>
</tr>
<tr>
<td></td>
<td>10 August – 10 September 1952</td>
</tr>
<tr>
<td>Vessel</td>
<td>Professor Mesyatsev</td>
</tr>
<tr>
<td>Gear</td>
<td>Petersen grab – 0.1-m² sampling area</td>
</tr>
<tr>
<td>No. of stations</td>
<td>70</td>
</tr>
<tr>
<td>No. of casts per station</td>
<td>2</td>
</tr>
<tr>
<td>Total no. of grab samples</td>
<td>134</td>
</tr>
<tr>
<td>Finest mesh size in process of rinsing samples, mm</td>
<td>0.75</td>
</tr>
<tr>
<td>Depth range, m</td>
<td>7–53</td>
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<tr>
<td>Mean depth, m</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>ZIN RAS</td>
</tr>
<tr>
<td></td>
<td>Kartesh</td>
</tr>
<tr>
<td></td>
<td>Petersen grab Ocean-50 (0.25 m²) sampling area</td>
</tr>
<tr>
<td>No. of stations</td>
<td>28</td>
</tr>
<tr>
<td>No. of casts per station</td>
<td>1</td>
</tr>
<tr>
<td>Total no. of grab samples</td>
<td>27</td>
</tr>
<tr>
<td>Finest mesh size in process of rinsing samples, mm</td>
<td>1</td>
</tr>
<tr>
<td>Depth range, m</td>
<td>5–70</td>
</tr>
<tr>
<td>Mean depth, m</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>IO RAS</td>
</tr>
<tr>
<td></td>
<td>15 July –17 July 2006</td>
</tr>
<tr>
<td></td>
<td>Vladimir Kuznetsov</td>
</tr>
<tr>
<td></td>
<td>Petersen grab Ocean-50 (0.25 m²) sampling area</td>
</tr>
<tr>
<td>No. of stations</td>
<td>38</td>
</tr>
<tr>
<td>No. of casts per station</td>
<td>3–5</td>
</tr>
<tr>
<td>Total no. of grab samples</td>
<td>38</td>
</tr>
<tr>
<td>Finest mesh size in process of rinsing samples, mm</td>
<td>1</td>
</tr>
<tr>
<td>Depth range, m</td>
<td>6–36</td>
</tr>
<tr>
<td>Mean depth, m</td>
<td>19</td>
</tr>
</tbody>
</table>

KFB = Karelian-Finnish Branch of the Academy of Sciences of USSR; ZIN RAS = Zoological Institute of the Russian Academy of Sciences, St. Petersburg; IO RAS = Institute of Oceanology of the Russian Academy of Sciences.
To test for differences between surveys in the biomass of 11 biomass-predominant and common bivalve species in 1952 and 2006, univariate techniques were applied such as ANOVA, the Mann–Whitney U-test, median test and Kolmogorov–Smirnov test (Hammer et al. 2001). Species composition and biomass data for these areas were compared using multivariate techniques (Clarke & Warwick 2001). The one-way ANOSIM test (PRIMER v6) was used to determine the differences in species composition and biomass between the studied years (overlapping stations), using 17 species of bivalves and seven species of echinoderms. Only species from the 1952 (mean values) and the 1981/90 surveys were compared. ANOSIM is analogous to analysis of variance (ANOVA) in univariate statistics. The 1952 data were not compared to the 2006 data because of the small number of overlapping stations. In the ANOSIM procedure, the probability of a priori groupings of samples was estimated by repeated permutations of data (i.e. repeated random relabelling of samples in the matrix). Initially, a global R statistic was calculated to determine whether significant differences exist between all groups (analogous to the global F test in ANOVA). If differences were significant at a global level, then pairwise comparisons between sample groups were conducted to test for differences between pairs. In global tests, the null hypothesis (i.e. ‘no difference between groups’) was rejected at a significance level of P < 0.05.

Possible changes in the community structure in terms of abundance and biomass were measured by the ABC (abundance/biomass comparison, statistics W) curves method. This method was applied only for stations where the biomass and abundance had been recorded adequately. The abundance–biomass comparison (ABC) curves were conducted using the PRIMER v.6.0 software package.

Non-metric multidimensional scaling (nMDS) based on Bray–Curtis similarity was carried out using logarithm-transformed biomass data (all replicates included). The data of different years were pooled into one dataset. The list of taxa contained species from the 1952 survey: 20 species of bivalves were included (other species of bivalves appearing in later surveys were pooled into group ‘Other bivalves’), 13 species of gastropods (plus ‘Other gastropods’ group), seven species of echinoderms (plus ‘Other echinoderms’ group), three species of cirripeds and one species of brachiopod. The rest of the taxa were entered as higher taxonomic groups (Porifera, Cnidaria, Polychaeta, Amphipoda, Cumacea, Decapoda, Panto poda, Bryozoa and Asciidae). Although the list of taxa did not include information about all species, the taxa identified to species level were the most important in terms of biomass.

Results

Biomass and abundance of macrobenthos

Biomass distribution in the Northern Onega Bay showed a consistent pattern in 1952 and 1981/90 (Fig. 2). This consistency was also found in the eastern part of the bay when the 1952 and 2006 data were compared. In the northern periphery of the bay, and generally in the Western and the Eastern Salma, the biomass was relatively low and this zone of low biomass extended to the coastal areas in the northwestern part (Fig. 2). The lowest biomass (5.5 g·m⁻²) was recorded at Station 4 near River Zolotitsa in 1952. In the coastal zone of the Solovetsky Islands, biomass varied greatly; however, most stations with biomass exceeding 1000 g·m⁻² were concentrated in this area. The highest biomass recorded was 9200 g·m⁻² at Station 237 in 1981/90 south of Bolshoi Solovetsky Island. In the central part of Onega Bay and off the Onega Peninsula coast the biomass was generally lower than around the islands (in most cases <500 g·m⁻²) but greater than in the north of the bay (Fig. 2). In general, the macrobenthic biomass in Onega Bay can be considered significant: it exceeded 100 g·m⁻² at more than 60% of all stations.

Among large taxonomic groups, bivalves made a major contribution to total benthic biomass, constituting at least 40% of the biomass of each survey (Fig. 2). Horse mussel Modiolus modiolus and quahog Arctica islandica together with barnacles Balanus crenatus and Verruca stroemia constituted the greatest biomass within all surveys. Cirripeds were the next most important contributors to the total benthic biomass (above 20%) in 1952 and 1981/90, followed by polychaetes. However, this was not the case in

![Fig. 2. Distribution of macrozoobenthos biomass (g·m⁻²) in Onega Bay in the years 1952, 1981/90 and 2006.](image-url)
the Southeastern Onega Bay in 2006, where the positions of these two groups were reversed (Fig. 3). Sponges, hydroids, brachiopods, bryozoans and echinoderms contributed to similar fractions of the total macrobenthic biomass (averaging 3–9%) in 1952 and 1981/90 (Fig. 3).

Median biomass values in the surveys were in the range 114–151 g m^{-2} and rather similar (Table 2). However, comparison of biomass values (using a non-parametric Mann–Whitney U-test) showed statistically significant differences between all stations in 1952 and in 1981/90 (P < 0.05) and between the 1981/90 and the 2006 stations (P < 0.01). This was due to some exceptionally high values (>2000 g m^{-2}) in 1981/90 (several stations around the Solovetsky Islands). No statistically significant differences in biomass were found between the 1952 and 2006 data (Table 2). No significant difference was detected between the 1952 stations and the overlapping 1981/90 stations.

Benthic abundance varied considerably between surveys from 10 to 43,604 ind m^{-2} (Table 2). Abundance in 1981/90 was notably higher (mean of 5182 ind m^{-2}) compared to the 1952 survey (mean of 2029 ind m^{-2}) and 2006 survey (mean of 2407 ind m^{-2}). The biomass/abundances ratio (B/A), or a mean mass of a specimen, was remarkably similar (Table 2) and was not significantly different between the 1952 and the 1981/90 surveys. The B/A ratio of the 2006 survey was lower than in the other two surveys (Mann–Whitney U-test, P < 0.01 for the 1952 and 2006 comparison and P < 0.05 for the 1981/90 and 2006 comparison). However, there was no significant difference in the B/A values for the 1952 stations overlapping with the 2006 survey (Table 2). In terms of abundance–biomass comparison (ABC curves) there was no significant difference between the 1952 survey (taking all stations or overlapped stations) and 1981/90 surveys.

Frequency of occurrence and biomass of particular taxa

Most of the bivalve species which were listed as dominant and subdominant in benthic communities of Onega Bay in 1952 (Ivanova 1957; Kudersky 1966) and the 1980s (Golikov et al. 1985; Lukanin et al. 1995; Naumov 2001) occurred with similar frequency in 1952 and 1981/90 (Table 3). Furthermore, Heteranomia spp., Nicania montagui, Nuculana sp., Modiolus modiolus and Mytilus edulis showed nearly the same values. Only Leionucula bellotii, Clinocardium cliaatum, Macoma calcarea occurred 1.6–2.1 times more frequently in 1981/90 compared to 1952, whereas Thyasira gouldii was about five times more common in this year (Table 3). Correlation between frequencies of occurrence of the bivalve species listed in Table 3 (without T. gouldii, which was the most dissimilar in this respect) in the 1952 and the 1981/90 surveys was high and statistically significant (r = 0.73, P < 0.005, n = 13).

In the 2006 survey area some of the bivalve species were found at a higher frequency than at the overlapping stations in 1952 (Table 3). In contrast, Heteranomia spp. was much rarer in 2006 than in 1952. Mytilus edulis and Chlamys islandica were found only in 1952. Furthermore, both absolute biomass and the biomass shares of particular species in 1952 and 1981/90 were also similar in many cases (Tables 3 and 4). Non-parametric tests indicate statistically significant differences in absolute biomass only for Elliptica elliptica, Heteranomia squamula, M. calcarea.
Table 2. Comparison of the macrobenthic biomass and abundance. For mean biomass, mean abundance and mean biomass ratio, the standard deviation is presented in brackets.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of stations</td>
<td>70</td>
<td>27</td>
<td>10</td>
<td>41</td>
<td>6</td>
</tr>
<tr>
<td>Benthic biomass (B) range, g·m⁻²</td>
<td>6–2188</td>
<td>11–9210</td>
<td>5–1195</td>
<td>2–2188</td>
<td>14–1706</td>
</tr>
<tr>
<td>Mean B, g·m⁻² (SD)</td>
<td>273 (371)</td>
<td>959 (2008)</td>
<td>190 (254)</td>
<td>332 (408)</td>
<td>374 (504)</td>
</tr>
<tr>
<td>Median B, g·m⁻²</td>
<td>151</td>
<td>142</td>
<td>114</td>
<td>188</td>
<td>68</td>
</tr>
<tr>
<td>Benthic abundance (A) range, ind·m⁻²</td>
<td>10–22,310</td>
<td>60–43,604</td>
<td>250–19,020</td>
<td>10–22,310</td>
<td>230–8630</td>
</tr>
<tr>
<td>Mean A, Ind·m⁻² (SD)</td>
<td>2029 (3685)</td>
<td>5182 (9528)</td>
<td>2407 (3540)</td>
<td>2452 (4182)</td>
<td>2328 (2956)</td>
</tr>
<tr>
<td>Median A, Ind·m⁻²</td>
<td>595</td>
<td>1332</td>
<td>1170</td>
<td>890</td>
<td>1985</td>
</tr>
<tr>
<td>B/A, range, g·m⁻²</td>
<td>0.02–1.62</td>
<td>0.01–1.24</td>
<td>0.01–0.58</td>
<td>0.02–1.62</td>
<td>0.02–0.53</td>
</tr>
<tr>
<td>Mean B/A, g·m⁻² (SD)</td>
<td>0.14</td>
<td>0.11</td>
<td>0.06</td>
<td>0.13</td>
<td>0.07</td>
</tr>
</tbody>
</table>

Table 3. Frequency of occurrence and mean contribution to the total biomass of common bivalves, cirripeds, echinoderms, gastropods, and brachiopods (in descending order of frequency of occurrence for the 1952 survey).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Bivalvia</td>
<td>FO ± SE</td>
<td>BS ± SE</td>
<td>FO ± SE</td>
<td>BS ± SE</td>
<td>FO ± SE</td>
</tr>
<tr>
<td>Arctica islandica</td>
<td>18 ± 3</td>
<td>49 ± 17</td>
<td>26 ± 8</td>
<td>30 ± 13</td>
<td>15 ± 7 ± 17</td>
</tr>
<tr>
<td>Chlamys islandica</td>
<td>10 ± 3</td>
<td>16 ± 6</td>
<td>22 ± 6</td>
<td>11 ± 5</td>
<td>15 ± 4 ± 11</td>
</tr>
<tr>
<td>Clinoocardium ciliatum</td>
<td>16 ± 3</td>
<td>24 ± 6</td>
<td>52 ± 10</td>
<td>11 ± 4</td>
<td>24 ± 7 ± 25</td>
</tr>
<tr>
<td>Elliptica elliptica</td>
<td>43 ± 4</td>
<td>13 ± 2</td>
<td>52 ± 10</td>
<td>5 ± 3</td>
<td>37 ± 8 ± 1</td>
</tr>
<tr>
<td>Heteranomia spp.</td>
<td>47 ± 4</td>
<td>4 ± 1</td>
<td>56 ± 10</td>
<td>1 ± 1</td>
<td>8 ± 4 ± 1</td>
</tr>
<tr>
<td>Hiastella sp.</td>
<td>27 ± 4</td>
<td>1 ± 1</td>
<td>56 ± 10</td>
<td>1 ± 1</td>
<td>13 ± 5 ± 1</td>
</tr>
<tr>
<td>Leiorunula belii</td>
<td>18 ± 3</td>
<td>1 ± 1</td>
<td>52 ± 10</td>
<td>1 ± 1</td>
<td>58 ± 8 ± 2</td>
</tr>
<tr>
<td>Macoma calcarea</td>
<td>9 ± 2</td>
<td>33 ± 9</td>
<td>7 ± 4</td>
<td>2 ± 1</td>
<td>55 ± 8 ± 20</td>
</tr>
<tr>
<td>Modiolus modiolus</td>
<td>24 ± 4</td>
<td>46 ± 5</td>
<td>26 ± 6</td>
<td>46 ± 10</td>
<td>53 ± 8 ± 4</td>
</tr>
<tr>
<td>Mytilus edulis</td>
<td>8 ± 2</td>
<td>18 ± 4</td>
<td>15 ± 7</td>
<td>12 ± 6</td>
<td>16 ± 4 ± 5</td>
</tr>
<tr>
<td>Nuculana sp.</td>
<td>20 ± 4</td>
<td>2 ± 1</td>
<td>22 ± 3</td>
<td>6 ± 2</td>
<td>7 ± 3 ± 1</td>
</tr>
<tr>
<td>Thyasira gouldi</td>
<td>10 ± 3</td>
<td>2 ± 1</td>
<td>63 ± 9</td>
<td>1 ± 1</td>
<td>37 ± 8 ± 1</td>
</tr>
<tr>
<td>Cirripedia</td>
<td>FO ± SE</td>
<td>BS ± SE</td>
<td>FO ± SE</td>
<td>BS ± SE</td>
<td>FO ± SE</td>
</tr>
<tr>
<td>Balanus balanus</td>
<td>37 ± 4</td>
<td>22 ± 4</td>
<td>4 ± 5</td>
<td>3 ± 2</td>
<td>44 ± 5 ± 24</td>
</tr>
<tr>
<td>Balanus crenatus</td>
<td>13 ± 3</td>
<td>31 ± 6</td>
<td>56 ± 10</td>
<td>21 ± 6</td>
<td>37 ± 8 ± 7</td>
</tr>
<tr>
<td>Verrucula stroemia</td>
<td>55 ± 4</td>
<td>15 ± 2</td>
<td>56 ± 10</td>
<td>8 ± 2</td>
<td>21 ± 7 ± 19</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>FO ± SE</td>
<td>BS ± SE</td>
<td>FO ± SE</td>
<td>BS ± SE</td>
<td>FO ± SE</td>
</tr>
<tr>
<td>Hemnica sp.</td>
<td>27 ± 4</td>
<td>1 ± 1</td>
<td>26 ± 8</td>
<td>1 ± 1</td>
<td>3 ± 1 ± 1</td>
</tr>
<tr>
<td>Ophiopholis aculeata</td>
<td>4 ± 2</td>
<td>2 ± 1</td>
<td>22 ± 8</td>
<td>2 ± 2</td>
<td>5 ± 2 ± 2</td>
</tr>
<tr>
<td>Ophiura robusta</td>
<td>27 ± 4</td>
<td>2 ± 1</td>
<td>59 ± 9</td>
<td>1 ± 1</td>
<td>5 ± 1 ± 1</td>
</tr>
<tr>
<td>Stegophiura nodosa</td>
<td>12 ± 3</td>
<td>4 ± 3</td>
<td>26 ± 8</td>
<td>3 ± 2</td>
<td>18 ± 6 ± 1</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>FO ± SE</td>
<td>BS ± SE</td>
<td>FO ± SE</td>
<td>BS ± SE</td>
<td>FO ± SE</td>
</tr>
<tr>
<td>Margritis g. greenlandicus</td>
<td>4 ± 2</td>
<td>1 ± 1</td>
<td>15 ± 7</td>
<td>1 ± 1</td>
<td>7 ± 3 ± 2</td>
</tr>
<tr>
<td>Puncturella noachina</td>
<td>4 ± 2</td>
<td>1 ± 1</td>
<td>7 ± 5</td>
<td>1 ± 1</td>
<td>6 ± 3 ± 1</td>
</tr>
<tr>
<td>Buccinum undatum</td>
<td>4 ± 2</td>
<td>6 ± 2</td>
<td>19 ± 7</td>
<td>1 ± 1</td>
<td>16 ± 6 ± 9</td>
</tr>
<tr>
<td>Brachiopoda</td>
<td>FO ± SE</td>
<td>BS ± SE</td>
<td>FO ± SE</td>
<td>BS ± SE</td>
<td>FO ± SE</td>
</tr>
<tr>
<td>Hemithiris psittacea</td>
<td>33 ± 4</td>
<td>8 ± 2</td>
<td>37 ± 9</td>
<td>10 ± 3</td>
<td>5 ± 1 ± 1</td>
</tr>
</tbody>
</table>

FO = frequency of occurrence (%); BS = biomass share (%); SE = standard error.
Table 4. Differences in biomass and statistical comparison of biomass data for dominant bivalve species at the stations in the overlapping area between the surveys in 1952 and 1981/90 in Onega Bay.

<table>
<thead>
<tr>
<th>Species</th>
<th>1952 (n = 36) Mean (SE)</th>
<th>1981/90 (n = 27) Mean (SE)</th>
<th>Mann-Whitney U-test (P)</th>
<th>Test of median (P)</th>
<th>Kolmogorov-Smirnov test K (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctica islandica</td>
<td>14.41 ± 7.98</td>
<td>39.34 ± 27.58</td>
<td>468.00 (0.56)</td>
<td>0.92</td>
<td>0.70 (0.70)</td>
</tr>
<tr>
<td>Chlamys islandica</td>
<td>25.54 ± 14.09</td>
<td>95.91 ± 70.33</td>
<td>461.50 (0.51)</td>
<td>0.54</td>
<td>0.55 (0.92)</td>
</tr>
<tr>
<td>Clinocardium ciliatum</td>
<td>15.97 ± 4.48</td>
<td>12.62 ± 5.49</td>
<td>470.50 (0.66)</td>
<td>0.39</td>
<td>0.63 (0.82)</td>
</tr>
<tr>
<td>Elliptica elliptica</td>
<td>30.08 ± 7.20</td>
<td>12.71 ± 7.13</td>
<td>242.50 (0.001)**</td>
<td>0.01*</td>
<td>1.91 (0.001)**</td>
</tr>
<tr>
<td>Modiolus modiolus</td>
<td>203.48 ± 70.89</td>
<td>466.97 ± 253.78</td>
<td>453.00 (0.45)</td>
<td>0.46</td>
<td>0.62 (0.84)</td>
</tr>
<tr>
<td>Nuculana spp.</td>
<td>1.85 ± 0.55</td>
<td>1.43 ± 0.44</td>
<td>419.50 (0.25)</td>
<td>0.61</td>
<td>0.76 (0.60)</td>
</tr>
<tr>
<td>Macoma calcarea</td>
<td>1.89 ± 0.83</td>
<td>1.43 ± 0.44</td>
<td>474.50 (0.73)</td>
<td>0.91</td>
<td>0.50 (0.97)</td>
</tr>
<tr>
<td>Heteranomia squamula</td>
<td>13.87 ± 3.18</td>
<td>3.42 ± 1.48</td>
<td>233.50 (0.001)**</td>
<td>0.001**</td>
<td>1.97 (0.001)**</td>
</tr>
<tr>
<td>Hiattella arctica</td>
<td>1.94 ± 0.52</td>
<td>4.93 ± 2.32</td>
<td>469.00 (0.86)</td>
<td>0.51</td>
<td>0.61 (0.85)</td>
</tr>
<tr>
<td>Macoma calcarea</td>
<td>0.19 ± 0.15</td>
<td>2.29 ± 1.4</td>
<td>381.00 (0.02)*</td>
<td>0.06</td>
<td>0.92 (0.37)</td>
</tr>
<tr>
<td>Tysaira gouldi</td>
<td>0.06 ± 0.03</td>
<td>0.45 ± 0.14</td>
<td>251.50 (0.001)**</td>
<td>0.001**</td>
<td>1.95 (0.001)**</td>
</tr>
</tbody>
</table>

*Different levels of statistical significance of differences. SE = standard error; P = probability of belonging to the same general set of variables.

and *T. gouldi* (Table 4). Biomass data for these and other common bivalves (17 species) for 49 overlapping stations were also tested for differences using a one-way ANOSIM test. No significant difference between the studied years was found (Table 5).

The 2006 survey indicated a greater contribution (averaged to nearly 67%) of *A. islandica*. In 1952 the contribution was lower but the species still made the greatest contributions to total benthic biomass (Table 3). Nonetheless, one should bear in mind that the 1952 and 2006 data allow little direct comparison due to the small number of widely scattered stations in the earlier survey versus much more closely set stations along the shoreward transects in 2006.

Amongst common cirripeds *Verucca stroemia* occurred at a very similar rate and made similar contributions to biomass in 1952 and 1981/90, whereas *Balanus balanus*, which occurred twice as frequently in 1952 compared to *B. crenatus*, was not common in 1981/90 or 2006. *Verucca stroemia* and *B. crenatus* occurred much more frequently than *B. balanus* in the 1981/90 and 2006 survey areas (Table 3).

The most common echinoderms in the 1952 and the 1981/90 surveys were (*in descending order*) *Ophiura robusta*, *Stegophiura nodosa*, *Ophiopilus aculeata* and *Henricia* sp. The frequencies of occurrence and average contributions to biomass were higher in 1981/90 for all species, although *S. nodosa* showed higher occurrence in 1952 in the area which overlapped with the 1981/90 survey. Again, the one-way ANOSIM test for seven species of relatively common echinoderms for 34 overlapping stations did not show a significant difference in biomass between the studied years (Table 4). In the overlapping area of the 2006 and 1952 surveys, *O. aculeata* did not occur in either year and other three species were not found in 1952 (Table 3).

Table 5. Comparison of the biomasses of common bivalves (17 species) and echinoderms (seven species) for all overlapping stations between the 1952 and the 1981/90 surveys using a one-way ANOSIM test.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Species</th>
<th>No. of species</th>
<th>No. of stations</th>
<th>Global R</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bivalvia</td>
<td>Arctica islandica; Chlamys islandicus; Clinocardium ciliatum; Elliptica elliptica; Heteranomia squamula; Hiattella arctica; Leionucula bellotii; Macoma calcarea; Modiolus modiolus; Mya truncata; Mytilus edulis; Nuculana minuta; Nuculana purnula; Pandora glacialis; Serripes groenlandicus; Tysaira gouldi</td>
<td>17</td>
<td>49</td>
<td>0.039</td>
<td>0.08</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>Asterias rubens; Henricia sanguinolenta; Ophiacantha bidentata; Ophiopilus aculeata; Ophiura robusta; Stegophiura nodosa; Strongylocentrotus pallidus</td>
<td>7</td>
<td>34</td>
<td>0.08</td>
<td>0.06</td>
</tr>
</tbody>
</table>

Macrobenthos of Onega Bay (White Sea, Russia)
Gastropods were not commonly found in the 1952 survey; only three species occurred with a frequency above 5%: Margarites groenlandicus, Punctarella noachina and Buccinum undatum. In 1981/90 these three were also the most frequently occurring species, with P. noachina occurring with a similar rate, whereas in 1952 the two other species were found more frequently (Table 3).

Hemithyris psittacea, the only brachiopod species living in the White Sea, showed a very similar occurrence rate and average contribution to total benthic biomass in 1952 and 1981/90. In 2006 the species was not as common as in the 1952 survey area overlapping with the 2006 survey (Table 3).

Comparison at the assemblage level

Results of the MDS analysis based on the biomass data for all taxa accounted for in the 1952 survey indicate considerable mixing of the samples of all surveys: variation between samples of the 1981/90 and the 2006 surveys is largely inside the variation of the 1952 survey performed at a wider spatial scale (Fig. 4). A pairwise ANOSIM test revealed no statistically significant differences between the 1952 and the 1981/90 data. However, differences at a statistically significant level (P < 0.05) were found between these surveys and the 2006 survey.

To compare the communities at a smaller scale, the study area was divided into sub-areas (Fig. 5). Comparison of the dominant pattern in particular sub-areas between the stations of the 1952 survey and the 1981/91 survey also did not indicate major shifts (Table 6). Sub-area F covered the northern stations of the 2006 survey. These stations were located near Station 65 of the 1952 survey, which had a similar species composition with Stations 16–19 of the 2006 survey. However, the biomass of Modiolus modiolus in 1952 was somewhat higher than in 2006 (Fig. 5, sub-area F). In Southeastern Onega Bay (Fig. 5, sub-area G) the community was also dominated by Arctica islandica in both 1952 and 2006.

Discussion

The benthic surveys considered in the present study were not designed to study inter-annual variation in benthic communities. When planning the 2006 survey the stations were intentionally set in the area which was covered the least by the surveys in earlier years. Furthermore, the methods of sampling and gears differed between surveys. Bearing this in mind, we expected to find greater differences between the surveys from three different decades. Median benthic biomass was very similar in all years of investigation and clearly different from other areas of the White Sea with similar depth and bottom topography. In particular, in the Gorlo (the shallow strait separating the outer part of the White Sea from its deep basin) and in the Dvina Bay the median biomass was one order of magnitude lower (Naumov 2001).

Neither the biomass of dominant bivalves and cirripeds nor the frequency of occurrence of the most common species showed any considerable changes between 1952 and 1981/90. The contribution to the total biomass of some bivalves and cirripeds (Modiolus modiolus, Arctica islandica, Chlamys islandica, Mytilus edulis, Elliptica elliptica, Balanus balanus, Verucca stroemia and, to lesser extent, Clinocardium ciliatum) did not change between 1952 and 1981/90. All these species were described as dominant in various benthic communities identified using different methods in the 1950s and the 1980s (Kudersky 1966; Golikov et al. 1985; Lukanim et al. 1995). Nuculana pernula and Nuculana minutula may be added to this list but it is possible that these morphologically similar species were poorly distinguished (Naumov 2006) in earlier surveys and so their presence cannot be confirmed with certainty. Furthermore, the frequency of occurrence and biomass of other common species (Heteranomia squamula, Hiatella sp., Nicania montagui, Hemithyris psittacea and common echinoderms) did not show much variation. At the assemblage level, few differences were revealed using multivariate statistics and direct comparison of the closely located stations from different surveys. The stability of the ABC curves and the average mass of a specimen also indicate the absence of shifts in benthic communities similar to those observed in some areas under the influence of eutrophication (Rosenberg 1987). Although the results of the 2006 survey appear somewhat different from the patterns of previous years this does not indicate major
Table 6. Benthic taxa composition (in terms of biomass) at stations of the 1952 and the 1981/90 surveys performed for sub-areas in Onega Bay.

<table>
<thead>
<tr>
<th>Survey</th>
<th>Subarea (see Fig. 5)</th>
<th>No. of samples</th>
<th>Dominant taxa</th>
<th>One-way ANOSIM test result</th>
</tr>
</thead>
<tbody>
<tr>
<td>1952</td>
<td>A</td>
<td>9</td>
<td><em>Hemithyris psittacea</em>, <em>Cirripedia</em>, <em>Nuculana minuta</em>, <em>Elliptica elliptica</em> and other bivalves</td>
<td>R = 0.176; P &gt; 0.05</td>
</tr>
<tr>
<td>1981/90</td>
<td></td>
<td></td>
<td><em>Hemithyris psittacea</em>, <em>Cirripedia</em>, <em>Elliptica elliptica</em> and other bivalves</td>
<td>No significant differences</td>
</tr>
<tr>
<td>1952</td>
<td>B</td>
<td>7</td>
<td><em>Modiolus modiolus</em>, <em>Cirripedia</em>, <em>Heteranomia squamula</em>, <em>Hydrozoa</em></td>
<td>R = 0.385; P &gt; 0.05</td>
</tr>
<tr>
<td>1981/90</td>
<td></td>
<td>3</td>
<td><em>Modiolus modiolus</em>, <em>Cirripedia</em>, <em>Heteranomia squamula</em>, <em>Ascidia</em></td>
<td>No significant differences</td>
</tr>
<tr>
<td>1952</td>
<td>C</td>
<td>10</td>
<td><em>Clinocardium ciliatum</em>, <em>Elliptica elliptica</em>, <em>Cirripedia</em>, <em>Ascidia</em></td>
<td>R = 0.634; P &lt; 0.05</td>
</tr>
<tr>
<td>1981/90</td>
<td></td>
<td>3</td>
<td><em>Arctica islandica</em>, <em>Clinocardium ciliatum</em>, <em>Serpies groenlandicus</em>, <em>Ascidia</em>, <em>Cirripedia</em></td>
<td>Significantly different</td>
</tr>
<tr>
<td>1952</td>
<td>D</td>
<td>7</td>
<td><em>Cirripedia</em>, <em>Modiolus modiolus</em>, <em>Chlamys islandicus</em>, <em>Hiatella sp.</em>, <em>Bryozoa</em>, <em>Hydrozoa</em></td>
<td>R = 0.138; P &gt; 0.05</td>
</tr>
<tr>
<td>1981/90</td>
<td></td>
<td>4</td>
<td><em>Cirripedia</em>, <em>Hemithyris psittacea</em>, <em>Modiolus modiolus</em>, <em>Chlamys islandicus</em>, <em>Hiatella sp.</em>, <em>Bryozoa</em>, <em>Hydrozoa</em></td>
<td>No significant differences</td>
</tr>
<tr>
<td>1952</td>
<td>E</td>
<td>8</td>
<td><em>Modiolus modiolus</em>, <em>Cirripedia</em>, <em>Ascidia</em>, <em>Hiatella sp.</em>, <em>Hemithyris psittacea</em></td>
<td>R = 0.323; P &lt; 0.05</td>
</tr>
<tr>
<td>1981/90</td>
<td></td>
<td>4</td>
<td><em>Ascidia</em>, <em>Cirripedia</em>, <em>Hemithyris psittacea</em>, <em>Nuculana minuta</em> and other bivalves</td>
<td>Significantly different</td>
</tr>
<tr>
<td>1952</td>
<td>G</td>
<td>9</td>
<td><em>Arctica islandica</em>, <em>Nicania montagu</em>, <em>Nuculana spp.</em>, <em>Elliptica elliptica</em></td>
<td>ANOSIM test failed</td>
</tr>
<tr>
<td>1981/90</td>
<td></td>
<td>2</td>
<td><em>Arctica islandica</em>, <em>Elliptica elliptica</em>, <em>Clinocardium ciliatum</em>, <em>Nuculana minuta</em></td>
<td></td>
</tr>
</tbody>
</table>

changes in the benthic communities because the survey in 2006 was designed in a different way and its overlap with the 1952 survey was minimal. However, even in this case, the dominant species *A. islandica*, *M. modiolus* and *V. stroemia* held their positions.

In spite of a similarity overall, there are apparent differences between the surveys which need to be discussed. First, the maximum and the average biomass of keystone species such as *M. modiolus*, *C. islandica* and *A. islandica* were higher in 1981/90 than in 1952. This may reflect population dynamics related to cohort growth and turnover. In clams and mussels, long-term population cycles have been known since the second half of the 20th century (Stephen 1938; Parsons *et al.* 1977; Luknin *et al.* 1989); these are not necessarily related to environmental variation (Naumov 2006). In the White Sea, a patch of benthic assemblages with a strong dominance of *A. islandica* (population density of about 15,000 ind·m⁻²) has been monitored in Chupa Inlet for more than 25 years. The structure and quantitative characteristics of this clam population at depths >10 m remained stable for 23 years, before the fraction of large (30–40 mm) specimens declined owing to a drastic natural elimination. In subsequent years, restoration of the population structure was observed, probably as a result of the re-distribution of the clams (Guerassimova *et al.* 2008).
A lower biomass of dominant bivalves in 1952 may also be explained by the use of different sampling methods. The Ocean-50 grab used in 1981/90 has a slightly larger sampling area (0.25 m²) than two casts of a Petersen grab (0.2 m²). It is possible that large sessile species with aggregated distribution were underestimated by taking two replicate samples of smaller size versus the one of larger size. Furthermore, an Ocean-50 grab is much heavier than a Petersen grab because their mass is proportional to L³, where L is a linear dimension of the open grab. A heavy grab is probably more effective in penetrating the dense coverage of large bivalves than a lighter one. Further studies using both theoretical models and field experiments are needed to check these hypotheses.

Some species which were not dominant in their biomass but are relatively common in Onega Bay showed an apparent increase in the frequency of occurrence and biomass between 1952 and 1981/90. These species include small clam Thyasira gouldi, echinoderms Ophiura robusta and Ophiopholis aculeata, and whelk Buccinum undatum. In 2006, T. gouldi was also common and B. undatum occurred with much higher frequency than found in previous surveys. In this case the differences in sampling methodology may also have biased estimates for these species. For example, one may suppose that such mobile and probably aggregating species such as ophiuran and whelks are underestimated by taking only two replicate samples of the Petersen grab. However, it is questionable whether this explanation also holds for T. gouldi. Alternative explanations would be trends for extension and/or increasing abundance in the aforementioned species. Regardless of whether these changes or trends are real or artefacts of sampling design, they are not essential in comparison with the apparent absence of shift in the dominance pattern in benthic communities and the relative stability of biomass characteristics of most common species at a decadal scale. Taking into account high spatial variability and methodological constraints of surveys, we may also speculate that such shifts could be potentially overlooked. However, the consistency of the dominance pattern in benthic assemblages in small sub-areas (Fig. 5) over decades suggests that this is not the case. Indeed, in the dynamics of the environmental conditions in the White Sea region we see hardly any major changes that could drive shifts in the dominance pattern in benthic communities.

The period from the early 1940s until the first half of the 1980s was characterised by general cooling, but from the mid-1980s onwards, temperatures increased (Tolstikov et al. 2004; Filatov et al. 2005b). For water temperature, the data from a permanent station at the entrance of the low-shore fjord in the Kandalaksha Bay, Chupa Inlet, which has unrestricted water exchange with the offshore part of the White Sea (Bahkov 1998; Howland et al. 1999), shows neither strong positive nor negative anomalies since the late 1950s. The average temperature for the 50–65 m layer indicates particularly little inter-annual variation; the anomalies do not significantly exceed 0.5 °C and show a weak correlation with the anomalies in the upper 15-m layer (Berger et al. 2003). As Onega Bay is open to the influence of the deep part of the White Sea, owing to tidal wave propagation and an anti-clockwise system of permanent currents (Bahkov 1998; Filatov et al. 2005a), the pattern of inter-annual variation of thermal regime is not expected to be very different from that in the entrance of Chupa Inlet. River discharge, which can potentially strongly affect benthic communities in the coastal zone, also shows no well expressed trends or major changes (Filatov et al. 2005b).

Modelling of yearly average primary production based on satellite chlorophyll data indicates that Onega Bay is one of the most productive areas in the White Sea (Romankевич & Vetrov 2004). A considerable part of the phytoplankton production and allochthonous organic matter supplied by river run-off is consumed by seston-feeding bivalves (M. modiolus, A. islandica, C. islandica, and M. edulis) and cirripeds, which constitute the majority of the biomass in Onega Bay. These bivalve species are long-living (Naumov 2006) and have few consumers – mostly flatfish, which do not predate on older age groups of M. modiolus, large clams and scallops (Ivanova 1957), and eiders, which are highly abundant in the area. Eiders use the area for breeding, moulting and wintering in the polynyas but mostly concentrate for feeding close to the shore, in particular on blue mussels, M. edulis (Bianki 1991; Galaktionov 2001; Makarevich & Krasnov 2005). It is therefore unlikely that predators have a strong impact on the population dynamics of dominant sessile benthic species at the scale of the entire Onega Bay. Due to their role in filtration of organic particles, influencing near-bottom hydrodynamics and producing shell material as substrate for epibenthos (Naumov 2006), the dominant bivalves and cirripeds may be considered keystone species-modifiers (Mills et al. 1993) in seabed biotopes. Thus the stability or quasi-periodic changes in their populations contribute to the relative stability of the subtidal macrobenthic communities in Onega Bay.

The characterisation of Onega Bay would be incomplete without mentioning that the anthropogenic influence on its marine ecosystem was low to moderate in the 20th century. Although the trend for eutrophication of the marine waters was seen in the White Sea in the 1980s compared to the 1950s (Maksimova 1991), the White Sea watershed area was not an area of intensive agriculture and pulp production in the second half of the 20th century (Terzhevsk et al. 2005), and natural organic matter
input from river run-off was always considerable (Romankevich & Vetrov 2004). Although there is pollutant transport with river run-off, much of the pollution is entrapped by so-called marginal filters in estuaries (Ivanov & Brizgalo 2005). In Onega Bay, background pollution with hydrocarbons and organochlorides is low; the trace metal concentrations in bivalve tissues may be somewhat higher than in the neighbouring Kandalaksha Bay but they are still not high compared with seas surrounded by areas of high population and industrial density (Savinov et al. 2001). Onega Bay has always been an important area for herring and navaga fishing for local and regional markets, but fishermen mostly used passive gears and there was practically no impact of bottom trawling and dredging on seabed habitats. Apart from pink salmon, which was introduced in the late 1950s–1960s, there are no alien species established in the region (Berger 2001).

It is of interest to compare the presumed stability of benthic communities in Onega Bay to examples known from the other shelf areas of similar scale. In the neighbouring Southwestern Barents Sea the response of zoobenthos to long-term fluctuations of temperature and the inflow of Atlantic waters is relatively rapid and manifests itself in changes of occurrence of the arctic and the boreal species (Galkin 1998; Denisenko 2008). However, the principal factor influencing variation of quantitative characteristics of infaunal benthic communities has been the bottom trawl fishery (Denisenko 2001; Carroll et al. 2009). In the 20th century, Skagerrak, Kattegat, the North and the Irish Seas show examples of significant changes in benthic (mostly infaunal) communities that are likely caused by eutrophication (Pearson et al. 1985; Rosenberg et al. 1987), bottom trawling, background pollution (Krönke 1990; Wieking & Krönke 2003; Türkay & Krönke 2004) and scallop dredging (Bradshaw et al. 2002). Beginning from the 1980s an increasing impact of climatic trends on benthic communities of the southern part of the North Sea can be traced (Beukema & Dekker 2003; Sonnewald 2008). The studies on the Black Sea benthos indicated that changes in the structure of bottom communities manifesting in the change of dominant species and the high magnitude of variation in abundance and biomass of common species may happen within a few years under the cumulative influence of the consequences of eutrophication and introduction of alien species. The misbalanced benthic communities are continuing to experience rapid changes in their quantitative species composition (Chikina & Kucheruk 2005; Kucheruk et al. 2009).

Amongst the seas around Europe, the White Sea and particularly Onega Bay may represent a rare case of a shallow-water benthic ecosystem which has not yet been modified by human impact. The specific oceanographical regime of the White Sea has possibly also made it resilient to climate variation in the past decades. Taking this into account, Onega Bay with its largely boreal and in several respects similar characteristics to the North Sea and the Western Baltic biota (Zenkevich 1963; Naumov 2001) is a prospective area for studies of natural variation in benthic communities and possible future climate-forcing in this yet undisturbed ecosystem belonging to the Northeast Atlantic realm.

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References


Macrobenthos of Onega Bay (White Sea, Russia)


The effect of temperature variability on ecological functioning of epifauna in the German Bight

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Keywords
Benthos; biological traits analysis; cold winter; ecosystem functioning; functional diversity; North Sea; temperature anomalies.

Abstract
Benthic epifauna was sampled in an area of 10 × 10 nautical miles in the German Bight. Samples were taken in January and July/August from 1998 to 2009. The ecological functioning of the epifaunal community was assessed using biological traits analysis (BTA). Twelve ecological traits of 26 epifaunal species were considered and analysed using non-metric multidimensional scaling (nMDS). Anomalies in the sea surface temperature (SST) close to the study area were mainly above the long-term mean during the study period. SST was exceptionally high during the autumn months between 2002 and 2006. Additionally, the cold winter of 1995–96 was clearly reflected in strong negative SST anomalies. Trait composition changed in 2002, mainly due to a decreasing trend of traits related to an opportunistic life mode from 1998–2002. Traits related to reproduction showed a much clearer response to the high autumn SST anomalies from 2002 to 2006 than other traits. We concluded that the cold winter resulted in an increase in opportunistic species in the study area followed by characteristic post-disturbance succession stages to the point of an established community in 2002. This indicates a recovery time of epifaunal communities in the German Bight of 7–8 years. Additionally, the results give evidence that climate-induced variability of SST in the German Bight affects mainly the reproduction of epifaunal species rather than other traits such as feeding type.

Introduction
In the North Sea ecosystem, a regime shift occurred in the late 1980s from a 'cold dynamic equilibrium' to a 'warm dynamic equilibrium' (Beaugrand 2004). This shift was linked to pronounced modifications in large-scale hydro-metrolologial forcing and ecosystem parameters, including a marked increase in oceanic inflow and sea surface temperature (Beaugrand 2004). The warm temperature period has continued to the present day (Hughes & Holliday 2006) and there is strong evidence to suggest that many different species and communities in the North Sea ecosystem are responding to these temperature changes. For example, the phenology of phyto- and zooplankton in the North Sea has changed and plankton communities have shifted due to an increasing prevalence of warm-water species (Edwards & Richardson 2004; Edwards et al. 2008; Kirby et al. 2008; Martens & van Beusekom 2008). Biogeographical shifts of fish species have been identified and interpreted as reflecting a response to increasing water temperature (Ehrich & Stransky 2001; Brander et al. 2003; Perry et al. 2005). Migration patterns of species have changed (Sims et al. 2001). Benthic communities in the Southern and Northern North Sea have been affected by temperature changes (Kröncke et al. 1998; Neumann et al. 2009a,b). However, the trend of increasing temperature was interrupted by extreme cold winter conditions in the North Sea region during 1995–1996. Cold winters influence benthic fauna greatly, through direct (enhanced mortality) and indirect (reduced reproduction and production) effects on the species, especially in shallow areas (Reiss et al. 2006;
Neumann et al. 2008a,b, 2009a,b). These effects are observed as a reduced number of species, diversity and biomass (Ziegelmeier 1970; Buchanan & Moore 1986; Beukema 1992; Kröncke et al. 1998). As the effects of cold winters might influence the ecosystem for several years, it is essential to understand them more precisely in order to interpret long-term dynamics in the North Sea ecosystem.

Limited attention has been paid to the question of how these climate-induced changes affect the functioning of the North Sea ecosystem despite a growing demand for the functional aspects of systems to be incorporated into conservation and management efforts (Bremner 2008; Frid et al. 2008). According to Jax (2005), the term ‘function’ in ecology refers to (i) processes and the causal relations that give rise to them, (ii) the role of organisms within an ecological system, (iii) the overall processes that sustain an ecological system and finally (iv) to the services a system provides for human or other organisms. Studies on species composition were often inadequate to address these issues as ecosystem processes are determined by the functional characteristics of the organisms involved, rather than by taxonomic identity (Odum 1969; Grime 1997; Hooper et al. 2002). The same conclusion was drawn by Diaz & Cabido (2001), who stated that ecosystem stability is strongly attributed to the functional traits of species and their interactions rather than to species composition per se.

Biological traits analysis (BTA), which was developed in terrestrial and freshwater ecology, is a useful analytical approach to describe different aspects of functioning (Bremner et al. 2003b). BTA has been applied successfully to assess fishing effects on benthic fauna (Bremner et al. 2003a, 2005; Tillin et al. 2006), to assess the functional diversity in different species assemblages (Bell 2007; Mouillot et al. 2007; Schratzberger et al. 2007) as well as for management and conservation purposes (Bremner 2008; Frid et al. 2008). BTA uses a comprehensive set of functional traits (e.g. mobility, feeding type, size, longevity, and reproductive technique), which can be used as indicators for ecosystem functioning. The wide range of traits used by BTA, the strong link between them and ecosystem processes (Diaz & Cabido 2001), as well as the sound theoretical framework (see Bremner 2008) are a considerable advance over traditional methods dealing with ecosystem functioning.

To understand the impact of temperature variability on ecosystem functioning in the German Bight, this study focused on a single component of the ecosystem, the mobile epifauna. We applied BTA on an epifaunal time series in the German Bight covering a period of 12 years with summer and winter sampling. Previous studies showed that the epifaunal communities in this area were severely affected by the cold winter in 1995–96, but also showed an increase in diversity and secondary production in conjunction with increasing sea surface temperature (Neumann et al. 2008a; Neumann et al. 2009b). The objectives of our study were (i) to assess the seasonal and annual effects of SST variability on the functional composition of epifauna and (ii) to compare these results with the outcome of the species composition analysis in the same area.

Material and Methods

Study site

The area of investigation (Box A; 10 × 10 nautical miles) was situated about 25 nautical miles northwest of the Island of Helgoland, in close proximity to the old Elbe glacial valley 30 m depth contour (54°17’ N–54°27’ N and 006°58’ E–007°15’ E) (Fig. 1). The mean depth of this area was 40 m and the water column was generally well mixed throughout the year. Sediments in the southwest corner of Box A were more than 20% mud (<63 μm fraction). This percentage gradually decreased towards the northeast (0–5%). The time series started in 1998 and were part of the German small scale bottom trawl survey (GSBTS) (Ehrich et al. 2007 for further information). Epifauna was sampled twice a year in January (first quarter) and in July/August (third quarter) on board the FRV Walther Herwig. Sampling did not take place in winter 1998 and 1999 due to ship time constraints.

Epifauna data

Epifauna was sampled with a standardized 2 m beam trawl made of galvanized steel with a chain matt attached.
The beam trawl was fitted with a 20-mm net and a cod end of 4 mm mesh size. A Scanmar depth-finding sonar was attached to the top of the net just behind the steel beam to determine the exact time and position of contact with the seabed. From the moment of contact with the ground, the beam was towed at a speed of about 1.5–2 knots for 5 min. Altogether, 197 beam trawls were taken between 1998 and 2009. In general, nine replicates were taken in each sampling season but the replicate number varied between 3 (winter 2000) and 13 (winter 2004) according to weather conditions. On average, 8.9 replicates were taken. Samples were sieved through 5-mm mesh and the epibenthic fauna was separated from the remains. Species were identified onboard to the lowest possible taxonomic level and abundance data were standardized to a tow length of 250 m (area sampled = 500 m²).

Temperature data
The Federal Maritime and Hydrographic Agency of Germany (BSH) provided weekly sea surface temperature (SST) data at the Helgoland Station (Hel; 54°9’9.6” N, 7°18’0” E) close to Box A. Monthly standardized temperature anomalies from 1998 to 2008 were calculated from the Helgoland station based on the 1968–2008 mean.

Biological trait analysis (BTA)
The epifaunal dataset was reduced to the 26 most dominant species in terms of abundance and occurrence in Box A, previously described by Neumann et al. (2008a,b). These species were coded in a ‘species by trait table’ (Fig. 2) to the extent they displayed the categories of 12 traits. Coding was done using a ‘fuzzy coding’ approach which uses positive scores to describe the affinity of species to trait categories (Chevenet et al. 1994). In this study, a scoring range from 0 (no affinity) to 4 (total affinity) was applied. For example, the shrimp Crangon allmanni was coded 0 (permanent attached), 0 (temporarily attached), 1 (Burrower), 2 (Crawler) and 1 (Swimmer) for the trait ‘adult mobility’. Ten of the traits used (including the categories) were adopted from Tillin et al. (2006) reflecting a wide range of ecological function and life-history modalities of species. The traits ‘fertilization type’ (internal, external) and ‘reproductive season’

<table>
<thead>
<tr>
<th>Trait</th>
<th>Categories</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mobility</td>
<td>Perm. attached; Temp. attached; Burrower; Crawler; Swimmer</td>
</tr>
<tr>
<td>Habitat</td>
<td>Infauna; Epifauna; Epizoic</td>
</tr>
<tr>
<td>Feeding type</td>
<td>Deposit; Filter/suspens.; Grazer; Scavenger; Predator</td>
</tr>
<tr>
<td>Food type</td>
<td>Algae; Invertebr./Vertebr.; Carnion; Detritus; Plankton; Suspend. org. matter; Microorg.</td>
</tr>
<tr>
<td>Size (cm)</td>
<td>small (1–2); small-medium (3–10); medium (11–20); medium-large (11–20); large (&gt; 50)</td>
</tr>
<tr>
<td>Adult longevity</td>
<td>&lt; 2; 2–5; 5–10; 10+</td>
</tr>
<tr>
<td>Age sexual maturity</td>
<td>&lt; 2; 2–5; 5–10; 10+</td>
</tr>
<tr>
<td>Reprod. technique</td>
<td>Asexual; Sexual (spawner); Sexual (egg lay/egg brood - mini adults); Sexual (egg lay/egg brood - plank. larval)</td>
</tr>
<tr>
<td>Reprod. frequency</td>
<td>Annual once; Annual (2 or more); Biennial; Semelparous</td>
</tr>
<tr>
<td>Reprod. season</td>
<td>Winter; Spring; Summer; Autumn</td>
</tr>
<tr>
<td>Dissemination</td>
<td>No pelagic life stage; Pelagic life stage; Low mobility adult; Highly mobile adult; Migratory</td>
</tr>
<tr>
<td>Fertilization type</td>
<td>Internal; External</td>
</tr>
</tbody>
</table>

Fig. 2. Stages of the biological trait analysis (BTA) including the trait variables with the corresponding number of categories used to describe ecological functioning of the epifaunal community in Box A.
Effect of temperature variability on epifauna

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Fig. 3. Anomalies in SST (°) at the station Helgoland (Hel) close to Box A, based on the 1968–2008 mean.

(autumn, winter, spring, summer) were added to focus on the reproduction of species, as temperature variability has a large impact on the reproduction cycles of species and on benthic–pelagic coupling in the North Sea (e.g. Edwards & Richardson 2004; Kirby et al. 2007, 2008). Trait category scores for each species present in a year/season were then weighted by their abundance in that year/season by multiplying the scores with abundance data and then summing the resulting values over all species (Fig. 2). The result is a ‘station by trait table’ which contains the frequencies of occurrence of biological traits in each year and season (Fig. 2).

It is important to mention that the BTA used here describes only a single aspect of functioning as it does not include other components of the ecosystem, nor does it quantify processes or properties.

Non-metric multidimensional scaling (nMDS) in the PRIMER v6 package (Plymouth Marine Laboratory) was applied to the station-by-trait table based on fourth root-transformed data. Similarities were calculated using the Bray–Curtis coefficient. This method describes the similarities between the years and seasons in terms of their trait composition and is appropriate for providing a general picture of functioning in marine assemblages (Bremner et al. 2006). An ANOSIM randomization test was performed to test the differences in trait composition between the years (H0: no differences in trait composition). The dissimilarity between these two periods was 21%. The most important trait categories contributing to this dissimilarity were categories which belonged to an opportunistic life mode, such as small size, early onset of sexual maturity and a short life span. Thus, the relative abundance of small species (1–2 cm) which have an age of maturity <2 years and an adult longevity of 2–5 years decreased continuously in the first years and seasons of the study period (Fig. 4). Shifts in trait composition around 2002 were also evident in the traits: adult mobility, feeding type, dissemination, as well as reproductive type, -frequency and -season (Fig. 5). For example, the proportion of deposit and filter/suspension feeders was much higher before 2003 (52–80%) whereas grazers, scavengers and particularly predators were the dominant feeding mode after 2003 (73–98%). Additionally, the abundance of migratory species was higher after 2003 (11–21%) than in the period before 2003 (1–7%). Traits such as adult mobility, reproductive type, reproductive frequency and reproductive season not only shifted between 2002 and 2003 but showed the highest percentages or even a seasonality in the period of the warm autumn months (2002–2007). The proportion of sexual egg layers with a planktonic larvae peaked in winter 2005 (75%) and 2006 (73%) and decreased slightly afterwards. The percentages of species which had their reproductive season in autumn and reproduce twice (or more) per year showed a clear seasonality. The highest abundance of

Results

SST temperature anomalies from 1995 to 2008

In general, the temperature anomalies were mainly above the long-term mean (1968–2008) at Helgoland Station from 1995 to 2008 (Fig. 3). However, the cold winter of 1995/96 was clearly reflected in strong negative SST anomalies from the start of 1996, which persisted until May 1997. Since 2002, the positive SST anomalies have often persisted throughout the year, and were exceptionally high during the autumn months in 2002–2006. For example, the highest yearly anomalies were found in September in 2002–2004 (2.1, 1.3 and 0.9) and in November and October in 2005 and 2006 (1.6 and 1.9). SST anomalies were exceptionally high at the first half of 2007 (January to June) ranging from 1.4 (June) to 2.1 (April), which (together with September 2002) is the highest recorded anomaly at that station in 1995–2008.

Biological trait analysis (BTA)

The nMDS analysis based on fourth root-transformed trait data revealed distinct changes in the trait composition of the epifauna in Box A in 2002 (Fig. 4). The ANOSIM randomization test confirmed significant differences in trait composition between the years 1998–2002 (winter) and 2002 (summer) to 2009 (R = 0.625, P < 0.001). The dissimilarity between these two periods was 21%. The most important trait categories contributing to this dissimilarity were categories which belonged to an opportunistic life mode, such as small size, early onset of sexual maturity and a short life span. Thus, the relative abundance of small species (1–2 cm) which have an age of maturity <2 years and an adult longevity of 2–5 years decreased continuously in the first years and seasons of the study period (Fig. 4). Shifts in trait composition around 2002 were also evident in the traits: adult mobility, feeding type, dissemination, as well as reproductive type, -frequency and -season (Fig. 5). For example, the proportion of deposit and filter/suspension feeders was much higher before 2003 (52–80%) whereas grazers, scavengers and particularly predators were the dominant feeding mode after 2003 (73–98%). Additionally, the abundance of migratory species was higher after 2003 (11–21%) than in the period before 2003 (1–7%). Traits such as adult mobility, reproductive type, reproductive frequency and reproductive season not only shifted between 2002 and 2003 but showed the highest percentages or even a seasonality in the period of the warm autumn months (2002–2007). The proportion of sexual egg layers with a planktonic larvae peaked in winter 2005 (75%) and 2006 (73%) and decreased slightly afterwards. The percentages of species which had their reproductive season in autumn and reproduce twice (or more) per year showed a clear seasonality. The highest abundance of
**Fig. 4.** nmMDS plot of biological trait composition in Box A from 1998 to 2009 including summer and winter sampling (top left). nmMDS plot was overlaid with the relative occurrence of the trait categories ‘small size (1–2 cm)’ (top right), ‘age at sexual maturity <2 years’ (bottom left) and adult longevity 2–5 years (bottom right). Data were fourth root-transformed.

**Fig. 5.** Percentages of trait categories of the trait variables adult mobility, feeding type, reproductive type, dissemination as well as reproductive frequency and -season in Box A from 1998 to 2009.
these species was found in winter 2003 to winter 2007, correlating to the winters following exceptional warm autumn months.

**Discussion**

The shift in trait composition in 2002 largely coincided with shifts in the epifaunal species composition in Box A (Neumann et al. 2008a,b), which was also observed in the shallow West and North Frisian coasts (Neumann et al. 2009a,b). In all these areas, exceptionally high abundances of the brittle star *Ophiura albida* were found in 1998, which decreased in subsequent years parallel to an increase in diversity, secondary production as well as abundance and biomass of other epifaunal species. The BTA revealed a decrease in traits related to an opportunistic life mode after summer 1998 (Fig. 4). The patterns found follow the theory on the effects of disturbance on communities going back to the models of Odum (Odum 1969) and Pearson–Rosenberg (Pearson & Rosenberg 1978). In the Pearson–Rosenberg model, the second stage in the faunal succession was characterized by the appearance of opportunistic species, which were able to recolonize a disturbed habitat faster than K-selective species. The opportunistic life mode (r-strategy) involves increased reproductive effort through early onset of maturity, short life span and small body size (Heip 1995) providing a selective advantage in disturbed environments by utilizing free resources faster than others. Thus, the decrease in small species (1–2 cm) with an age of maturity <2 years and an adult longevity of 2–5 years confirmed (according to the BTA) that the community in Box A was at a succession stage between the opportunistic dominance and the established community between 1998 and 2002. The occurrence of seasonal variation formed a decisive part of ‘persistence stability’ in benthic communities following catastrophic events in temperate areas with a highly dynamic physical regime (Arntz & Rumohr 1982). Seasonality was found for the traits reproductive frequency and reproductive season since 2003, but other traits also show conspicuous changes between 2002 and 2003 (Fig. 5). For instance, the proportions of predators, scavengers and grazers were much higher after winter 2003, whereas those of deposit and filter/suspension feeders decreased. In conjunction with the shift in overall trait composition in 2002, this indicated a shift in the community from the disturbance stage after the cold winter of 1995/96 to the recovery stage between 2002 and 2003. Thus, the variability of trait composition underpins the hypothesis that the cold winter resulted in the outbreak of opportunists, followed by characteristic post-disturbance succession stages to the point of an established community in 2002/2003 (Neumann et al. 2008a,b). The effect of cold winters on ecosystems was less clear in the later years due to the clear response of ecosystem components to the warming of the North Sea. However, cold winters are also part of climate variability and their impacts have been observed in long-term records of plankton (Martens & van Beusekom 2008) and benthic infauna (Kröncke et al. 1998; Schröder 2005). The current study revealed that the recovery time of epifaunal communities after cold winters was 7–8 years, compared to a much faster recovery in plankton communities (<1 year) and benthic infauna communities (2–5 years) in the German Bight (Schröder 2003; Martens & van Beusekom 2008). The prolonged recovery time of epifauna in shallow, well-mixed areas has important implications for the assessment of ecosystem health and consequently for management and conservation strategies.

Succession of the epifaunal community in Box A was mainly driven by biotic factors such as trophic interactions (Neumann et al. 2008a,b). During our study, SST anomalies at the station close to Box A were mainly above the long-term mean of 1968–2008, with exceptionally high anomalies in the autumn months of 2002–2006. It is obvious that traits related to the reproduction of species such as reproductive type, -frequency and -season have shown a clear response to these high autumn water temperatures. Thus, a high proportion of sexual egg layers with planktonic larvae were found during the period of high autumn anomalies. Additionally, higher abundances of species which reproduce in autumn and are able to reproduce twice a year were found in the winters after the warm autumn months. Direct positive effects of temperature on key stages of reproduction are well known for many species which were found in Box A. For example, the larval development of the swimming crab *Liocarcinus holsatus* (from hatching to metamorphosis) is faster with increasing temperature (Choy 1991). Furthermore, the duration of the larval stage as well as the frequency of breeding of *Pandalus* spp. is positively linked to temperature (Bergström 2000), as has also been observed in other caridean species (Wear 1974). Henderson et al. (2006) found that the recruitment of the shrimp *Crangon crangon* in autumn was correlated to SST and the winter index of the North Atlantic Oscillation. Similar changes were also observed in planktonic communities where, in particular, echinoderm and decapod larvae were found in higher abundances and/or earlier due to temperature-induced shifts in the reproduction cycle of benthic species (Lindley et al. 1993; Greve et al. 2001; Edwards & Richardson 2004; Kirby et al. 2007; Richardson 2008).

In contrast to traits related to reproduction, traits such as feeding type and dissemination showed no obvious response to the exceptional warm SST in autumn but a clear shift in winter 2003 (when there was a higher...
proportion of predators, scavengers, grazers and migratory species) in relation to overall positive anomalies of SST. However, it was difficult to determine whether these changes could be attributed to the climate-induced variability of SST or whether the trait compositions just reflect the stage of the common community following the succession after the cold winter. As Neumann et al. (2008a,b, 2009a,b) argued that the epifauna in the shallow Southeastern North Sea were influenced by increased food supply due to a much longer period of primary production in conjunction with higher SSTs (Hughes & Holliday 2007), we expected higher proportions of organisms such as deposit feeders in this study, but that was not the case. However, the increased abundance of epifaunal predators might be attributed to higher abundances of, for example, deposit feeders of lower trophic levels (i.e. benthic infauna, meiofauna) which in turn benefited from increased food supply. Thus, a higher proportion of predators since 2003 in Box A might also be attributed to climate-induced temperature increase, especially as Henderson et al. (2006) also suggested that there must also be an increase in food availability if an increase of larval development due to higher temperature is to be translated into higher recruitment.

The results of the BTA primarily revealed a greater impact of temperature variability on traits related to reproduction than on feeding traits in Box A. Therefore, we assumed that the climate-induced temperature variability indeed had a greater influence on the recruitment of epifauna than on the food availability in the study area. In contrast, food supply was found to be an important factor influencing epifaunal species in the northern, stratified North Sea (Neumann et al. 2009a,b), which were regarded to be food limited (Davies & Payne 1984). Further analysis, including our data from the Northern North Sea, should be used to test these hypothesized functional differences between the Northern and Southern North Sea.

We are aware that we will have missed some aspects of functioning as we excluded rare species in the BTA and thus their contribution to functionality. Additionally, we do not cover all aspects of functioning due to the choice of only 12 functional traits in the BTA. Two expert workshops in Plymouth and London have identified 10 key aspects of marine system functioning and 24 corresponding functional traits for the BTA (Frid et al. 2008). We excluded traits such as 'Energy transfer efficiency' or 'Intra-specific sociability' to reduce the demand for functional data, which were mostly impossible to get. However, this does not greatly affect our conclusions. The definition of functioning by Jax (2005) given in the introduction emphasizes both processes and the role of single components. Although our study only incorporates functional aspects of one single component (the benthic epifauna), it provides useful information on how the functional composition of epifauna was linked to environmental changes. But there is an obvious need for holistic studies that include more biotic components as well as ecological processes.

**Acknowledgements**

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**References**


Zoobenthos as an environmental quality element: the ecological significance of sampling design and functional traits

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Abstract

The EC Water Frame Directive (WFD) states that all coastal water bodies must achieve ‘good ecological status’ by the year 2015. A range of different classification methods have been developed and used to define ecological status to support the WFD. The aim of this study was to compare the effects of using two different mesh sizes of sieve (1.0 and 0.5 mm) on zoobenthic assemblages and on the ecological status of benthic macrofauna (using the Brackish water benthic index, BBI) in three ecologically distinct archipelago areas (Inner, Middle and Outer) in the Åland Islands, Northern Baltic Sea. We performed a biological trait analysis (BTA) to evaluate differences in the functional (trait) diversity of macrofauna collected using different mesh sizes and estimate the ecological relevance of mesh size. The results showed that sieve mesh size had significant effects on the recorded number of species, abundance, and total biomass of the zoobenthos. Small-bodied species and juveniles (e.g. Macoma balthica) were not observed when using a 1.0-mm mesh. The ecological status (sensu WFD) was only slightly affected by the mesh size, and all areas had good or high ecological status. BTA showed a difference in trait composition when using 0.5- or 1.0-mm mesh, particularly in the Outer area, where the proportion of small-sized species was high. Our results highlight how biological traits, in addition to species number and biomass, can play a key role when analyzing ecosystem structure for assessment and classification of coastal ecosystems. We show that combining traditional monitoring for the EU WFD with a functional analysis strengthens our ability to interpret environmental quality, and thus increases the precision of our advice for management purposes.

Introduction

Eutrophication is one of the most severe environmental issues in the Northern Baltic Sea, affecting both pelagic and benthic environments, in shallow and deep areas (Elmgren 1989; Bonsdorff et al. 1997; HELCOM 2009). Zoobenthos is widely used as an indicator of change in environmental conditions, as the organisms are relatively stationary and several species live for many years. Thus changes in environmental conditions are reflected in zoobenthos as altered community parameters. Increased disturbance of coastal areas leads to changes in species number and the composition of assemblages, as well as in their abundance and biomass (Pearson & Rosenberg 1978; Cederwall & Elmgren 1980; Diaz & Rosenberg 1995; Norkko & Bonsdorff 1996; Bonsdorff & Pearson 1999; Perus & Bonsdorff 2004).

In the Northern Baltic Sea, the number of benthic species is low primarily due to brackish water conditions (salinities vary between 3 and 7 psu). Species are either of marine or limnic origin and they live at the limits of their physiological tolerance (Bonsdorff 2006).
salinity, the organisms are small in size compared with their relatives in fully marine areas. Hence, the size-spectrum of benthic organisms is narrow, and most organisms have an adult size smaller than a few centimeters (although certain polychaetes may reach 10 cm in length). To fully illustrate and understand community dynamics, individuals’ size must be considered a priori when choosing methods for the study. Sieve mesh sizes of 1 mm or more are widely used for benthic surveys in marine areas (Borja et al. 2009 and references therein), while a 0.5-mm sieve mesh is more often used in local studies in the Northern Baltic Sea (Perus et al. 2007).

Assessments of anthropogenic effects on benthic systems have mostly been based on taxonomic composition and relative abundance of taxa, which are still valuable and easy to comprehend, serving as a base for further assessments (Blomqvist & Bonsdorff 1986; Bonsdorff & Blomqvist 1993; Perus & Bonsdorff 2004). However, recent studies have questioned the use of only species number and other basic parameters as measures of ecosystem health and functioning, especially as marine benthic systems harbour great numbers of phyla for which the taxonomic divisions are still uncertain (Warwick & Sommerfeld 2008). The increasing need for broadening of the quality concept for habitats or coastal areas and accepting the importance of ecosystem functioning, has promoted a scientific and applied discussion about present quality indices, what they describe and how they fit modern management approaches (Frid et al. 2008; Tillin et al. 2008; Borja et al. 2009). The ability of management directives (e.g. sampling methods), ecological indices and other measures of anthropogenic stress to encompass different scales of functioning and biodiversity during ecosystem change has been questioned. For example, the contribution of some species to the functioning of the ecosystem may decrease and that of other species increase during environmental change, and to include this requires an appropriate time and spatial sampling scale (Thrush et al. 1997, 2000; Yachi & Loreau 1999; Stachowicz et al. 2002). Further, organisms that appear to perform similar roles may not always respond to stress in the same way (Ramsay et al. 1998). Hence, the next step is to connect the changes in abiotic characteristics of the habitat or environment, the number and abundance (or biomass) of species (species diversity) and the functioning of these species (functional diversity) in order to best identify and direct management efforts (Bremner et al. 2003; Jax 2005; Bremner 2008). According to the EU Water Frame Directive (2000/60/EG; WFD) all coastal waters should achieve a good ecological status by 2015. For this purpose, water areas are being classified using biological quality elements (macrophytes, phytoplankton, zoobenthos) and divided into five classes of ecological status: high, good, moderate, poor and bad (2000/60/EG WFD; Borja et al. 2000; Rosenberg et al. 2004; Perus et al. 2007; Josefsson et al. 2009). As the EU WFD classifies the entire Baltic Sea as one eco-region, this implies that the same quality elements and indicators should be valid across the entire sea. As has been shown in numerous recent studies, this is not the case (Perus & Bonsdorff 2004; Leonardsson et al. 2009; Rosenberg et al. 2009). Not only must species-sensitivity values be set according to regional ecological baselines, but also indicators other than just presence/absence, abundance and biomass must be included. One potential way forward is to include functioning (cf. Bonsdorff & Pearson 1999) and specific biological traits (Bremner 2008). In the case of the Northern Baltic Sea species, size must also be considered.

The aim of this study was to investigate how different mesh sizes of sieve affect the results of benthic studies both structurally and functionally. We studied the effects of macrofauna assemblage observations, using two sieve mesh sizes: 1.0 or 0.5 mm. The effects were measured on basic community parameters, as well as on the ecological status of the environment, along an environmental gradient from inner to outer archipelago using a specially developed index, the brackish water benthic index (BBI; Perus et al. 2007). In addition we performed a biological trait analysis (BTA; Bremner et al. 2003) to evaluate differences in functional (trait) diversity of different mesh sizes and estimated the ecological relevance of mesh size choice in relation to the selected macro-habitats.

**Study Areas**

The field sampling for this study was conducted in three areas (macro-habitats) of different exposure and degree of organic input to the sediments in the Åland archipelago (N Baltic Sea): Inner, Middle and Outer archipelago areas (Fig. 1). The Inner area was sheltered from the open sea and had limited water exchange. It was directly affected by human activities, mainly agriculture and food industry. The Middle area was semi-exposed and moderately affected by local sources of eutrophication. The Outer area was exposed to the open sea with high water exchange rates. It was only slightly affected by local human activities, and had low nutrient levels in comparison with the other areas studied. The sediment quality ranged from sand/gravel in the Outer exposed areas, with low organic content (mean 1.8%) to clay/mud with high organic content (mean 5.6%) in the Inner sheltered areas (Table 1). The entire region (Fig. 1) has been thoroughly studied for benthic infauna since the early 1970s and there were comprehensive records of the benthic assemblages in these areas (e.g. Helminen 1975; Bonsdorff et al. 1991, 2003; Perus et al. 2001; Perus & Bonsdorff 2004).
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Fig. 1. Map of the study areas in the Åland archipelago, Northern Baltic Sea. I, Inner area; M, Middle area; O, Outer area.

Table 1. Site characteristics of the three archipelago areas. The four variables, Depth, Salinity, Oxygen (O2 %) in bottom water and Organic content in sediment are presented as: mean (min–max), the variable Dominating sediment type with the following abbreviations; C, clay; M, mud; S, sand; G, gravel.

<table>
<thead>
<tr>
<th>Archipelago area</th>
<th>Site characteristics</th>
<th>Inner</th>
<th>Middle</th>
<th>Outer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Depth m</td>
<td>10.7 (5–16)</td>
<td>11.2 (6–27)</td>
<td>14 (4–26)</td>
</tr>
<tr>
<td></td>
<td>Salinity, %</td>
<td>5.6 (5.6–5.7)</td>
<td>5.6 (5.3–5.8)</td>
<td>6.0 (5.4–6.2)</td>
</tr>
<tr>
<td></td>
<td>O2 % in bottom water</td>
<td>86 (80–91)</td>
<td>93 (87–99)</td>
<td>94 (86–113)</td>
</tr>
<tr>
<td></td>
<td>Dominating sediment type</td>
<td>C, MC</td>
<td>C, MC, CG</td>
<td>CS, S, SG</td>
</tr>
<tr>
<td></td>
<td>Organic content in sediment (loil), %</td>
<td>5.6 (2.7–8.6)</td>
<td>5.5 (0.9–9.2)</td>
<td>1.8 (0.4–10.7)</td>
</tr>
</tbody>
</table>

Material and Methods

Sampling was conducted between 14 August 2007 and 7 September 2007 when the animal summer-recruitment had occurred. In all areas, zoobenthic samples were taken using an Ekman-Birge grab sampler (289 cm²) from two depth zones: <10 m (hereafter called ‘shallow’) and >10 m (hereafter called ‘deep’). Five replicate samples were taken from six stations in each area; three on shallow and three on deep bottoms. The samples were sieved through both 1.0- and 0.5-mm screens (reported as 1.0 and 0.5 mm pooled). Fauna were identified to the lowest possible taxonomic level, counted and weighed (wet weight). The length of individual Macoma balthica was measured to the nearest mm for estimates of population structure and recruitment success. A paired t-test was used to compare the number of species, abundance and biomass between the 0.5- and 1.0-mm mesh results in the different depth zones and areas. An overall analysis of mesh size effects was done using two-way ANOVA, with sieves (0.5 and 1.0 mm) and areas...
Ecological status

The ecological status *sensu* WFD was measured using the BBI equation 1 (Perus et al. 2007). It was adopted from the benthic quality index (BQI; Rosenberg et al. 2004) and adjusted for low-saline coastal areas, with low species numbers, and the sensitivity values for the species have been adjusted to their actual environment (cf. Rumohr et al. 1996). BBI follows the assumption that biodiversity increases with increasing distance from a pollution source along a gradient of disturbance, and can take values between 0 and roughly 1 (Pearson & Rosenberg 1978; Perus et al. 2007).

\[
\text{BBI} = \frac{\left( \frac{\text{BQI}}{\text{BQI}_{\text{max}}} \right) + \left( \frac{\text{H}'}{\text{H}_{\text{max}}} \right)}{2} \times \left[ \left( 1 - \frac{1}{\text{S} \text{AB}} \right) + \left( 1 - \frac{1}{\text{S}} \right) \right]
\]

where \( \text{BQI} \) = benthic quality index (*sensu* Rosenberg et al. 2004); \( \text{BQI}_{\text{max}} \) = maximum BQI-value recorded within each type after calculating all available data within the national Finnish zoobenthos database 'Hertta' (http://www.ymparisto.fi); \( \text{H}' \) = Shannon-Wiener diversity index (\( \log_2 \)-base); \( \text{H}_{\text{max}} \) = maximum \( \text{H}' \)-value recorded within type after calculating all available data within national zoobenthos database; \( \text{AB} \) = total abundance at each station; and \( \text{S} \) = number of species/taxa at each station.

Biological trait analysis (BTA)

For the BTA we selected 10 specific traits representing the principal aspects of morphology, life-history, feeding habit, and movement of the studied taxa (Table 2). These were chosen to maximize the differences among species or taxa, and thus to elucidate representative trait patterns in sampling design and differences between areas. The 10 traits were separated into sub-categories, i.e. modalities. Body design, for example, was divided into vermiform unsegmented, vermiform segmented, bivalved, turbinate and articulate. This resulted in a total of 45 different trait modalities for the species-pool selected (Table 2). The division of traits and categories was deduced from Bonsdorff & Pearson (1999), Pearson (2001), and Bremner et al. (2003, 2006a,b), and revised and applied to fit the Baltic Sea benthic species (A. Törnroos unpubl. data).

Individual taxa were then coded for the extent to which they display the modalities in a scoring range between 0 and 3, with 0 being no affinity to a modality and 3 being total affinity. The category scores were then standardized to 1 within a trait. This ‘fuzzy coding’ procedure (Chevenet et al. 1994) allows taxa to exhibit the modalities of a variable (trait) to different degrees. The procedure was developed and first applied to terrestrial plants and freshwater invertebrates (Olff et al. 1994; Townsend & Hildrew 1994) but has now also been introduced for marine systems (Bremner et al. 2003, 2006a). For our purposes, data on traits were obtained from the primary and secondary literature and by consulting expert advice (A. Törnroos unpubl. data). Thus, relevant and reliable information on all traits was obtained for all taxa sampled. This procedure resulted in a taxa by trait matrix, one of two tables included in the BT analysis. To link the abundance of taxa at each station and mesh size with the traits displayed by the taxa, we conducted a co-inertia analysis (CoI; Dolédec & Chessel 1994). This analysis assesses the co-structure between two data tables, in this case a ‘taxa by station’ table and a ‘taxa by trait’ table, and simultaneously ordinates the two tables, maximizing both the variance from the individual tables and the correlation between them (Dolédec & Chessel 1994; Dray et al. 2003). As a first step, two separate ordinations were conducted: a centered PCA (principle component analysis) on the “taxa by station” table and a PCA (fuzzy correspondence analysis) on the “taxa by trait” table (Chevenet et al. 1994; Charvet et al. 1998). These were then used in the CoI analysis, and the significance of the resulting co-structure was examined with the RV coefficient (a measure of similarity between squared symmetric matrices). To evaluate if the value of RV significantly differed from zero, a Monte-Carlo random permutation test was performed (n repetitions = 999) (Dolédec & Chessel 1994). To investigate trait patterns in relation to mesh size along the environmental gradient, we conducted two separate CoI analyses; one on the Inner area stations, and one on the Outer area stations. This was done to best elucidate patterns in the two areas, and to prevent the uneven abundance distribution in the inner archipelago to mask the more even pattern (lower variability) of the outer archipelago. BTA was thus not conducted on the Middle area, as we wanted to highlight the opposite ends of the range of environmental and faunal abundance. Prior to the analysis, down weighting of abundant taxa was done using square-root transformation. The scores were plotted on ordination maps, with each point representing the abundance-weighted biological trait composition of each station. All analyses were done in the R environment (R Development Core Team 2009).
Table 2. Biological traits (10) and modalities (45) ascribed to species and used in the BTA. Labels listed correspond to trait modalities in Fig. 5.

<table>
<thead>
<tr>
<th>Biological traits</th>
<th>Trait modalities</th>
<th>Labels</th>
<th>Explanations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean size</td>
<td>0.1–1 mm</td>
<td>VS</td>
<td>Very small</td>
</tr>
<tr>
<td></td>
<td>1–5 mm</td>
<td>S</td>
<td>Small</td>
</tr>
<tr>
<td></td>
<td>5 mm–1 cm</td>
<td>SM</td>
<td>Small-medium</td>
</tr>
<tr>
<td></td>
<td>1–3 cm</td>
<td>M</td>
<td>Medium</td>
</tr>
<tr>
<td>Body design</td>
<td>Vermiform</td>
<td>Vermi_uns</td>
<td>Wormlike, lacking true segments</td>
</tr>
<tr>
<td></td>
<td>unsegmented</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Vermiform</td>
<td>Vermi-seg</td>
<td>Wormlike, semi-independent units</td>
</tr>
<tr>
<td></td>
<td>segmented</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bivalved</td>
<td>Bivalved</td>
<td>Shell with two valves jointed by a ligament</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Turbinated</td>
<td>Turbinate</td>
<td>Whorled shell</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Articulated</td>
<td>Articulate</td>
<td>Jointed, arthrous</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Larval type</td>
<td>Planktotrophic</td>
<td>Planktotrophic</td>
<td>Feeding on materials captured from the plankton</td>
</tr>
<tr>
<td></td>
<td>Lecitotrophic</td>
<td>Lecitotrophic</td>
<td>Nourished on internal resources, yolk</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Direct development</td>
<td>Direct_dev</td>
<td>Direct_dev</td>
<td>Direct development of mini adults</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Living habit</td>
<td>Attached</td>
<td>Attached</td>
<td>Adherent to substratum (&gt;95% of adult time)</td>
</tr>
<tr>
<td></td>
<td>Tube-dweller</td>
<td>Tube_dweller</td>
<td>In or on sediment, in water column</td>
</tr>
<tr>
<td></td>
<td>Burrow_dweller</td>
<td>Burrow_dweller</td>
<td>In or on sediment, in water column</td>
</tr>
<tr>
<td></td>
<td>Free-living</td>
<td>Free</td>
<td>In or on sediment, in water column</td>
</tr>
<tr>
<td>Environmental position</td>
<td>Infauna (&gt;5 cm)</td>
<td>Inf_deep</td>
<td>Living within substrate, deeper than 5 cm</td>
</tr>
<tr>
<td></td>
<td>Infauna middle (2–5 cm)</td>
<td>Inf_middle</td>
<td>Living within substrate, between 2 and 5 cm</td>
</tr>
<tr>
<td></td>
<td>Infauna (top 2 cm)</td>
<td>Inf_top</td>
<td>Living within top 2 cm of substrate</td>
</tr>
<tr>
<td>Epibenthic</td>
<td>Epibenthic</td>
<td>Epibenthic</td>
<td>Living on the surface of substrate</td>
</tr>
<tr>
<td>Benthic-pelagic</td>
<td>Bent_pel</td>
<td>Bent_pel</td>
<td>Living in the water column but (primarily/occasionally) feeds on the bottom</td>
</tr>
<tr>
<td>Feeding habit</td>
<td>Detritivore</td>
<td>Detritivore</td>
<td>Feeds on detritus</td>
</tr>
<tr>
<td></td>
<td>Omnivore</td>
<td>Omnivore</td>
<td>Feeds on mixed diet of plant and animal material</td>
</tr>
<tr>
<td></td>
<td>Herbivore</td>
<td>Herbivore</td>
<td>Feeds on plants</td>
</tr>
<tr>
<td></td>
<td>Carnivore</td>
<td>Carnivore</td>
<td>Feeds on animals (predator)</td>
</tr>
<tr>
<td></td>
<td>Scavenger</td>
<td>Scavenger</td>
<td>Feeds on dead organic material</td>
</tr>
<tr>
<td>Resource capture method</td>
<td>Jawed</td>
<td>Jawed</td>
<td>Jaws, mandibles</td>
</tr>
<tr>
<td></td>
<td>Siphon</td>
<td>Siphon</td>
<td>Both with and without jaws</td>
</tr>
<tr>
<td></td>
<td>Tentaculate</td>
<td>Tentaculate</td>
<td>Temporary (e.g. Mytilus edulis)</td>
</tr>
<tr>
<td></td>
<td>Pharynx</td>
<td>Pharynx</td>
<td>Both with and without jaws</td>
</tr>
<tr>
<td></td>
<td>Radula</td>
<td>Radula</td>
<td>Rasping</td>
</tr>
<tr>
<td>Mobility</td>
<td>Sessile</td>
<td>Sessile</td>
<td>Temporary (e.g. Mytilus edulis)</td>
</tr>
<tr>
<td></td>
<td>Semi-mobile</td>
<td>Semi_mobil</td>
<td>Both with and without jaws</td>
</tr>
<tr>
<td></td>
<td>Mobile</td>
<td>Mobil</td>
<td>Both with and without jaws</td>
</tr>
<tr>
<td>Movement method</td>
<td>Byssus</td>
<td>Byssus</td>
<td>Occasional movement with byssus threads</td>
</tr>
<tr>
<td></td>
<td>Swimmer</td>
<td>Swimmer</td>
<td>Fins, legs, appendages via undulatory movement</td>
</tr>
<tr>
<td></td>
<td>Raft/drift</td>
<td>Raft_drift</td>
<td>Rafting on e.g. algal mats, drifting</td>
</tr>
<tr>
<td></td>
<td>Crawler</td>
<td>Crawler</td>
<td>On substrate via muscles, legs or appendages</td>
</tr>
<tr>
<td></td>
<td>Burrower</td>
<td>Burrower</td>
<td>Lives and or moves in a burrow</td>
</tr>
<tr>
<td></td>
<td>Tube-builder</td>
<td>Tube_builder</td>
<td>Lives and moves in a tube</td>
</tr>
<tr>
<td>Sediment transportation</td>
<td>No transport</td>
<td>No_trans</td>
<td>No transport</td>
</tr>
<tr>
<td></td>
<td>Diffusive mixing</td>
<td>Diff_mixing</td>
<td>Random diffusive transport (e.g. reworking, excavation)</td>
</tr>
<tr>
<td></td>
<td>Surface deposition</td>
<td>Surf_deposition</td>
<td>Surface deposition of particles, ‘regeneration’ (e.g. excavation, egestion)</td>
</tr>
<tr>
<td></td>
<td>Conveyer belt transport</td>
<td>Conv_belt_trans</td>
<td>Translocation of sediment, depth to surface (e.g. egestion, excavation, defecations)</td>
</tr>
<tr>
<td></td>
<td>Reverse conveyer</td>
<td>Rev_conv_belt_trans</td>
<td>Subduction of particles from surface to depth (e.g. egestion, excavation)</td>
</tr>
</tbody>
</table>

Results

Basic community parameters

Benthic faunal assemblages in the studied areas of the Åland archipelago consisted of 30 species/taxa (Table 3). In the Inner area, the zoobenthic assemblage was dominated by gastropods and oligochaetes, typically occurring on muddy bottoms. Macoma balthica was also abundant and dominated by biomass. In the Middle area, the assemblage was similar but M. balthica dominated both numerically and by biomass. The invasive polychaete Marenzelleria sp. was relatively abundant in this area. The Outer area was
Table 3. Species list of the soft-bottom communities in the three archipelago areas (Inner, Middle and Outer) from both shallow and deep samples. X indicates if a species was present. Total number of species on shallow versus deep stations are given at the bottom of the table. Total # spp, total number of species in each area.

<table>
<thead>
<tr>
<th>Species/taxa</th>
<th>Inner area</th>
<th>Middle area</th>
<th>Outer area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Shallow</td>
<td>Deep</td>
<td>Shallow</td>
</tr>
<tr>
<td>Nemertea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyanophthisma obscura</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Priapulida</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Halicryptus spinulosus</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annelida</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Hamathoe sarsi</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Manayunkia aestuaria</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Marenzelleria spp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Hediste diversicolor</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Pygospio elegans</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Molusca</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Cerastoderma glaucum</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macoma balthica</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Mytilus edulis</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Hydrobia spp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Radix spp.</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Limapontia capitata</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Potamopyrgus</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>antipodarum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Theodoxus fluviatilis</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arthropoda</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acarina</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Semibalanus</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>limprvis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Idotea chelipes</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Jaera abdorlons</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Gammanus sp.</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leptocheius pilosus</td>
<td>X</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Monoporeia affinis</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corophium volutator</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saduria entomon</td>
<td>X</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Neomyis integer</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Chironomus plumosus</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Total shallow versus deep</td>
<td>16</td>
<td>11</td>
<td>19</td>
</tr>
<tr>
<td>Total # spp</td>
<td>18</td>
<td>22</td>
<td>19</td>
</tr>
</tbody>
</table>

Table 4. Results of paired t-test analysis of mesh size effects on number of species, abundance and biomass in the Inner, Middle and Outer areas.

<table>
<thead>
<tr>
<th>Species</th>
<th>df</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inner archipelago</td>
<td>29</td>
<td>9.497</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Middle archipelago</td>
<td>29</td>
<td>15.56</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Outer archipelago</td>
<td>34</td>
<td>11.29</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Abundance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inner archipelago</td>
<td>29</td>
<td>6.595</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Middle archipelago</td>
<td>29</td>
<td>7.236</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Outer archipelago</td>
<td>34</td>
<td>8.253</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Biomass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inner archipelago</td>
<td>29</td>
<td>5.373</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Middle archipelago</td>
<td>29</td>
<td>8.142</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Outer archipelago</td>
<td>34</td>
<td>9.106</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

characterized by *M. balthica* and other bivalves (*Mytilus edulis* and *Cerastoderma glaucum*) together with *Marenzelleria* sp. The amphipod *Monoporeia affinis* was also common in this area. As both the shallow and the deep stations in all areas showed identical patterns regarding species number, abundance and biomass (P > 0.05, unpaired t-test), the two depth zones were pooled in the statistical analysis.

The number of species found in each area was significantly lower using the 1.0-mm mesh than the 0.5-mm mesh. In the Inner area, 18 species were found using the 0.5-mm mesh and 14 using the 1.0-mm mesh. In the Middle area, 22 species were recorded (19 with the larger mesh alone). The Outer area had the highest total species number: 28 with the 0.5-mm mesh and 27 with the 1.0-mm mesh (Table 3). The mean number of species was significantly higher using the 0.5-mm mesh compared with the 1.0-mm mesh (P < 0.0001; paired t-test) in all archipelago areas (Table 4). In the overall analysis using a 2-way ANOVA there was a significant difference in species number both between the sieves (P < 0.0001) and between the areas (P < 0.0001) (Table 5; Fig. 2A).

The total abundance values were significantly higher with the 0.5-mm mesh than with the 1.0-mm mesh in all areas (P < 0.0001; paired t-test) (Table 4). For both mesh sizes the abundance was lowest in the Inner area and highest in the Outer area. In the overall analysis using a 2-way ANOVA there was a significant difference in abundance both between sieves (P < 0.0001) and among areas (P = 0.0162) (Table 5; Fig. 2B).

Biomass values were also lowest in the Inner area and highest in the Outer area, and they were significantly higher in the 0.5-mm mesh fraction in all areas (P < 0.0001; paired t-test) (Table 4). In the overall analysis using a 2-way ANOVA there was a significant difference in abundance both between sieves (P < 0.0001) and among areas (P = 0.0043). There was also a significant interaction (P = 0.0043) between mesh and area (Table 5; Fig. 2C).

In all areas, both the abundance and the biomass estimates of the numerically dominant species were reduced significantly when using only the 1.0-mm mesh (Fig. 3).
Zoobenthos as an environmental quality element

Table 5. Results of 2-way ANOVA analysis of mesh size effects on number of species, abundance and biomass in the Inner, Middle and Outer areas.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of species</td>
<td>4</td>
<td>101.8</td>
<td>25.45</td>
<td>3.99</td>
<td>0.031</td>
</tr>
<tr>
<td>Mesh</td>
<td>1</td>
<td>83.44</td>
<td>83.44</td>
<td>149.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Area</td>
<td>2</td>
<td>172.9</td>
<td>86.45</td>
<td>25.50</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Interaction</td>
<td>2</td>
<td>0.822</td>
<td>0.411</td>
<td>0.735</td>
<td>0.4947</td>
</tr>
<tr>
<td>Subjects (matching)</td>
<td>16</td>
<td>54.25</td>
<td>3.390</td>
<td>6.063</td>
<td>0.0004</td>
</tr>
<tr>
<td>Residual</td>
<td>16</td>
<td>8.948</td>
<td>0.559</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abundance</td>
<td>4</td>
<td>60,830,000</td>
<td>15.2</td>
<td>35.34</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Mesh</td>
<td>1</td>
<td>60,830,000</td>
<td>60,830,000</td>
<td>15.2</td>
<td>35.34</td>
</tr>
<tr>
<td>Area</td>
<td>2</td>
<td>55,890,000</td>
<td>27,950,000</td>
<td>15.2</td>
<td>35.34</td>
</tr>
<tr>
<td>Interaction</td>
<td>2</td>
<td>6,332,000</td>
<td>3,166,000</td>
<td>15.2</td>
<td>35.34</td>
</tr>
<tr>
<td>Subjects (matching)</td>
<td>16</td>
<td>82,930,000</td>
<td>5,183,000</td>
<td>15.2</td>
<td>35.34</td>
</tr>
<tr>
<td>Residual</td>
<td>16</td>
<td>27,540,000</td>
<td>1,721,000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>4</td>
<td>18.00</td>
<td>18.00</td>
<td>33.67</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Mesh</td>
<td>1</td>
<td>18.00</td>
<td>18.00</td>
<td>33.67</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Area</td>
<td>2</td>
<td>67,730</td>
<td>33,860</td>
<td>15.2</td>
<td>35.34</td>
</tr>
<tr>
<td>Interaction</td>
<td>2</td>
<td>3,332,000</td>
<td>1,666,000</td>
<td>15.2</td>
<td>35.34</td>
</tr>
<tr>
<td>Subjects (matching)</td>
<td>16</td>
<td>69,230</td>
<td>4,327</td>
<td>15.2</td>
<td>35.34</td>
</tr>
<tr>
<td>Residual</td>
<td>16</td>
<td>8,553</td>
<td>0.5345</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Oligochaetes, which were abundant in the Inner and Middle area, were reduced by 96–99% when using only a 1.0-mm mesh size. Ostracods were reduced by 97% in the Inner area and by 100% in the Middle and Outer areas, and polychaetes, namely Marenzelleria sp, were reduced by 75% in the Outer area when using the 1.0-mm mesh. The Baltic clam, M. balthica, dominated in all areas by biomass (58–78%), but abundance estimates were reduced significantly, when the 1.0-mm mesh was used.

The size distribution of M. balthica was affected by mesh size: when the 1.0-mm mesh was used, the number of individuals measuring 1 and 2 mm in size (i.e. the annual spat) was reduced markedly. In the Inner area, 96% of 1-mm-sized M. balthica and 32% of 2-mm-sized individuals were lost using the 1.0-mm mesh. In the Middle area, the corresponding values were 100% (1 mm) and 45% (2 mm), and in the Outer area 99% (1 mm) and 47% (2 mm). Both sieves captured equal numbers of clams of size classes 3 mm and larger. Thus the main difference was the loss (or underestimation) of recruiting individuals, which may affect the evaluation of the ecological status of a benthic habitat.

Ecological status

This survey showed that zoobenthos as an ecological quality element resulted in evaluation of a relatively good overall status (Fig. 4). All but one sampled station and all three areas were classified as ‘good’ (1.0-mm mesh) or ‘high’ (0.5-mm mesh) ecological status. The BBI itself was highest in the Outer area, but as the class boundaries are different for the different areas (and depths), the ecological status was similar to the other areas.

Biological traits

The CoI analyses for the Inner and Outer area stations illustrated the relationship between taxon composition and abundance at shallow and deep stations with the two mesh sizes, and biological traits. A clear difference in the trait composition was identified between the two archipelago areas in terms of number of modalities found. In the Inner area, no scavengers (feeding type) or tube builders (movement type) were registered, resulting in 43 modalities compared with 45 in the Outer area.

The significance of the resulting correlation (noted R value in Table 6) between the two sets of coordinates was...
examined with the Monte-Carlo test. The test showed that the Outer area had a borderline significance for a non-random pattern (RV = 0.254, P = 0.071). However, the opposite was true for the Inner area (RV = 0.268, P = 0.297). Still, we chose to present both results to illustrate the trend and more evident pattern in the Outer area compared with the Inner one, considering the higher species diversity and more equal abundance of species (Figs 5 and 6).

In the BTA of the Outer area, axes 1 and 2 of the co-inertia analysis accounted for 90% (65% and 25%, respectively) of the variability in biological trait composition between the stations. A clear separation between shallow and deep stations along the second axis could be seen, especially for the outer archipelago (Fig. 6). Along the first axis of the ordination, the two mesh sizes were separated for both shallow and deep stations, the larger size being grouped more towards the centre and the smaller mesh size samples more spread out, i.e. separated from the others (Figs 5 and 6). This means that the mesh size of the sieve influences the functional analysis, and implies that for a reliable analysis of biological traits in these relatively species-poor assemblages, information is needed for all species that can be sampled (Fig. 6). The shallow areas were characterized by small-sized detritivores (species obtaining food through suspension, surface and/or sub-surface feeding) with a diffusive sediment transport mode (taxa such as *Macoma balthica*, *Potamopyrgus antipodarum* and *Chironomidae*). The deeper areas showed a compilation of detritivores performing no sediment
transport (e.g. *Mytilus edulis*) and omnivorous tube-builders performing reversed conveyor belt transport (taxa such as *Marenzelleria* sp. and *Pygospio elegans*).

**Discussion**

The results from this study showed that the choice of mesh size (1.0 or 0.5 mm) in the sieve affected all basic community parameters, in all areas and at both depths (shallow and deep). The number of species, abundance and biomass were all significantly reduced when using the larger mesh size alone. The number of species dropped by 42% in the Inner and Middle area, and by 25% in the Outer area. Also, some species, such as oligochaetes and polychaetes, were sampled in significantly reduced numbers with the 1.0-mm mesh. Small-sized species, such as ostracods and small polychaetes (e.g. *Manayunkia aestuaria*), as well as juveniles of many species, were lost completely when the larger mesh size was used. In other words, the benthic community may look very different when using different mesh sizes. When many species are seemingly lost (due to large mesh size) from an area with naturally low biodiversity, the ecological assessment and representation of that assemblage will be wrong. It is impossible to obtain a representative picture of the overall biodiversity and ecosystem functioning if only the most widespread and most abundant species are studied (Elingsen *et al.* 2007).

The mesh size of sieve also had a significant effect on the registered population structure of the bivalve *Macoma balthica*, which is a key species in the Northern Baltic Sea (Segersträle 1962; Olafsson 1989). Population structure and recruitment success of the species are often used as indicators of the environmental conditions. Adult *M. balthica* are quite tolerant and can withstand stressed environmental conditions for some time, whereas juveniles are sensitive even to small disturbances in the environment (Bonsdorff *et al.* 1995). When the 1.0-mm mesh was used, most juveniles (1–2 mm in size) were lost, and thus the whole annual recruitment could be missed from any analysis. It is thus impossible to make estimates on recruitment success and population structure if the larger mesh size is used.

The estimate of the ecological status according to the EU-WFD is done using several different indices, and almost every country has developed an index of their own, suitable for their particular environment (Diaz *et al.* 2004; Zettler *et al.* 2007; Borja *et al.* 2009; Josefsson *et al.* 2009; Leonardsson *et al.* 2009). For the Northern Baltic Sea, BBI has been developed to account for the low salinity and low species numbers in the area (Perus *et al.* 2007). Due to the complex topography and the gradients

### Table 6. Main characteristics of co-inertia analyses.

<table>
<thead>
<tr>
<th></th>
<th>Axis</th>
<th>Covar</th>
<th>Var1</th>
<th>Var2</th>
<th>Iner1</th>
<th>Iner2</th>
<th>R value</th>
</tr>
</thead>
<tbody>
<tr>
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</table>

Covar, covariance between both sets of coordinates of co-inertia analysis; Var1, Inertia of the abundance data projected onto co-inertia axes; Var2, Inertia of the trait data projected onto co-inertia axes; R value, correlation between both sets of coordinates resulting from the co-inertia analysis; Iner1, maximum inertia projected onto axes of the simple analysis of abundance data (eigenvalues of centered PCA); Iner2, maximum inertia projected onto axes of the simple analysis of trait data (eigenvalues of FCA).
of salinity and exposure in the archipelago areas, the BBI has different class boundaries for different areas and depth-zones (Perus et al. 2007). In the Inner and Outer archipelago areas, the status was somewhat better in the shallow than in the deeper areas. In our study the ecological status was good or even high in all areas and depths, except for one deep station in the Inner area, where the status was moderate (0.5 mm) or bad (1.0 mm). Identifying the border between moderate and good is critical, as all water areas should have a good ecological status by 2015. In our study, the proportion of sites with a good ecological status was the same irrespective of mesh size. However, the status was generally somewhat better when a 0.5-mm mesh rather than a 1.0-mm one was used. Using a 1.0-mm mesh would certainly not overestimate the ecological status, and sometimes a conservative estimate may be desired. As the estimated ecological status using the BBI was uniformly and significantly higher using the 0.5-mm mesh than the 1.0-mm mesh, important ecological information is lost using only the larger mesh size. On the other hand, the more conservative estimate may be valid from a management point of view (Fig. 4). For the Åland archipelago, similar estimates of ecological status have been obtained using macrophytes as biological parameters (Söderström 2008).

BTA was found to be a useful approach in the coastal areas of the Northern Baltic Sea. Our analysis – one of the first in this region (but see Boström et al. 2010) – serves to highlight the issue of time consumption versus sampling effort (e.g. mesh size choice) and reliability of comprehensible results in management. When choosing a less time-consuming and thereby more economical sampling method (e.g. 1.0-mm mesh size), the ecological perception of a system is adversely affected. Although the larger mesh size did not overestimate the ecological status, the ecological functionality of the system in question could be wrongly interpreted if all species and their functional traits are not covered. However, the application of functional multi-trait analyses, such as BTA, to species level or even more properly individual level, is still time-consuming, taxonomically difficult and needs further refinement (Albert et al. 2010). The difference in trait composition when using 0.5- or 1.0-mm mesh showed a significant trend, particularly in the Outer archipelago,
where the proportion of small-sized species is high. A functional approach to classifying and assessing habitat and ecosystem quality is generally agreed upon today and may be the most relevant for delivering ecosystem-based targets (Bremner 2008; Tillin et al. 2008). Discussion about drawbacks and problems still concerned with the approach have focused mainly on the operational measures of functioning, methods to best elucidate functioning and the extensive species-specific information required in analysis (Bremner et al. 2003, 2006a,b; Tillin et al. 2008). However, the scale on which functioning is studied is also significant (Hewitt et al. 2008). As shown in this study, it is particularly essential to consider the scale at which one samples, not only the spatial scale that concerns the design (e.g. between or within habitats and within landscapes). The choice of mesh size, and thereby inclusion or exclusion of both rare and common species in analysis, is essential to the conclusions of habitat quality, ecosystem stability and functioning.

The functional consequences of sampling method on the scale of mesh size of sieve, have not to our knowledge been thoroughly evaluated. Our findings suggest this can markedly affect the measurement of benthic functioning of coastal areas. We also show that it is important to differentiate between the shallow (<10 m; photic zone) and deeper (>10 m; euphotic zone) areas in complex archipelago areas, where the shoreline is long and topography is complex (Granö et al. 1999).

Concluding Remarks

Our results highlight how biological traits, in addition to species number and biomass, can play a key role in analyzing ecosystem structure and in assessment and classification of coastal systems, and for our understanding of the complexity of ecological functioning of these systems (Bremner 2008; Hewitt et al. 2008).

In conclusion, the ecological implications of using larger mesh sizes of the sieve (1.0 mm is recommended for the Baltic Sea in the WFD) instead of smaller is that, in shallow areas, individuals of small species and their particular traits are not sufficiently sampled, i.e. they may be lost in a functional perspective. In deeper areas, especially trait modalities linked to the essential process of
biorbution are lost. From an ecological point of view, a broader trait composition is obtained with 0.5-mm mesh sizes, generating a more reliable and complete picture of ecosystem functioning. We also show that combining traditional monitoring for the EU WFD with a functional analysis of the benthic assemblages strengthens our ability to interpret environmental quality, and thus increases the precision of our advice for management purposes.

Acknowledgements
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References


Assessment of benthic ecosystem functioning through trophic web modelling: the example of the eastern basin of the English Channel and the Southern Bight of the North Sea

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Abstract

Benthic organisms appear to be accurate proxies for assessing coastal ecosystem structures and changes due to climatic and anthropogenic stresses. Functional studies of benthic systems are relatively recent, mainly because of the difficulties in obtaining the basic parameters for each benthic compartment (i.e. detritus, bacteria, meiofauna and macrofauna). Our study focuses on the eastern basin of the English Channel and the Southern Bight of the North Sea. Trophic web modelling was used to assess the functioning of the three main benthic community assemblages. To test and assess the relative importance of factors assumed to influence trophic structure (geographical environment and sedimentary particle size distribution), the study area was subdivided into divisions defined a priori according to the two main structural factors of community distribution; geographic distribution and sedimentary patterns. Then, a steady state trophic model utilising the inverse method was applied to a diagram composed of eight compartments, including detritus, bacteria, meiofauna, macrobenthos and fish. For each compartment, six physiological parameters were assessed, based on our own data, empirical relationships and literature data. This method allowed estimation of the flux of matter and energy within and between the units of the benthic system and assessment of the amount of trophic energy stored in these units (available mostly to fish). Our results showed that suspension-feeders control most of the matter transfer through the macrobenthic food-web, except in the fine sand community, where deposit-feeders play a dominant role. The results also showed that, whatever the geographic area, trophic structure is strongly linked to the sedimentary conditions. As benthic communities are connected through hydrodynamics, a model of the entire eastern basin of the English Channel would appear to be acceptable. However, the main sediment types must be taken into account when establishing relationships between the functional units.
Introduction

Ecosystem functioning has become one of the main fields of interest in marine ecology (see Hooper et al. 2005 for a review). According to Christensen et al. (1996), ecosystem functioning includes three main phenomena: ecosystem properties (i.e. the different functional compartments of an ecosystem and the rates of the processes that link the compartments together), ecosystem goods (i.e. the direct market values of an ecosystem) and ecosystem services (i.e. the direct or indirect benefits that ecosystems provide to humans). Marine benthic communities were initially assessed using qualitative methods that identify the taxonomic composition of the community. Although such methods highlight environmental stress (Bilyard 1987) such as resistance to anthropogenic disturbances (Pearson & Rosenberg 1978), it is quite difficult to obtain information about the functioning of the ecosystem from these methods (Warwick et al. 2002). However, other methods based on quantitative examination have been developed to better investigate the function of benthic invertebrates in the ecosystem. These new tools include work on mesocosms (Solan et al. 2003), biological traits analysis (Bremner et al. 2006) or trophic web modelling (Chardy & Dauvin 1992). The trophic web modelling tool appears to be essential for synthesising data, developing theories and discriminating between alternative competing explanations of how ecosystems function (Underwood 1990, 1996). Among the different trophic web models already developed, steady-state/dynamic-process models provide the most explicit representation of trophic interaction (Whipple et al. 2000), particularly the steady-state inverse model (Chardy 1987; Vézina & Platt 1988; Vézina 1989).

The benthic communities in the eastern English Channel have been widely studied using both qualitative descriptive methods (Dauvin 1997a) and quantitative analyses (Kaiser et al. 1998; Ellien et al. 2000; Newell et al. 2001). However, few studies have addressed trophic relationships in this area, with those that have, focusing on local scales only (the Bay of Somme, Rybarczyk et al. 2003, and the Bay of Seine, Rybarczyk & Elkaim 2003). In this context, there is a need for large-scale assessment of energy flow and trophic structure of the system, which can be well approximated using trophic web modelling.

The main objective of this study was to test whether the trophic structure of benthic communities, through the relationships among benthic invertebrates, depends mainly on geography or on sediment type. Both of these factors are considered to have a strong correlation with hydrodynamic patterns, which influence the organisation of the benthic communities in the area (Dauvin 1997a). We utilised the inverse model simulation technique for this purpose, which estimates carbon flows through the benthic ecosystem; this was done using the quantitative dataset for a large spatial area in the eastern basin of the English Channel.

Material and methods

Study site

The area studied is the eastern basin of the English Channel and the southern part of the North Sea, called the Southern Bight. This epicontinental sea is a shallow water zone (maximum 50 m) that is subjected to a variety of hydrodynamic forces. The tidal range in the area is high, reaching about 9 m on the French coast of the Bay of Somme (Salomon & Breton 1991). The tidal current velocities are highly variable, usually being stronger near the French coast than the English coast (Salomon & Breton 1991). The water generally moves from the English Channel to the North Sea, although a long period of strong easterly winds can reverse this trend (Salomon & Breton 1991). These patterns are also modified by coastal geography and the presence of three estuaries (the Seine estuary, the Somme estuary and the Scheldt-Rhine-Meuse estuary complex). Local hydrodynamics creates particular structures, such as the gyres that retain the water masses in a restricted zone near the Barfleur Cape in the north-western part of the Bay of Seine and the Isle of Wright.

The particle size of the sediment is strongly correlated with the hydrodynamics described above, with a sedimentary gradient (Fig. 1) ranging from coarse sediments in the middle of the Dover Strait to fine sediments in the area’s bays and estuaries (Larsonneur et al. 1982). This differential sedimentation leads to a bio-sedimentary gradient from pebbles and gravel to fine sand in the places where five main communities have been identified previously (Cabioch & Glaçon 1975, 1977; Cabioch et al. 1978): (i) the pebble and gravel community with sessile epifauna and Ophiothrix fragilis (Echinodermata); (ii) the coarse sand community with Branchiostoma lanceolatum (Cephalochordata); (iii) the fine-to-medium clean sand community with Ophelia borealis (Polychaeta); (iv) the muddy fine sand community with Abra alba (Mollusca); and (v) the ‘muddy heterogeneous’ community with a mix of species from the pebble and gravel community, the coarse sand community and the muddy fine sand community. Additionally, the offshore English Channel is mainly composed of coarse sand to pebble substrates, whereas the fine sand is confined to bays and the littoral fringe.

Sampling strategy

Macrofaunal material was collected between 2006 and 2008 in an area ranging from the eastern basin of the
English Channel to the southern bight of the North Sea (from 0° longitude to the Franco-Belgian border). The main objective was to update the benthic invertebrate knowledge 30 years after the first extensive benthic sampling in the English Channel (during the RCP Manche survey, Cabioch & Glaçon 1975, 1977; Cabioch et al. 1978). The secondary objective was to supply the first quantitative description of the benthic communities over the entire area, to allow assessment of the trophic structure of the benthic communities and aid the complex planning and decision-making required for managing anthropogenic pressure in this dynamic area (Martin et al. 2009).

Quantitative samples were taken with a 0.25-m² Hamon grab (two samples for the macrobenthic fauna and one sample for sediment). As our focus was on the macrobenthic component of the total benthic biomass, samples were sieved through a 2-mm mesh (which allows more than 95% of macrobenthic biomass to be retained, see Ghertsos 2002). The samples were then sorted, and the organisms were identified to species level where feasible. Biomass was determined with the ash-free-dry-mass method to reduce the variation within and between species due to gut content (van der Meer et al. 2005).

To extend and improve the spatial resolution of the study area, two other quantitative databases were also included in this study. The first one covers the entire Bay of Seine (see Ghertsos 2002 and Dauvin & Ruellet 2008 for details). The second covers the French coast from the Pointe d’Ailly to the Belgium border (see Desroy et al. 2003 for details). Thus, a total of 403 quantitatively sampled sites from the Bay of Seine to the Southern Bight were available for trophic web analysis (Fig. 1). All macrofaunal/sediment material was gathered and processed using the same basic methods.

Modelling strategy
Many trophic web models have been applied to very large spatial areas, such as the North Sea (Mackinson & Daskalov 2007), the Irish Sea (Lees & Mackinson 2007) and the Baltic Sea (Harvey et al. 2003). To test whether such a large-scale model would be appropriate for the eastern basin of the English Channel, we examined trophic structure at different spatial scales. To accomplish this, an a priori division of the area was made based on the two main factors assumed to influence the benthic communities and their organisation (taking into account that the sediment factor is influenced by hydrodynamics which, in turn, is influenced by the geographic factor). The area was split into three geographic divisions (Bay of Seine, Dover Strait and North Sea) and three main sediment divisions following the dominant sediment types in the area (i.e. gravel and pebbles, coarse sand and fine sand).
(Fig. 1). Following Kröncke et al. (2004) and Kröncke (2006), the expression ‘geography’ here refers to all environmental variables acting over a spatial area (e.g. hydrodynamism, freshwater inputs, food supply and quality). Simulations were then run for the three geographic divisions and the three sediment divisions, and the outputs from these simulations were compared. Simulations were also run for each sediment type within the three geographic divisions. Thus, there were three sub-divisions for each division, except for the Bay of Seine, which lacks fine sand communities, resulting in a total of eight subdivisions in the study area.

Model formulation and principles

Trophic web structure was assessed using a trophic inverse model originally introduced by Vézina & Platt (1988) for the pelagic food-web of the English Channel and the Celtic Sea, which since then has been used by a number of authors in various marine ecosystems (Chardy et al. 1993a,b; Niquil et al. 2001; Leguerrier et al. 2003). The inverse method-based steady state model is a diagnostic method that, although it does not incorporate a temporal dimension, can provide a comprehensive description of the general trophic structure of an ecosystem. Our model is composed of eight biotic and abiotic compartments and is used to estimate the carbon flows resulting from secondary benthic production (Chardy & Dauvin 1992). The information required for direct estimation of most of the flows in such a food-web model is either not available or is very difficult to obtain. Thus, it seems more appropriate to use the flow balance principle, as the inputs are equal to the sum of the outputs and the rate of the biomass standing stock is under steady-state conditions (Vézina & Platt 1988).

This kind of inverse problem can be encountered in all research fields where the number of observations is less than the number of parameters that need to be known in order to describe the system (Vézina & Platt 1988). To solve this kind of inverse problem, Tarantola & Valette (1982) have proposed three fundamental conditions:

- Having a given state of information about the values of the observed parameters.
- Having information about the unknown parameters (we assume that an a priori decision is made about the unknown parameter values associated with an interval of confidence).
- Having the necessary information about the theoretical relationships between known data and unknown parameters.

In trophic web studies, the known data are estimations of the biomass standing stock in each benthic compartment (i.e. the biomass values of each compartment); the unknown parameters are the physiological parameters (e.g. ingestion rate, egestion rate). These parameter values are taken from data reported in the literature and/or from empirical relationships. From these data, a mean value is calculated for each parameter, and the model allows this value to move between an upper and a lower bound, which are determined by the confidence interval of the mean. The relationships linking these bounds are mainly the trophic preferences. This method yields the annual average of the carbon flows connecting the different functional compartments.

The functional diagram (Fig. 2) of the benthic compartment needs to be simple enough to fit the different benthic communities but also accurate enough to express the knowledge about the benthic compartments in the eastern basin of the English Channel and the Southern Bight of the North Sea. We define the functional compartments based on the available knowledge about the trophic compartment and on the size of the benthic organism (this criterion is mainly used to divide the benthic organisms between macrofauna and meiofauna compartments). This is a steady-state model, an annual average representation of biomasses and flows. Temporal biomass variations are not considered (dX/dt) = 0. The steady-state hypothesis is expressed by the general equation:

\[
\frac{dX_i}{dt} = \sum_{j=1}^{m} \left( I_{i,j} X_j C_{ji} \right) \left( 1 - E_{ii} \right) - \left( M_{ii} + R_{ii} \right) X_i = 0
\]

where \( \sum F_{ji} \) sum of the flows going from ‘\( j \)’ to ‘\( i \)’ (sum of the inputs, consumption of ‘\( i \)’); \( \sum F_{ip} \) sum of the flows going from ‘\( i \)’ to the other compartment ‘\( p \)’ and to the general outputs of the system (sum of outputs: preditory mortality, non-preditory mortality, egestion and respiration).

At the scale of compartments, the steady-state is expressed by the balance of the processes:

\[
\frac{dX_i}{dt} = \sum_{j=1}^{m} \left( I_{i,j} X_j C_{ji} \right) \left( 1 - E_{ii} \right) - \left( M_{ii} + R_{ii} \right) X_i - \sum_{p=1}^{n} \left( I_{p,j} X_p C_{ip} \right) = 0
\]

where: \( j = 1…m \), is \( m \) number of prey available for ‘\( i \)’; \( p = 1…n \), is \( n \) number of predators of ‘\( i \)’; \( I_i \) is annual ingestion rate of ‘\( i \)’; \( X_i \) is the biomass of the compartment ‘\( i \)’; \( C_{ji} \) is the feeding preference of the compartment ‘\( i \)’ for the resource ‘\( j \)’; \( E_{ii} \) is the annual egestion rate of ‘\( i \)’; \( M_{ii} \) is the annual non-predatory mortality rate of ‘\( i \)’; and \( R_{ii} \) is the annual respiration rate of ‘\( i \)’.

The annual production/biomass (P/B) ratios for all seven compartments, from which the physiological param-
Fig. 2. Functional diagram of the benthic ecosystem in the eastern part of the English Channel and the southern Bight of the North Sea. Trophic fluxes: faeces + non-predatory mortality; Respiration.

Not all P/B values were obtained with empirical data. As only the largest benthic organisms (2-mm sieve) were considered in this study, juveniles and small species were ignored for the biomass estimation. All the large species were assumed to be adults and we therefore decided to take the smallest P/B found for each compartment. For bacteria, we chose a value of 3700, which is an intermediate value between that of 9470 proposed by Mackinson & Daskalov (2007) and 167 proposed by Améziane et al. (1996). The P/B of 0.95 for the deposit-feeders and 0.8 for the suspension-feeders are the means of the P/B for all the deposit-feeder species and the P/B of bivalves, as calculated by several authors working in highly different environments (Warwick & Price 1975; Warwick et al. 1978; Warwick 1980; Warwick & George 1980; George & Warwick 1985). The deposit-feeder value agrees with the P/B of the compartment ‘small infauna (polychaetes)’ proposed by Mackinson & Daskalov (2007). The lowest meiofauna P/B value (9) proposed in the literature by Gerlach (1971), was chosen to illustrate the auto-predation phenomenon that occurs in this group. The carnivore P/B value (0.65) was the calculated mean of the polychaete predator P/B value given by George & Warwick (1985) for a hard-bottom community. The omnivore compartment has a value close to carnivores (0.7). This value was also chosen based on the mean omnivore values calculated from those given by George & Warwick (1985) (between 0.2 and 0.4) and those used by Mackinson & Daskalov (2007) (0.55 for the ‘crab’ compartment and 3 for the ‘shrimp’ compartment).

The respiration rate was derived from the allometric equation developed by Schwinghamer et al. (1986): \( \log_{10} Ra = 0.367 + 0.993 \log_{10} Pa \), where Ra is the annual respiration rate (in kCal year\(^{-1}\)) and Pa is the annual production rate (in kCal year\(^{-1}\)). The egestion parameter was determined from values found in the literature. Ingestion rates were deduced from P/B values, assuming that egestion and respiration are known. The biomass of the four macrobenthic compartments – deposit-feeder & mixed, suspension-feeder, carnivore and omnivore – was taken from the present work. The bacteria biomass was considered to be similar to values provided by Améziane et al. (1996) for the Bay of Morlaix in the Western English Channel and the meiofauna and fish biomasses were considered to be similar to those in the North Sea (Mackinson & Daskalov 2007). These three compartments...
Table 1. Main characteristics of the functional compartments of the different divisions and sub-divisions in the eastern part of the English Channel and the Southern Bight of the North Sea and values of biotic rates used in the simulations.

<table>
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<td>0.25</td>
<td>0.17</td>
<td>3800</td>
<td>1100</td>
<td>0.08</td>
<td>0.25</td>
<td>0.26</td>
</tr>
<tr>
<td>DSGP</td>
<td>0.17</td>
<td>4000</td>
<td>1100</td>
<td>0.08</td>
<td>0.3</td>
<td>0.15</td>
<td>0.15</td>
<td>3700</td>
<td>1100</td>
<td>0.075</td>
<td>0.25</td>
<td>0.15</td>
<td>0.06</td>
<td>3700</td>
<td>1100</td>
<td>0.075</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td>BSGP</td>
<td>0.17</td>
<td>3700</td>
<td>1100</td>
<td>0.07</td>
<td>0.25</td>
<td>0.25</td>
<td>0.17</td>
<td>3700</td>
<td>1100</td>
<td>0.07</td>
<td>0.25</td>
<td>0.25</td>
<td>0.17</td>
<td>3700</td>
<td>1100</td>
<td>0.065</td>
<td>0.3</td>
<td>0.3</td>
</tr>
</tbody>
</table>

B = annual mean biomass in g cm⁻² year⁻¹; P/B = turn-over rate in year⁻¹; I = ingestion in year⁻¹; R = respiration per year; M = non predatory mortality per year; E = egestion; NS = North Sea; DS = Dover Strait; BS = Bay of Seine; GP = gravel and pebbles sediment; C = Coarse sand sediment; F = Fine sand sediment; Tct = Total area; B = benthic bacteria; DF&M = Deposit-Feeder and Mixed; S = Suspension-Feeder; Me = Meiofauna; C = Carnivore; O = Omnivore; F = Fish.
(bacteria, meiofauna and fish) had the same biomass in each of the models applied for each division and subdivision of our study area. The physiological parameters are presented in Table 1.

Diet preference values were determined according to three different sources of information. Diet data were preferentially taken from experimental studies of gut contents for particular species (e.g. Fauchald & Jumars 1979; Langdon & Newell 1990) or groups of species (Lopez et al. 1989). Data from stable isotope studies were also used, where available (e.g. Le Loc’h & Hily 2005; Carlier et al. 2007). Finally, some remaining missing data were also taken from previous published trophic web models (e.g. Chardy & Dauvin 1992; Améziane et al. 1996; Leguerrier et al. 2003).

To assess and compare the functioning of each sector of the eastern basin of the English Channel and the Southern Bight of the North Sea, simulations were based on the same initial mean values for ingestion, egestion, P/B, non-predatory mortality and initial matter input. However, the model was allowed to select each parameter’s value within the confidence interval of the mean for each simulation. The values of biomass and respiration were fixed for each simulation (i.e. the model was not allowed to change them). The simulation outputs for each division and sub-division were the average annual carbon flows per square metre that link all functional compartments.

Compartment status

We sub-divided the benthic ecosystem into eight compartments defined by feeding mode and size. The general structure of the diagram (Fig. 2) uses the main components previously proposed by Chardy et al. (1993a,b), to which we added the omnivore and the demersal fish compartments. Omnivores have been separated from carnivores because, as scavengers that recycle organic matter, they have a different function in the ecosystem. The fish compartment was added to ‘close’ the benthic trophic web.

- **Fi.** The initial flow. This is the necessary amount of organic matter for the whole ecosystem to function. It translates as the net sedimentation of pelagic detritus (dead phytoplankton cells, faeces) that can be used by benthic organisms.
- **X1.** Detritus. This is an inactive compartment. It appears to be a cross-road from which the carbon is passed to higher levels, receiving matter from outside the system (Fi) as well as from inside the trophic web itself (i.e. egestion, non-predation mortality).
- **X2.** Bacteria. Benthic bacteria are associated with particles of detritus.
- **X3.** Deposit-feeders and Mixed. This group includes strict deposit-feeders that feed only on detritus at the sediment layer, but also organisms that are able to feed as either deposit-feeders or suspension feeders. No distinction has been made between sub-surface and surface deposit-feeders, as they all feed on detritus and bacteria.
- **X4.** Suspension-feeders. This group is mainly composed of filter-feeding bivalves that feed in the water–sediment interface. They feed more on fresh matter than the deposit-feeder group does (e.g. phytoplankton, microphytobenthos, fresh detritus). They can also feed on bacteria bound to particles. Langdon & Newell (1990) have estimated that the bacteria could represent 3.5 and 25.8% of carbon needs in oysters and mussels, respectively. As phytoplankton is not represented in our model, the trophic preference of suspension-feeders was integrated by including a preference for benthic bacteria and a lesser egestion.
- **X5.** Meiofauna. Nematodes are often the most abundant organisms in the permanent meiofauna (Boaden 2005). Most of the meiofaunal organisms feed on detritus and bacteria, but some of them are also carnivores, including cannibalism.
- **X6.** Carnivores. This group is composed of predators and carnivores. They only feed on living or almost living organisms; motile nemertean and polychaete predators are the most representative organisms in this group.
- **X7.** Omnivores. This group consists of species that have an opportunistic feeding mode. These species will always prefer to feed on fresh material, but they can also feed as scavengers on dead bodies and detritus. This group is mainly composed of decapods and some gastropods.
- **X8.** Fish. The only vertebrate compartment of this trophic web, this group is composed of carnivorous demersal fish that feed on every macrobenthic compartment in the model.

Results

The sum of the average biomass values of benthic invertebrates in the whole study area is 5.253 g/cm², composed mostly of suspension-feeders (77%), then deposit-feeders and mixed (8%), with omnivores and carnivores having similar proportions (7.5 and 6%, respectively) and meiofauna having the smallest proportion (1.5%).

To assess the trophic structure of each division and subdivision of our study area, the first step was to identify the preferred trophic pathway (i.e. the main compartments through which most of the carbon will transit). The fish compartment (X8) is always the most important predator...
in each of the macrobenthic compartments. To obtain a more accurate picture of the carbon flow through the macrobenthic compartments, we did not take the fish compartment into account when determining the trophic pathways; fish were only considered as the top predators, which came into play following one of the two last macrobenthic compartments (i.e., carnivore and omnivore).

The preferential trophic pathway for the whole study area begins in the detritus compartment. Most of the carbon in this first compartment is absorbed by the bacteria in the second compartment (87.1% of the uptake); the suspension-feeders feed mainly on bacteria (72.4%). The main predators of the suspension-feeder compartment are the fish (59.4%), although the main benthic invertebrate's predators are the omnivores (21.8%). Thus, the total area was considered to have a ‘suspension-feeder/omnivore’ trophic pathway (Fig. 3A).

Comparison of the divisions

The sum of the average biomass values of benthic invertebrates from each trophic compartment in the different divisions of our study area reached values of 0.462, 0.794 and 0.508 gC·m⁻² for the three geographical divisions (North Sea, the Dover Strait and the Bay of Seine, respectively) and 0.419, 0.917 and 0.761 gC·m⁻² for the three main sediment divisions (gravel and pebbles, coarse sand and fine sand, respectively).

In the geographic divisions, suspension-feeders were always dominant in terms of biomass proportions, ranging from 33.3% in the North Sea to 73.7% in the Dover Strait. This pattern was also observed in the sediment divisions, where the biomass proportions of the suspension-feeders were always between 59.2% in the gravel and pebbles and 69.1% in the fine sand. The highest biomass proportion for the deposit-feeders and mixed was found in the North Sea geographic division, with 18.6%, and in the fine sand sediment division, with 10.9%. Carnivores and omnivores have quite similar proportions in the Dover Strait (4.4 and 5%, respectively) and in the North Sea (16.5 and 13.6%, respectively), but the carnivores clearly dominate (20.6%) the omnivores (9.8%) in the Bay of Seine. However, all the sediment divisions have quite similar proportions for these two compartments (8.1% for the carnivores and 8.6% for the omnivores in...
the gravel and pebbles, 1.9 and 4.4% in the coarse sand and 4.7 and 4.7% in the fine sand).

Like the trophic pathway for the whole study area, the Bay of Seine had a 'suspension-feeder/omnivore' pathway. However, the Dover Strait and the North Sea sites had a different type of trophic pathway, with both of them having a 'suspension-feeder/carnivore' pathway.

Each of the sediment divisions had a different type of trophic pathway (Table 2a). The gravel and pebbles division had the same 'suspension-feeder/carnivore' trophic pathway as the whole study area, the Dover Strait and the North Sea, denoted in this paper as TP1. The coarse sand division had the same 'suspension-feeder/omnivore' trophic pathway as the whole Bay of Seine, denoted TP2. Finally, the fine sand division had the pathway that differed the most, mainly because the principal primary consumers switch from being suspension-feeders to being deposit-feeders and mixed. This switch gives this division a 'deposit-feeder and mixed/carnivore' trophic pathway, denoted TP3.

### Discussion

Food-web studies and trophic network analysis provide powerful tools for identifying the global functional properties of benthic communities (Chardy et al. 1993a,b). New techniques for describing and quantifying the flows of organic matter between compartments have been developed at the same time as numerical methods such as trophic models. One of these numerical methods for flow network assessment in trophic web is the trophic inverse model used in this study. This model is based on an underlying inverse method (Chardy 1987), which states that the sum of inputs is equal to the sum of outputs (Vézina & Platt 1988).

Since this model arrived in the late 1980s (Vézina & Platt 1988; Vézina 1989; Chardy et al. 1993a,b) it has been widely used in many different environments and biotic compartments, such as the French coast of Brittany in the Western English Channel (Chardy 1987; Chardy & Dauvin 1992; Chardy et al. 1993a,b; Améziane et al. 1996), the intertidal mudflat on the French Atlantic coast (Leguerrier et al. 2003, 2004), Arcachon Bay (Blanchet 2004), the Baltic Sea (Harvey et al. 2003), the coast of Norway (Salvanes et al. 1992), the Mediterranean (Coll

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**Table 2.** (a) Compartments for each of the three preferential trophic pathways identified. (b) Preferential trophic pathway for each division and sub-division of the Eastern English Channel and the Southern Bight of the North Sea.

<table>
<thead>
<tr>
<th>(a) N° preferential trophic pathway</th>
</tr>
</thead>
<tbody>
<tr>
<td>TP1 Detritus-Bacteria-Suspension-feeder-Omnivore-Fish</td>
</tr>
<tr>
<td>TP2 Detritus-Bacteria-Suspension-feeder-Carnivore-Fish</td>
</tr>
<tr>
<td>TP3 Detritus-Bacteria-Deposit-feeder and Mixed-Car-nivore-Fish</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(b) sediment/site</th>
<th>Bay of Seine</th>
<th>Dover Strait</th>
<th>North Sea</th>
<th>whole</th>
</tr>
</thead>
<tbody>
<tr>
<td>gravel and pebbles</td>
<td>TP1</td>
<td>TP2</td>
<td>TP3</td>
<td>TP2</td>
</tr>
<tr>
<td>coarse sand</td>
<td>TP1</td>
<td>TP1</td>
<td>TP1</td>
<td>TP1</td>
</tr>
<tr>
<td>fine sand</td>
<td>TP3</td>
<td>TP3</td>
<td>TP3</td>
<td>TP3</td>
</tr>
<tr>
<td>whole</td>
<td>TP1</td>
<td>TP2</td>
<td>TP2</td>
<td>TP1</td>
</tr>
</tbody>
</table>
Assessment of benthic ecosystem functioning

In the English Channel. Thanks to a large tidal range, the hydrographical influence of large rivers and the morphology of the Eastern English Channel coast, hydrodynamics in the Channel vary greatly and have a complex pattern (Solomon & Breton 1991). These hydrodynamics lead to differential particle-size sedimentation, with a gradient ranging from pebbles and gravel to fine sand (Larsonneur et al. 1982).

Depending on the sediment type, different benthic species are able to settle and to undergo a successful metamorphosis (Gray 1974). Previous authors have identified five main bio-sedimentary structures, which have been studied since the late 1970s (see Dauvin 1997a). For this study, we chose three sediment divisions; coarse sediment – gravel and pebbles; intermediate sediment – coarse sand; and fine sediment – fine sand. These sediment divisions were associated with three geographic divisions: the Bay of Seine, the Dover Strait and the North Sea (Fig. 1). This first quantitative approach at such a large spatial scale as the Eastern English Channel allowed us to compare the trophic structure in the various sediment and geographic divisions through trophic web modelling.

However, inverse methods are based on the parsimony principle (Vézina & Platt 1988). Thus, many flows can be underestimated or overestimated (Leguerrier et al. 2003).

We used similar input parameters to ensure an identical estimation error, so that comparisons of the divisions and sub-divisions would remain possible. We also tested each of the model outputs by randomly selecting different values of particular organic matter (P.O.M.), flow entering the system inside a confidence interval. We then compared the different outputs of each division and sub-division, to make sure that they were consistent. Moreover, sensitivity analyses showed that outputs from inverse methods were robust (Marquis et al. 2007). Using the preferred trophic pathway identified for each division (Table 2a), we found only slight differences among geographic divisions; the trophic pathways in the Dover Strait and the North Sea were similar and were themselves similar to the preferred pathway for whole area (TP1) (Table 2b). Only the Bay of Seine was found to be different (TP2).

However, the trophic pathways in the sediment divisions were very different from each other (Table 2b). For example, in the gravel and pebbles and coarse sand sediment divisions, the suspension-feeders were dominant. Of the 10 suspension-feeder species that contribute most to the biomass, five species were observed in both of the communities. The presence of these five species could be seen as enhancing the efficiency of the suspension-feeder compartment in terms of trophic web matter transfer. In the higher levels of the trophic web of these divisions, the switch from carnivore in the gravel and pebbles sediment...
### Table 3. Ten main contributive species to the mean biomass of sediment divisions for each trophic compartment.

<table>
<thead>
<tr>
<th></th>
<th>deposit-feeder and mixed</th>
<th>suspension-feeder</th>
<th>carnivore</th>
<th>omnivore</th>
</tr>
</thead>
<tbody>
<tr>
<td>GP Arcopagia crassa</td>
<td>3.725</td>
<td>6.316</td>
<td>0.145</td>
<td>1.881</td>
</tr>
<tr>
<td>Cirriformia tentaculata</td>
<td>1.250</td>
<td>5.963</td>
<td>0.136</td>
<td>1.394</td>
</tr>
<tr>
<td>Chaetopterus variopedatus</td>
<td>0.443</td>
<td>5.093</td>
<td>0.077</td>
<td>1.263</td>
</tr>
<tr>
<td>Golfingia (Golfingia) elongata</td>
<td>0.273</td>
<td>3.926</td>
<td>0.059</td>
<td>0.837</td>
</tr>
<tr>
<td>Upogebia deltata</td>
<td>0.271</td>
<td>3.129</td>
<td>0.045</td>
<td>0.635</td>
</tr>
<tr>
<td>Echinocardium cordatum</td>
<td>0.195</td>
<td>2.611</td>
<td>0.011</td>
<td>0.325</td>
</tr>
<tr>
<td>Callianassa tyrrhena</td>
<td>0.191</td>
<td>2.286</td>
<td>0.008</td>
<td>0.229</td>
</tr>
<tr>
<td>Euclymene kumbriocides</td>
<td>0.179</td>
<td>2.080</td>
<td>0.007</td>
<td>0.173</td>
</tr>
<tr>
<td>Golfingia (Golfingia) margaritacea</td>
<td>0.159</td>
<td>2.052</td>
<td>0.006</td>
<td>0.135</td>
</tr>
<tr>
<td>Cs Echinocardium cordatum</td>
<td>6.848</td>
<td>42.358</td>
<td>1.037</td>
<td>2.153</td>
</tr>
<tr>
<td>Arcopagia crassa</td>
<td>6.197</td>
<td>20.484</td>
<td>0.660</td>
<td>1.025</td>
</tr>
<tr>
<td>Amphitrite johnstoni</td>
<td>4.110</td>
<td>3.116</td>
<td>0.352</td>
<td>1.019</td>
</tr>
<tr>
<td>Cirriformia tentaculata</td>
<td>1.250</td>
<td>2.912</td>
<td>0.339</td>
<td>0.753</td>
</tr>
<tr>
<td>Tellina fabula</td>
<td>1.014</td>
<td>2.306</td>
<td>0.245</td>
<td>0.583</td>
</tr>
<tr>
<td>Callianassa tyrrhena</td>
<td>0.703</td>
<td>2.080</td>
<td>0.193</td>
<td>0.533</td>
</tr>
<tr>
<td>Tellina tenuis</td>
<td>0.673</td>
<td>1.793</td>
<td>0.188</td>
<td>0.515</td>
</tr>
<tr>
<td>Callianassa tyrrhena</td>
<td>0.703</td>
<td>1.622</td>
<td>0.174</td>
<td>0.464</td>
</tr>
<tr>
<td>Echitrus echiturus</td>
<td>0.395</td>
<td>1.493</td>
<td>0.114</td>
<td>0.346</td>
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<tr>
<td>Callianassa subterranea</td>
<td>0.382</td>
<td>11.750</td>
<td>1.017</td>
<td>0.986</td>
</tr>
<tr>
<td>Fs Echinocardium cordatum</td>
<td>12.955</td>
<td>4.446</td>
<td>0.400</td>
<td>0.642</td>
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<tr>
<td>Cirriformia tentaculata</td>
<td>1.250</td>
<td>3.897</td>
<td>0.353</td>
<td>0.573</td>
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<tr>
<td>Coelobita gibbula</td>
<td>0.675</td>
<td>0.322</td>
<td>0.322</td>
<td>0.456</td>
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<tr>
<td>Tellina fabula</td>
<td>0.352</td>
<td>2.225</td>
<td>0.322</td>
<td>0.456</td>
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<tr>
<td>Ovenia fusiformis</td>
<td>0.284</td>
<td>2.080</td>
<td>0.318</td>
<td>0.263</td>
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<tr>
<td>Tellina tenuis</td>
<td>0.262</td>
<td>1.927</td>
<td>0.288</td>
<td>0.151</td>
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<tr>
<td>Macoma balthica</td>
<td>0.248</td>
<td>1.921</td>
<td>0.266</td>
<td>0.145</td>
</tr>
<tr>
<td>Callianassa subterranea</td>
<td>0.244</td>
<td>1.827</td>
<td>0.107</td>
<td>0.074</td>
</tr>
<tr>
<td>Acrocinia brachiata</td>
<td>0.179</td>
<td>1.245</td>
<td>0.094</td>
<td>0.065</td>
</tr>
<tr>
<td>Upogebia deltata</td>
<td>0.174</td>
<td>1.168</td>
<td>0.068</td>
<td>0.054</td>
</tr>
</tbody>
</table>

**B** = mean annual biomass of the species in g m⁻² year⁻¹ (ash-free dry weight); **GP** = Gravel and pebbles; **Cs** = Coarse sand; **Fs** = Fine sand.

The shift from deposit-feeder to carnivore dominance in the coarse sand sediment is more difficult to explain. This could be because the omnivores in coarse sand have a more regular biomass distribution among the 10 species that dominate the biomass (Table 3).

The trophic pathway also switches from suspension-feeder dominance to deposit-feeder and mixed dominance between coarse sand and fine sand, despite the fact that both divisions have quite similar species. This switch can be explained by the increase in biomass of one deposit-feeder species, the sea urchin *Echinocardium cordatum*, associated with the decrease in biomass of the dominant suspension-feeder species, *Ensis directus*, which has its biomass value divided by four in the fine sand sediment division. Finally, the switch between carnivore dominance in fine sand to omnivore dominance in coarse sand, seems to be due mostly to the absence of a significant decrease in the large omnivorous cnidarian *Urticina felina* and molluscs *Buccinum undatum* and *Nassarius reticulatus*, which contribute most to the biomass of the coarse sand sediment division.

In his trophic model of the benthic trophic web in Arcachon Bay, Blanchet (2004) found the same deposit-feeder dominance in a similar fine sediment type, but with a large difference in the mean deposit-feeder biomass (0.08 g C m⁻² in our study compared with 0.52 g C m⁻² in Arcachon Bay), probably due to the presence of the seagrass *Zostera noltii*. Unfortunately, further comparisons of our results with those of adjacent marine areas are quite difficult to carry out. The models of Mackinson & Daskalov (2007) for the North Sea, and Lees & Mackinson (2007) for the Irish Sea, mainly deal with fisheries management. In addition, these authors did not investigate trophic structure at the benthic level and the functional compartments utilised were very different. In the Maremnes-Olérons, Leguerrier *et al.* (2003) sought to highlight the differences between the carbon flows of cultivated oysters and those of non-cultivated benthos, and the models made for the Western English Channel (Chardy & Dauvin 1992; Améziane *et al.* 1996) were used mainly to investigate benthic–pelagic relationships, and used different compartments.
Comparison among sub-divisions tends to show that the importance of the geographic factor is low. In fact, for the geographic coarse sand and the fine sand sub-divisions, no matter what geographic location is considered, the trophic structure always follows the trophic pathway of the sediment type to which it belongs (Table 2b). However, no clear pattern appeared for the gravel and pebbles sediment. This lack of a clear pattern can be explained by the sampling method; all the sites were sampled with the quantitative Hamon grab sampling gear which reaches its functional limits in pebbles and stony bottoms. Thus, it appears that the gravel and pebbles sediment was under-sampled. In addition, among the three sediment types, gravel and pebbles appear to be the least accurate in terms of representing benthic organisation and functioning, which could explain the lack of a clear pattern observed in this division. It is unclear even for the coarse sand and fine sand sediment types whether the observed features are natural or directly dependent on the sampling strategy. In their study of the effects of sampling effort on food-web structure, Martinez et al. (1999) showed that major trophic web properties like food chain length appear to be robust to variation in sampling resolution. However, further investigations are required to confirm this conclusion, particularly assessment of the other bio-sedimentary communities of the Eastern English Channel and the Southern North Sea (i.e. muddy-fine sand and mud). The use of a 2-mm sieve is appropriate for sampling large-sized species, but can underestimate small species, including some deposit-feeders and mixed. However, more than 95% of macrobenthic biomass is retained on 2-mm sieve mesh (Ghertsos 2002) and the predominantly pebbles to coarse sand communities of the Eastern English Channel are dominated by large-sized suspension-feeder species (Dauvin & Ruellet 2008), so this bias is mainly restricted to the less common fine sediments.

According to Vézina & Platt (1988), the inverse methods provide a strong foundation for an effective comparative analysis of food-web dynamics. This study allowed us to determine that there is variation in trophic organisation in the Eastern English Channel and the Southern North Sea, depending on the scale of observation. In this respect, the sediment division (the bio-sedimentary division) appears to be the most important factor controlling benthic ecosystem functioning in the area, with the possible exception of the Bay of Seine due to its very particular features (i.e. an enclosed bay in close proximity to a river). The trophic organisation of the overall area is an integration of the specific properties of each individual functional unit. Thus, views of the trophic structure of the system can differ depending on the scales and factors considered. Further investigations are needed to identify and determine the spatial limits of the individual functional units, as well as their intrinsic properties.

Limitations and Perspectives
A model is a conceptual representation of a particular ecosystem, which has the primary advantage of gathering and summarising the current knowledge of ecosystem functioning (Barnsley 2007). This study shows that inverse models are extremely useful for investigating the trophic structure of benthic ecosystems. Our trophic inverse model allowed us to determine the specific conditions under which the detritic compartment is utilised and to identify which flows are the most important for overall functioning of the system. The comparisons of the different sediment and geographic divisions were also useful for understanding the variations in ecosystem functions, for identifying general information about benthic functioning, and thus for providing a basis for comparison with other benthic ecosystems.

However, using this kind of model is only possible when quantitative data are available, which leads to the main problem with a study such as ours; as far as the benthic compartment is concerned, inverse models can only be used for sediment types in which a quantitative sampling gear can operate. Pebbles and stony sediment are excluded, unless SCUBA divers are employed, which involves much more work compared with the soft-bottom communities.

Another inconvenience of inverse models is that they require access to many physiological parameters that are hard to obtain. One solution to overcome this difficulty is to derive all necessary physiological parameters (e.g. respiration, ingestion) from the P/B value for each compartment. The P/B values for many species and/or compartments are widely available in the literature, but they vary greatly depending on the authors. This variation can be explained by the different methods used for the assessment, but also by the intrinsic properties of P/B. The annual P/B of a cohort usually decreases with age; it follows that populations dominated by older year classes will have a lower P/B than those composed of younger individuals (Warwick 1980). Another solution would be the coupling of this kind of work with other modelling methods such as the model of size spectra developed by Jennings et al. (2002) for the benthic system. This method assumes that organisms with higher body mass feed at higher trophic levels, meaning that it requires fewer parameters to assess the main energy flow through the food-web.

To the problem of variation in this well known compartment, it is necessary to add the problem of the compartments about which little is known – the black boxes such as benthic bacteria or meiofauna. As few studies
of these compartments are available, it is extremely difficult to gather the necessary parameters which, by virtue of their lack of attention, are plagued by incertitude.

Another problem is that macrobenthic communities are well known for having large fluctuations in biomass and abundance from year to year, mainly due to predation on larvae in the plankton (Thurston 1946) or newly settled juveniles. In addition, high adult mortality can also occur (Warwick 1980). For these reasons, the trophic representation for 1 year may not be valid the following year. This is particularly evident in populations that are dominated by species with long-lived planktonic larvae, which are considered to have highly unstable dynamics (Thurston 1946).

Our study has shown that, as far as the benthic compartment is concerned, a large-scale spatial model seems to be acceptable for our study area, as the benthic communities are all influenced by hydrodynamics. Nonetheless, as benthic trophic functioning is variable and strongly dependent on sediment type, this model would have to take into account at least the three main sediment types (i.e. gravel and pebbles, coarse sand and fine sand).

Acknowledgements

The authors wish to thank Dr Aurélie Foveau, Aurore Savina, Emilie Houillez and Amélie Charnoz for their help in the sorting and identification of the species, Eric Lecuyer, Dr Nicolas Desroy, Dr Nicolas Spilmont and the officers and crew of the RV Cotes de la Manche for their effort at sea, Lisa Spencer and Dr Julie Bremer for correcting the English syntax and grammar, and two anonymous referees for their helpful suggestions and comments. This work was carried out with financial contribution of the European Union’s Interreg IIIa scheme (European Regional Development Funds) CHARM 2 project coordinated by A. Carpentier, Ifremer, Boulogne-sur-mer.

References


Original Article

Epiphytes and associated fauna on the brown alga Fucus vesiculosus in the Baltic and the North Seas in relation to different abiotic and biotic variables

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2 Institute of Mathematics and Natural Sciences, Tallinn University, Tallinn, Estonia
3 Coastal Research and Planning Institute, University of Klaipėda, Klaipėda, Lithuania
4 Marine Systems Institute, Tallinn University of Technology, Tallinn, Estonia
5 Laboratory of Marine Ecology, Institute of Biology, University of Latvia, Salaspils, Latvia

Keywords
Community composition; dominance structure; epibionts; fucoids; host frond; marine benthos; mobile invertebrates; seaweeds; spatial variability; wave exposure.

Abstract

Fucus vesiculosus L. is an important habitat-forming macroalga both in the saline and high diverse North Sea and the diluted and low diversity Baltic Sea. Despite its importance, comparisons of the spatial patterns of its epiphytes have rarely been reported. In this study we examined the species composition and density of macro-epiphytes and mobile fauna on the canopy-forming macroalga F. vesiculosus inhabiting different regimes of wave exposure in the North and Baltic Seas. The North and Baltic Seas had distinct epiphyte and mobile faunal communities. Wave exposure and segments of host fronds significantly contributed to the variability in species composition and dominance structure of epiphytes on F. vesiculosus in the North Sea and Baltic Sea. The study indicated that there is no clear spatial scale where environmental variables best predicted epiphytic and mobile faunal communities, and the formation of epiphytic and faunal communities is an interplay of factors operating through micro- to regional scales.

Introduction

Epiphytism and competition for a substrate is a widespread phenomenon in marine communities, especially in the rocky intertidal zone (Paine 1990; Kraberg & Norton 2007). Many algal species can grow on some host species or even are obligatory epiphytes (Pavia & Åberg 1999) providing potential for mutualistic interspecific associations (Stachowicz & Whitlatch 2005).

Fucoids are widely distributed perennial brown macroalgae in the intertidal Northeastern Atlantic with an important role in structuring intertidal communities (Lüning 1990). They can also extend to brackish non-tidal Baltic waters. Fucus vesiculosus L. is an important habitat-forming macroalga both in the saline and high diverse North Sea and the diluted and low diversity non-tidal Baltic Sea (Kiirikki 1996a; Berger et al. 2004; Torn et al. 2006; Rohde et al. 2008). Fucus vesiculosus hosts a large variety of macroalgal species (Rindi & Guiry 2004), which provide suitable habitat for sessile invertebrates (Johnson & Scheibling 1987) and associated invertebrates, mainly grazers (Orav-Kotta & Kotta 2004; Räberg & Kautsky 2007). Despite its importance, comparisons of the spatial patterns of its epiphytes have rarely been reported (Rindi & Guiry 2004; Fraschetti et al. 2005).

Epiphytic organisms, such as micro- and macroalgae, invertebrates and bacteria, are often present on the thallus of perennial macroalgae. Their abundance is largely determined by abiotic factors, e.g. water motion and nutrient availability. The ability of epiphytes to tolerate regular desiccation during low tides determines their spatial distribution (Molina-Montenegro et al. 2005). Elevated
nutrient loading is expected to increase both the number of epiphytic algae and invertebrates. However, the relationship varies among regions and is modulated by a number of other environmental variables, e.g. wave exposure, regional species pool, characteristics of the host plant and herbivory (Kotta et al. 2000; Worm et al. 2002; Kotta & Witman 2009). Among biotic interactions, intraspecific competition for space and light and the presence of adequate food resources for invertebrates are important (Lobban & Harrison 2000).

The ability of host algae to resist and avoid epibionts has great importance (Honkanen & Jormalainen 2005), affecting the photosynthetic rate and growth of host algae (Korpinnen et al. 2007). The position within the thallus of seaweeds is important factor structuring epiphyte communities (Lobban & Baxter 1983; Cardinal & Lesage 1992; Longtin et al. 2009). Large epiphytes are associated with the basal disk; ephemeral epiphytes appearing on the tips of the host fucoid fronds (Arrontes 1990). The cover of epiphytes often increases with the age of algae.

The objective of this study was to examine the species composition and density of epiphytes and mobile fauna on the canopy-forming macroalga F. vesiculosus inhabiting at different regimes of wave exposure in the North and Baltic Seas. We considered epiphytes hereafter as organism-on-a-plant concept (sensu Wahl 2009; Steel & Wilson 2003, references therein). Thus, epiphytes in this report comprise any macroalgae and sessile invertebrates on the host algae. Mobile fauna is defined here as motile macroinvertebrates associated with the host macroalgae.

We tested the following hypotheses:
1 The occurrence and cover of epiphytes are specific to the frond segment of host macroalgae.
2 The occurrence and cover of epiphytes are related to the wave exposure of the site.
3 The relationship between abiotic (exposure), biotic factors (frond segment) and epiphytes (species composition, cover) varies among different marine regions (North versus Baltic Seas).

Material and Methods

Study area

The study was performed in the North Sea and the Baltic Sea. In each region we selected three sites differing in exposure level. The used exposure levels according to the EUNIS classification were as follows: sheltered, moderately exposed and exposed. In the North Sea the sampling was done on the southwest coast of Norway in Raunefjord and Korsfjord in summer 2007 (Fig. 1). The North Sea study area contains numerous small and large islands separated by wide or narrow sounds. The bottom relief of the area is steep and very uneven. Espegrend Marine Biological Station (N1; 60.273°N, 5.218°E) represented sheltered, Loholmen (N2; 60.266°N, 5.211°E) moderately exposed and Store Kalsoy (N3; 60.113°N, 5.069°E) exposed areas. During sampling, salinity ranged between 30 and 33 psu and tidal range was c. 1 m in the sampling area.

In the Baltic Sea, samples were collected from the Gulf of Riga and the Baltic Proper in summer 2008 (Fig. 1).
The Gulf of Riga is a wide, shallow, semi-enclosed brackish water ecosystem. In general, the bottom relief of the area is quite flat, with gentle slopes towards deeps. The northern part of the Gulf is characterized by a wide coastal zone with diverse bottom topography and extensive reaches of boulders. The coasts of the Baltic Proper are very exposed, hydrodynamically active and characterized by a steep coastline. The inner part of Köigute Bay, the Gulf of Riga (B1; 58.374°N, 22.972°E) represented a sheltered area, the outer part of Köiguste Bay (B2; 58.370°N, 22.982°E) a moderately exposed area, and Küderna Bay, the Baltic Proper (B3; 58.568°N, 22.302°E) an exposed area. During sampling, salinity ranged between 4 and 7 psu. The Baltic Sea is nearly tideless, with an average daily tidal component of 15 cm (Schiewer 2008). The water level fluctuations in the area are mainly caused by the meteorological forcing with a seasonal sea level mean range of 30 cm (e.g. Suursaar & Sooäär 2007).

Sampling
In the North Sea, samples were taken at low tide on the upper littoral zone in the middle of F. vesiculosus belt. In the Baltic Sea samples were collected by a diver from a Fucus vesiculosus belt at 0.5-1 m depth. Four replicates of host algae were collected randomly with the aid of a rope that was placed along the shore and marked at every metre. Four marks were randomly selected and host plants were collected nearest to the respective marks on the rope. Samples were transported in plastic bags to the laboratory for the further analyses within 24 h. Mobile fauna were removed from host thalli, counted and identified to the lowest taxonomic level possible using a dissecting microscope (magnification 4–10×). The cover of epiphytes were estimated on a six-grade scale (0 – absence, 1 – from 1 to 20%, 2 – from 21 to 40%, 3 – from 41 to 60%, 4 – from 61 to 80% and 5 – from 81 to 100% of cover on host plant) separately on basal, middle and distal segments of each host frond (Rindi & Guiry 2004) (Fig. 2).

Data analysis
All multivariate analyses were conducted using PRIMER 6 software (Clarke & Gorley 2006). Hierarchical permutational multivariate analysis of variance (PERMANOVA) (Anderson et al. 2008) was used separately for epiphytes and mobile fauna to examine differences in the patterns of variation in composition, cover and abundance between regions (fixed factor), wave exposure (nested in region, fixed factor) and frond segment of host macroalgae (nested in region and wave exposure, fixed factor). Due to the mobility of organisms, frond segment was not considered an important factor for mobile or associated fauna. Therefore, 2-factor PERMANOVA was used to determine the abundances of mobile invertebrates.

Prior to analysis, a Bray–Curtis similarity matrix was calculated using raw data (untransformed) and presence/absence transformation to detect whether the potential differences between the assemblages of the epibiota were due to differences in relative abundances or species composition (Clarke & Warwick 2001).

When a factor with more than two levels (i.e. wave exposure and host frond segment) was identified as significant (P < 0.05), post-hoc PERMANOVA pair-wise tests were conducted to detect which levels were responsible for significant interactions. Taxa responsible for observed differences were identified by similarity percentages (SIMPER), where the cut-off percentage was set to 90. Non-metric multidimensional scaling (nMDS) was used to present visual images of the differences in composition of epiphytic and mobile faunal assemblages in distinct marine regions, exposure levels and frond segment of the host.

Results
A total of 27 epiphytic and mobile faunal taxa were recorded on the fronds of Fucus vesiculosus in the studied areas: 8 taxa of macroalgae, 5 taxa of sessile invertebrates (i.e. suspension-feeders) and 14 taxa of mobile invertebrates (mainly herbivores) (Table 1).

All investigated factors significantly contributed to the variability in species composition and coverage of epiphytic and mobile faunal communities on F. vesiculosus (PERMANOVA, Table 2). Epiphytic and mobile fauna communities were clearly differentiated in species...
composition and dominance structure between the North and Baltic Seas (Table 2, PERMANOVA: P = 0.001). The epiphytes and mobile fauna taxa contributing most to the regional variability were the brown algae *Pylaiella littoralis*, *Elachista fucicola*, the tube-building polychaete *Spirorbis spirorbis*, and the herbivorous snail *Theodoxus fluviatilis* (Supporting Information Tables S1–S4).

The species composition of epiphytic community (presence/absence transformed data) on their host was significantly different between every level of wave exposure in both the North and Baltic Seas (P < 0.05), except for moderately exposed versus sheltered sites in the North Sea (PERMANOVA pair-wise test: P = 0.092). Dissimilarities between different exposure levels were mostly due to *Elachista fucicola* and *Pylaiella littoralis* (Supporting Information Table S5).

Similarly, the dominance structure of epiphytic community (untransformed data) on their host was significantly different between every level of wave exposure in both the North and Baltic Seas (P < 0.05), except for moderately exposed versus sheltered sites in the North Sea (PERMANOVA pair-wise test: P = 0.078). Dissimilarities between different exposure levels were mostly due to *E. fucicola* and *P. littoralis* (Supporting Information Table S6).

The species composition (presence/absence data) and dominance structure (untransformed data) of mobile fauna community differed significantly for every exposure level in the North and Baltic Seas (PERMANOVA pair-wise test: P < 0.05). Dissimilarities between different exposure levels were mainly due to *Gammarus* spp.,

### Table 1. Recorded epiphytes and mobile fauna on the host *Fucus vesiculosus* at three study sites in the North (NS) and Baltic Sea (BS).

<table>
<thead>
<tr>
<th>No.</th>
<th>Taxon</th>
<th>Region</th>
<th>Wave exposure</th>
<th>Frond segment of host</th>
<th>NS: Mean cover/abun ± SE</th>
<th>BS: Mean cover/abun ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Electra crustulenta</em> (Pallas, 1766)</td>
<td>BS</td>
<td>S, ME</td>
<td>B, M, D</td>
<td>0.25 ± 0.07</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td><em>Electra pilosa</em> (L.)</td>
<td>NS</td>
<td>S, ME</td>
<td>B, M, D</td>
<td>0.47 ± 0.14</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td><em>Spirorbis spirorbis</em> (Linnaeus, 1758)</td>
<td>NS</td>
<td>S, ME</td>
<td>B, M, D</td>
<td>1.03 ± 0.18</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td><em>Balanus improvisus</em> Darwin, 1854</td>
<td>BS</td>
<td>E</td>
<td>M</td>
<td>0.03 ± 0.03</td>
<td>6.5 ± 2.21</td>
</tr>
<tr>
<td>5</td>
<td><em>Gammarus</em> spp.</td>
<td>BS, NS</td>
<td>S, ME, E</td>
<td></td>
<td>0.33 ± 0.26</td>
<td>6.17 ± 1.60</td>
</tr>
<tr>
<td>6</td>
<td><em>Idotea balthica</em> (Pallas, 1772)</td>
<td>BS, NS</td>
<td>S, ME, E</td>
<td></td>
<td>1.5 ± 0.4</td>
<td>6.17 ± 1.60</td>
</tr>
<tr>
<td>7</td>
<td><em>Idotea chelipes</em> (Pallas, 1766)</td>
<td>BS, NS</td>
<td>S, ME, E</td>
<td></td>
<td>0</td>
<td>0.25 ± 0.25</td>
</tr>
<tr>
<td>8</td>
<td><em>Jaera albifrons</em> Leach, 1814</td>
<td>BS</td>
<td>ME</td>
<td></td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td><em>Cyanophthalma obscura</em> (Schüttze)</td>
<td>BS</td>
<td>E</td>
<td></td>
<td>0.08 ± 0.08</td>
<td>0.08 ± 0.08</td>
</tr>
<tr>
<td>10</td>
<td><em>Gibbula cineraria</em> (L.)</td>
<td>NS</td>
<td>ME</td>
<td></td>
<td>0.08 ± 0.08</td>
<td>0</td>
</tr>
<tr>
<td>11</td>
<td><em>Hydrobia</em> spp.</td>
<td>BS</td>
<td>S, ME, E</td>
<td></td>
<td></td>
<td>14.92 ± 6.24</td>
</tr>
<tr>
<td>12</td>
<td><em>Lacuna vincuta</em> (Montagu)</td>
<td>NS</td>
<td>E</td>
<td></td>
<td>0.17 ± 0.11</td>
<td>0</td>
</tr>
<tr>
<td>13</td>
<td><em>Littorina littorea</em> (L.)</td>
<td>NS</td>
<td>S, ME, E</td>
<td></td>
<td>7.17 ± 1.62</td>
<td>0</td>
</tr>
<tr>
<td>14</td>
<td><em>Littorina obtusata</em> (L.)</td>
<td>NS</td>
<td>S, ME, E</td>
<td></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>15</td>
<td><em>Lymnaea peregra</em> (Müller)</td>
<td>BS</td>
<td>ME, E</td>
<td></td>
<td>0.17 ± 0.17</td>
<td>0.42 ± 0.26</td>
</tr>
<tr>
<td>16</td>
<td><em>Mytilus edulis</em> L.</td>
<td>NS</td>
<td>S</td>
<td></td>
<td>0.17 ± 0.17</td>
<td>0</td>
</tr>
<tr>
<td>17</td>
<td><em>Mytilus trossulus</em> Gould</td>
<td>BS</td>
<td>E</td>
<td></td>
<td>0</td>
<td>0.42 ± 0.29</td>
</tr>
<tr>
<td>18</td>
<td><em>Theodoxus fluviatilis</em> (L.)</td>
<td>BS</td>
<td>S, ME, E</td>
<td></td>
<td>0</td>
<td>39.17 ± 6.47</td>
</tr>
</tbody>
</table>

### Macrocystaceae

<table>
<thead>
<tr>
<th>No.</th>
<th>Taxon</th>
<th>Region</th>
<th>Wave exposure</th>
<th>Frond segment of host</th>
<th>NS: Mean cover/abun ± SE</th>
<th>BS: Mean cover/abun ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>19</td>
<td><em>Ceramium tenuicorne</em> (Kützing) Waern</td>
<td>BS, NS</td>
<td>ME, E</td>
<td>B, M, D</td>
<td>0.08 ± 0.06</td>
<td>0.28 ± 0.09</td>
</tr>
<tr>
<td>20</td>
<td><em>Ceramium virgatum</em> Roth</td>
<td>BS, NS</td>
<td>ME, E</td>
<td>B, M, D</td>
<td>0.08 ± 0.06</td>
<td>0.28 ± 0.09</td>
</tr>
<tr>
<td>21</td>
<td><em>Chaetomorpha</em> sp.</td>
<td>NS</td>
<td>S</td>
<td>M, D</td>
<td>0.06 ± 0.04</td>
<td>0</td>
</tr>
<tr>
<td>22</td>
<td><em>Chordaria flagelliformis</em> (Müller) Agarth</td>
<td>NS</td>
<td>ME</td>
<td>M</td>
<td>0.06 ± 0.06</td>
<td>0</td>
</tr>
<tr>
<td>23</td>
<td><em>Cladophora glomerata</em> (L.) Kützing</td>
<td>BS, NS</td>
<td>S, ME, E</td>
<td>B, M, D</td>
<td>0.03 ± 0.03</td>
<td>0.36 ± 0.09</td>
</tr>
<tr>
<td>24</td>
<td><em>Elachista fucicola</em> (Velley) Arenschnou</td>
<td>BS, NS</td>
<td>S, ME, E</td>
<td>B, M, D</td>
<td>0.72 ± 0.17</td>
<td>0.19 ± 0.08</td>
</tr>
<tr>
<td>25</td>
<td><em>Pylaiella littoralis</em> (L.) Kjellman</td>
<td>BS, NS</td>
<td>S, ME, E</td>
<td>B, M, D</td>
<td>0.06 ± 0.04</td>
<td>1.14 ± 0.26</td>
</tr>
<tr>
<td>26</td>
<td><em>Ulva intestinalis</em> L.</td>
<td>NS</td>
<td>S, ME, E</td>
<td>B, M, D</td>
<td>0.14 ± 0.06</td>
<td>0</td>
</tr>
</tbody>
</table>

### Hydrozoa

<table>
<thead>
<tr>
<th>No.</th>
<th>Taxon</th>
<th>Region</th>
<th>Wave exposure</th>
<th>Frond segment of host</th>
<th>NS: Mean cover/abun ± SE</th>
<th>BS: Mean cover/abun ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>27</td>
<td><em>Dynamena pumila</em> (L.)</td>
<td>NS</td>
<td>ME</td>
<td>B, M, D</td>
<td>0.11 ± 0.07</td>
<td>0</td>
</tr>
</tbody>
</table>

S, Sheltered; ME, moderately exposed; E, exposed site. B, basal; M, middle; D, distal segment of host alga.

Means and standard errors were calculated from untransformed coverage and abundance data.
Littorina spp. and Theodoxus fluviatilis (Supporting Information Tables S7 and S8).

Different segments of host fronds had significantly different species composition of epiphytic communities at the moderately exposed site in the North Sea (between middle and distal segments; \( P = 0.033 \)) and at exposed (between middle and distal segments; \( P = 0.03 \)) and sheltered sites in the Baltic Sea (between basal and distal segments; \( P = 0.031 \)). Different segments of host fronds had significantly different dominance structure of epiphytic communities (untransformed data) at the sheltered site in the North Sea (between basal and distal segments; \( P = 0.026 \)) and at exposed (between middle and distal segments; \( P = 0.023 \)) and sheltered sites in the Baltic Sea (between basal and distal segments; \( P = 0.03 \)).

The differences in species composition and dominance structure were mainly caused by E. fucicola and P. littoralis (Supporting Information Tables S9 and S10).

According to nMDS ordination, the epiphytic community composition and structure on host macroalgae clearly differed between sea regions in epiphyte coverage and also in mobile fauna abundance. It is also possible to detect a separate effect of wave exposure on epiphytic and mobile fauna community composition and structure within the two sea regions. However, the distinctions are larger for regions than for exposure levels. Nevertheless, in some instances the differences were very clear, e.g. epiphytes were totally absent at the exposed site of the North Sea (Fig. 3).

**Discussion**

We predicted that the occurrence and cover of epiphytes would be specific to the frond segments of host macroalgae. The results agreed with the hypothesis as different parts of host seaweeds had different epiphytic and mobile fauna species composition and dominance structure. The distal segment of host frond had the lowest coverage and the lowest species richness of epiphytes. This pattern is due to the high metabolic activity of apical (new) parts of Fucus vesiculosus thallus where the host alga produces allelopathic compounds such as phlorotannins (Wikström & Pavia 2003). Also, the topmost parts of fucoid algae have an anti-fouling strategy of periodically shedding surface cell layers (Kuirikki 1996b), which reduces the probability of epibionts settling and becoming established on the host plant. A similar strategy of mechanical defence has been observed in red algal hosts (Nylund & Pavia 2005).

We also predicted that the occurrence and cover of epiphytes would be related to the wave exposure of the site.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P(perm)</th>
<th>Unique perms</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Epiphytic coverage</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Presence/absence transformed</td>
<td></td>
<td>Region</td>
<td>1</td>
<td>15,498</td>
<td>15,498</td>
<td>41.016</td>
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<tr>
<td></td>
<td></td>
<td>Wave exposure (Region)</td>
<td>4</td>
<td>36,967</td>
<td>9241.6</td>
<td>24.459</td>
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<td></td>
<td></td>
<td>Frond segment (Wave exposure (Region))</td>
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<td>13,869</td>
<td>1155.7</td>
<td>3.0588</td>
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<td></td>
<td></td>
<td>Res</td>
<td>54</td>
<td>20,403</td>
<td>377.84</td>
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<tr>
<td></td>
<td></td>
<td>Total</td>
<td>71</td>
<td>86,736</td>
<td></td>
<td></td>
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<tr>
<td>Untransformed</td>
<td></td>
<td>Region</td>
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<td>18,220</td>
<td>18,220</td>
<td>33.454</td>
</tr>
<tr>
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<td>Wave exposure (Region)</td>
<td>4</td>
<td>50,430</td>
<td>12,607</td>
<td>23.149</td>
</tr>
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<td></td>
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<td>Frond segment (Wave exposure (Region))</td>
<td>12</td>
<td>19,143</td>
<td>1595.2</td>
<td>2.929</td>
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<tr>
<td></td>
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<td>Res</td>
<td>54</td>
<td>29,410</td>
<td>544.63</td>
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<tr>
<td></td>
<td></td>
<td>Total</td>
<td>71</td>
<td>117,200</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mobile faunal abundance</td>
<td></td>
<td>Presence/absence transformed</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Region</td>
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<td>42,429</td>
<td>42,429</td>
<td>123.9</td>
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<td></td>
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</table>

Res, Residual.
Some epiphytic (e.g. *Spirobranchus spirorbis*, Bryozoa, *Cladophora glomerata*, *Pylaiella littoralis*) and mobile faunal species (e.g. *Jaera albifrons*) were not observed at exposed study sites, suggesting that occurrence and cover/abundance are related to the exposure level of a site. This pattern is explained by the high hydrodynamic pressure on the thallus of *Fucus vesiculosus* at highly exposed sites, which removes epiphytic algae and prevents benthic suspension feeders from settling on the algae.

We also predicted that the relationship between abiotic (exposure), biotic factors (host frond segment) and epiphytes (species composition, cover) would vary among different marine regions (North versus Baltic Seas). Indeed, our study showed that the North and Baltic Seas had different epiphytic and mobile faunal species compositions and dominance structures. The epiphytic and mobile faunal taxa contributing most to the dissimilarity between North and Baltic Sea communities were the brown alga *P. littoralis* and the herbivore *Theodoxus fluviatilis*, respectively. Both species have a strong degree of tolerance to lowered salinity which consequently enables them to thrive in the low salinity environment. This suggests that salinity determines interregional differences in epiphyte communities between North and Baltic Seas (Kangas & Skoog 1978; Russell 1994; Snoeij 1999). *Theodoxus fluviatilis* was consistently absent in the North Sea study sites, causing high dissimilarities in abundance among regions.

This study also showed a higher variability of epiphytes and mobile faunal community structure in the Baltic Sea than in the North Sea. It has been proposed that processes affect ecosystems simultaneously at various spatial and temporal scales (Denny et al. 2004; Fraschetti et al. 2005; Kotta et al. 2008). The relative importance of small- and large-scale processes on the formation of marine communities is little known and it is likely the patterns vary among regions (e.g. Hewitt et al. 2007; Kotta & Witzman 2009). Our study indicates that large-scale factors mostly determine the distribution patterns of epiphytes in the North Sea and within these patterns, processes operating at microscale (e.g. due to frond segment) further modify the epiphyte communities. On the other hand,
large-, meso- and microscale processes are all equally important in determining the distribution patterns of epiphytes in the Baltic Sea.

In general, associated faunal community composition was different between all levels of wave exposure in both marine regions, whereas epiphytic composition and structure did not significantly differ between moderately exposed and sheltered sites in the North Sea. This indicates that epiphytic algae inhabiting the North Sea tolerate a larger range of exposure than those inhabiting the Baltic Sea.

The effect of host frond segments on the patterns of epiphytes varied among North and Baltic Seas, supporting the hypothesis that there are different factors (levels) forming different epiphytic communities on *F. vesiculosus* in the Baltic and North Sea. It seems likely that at smaller spatial scales, biotic factors (i.e. frond segment) play a more important role in epiphytic communities in the Baltic Sea, whereas abiotic factors (i.e. wave exposure) are more important in the North Sea.

Our understanding of the causes of local species diversity in marine habitats mostly originates from observations performed at small spatial scales. Comparing local and regional variability of epiphyte communities, our study clearly demonstrated that regional differences define broad patterns of species diversity and are among the most significant factors explaining population variability in these marine environments. However, our study was limited to two-region cases and further studies from multiple regions may provide us with a generic knowledge of the processes shaping epiphyte communities. Besides the spatial aspect, epiphytes are known to have a strong component of seasonal variability (Borum 1985; Vairappan 2007; Torn et al. 2010). This was not considered in the current study but may be highly relevant, as different regions are characterized by different types and intensity of seasonality.

To conclude, all investigated factors contributed significantly to the variability in species composition and coverage of epiphytes and mobile faunal communities on *F. vesiculosus*. The North and Baltic Seas each had distinct epiphyte and mobile faunal communities. Within the studied regions, wave exposure and frond segment contributed significantly to the variability in species composition and dominance structure of epiphytes on *F. vesiculosus* in the North Sea and Baltic Sea. Large-scale factors greatly determine the distribution patterns of epiphytes in the North Sea, whereas large-, meso- and microscale processes were all equally important in determining the distribution patterns of epiphytes in the Baltic Sea. The study indicated that there is no clear spatial scale where environmental variables best predicted epiphyte and mobile faunal communities. The formation of epiphytic and mobile faunal communities is an interplay of factors operating through micro- to regional scales.

**Acknowledgements**

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**References**


**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Results of SIMPER analyses testing for differences in the species composition of epiphytic communities on *Fucus vesiculosus* between the North and Baltic Seas (presence/absence transformed data, coverage of epiphytes on host).

**Table S2.** Results of SIMPER analyses testing for differences in the dominance structure of epiphytic communities on *Fucus vesiculosus* between the North and Baltic Seas (untransformed data, coverage of epiphytes on host).

**Table S3.** Results of SIMPER analyses testing for differences in the species composition of mobile faunal communities on *Fucus vesiculosus* between the North and Baltic Seas (presence/absence transformed data, abundance of fauna on host).

**Table S4.** Results of SIMPER analyses testing for differences in the dominance structure of mobile faunal communities on *Fucus vesiculosus* between the North and Baltic Seas (untransformed data, abundance of fauna on host).

**Table S5.** Results of SIMPER analyses testing for differences in the species composition of epiphytic communities on *F. vesiculosus* between different wave exposure levels (presence/absence transformed data, coverage of epiphytes on host).

**Table S6.** Results of SIMPER analyses testing for differences in the dominance structure of epiphytic communities on *F. vesiculosus* between different wave exposure levels (untransformed data, coverage of epiphytes on host).

**Table S7.** Results of SIMPER analyses testing for differences in the species composition of mobile faunal communities on *F. vesiculosus* between different wave exposure levels (presence/absence transformed data, abundance of fauna on host).

**Table S8.** Results of SIMPER analyses testing for differences in the dominance structure of mobile faunal communities on *F. vesiculosus* between different wave exposure levels (untransformed, abundance of fauna on host).

**Table S9.** Results of SIMPER analyses testing for differences in the species composition of epiphytic communities on *F. vesiculosus* between different frond segments (presence/absence transformed data, coverage of epiphytes on host).

**Table S10.** Results of SIMPER analyses testing for differences in the dominance structure of epiphytic communities on *F. vesiculosus* between different frond segments (untransformed data, coverage of epiphytes on host).

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Food resource use in sympatric juvenile plaice and flounder in estuarine habitats
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Keywords
Adaptation; coastal habitats; flatfish; Irish Sea; Platichthys flesus; Pleuronectes platessa; trophic niche.

Abstract
Environmental conditions in estuarine habitats can vary greatly and influence the composition of fish assemblages and their trophic interrelationships. We investigated feeding habits and patterns of diet overlap in juvenile plaice (Pleuronectes platessa) and flounder (Platichthys flesus) from two estuarine habitats in the Irish Sea. Plaice was found to vary its diet significantly across environments, whereas flounder exhibited a more consistent and homogeneous feeding pattern. Importantly, sympatric fish sampled at the same station were shown to reduce diet overlap. The results support the view that environmental heterogeneity in estuaries maintains a wide range of selective forces, the net outcome of which can produce a diverse array of feeding adaptations among interacting species.

Introduction
Despite extensive habitat destruction, pollution and long-term irresponsible exploitation regimes (Lotze et al. 2006), estuarine and coastal areas still retain a pivotal role in aquatic production processes, conservation, resource use, economy and commerce. Most of such ‘transitional’ habitats represent vital ‘nurseries’ for the juvenile stages of several commercially important fish (Beck et al. 2001; Kraus & Secor 2005), providing abundant food resources, shelter and favourable conditions for rapid growth (Haedrich 1983). Yet, estuaries, lagoons and tidal flats are also characterised by an unparalleled spatial and temporal environmental heterogeneity (Elliott & Quintino 2007), which necessarily poses severe adaptive challenges to the organisms that spend at least part of their life cycle therein.

One main ecological challenge is to be able to partition resources in a densely populated and variable environment. Similar species that occupy the same habitat at the same time will likely consume slightly different prey to minimise niche overlap (Schoener 1974), and a number of studies have shown this to be the case for fish inhabiting coastal ecosystems (Beyst et al. 1999; Darnaud et al. 2001; Mariani et al. 2002; Platell et al. 2006; Russo et al. 2008). Juveniles of flatfish species (Order Pleuronectiformes) are found in abundance in estuarine and coastal fish assemblages worldwide, making them good candidates for studies of resource partitioning. In particular, European flounder (Platichthys flesus L.) and plaice (Pleuronectes platessa L.) represent key species in cold temperate areas in the Northeast Atlantic and the latter especially sustains a very valuable commercial fishery. After hatching, juvenile flounder and plaice use shallow nursery grounds during the first months of life, between March and October (Russell 1976; Gibson 1994; Raffaelli & Hawkins 1996), exhibiting at this time a high degree of spatial overlap.

Despite the reported similarity in diet (Gibson 1994; Piet et al. 1998), most studies suggest that sympatric plaice and flounder segregate trophic niches (Aarnio et al. 1996; Beyst et al. 1999; Ameczua et al. 2003; Andersen et al. 2005; Russo et al. 2008). Most comparative studies emphasise inter-specific variation and competition in a specific spatial context – sometimes going as far as providing mechanistic explanations for the observed variation.
in diet (Bels & Davenport 1996; Gronkjaer et al. 2007; Russo et al. 2008) – but tend to overlook the overall role of coastal environmental heterogeneity in influencing the adaptive responses of species.

Here we compare the feeding habits of sympatric flounder and plaice in two different estuarine environments in the Irish Sea and we test the hypothesis that local conditions will affect the dietary patterns in these species, resulting in spatial variations in their trophic inter-relationships.

Material and Methods

Study area
The study was carried out in two inshore tidal inlets in the Irish Sea: North Bull Island (53°22’ N, 6°07’ W), in Dublin Bay, and Wexford Harbour (52°20’ N, 6°27’ W), at the southernmost end of the Irish Sea basin (Fig. 1). North Bull Island has previously been shown to have higher average salinity (37 psu) and lower average temperature (17 °C) than Wexford Harbour (27 psu and 19 °C) throughout the year (Craig et al. 2008). Both localities are characterized by sandy/muddy bottoms, which remain completely exposed during low tide. Within each location, two stations ~500 m apart were chosen for sampling.

Sampling
Juveniles of plaice and flounder were collected using a 10-m long, 4-m high, hand-dragged seine (2-mm mesh), between June and July 2008, which corresponds to the period of maximum abundance and activity of 0-group flatfishes in inshore tidal areas in the Northeast Atlantic (Gibson 1994; Raffaelli & Hawkins 1996). In each locality, specimens were collected once a week, over 4 weeks, during daytime, at high and low tide, to maximize the representation of the sample for both species. Specimens were counted each time, and a random subsample was sacrificed using an overdose of phenoxyethanol and later placed in a 5% formalin solution for preservation and identification.

Data processing and analysis
All preserved individuals were measured with a calliper (fork length, \(L_f\), to the nearest mm) and their stomach contents emptied into a Petri dish and observed under a stereomicroscope. Prey items were classified to the lowest taxonomic level possible and recorded as present or absent.

The multivariate dataset was explored and represented using a two-dimensional unconstrained principal coordi-
nate ordination (PCO) based on Gower's dissimilarity measure (Gower 1966). Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was then used to analyse the variation in feeding habits of plaice and flounder between and within the two different estuarine habitats. The experiment consisted of a three-way design with 'Species' ('Spe', two levels) as a fixed factor, 'Locality' ('Loc', two levels) as a random and crossed factor, and 'Station' ('Sta', two levels) as a random factor nested in 'Locality'. Pairwise tests were also conducted to pinpoint the levels responsible for significant interactions.

Feeding was also examined by comparing the variation of most abundant taxa, which were 'pooled' into taxonomical/ecological guilds as follows: 'Copepods' (comprising Harpacticoida, Cyclopoida and Calanoida), 'Worms' (comprising Polychaeta, Oligochaeta and Nematoda), 'Amphipoda + Isopoda', and 'Other Malacostraca' (comprising Mysidacea, Brachyura and Caridea). These data were analysed by univariate ANOVA, applying the same design described for PERMANOVA, and after testing for homogeneity of variance using the Cochran's C-test (Underwood 1997). Student-Newman-Keuls (SNK) tests were used for post hoc multiple pairwise comparisons.

Results

A total of 1144 flounder and 810 plaice were collected. Flounder were dominant in Wexford Harbour (975 versus 184) and plaice in North Bull Island (626 versus 169) (Fig. 1).

A total of 202 fish were examined for stomach contents: 50 flounder (31 + 19) and 50 plaice (30 + 20) from two stations in North Bull Island, 50 flounder (30 + 20) and 52 plaice (36 + 16) from the two stations in Wexford Harbour. Fish size ranged between 22 and 127 mm and no differences were observed between species and locations (ANOVA: $F = 1.42$, df = 3, $P = 0.24$) and none of them had an empty stomach. Twenty-one different prey items were identified, with mysids being generally the primary resource for flounder and polychaetes being the most abundant prey in plaice (Table 1).

PCO ordination of sample centroids showed a more clumped distribution for flounder and a greater scattering of the plaice data points (Fig. 2). PERMANOVA detected significant differences for both the interactions: Spe*Loc and Spe*Sta(Loc), as well as for the effect 'Station(Loc)', revealing the dependence of locality-specific variation in governing feeding interactions between these species.

<table>
<thead>
<tr>
<th></th>
<th>FB1 (19)</th>
<th>FB2 (31)</th>
<th>FW1 (30)</th>
<th>FW2 (20)</th>
<th>PB1 (30)</th>
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Numbers in brackets in the column headers refer to sample size. Values in bold represent 'important' (>25%) or 'dominant' (>50%) prey items, according to Albertine-Berhaut (1973).
Fig. 2. Ordination plot of sample centroids inferred with Principal coordinate analysis. F is for flounder (black), P is for plaice (grey), B is for ‘North Bull Island’ (triangles) and W is for ‘Wexford Harbour’ (circles).

Table 2. Results summary table for PERMANOVA procedure conducted on presence/absence stomach content data. Values in bold are significant with $\alpha = 0.05$.

<table>
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<th>source</th>
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<th>pseudo-F</th>
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<td>0.114</td>
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<td>0.041</td>
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<td>11,756</td>
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<tr>
<td>residual</td>
<td>191</td>
<td>2697.5</td>
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<td></td>
</tr>
<tr>
<td>total</td>
<td>198</td>
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</table>

(Table 2). Pairwise tests conducted on both interactions showed consistent significant differences between species within stations but only plaice was shown to vary its diet significantly between locations.

Univariate analyses were also informative in describing diet variation between and within species (Fig. 3). Significant differences between species were detected in the category ‘Worms’ ($F = 32.5$, $P = 0.01$). The interactions Spe*Loc for ‘Other Malacostraca’ ($F = 42.9$, $P = 0.02$) and Spe*Sta (Loc) for ‘Copepods’ ($F = 4.3$, $P = 0.01$) were also significant, and the Spe*Loc interaction for both ‘Copepods’ ($F = 10.7$, $P = 0.08$) and ‘Amphipoda + Isopoda ($F = 14.4$, $P = 0.06$) were only marginally above the probability threshold. SNK tests confirmed significant differences between plaice and flounder across all stations in terms of ‘Copepods’, but only in Wexford for ‘Other Malacostraca’.

Fig. 3. Frequencies of four main food categories in plaice and flounder from two estuaries. Results of univariate ANOVA tests are in the text.

Discussion

The study of the feeding habits and resource partitioning in closely related fish can be very useful to understand the flows of energy across the food web (Darnaude, 2005) and provide important insights into the trophic flexibility of interacting species (Mariani et al. 2002; Platell et al. 2006; Russo et al. 2008). Yet, the quantification of diet overlap or niche segregation – even when supported by robust explanations of the processes underlying the patterns – may still only provide a very narrow picture of the true flexibility of a species’ trophic ecology.

This study expands the analysis of resource partitioning between two common flatfish, plaice and flounder, by taking into consideration the naturally high environmental heterogeneity of estuarine habitats, and performing diet comparisons in two different estuarine habitats.

Wexford Harbour was found to be dominated by flounder, whereas North Bull Island showed a predominance of plaice. This is probably linked to the lower salinities observed year-round in Wexford (Craig et al. 2008) and the well-known pronounced preference of flounder for brackish environments. This species appeared to exhibit a more spatially homogeneous food spectrum (clumped scatter of data in Fig. 2) relative to plaice,
which exhibits remarkable diet changes between the two study locations (wider distribution of data in Fig. 2).

Univariate tests on the most abundant prey items (Fig. 3) illustrate well the extent and nature of diet variation between and within plaice and flounder. Plaice seems to be the most efficient forager of polychaetes and other worm-like prey, whereas flounder consistently consumes a greater amount of malacostraca, particularly mysids (Table 1). The frequency of different preys across flounder samples is much more even than in plaice: for instance, considerable frequencies of copepods, decapods and bivalves are found in the stomachs of plaice from North Bull Island, whereas virtually only polychaetes and amphipods are consumed in Wexford. One explanation may reside in the fact that Wexford is a flounder-dominated habitat, which might drive the less numerous plaice to select only preys, such as polychaetes and amphipods, that are not ‘preferred’ by flounder, as indeed appears to be the case in Wexford Harbour. Intra-specific competition may also play a role, prompting plaice to select a wider range of prey in the location where it is more frequent and dominant (i.e. North Bull Island).

On the other hand, flounder does not seem to go through the same ‘diet switch’, when the two estuaries are compared. The only prey categories affected are amphipods and isopods, which show a slow frequency in Wexford (Fig. 3), although this is counterbalanced by the intense consumption of other malacostraca (especially mysids). Without a parallel investigation on the abundance of potential prey (Wouters & Cabral 2009), it remains difficult to assess to what extent the results may be influenced by differential availabilities of resources; however, the present data unambiguously show that estuarine environmental heterogeneity determines changes in resource use in plaice and flounder and that the responses are different for each species, resulting in the variation of patterns of trophic inter-relationships between species.

The feeding habits of plaice and flounder vary between and within localities (Table 2), resulting in very interesting patterns at finer scales: plaice in Wexford consumed significantly different prey than plaice in Bull Island, and in each station within estuary, plaice and flounder consistently preyed upon different items, effectively reducing niche overlap. This view of trophic niches and resource use makes the fluctuating, unstable, seemingly chaotic estuarine habitat a much more fine-tuned, sophisticated, elegantly functioning system than generally believed. Further studies including a greater number of estuaries, and possibly a greater number of species, may add operational complexity, but would certainly help to characterise these mechanisms with greater confidence.

Conclusions

We have shown that the patterns of niche overlap and resource partitioning between plaice and flounder in estuarine habitats vary depending on the specific system studied. This strengthens the view that estuaries, lagoons and other transitional habitats may represent a heterogeneous ‘mosaic’ of selective forces (Weinig & Schmit 2004), which is crucial to the evolution of the life-histories of coastal marine fish (Mariani 2006) and perhaps influences the functioning of more ‘extended’ phenotypic traits (sensu Dawkins 1982), such as trophic interactions and community structure.

Future studies should attempt to evaluate whether the observed trophic flexibility results entirely from phenotypic plasticity (Gronkjaer et al. 2007) or also to some extent from genomic adaptation.

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References


Albertine-Berhaut I. (1973) Biologie des stades juveniles de teleostees, Mugilidae, Mugil auratus Riso 1810, Mugil capito Cuvier 1829 et Mugil saliens Riso 1810. Regime alimentaire. Station Marine d’Endoume, Marseille. 2 pp 251–266.


ORIGINAL ARTICLE

mtDNA differentiation in the mussel Mytilus galloprovincialis Lmk. on the Iberian Peninsula coast: first results

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Keywords
Atlantic Ocean; genetic differentiation; Mediterranean Sea; mitochondrial DNA; Mytilus galloprovincialis.

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Abstract
The nucleotide sequence of the VD1 domain of the Long Unassigned Region in the F mitochondrial DNA genome was studied for 135 Iberian mussels, 78 from the Atlantic and 57 from the Mediterranean. Significant genetic differentiation between Atlantic and Mediterranean Mytilus galloprovincialis samples was found (FST = 0.262, P < 0.00001). The four main clusters observed in the neighbor-joining tree of haplotypes were not exclusive for a specific region, but a clear geographic pattern could be observed. One of the clusters contained 86% of the Atlantic individuals and the remaining three clusters were predominantly Mediterranean. The Atlantic–Mediterranean differentiation of the mitochondrial DNA haplotypes was in agreement with previous data describing the same partitioning in M. galloprovincialis and in many other marine organisms, using different kinds of genetic markers. In all cases the Almeria Oran Oceanographic front has been associated to this genetic discontinuity.

Introduction
In Europe, the mussel Mytilus galloprovincialis Lmk. is distributed in the Black Sea, the Mediterranean and on the Atlantic coast from the Iberian Peninsula as far north as the British Isles (Gosling 1992). The Iberian Peninsula occupies an intermediate location in this distribution, between the Atlantic and Mediterranean regions.

Extensive genetic studies of M. galloprovincialis populations in the Iberian Peninsula have been carried out using allozyme polymorphisms (Sanjuan et al. 1994, 1997; Quesada et al. 1995a), mtDNA RFLPs (Quesada et al. 1995b; Sanjuan et al. 1996) and microsatellites (Diz & Presa 2008). In all cases, results agree on the existence of a strong genetic discontinuity between Atlantic and Mediterranean populations associated to the Almeria Oran Oceanographic front (AOOF). However, the direct analysis of nucleotide variation would provide a deeper insight into the population dynamics of the species, on both sides of the Gibraltar Strait, than is offered by allozymes, restriction enzyme analyses or microsatellites.

Currently, analysis of mitochondrial DNA (mtDNA) sequences is one of the most widely used tools in molecular phylogenetics studies due to uniparental inheritance, abundance of selectively neutral mutations, low rate of recombination and technical simplicity. Skibinski et al. (1994) and Zouros et al. (1994) described the existence of doubly uniparental inheritance (DUI) of the mtDNA in the Mytilidae family. DUI involves the existence of heteroplasmic males carrying a maternal (F) and a paternal (M) mitochondrial genome, and homoplasmic females bearing only the F genome. Thus, the F genome is maternally transmitted to offspring, whereas the M genome is paternally transmitted to male progeny only. In species with DUI, maternal lineages provide more reliable information for population and phylogenetic studies, as M lineages are not appropriate for phylogeographic studies due to their very fast evolution and liability to invasion from the F lineage (Ladoukakis et al. 2002). The mitochondrial genome of Mytilus is divided into two parts: the core that contains all protein, rRNA and tRNA coding genes and a few noncoding regions of <500 bp, and the LUR (large
mtDNA differentiation in Iberian *M. galloprovincialis* Lmk.

unassigned region). Cao *et al.* (2004) have divided the LUR into three parts: the first variable domain (VD1), the conserved domain (CD), and the second variable domain (VD2). These domains seem to be equivalent to those found in human mtDNA and contain sequence motifs which are known to be involved in the replication and transcription of the molecule. These observations suggest that the LUR is the main control region of the mitochondrial genome (Cao *et al.* 2004). The high degree of nucleotide variability makes VD1 domain an excellent tool in order to analyse genetic variation in the mussel *M. galloprovincialis*.

Thus, the aim of this work was to assess the degree of variation and differentiation, and to infer the population dynamics processes leading to the current patterns of genetic variation in the *M. galloprovincialis* populations living on the Iberian coast using the nucleotide sequence tool in order to analyse genetic variation in the mussel *M. galloprovincialis*.

Material and Methods

A total of 135 individuals of *M. galloprovincialis* were collected in two Atlantic and two Mediterranean locations on the Iberian Peninsula coast (Fig. 1). After dissection, total DNA was extracted from gonadal tissue using the procedure of DeSalle *et al.* (1993).

Amplification of the large unassigned region (LUR) of the mitochondrial genome was carried out in a final volume of 50 μL containing 10 mM Tris–HCl, pH 9.0, 2 mM MgCl₂, 50 mM KCl, 0.1% Triton X-100; 0.2 mM of each dNTP (Amersham Pharmacia Biotech); 0.06 μM of each primer (UNFOR1 and UNREV1; Cao *et al.* 2004); 1.5 U of Taq DNA polymerase (EcoTaq, Ecogen) and 3 μL of the extracted DNA. An initial denaturation at 94 °C for 3 min, 40 PCR cycles (94 °C: 1 min, 55 °C: 1.5 min, 72 °C: 1 min) and a final extension at 72 °C for 6 min were carried out in a GeneAmp PCR System 9700 thermal cycler (Applied Biosystems).

The PCR products were visualized by UV transillumination after electrophoresis in 1.5% SeaKem LE agarose gels (FMC BioProducts) containing ethidium bromide. Double-stranded DNA from PCR reactions was cleaned using the Qiaquick PCR purification kit (Qiagen GmbH), following the manufacturer’s instructions.

From purified PCR products, both strands of a fragment of 575 bp, belonging to the VD1 domain of the female mtDNA LUR, was sequenced in two separated sequencing reactions using the CEQ Dye Terminator Cycle Sequencing Kit (Beckman Instruments) and two different primers specific for the female mtDNA molecule. Finally, fragments were migrated in a Beckman CEQ2000 DNA sequencer (Beckman Instruments) at the Facultade de Bioloxia, Universidade de Vigo. Sequences were read and edited using the software provided with the sequencer and aligned with CLUSTAL X version 2.0.9 (Larkin *et al.* 2007).

Nucleotide diversity (Tajima 1983; Nei 1987) for each sample was estimated in the MEGA software v4.0.2. Gene diversity estimated from haplotype frequencies (Nei 1987) as well as population pairwise FST distances (Reynolds *et al.* 1983; Slatkin 1995) between all pairs of populations, were computed using the ARLEQUIN software package v3.1 (Excoffier *et al.* 2005). In the case of pairwise FST distances we have applied the Bonferroni method, a multiple-comparison correction used when several statistical tests are being performed simultaneously. To avoid spurious positives, the alpha value was lowered to account for the number of comparisons being performed.

Haplotype phylogenetic relationships were estimated with a neighbor-joining (NJ) method (Saitou & Nei 1987) conducted by the MEGA software v4.0.2 (Tamura *et al.* 2007), using the gamma-corrected Tamura–Nei distance (Tamura & Nei 1993). Support for the tree was obtained by 1000 bootstrap replicates (Felsenstein 1985).

Results

A total of 135 individuals were sequenced for 575 bp of the VD1 domain of the female mtDNA. Seventy-six variable sites were observed, defining 40 different haplotypes whose frequencies in each of the four samples are detailed in Table 1. The sequence of haplotype h12 was deposited in GenBank (accession no. HQ675011). Four of these...
Table 1. Relative frequencies of the 40 haplotypes found in this study. Numbers in parentheses are sample sizes. Sample codes are indicated in Fig. 1.

<table>
<thead>
<tr>
<th>Haplotype</th>
<th>Atlantic</th>
<th>Mediterranean</th>
</tr>
</thead>
<tbody>
<tr>
<td>GSU33</td>
<td>0.36</td>
<td>0.31</td>
</tr>
<tr>
<td>GBA45</td>
<td>0.34</td>
<td>0.09</td>
</tr>
<tr>
<td>GSA17</td>
<td>0.06</td>
<td>0.02</td>
</tr>
<tr>
<td>GSU29</td>
<td>0.05</td>
<td>0.04</td>
</tr>
<tr>
<td>GSU30</td>
<td>0.03</td>
<td>0.02</td>
</tr>
<tr>
<td>GSU31</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>GSU32</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>GSU33</td>
<td>0.01</td>
<td>0.00</td>
</tr>
<tr>
<td>GSU34</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>GBA03</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>GBA04</td>
<td>0.02</td>
<td>0.00</td>
</tr>
<tr>
<td>GBA17</td>
<td>0.02</td>
<td>0.00</td>
</tr>
<tr>
<td>GBA22</td>
<td>0.02</td>
<td>0.00</td>
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<tr>
<td>GBA27</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>GBA29</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>GBA37</td>
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<tr>
<td>GBA40</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>GBA46</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>GCQ12</td>
<td>0.04</td>
<td>0.01</td>
</tr>
<tr>
<td>GCQ16</td>
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<td>0.00</td>
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</tbody>
</table>

haplotypes (h11, h12, GBA04 and GCQ126) showed a previously described duplication (Cao et al. 2004; Śmietańka et al. 2004) of 36 bp, spanning from nucleotides 262 to 297 of the sequence of haplotype h12. Haplotypes appearing more than once are named with numbers (h01–h14) and the ‘singletons’ are named by the code of the individual carrying the haplotype.

There was only one haplotype (h10) present in all the samples. Haplotypes h01 and h05 were the commonest among the Atlantic samples (frequencies of 34 and 14%, respectively), whereas haplotypes h08, h09 and h10 were the most abundant in the Mediterranean, where they reach frequencies of 14–19%. It is noteworthy that the percentage of singleton haplotypes, calculated over the total number of individuals, was much higher in the Atlantic (30%) than in the Mediterranean (5%). When calculated over the number of haplotypes, the value was also distinctly higher in the Atlantic (66%) than in the Mediterranean (21%). All the populations showed similar degrees of diversity at the haplotype level. Haplotype diversity (h) averaged 0.87 in the Atlantic samples and 0.9 in the Mediterranean samples. Conversely, the average of nucleotide diversity (π) in the Mediterranean (0.025) was almost double the value in the Atlantic (0.013), although an unpaired t-test resulted in a probability of 0.0815. More extensive sampling will be necessary to clarify this apparent difference in nucleotide diversity.

The population pairwise FST distances (data not shown) yielded highly significant values for the Atlantic–Mediterranean pairs (P < 0.00001) and nonsignificant values for the Mediterranean pairs (P = 0.748). When the Atlantic populations were compared, the FST distance was found significant at the 5% level, although it became nonsignificant after application of Bonferroni correction for the six pairwise comparisons (alpha level was lowered from 0.05 to 0.0083). The FST value between the Atlantic and the Mediterranean pooled samples (0.262) was highly significant (P < 0.00001).

The NJ tree (Fig. 2) showed four main clusters supported for bootstrap values higher than 70%. The largest cluster, supported by a bootstrap value of 97%, included 86% of the Atlantic individuals, and 29 different haplotypes (24 exclusively Atlantic). The remaining three clusters were predominantly Mediterranean, encompassing 81% of the individuals of this geographic region.

Discussion

The results of the analyses applied in this study were consistent with the existence of a significant genetic discontinuity between the Atlantic and Mediterranean populations of Mytilus galloprovincialis on the Iberian coasts. On the one hand, the population pairwise FST distances showed high differentiation between the Atlantic and the Mediterranean populations, but nonsignificant differences within each group. On the other hand, the NJ tree displayed four highly differentiated clusters representing four groups of haplotypes separated, one from each other, by a minimum of 10 mutational steps. Although no cluster is exclusive for a specific region, a clear geographic pattern differentiates the largest cluster, which includes 86% of the Atlantic individuals, and the remaining three clusters, predominantly Mediterranean.
between two haplotypes was three mutational steps. In Atlantic haplotypes belonged to the same cluster, and the largest difference at the nucleotide diversity level, the Atlantic haplotypes showed a higher degree of homogeneity, as all of them belonged to the same cluster, and the largest difference between two haplotypes was three mutational steps. Using the same reasoning, the remaining haplotypes were defined as Mediterranean. At the nucleotide diversity level, the Atlantic haplotypes showed a higher degree of homogeneity, as all of them belonged to the same cluster, and the largest difference between two haplotypes was three mutational steps. In contrast, Mediterranean haplotypes are much more diverse, belonging to three clearly differentiated clusters. This scenario explains the high π value in the Mediterranean. The apparent contradiction between the difference in the π value and the similarity of haplotype diversities (0.87 and 0.90) is explained by the high frequency of singletons in the Atlantic cluster, typical of populations that have gone through episodes of recent expansion. The low number of haplotypes in the Mediterranean clusters could be explained by recent bottleneck effects that reduced genetic diversity.

These results were in agreement with previous findings describing an Atlantic–Mediterranean partitioning in *M. galloprovincialis* (Sanjuan et al. 1994, 1996, 1997; Quesada et al. 1995a,b, 1998; Ladoukakis et al. 2002; Smietanka et al. 2004; Diaz & Presa 2008) using different kinds of genetic markers (allozyme polymorphisms, mtDNA restriction fragment length polymorphisms, mtDNA sequences and nuclear microsatellites). In all cases this genetic discontinuity has been associated with the Almeria Oran Oceanographic front (Fig. 1; Tintore et al. 1988), a strong marine surface current between Almeria (Spain) and Oran (Algeria). The strong current and a sharp change in oceanographic conditions (higher salinity and temperature in the eastern part of the front) could represent an important obstacle to the dispersal of mussel larvae.

A process of vicariance due to isolation of both populations is consistent with the clear genetic differentiation observed between the Atlantic and Mediterranean. The narrowing of the Gibraltar Strait in the Pleistocene (Pie-lou 1979) could account for the isolation of the Mediterranean basin. Subsequently, after the opening of the Gibraltar Strait, the AOOF would have acted as a partial barrier for genetic flow, maintaining some degree of the differentiation previously established.

In spite of this barrier to gene flow there are significant proportions of typically Atlantic haplotypes present in the Mediterranean and vice versa. Specifically, we have observed that 14% of the Atlantic individuals carry Mediterranean haplotypes and 19% of the Mediterranean mussels carry Atlantic haplotypes. This asymmetric gene flow explains the mixing of Atlantic and Mediterranean individuals in all the main clusters of the tree. It is congruent with the predominantly eastward direction of the surface water circulation through the Straits of Gibraltar (Perkins et al. 1990) and has been described previously in *M. galloprovincialis* using mtDNA RFLPs (Quesada et al. 1998). However, this difference is not statistically significant and more samples should be analyzed to provide more support for the asymmetry of the gene flow.

**Summary**

All the results in this study are consistent with a process of isolation, followed by restricted secondary contact, generating the current patterns of genetic differentiation between the Atlantic and Mediterranean populations of *Mytilus galloprovincialis* in the Iberian Peninsula. The
temporary closing of the Mediterranean Sea, followed by the opening of the Strait of Gibraltar and subsequent gene flow restricted by the AOOF, would be a plausible geological scenario explaining this situation. Nevertheless, a more exhaustive sampling would be necessary to provide better evidence of the recent dynamics of Atlantic and Mediterranean populations, and the interactions between them.

References


Excoffier L., Laval G., Schneider S. (2005) Arlequin ver. 3.5.0: an integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online, 1, 47–50.


**Paramuricea clavata** (Anthozoa, Octocorallia) loss in the Marine Protected Area of Tavolara (Sardinia, Italy) due to a mass mortality event

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**Keywords**
Conservation; global warming; Octocorals; Vibrio.

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**Abstract**
Recent studies highlight an increase in the frequency and intensity of marine mass mortalities of several species over the past 30–40 years, mainly in tropical and temperate areas. In the Mediterranean Sea these episodes particularly affect benthic suspension feeders, such as sponges and cnidarians. The main objective of this work was to document the loss of one of the main Mediterranean seas-ecosystems, *Paramuricea clavata* forests at the Marine Protected Area of Tavolara Punta Coda Cavallo, Sardinia (Italy), during the summer of 2008. Data regarding colony height, density, level of damage, and microbiological community were collected at two sites. Such parameters help us understand how mass mortality mechanisms act on this ecosystem engineer. We identified a change in size class distribution following a mass mortality that leaves mainly small colonies with a decrease in habitat complexity. Several tests on water chemistry demonstrate that the mortality event was not caused by local contamination. Moreover, microbiological tests on potential pathogenic agents suggest that bacteria belonging to the genus *Vibrio* are present as an opportunistic and not an etiological cause of *P. clavata* mortality events. Possible restoration approaches are discussed.

**Introduction**
Marine communities appear to be facing one of the worst periods in their recent history. The direct negative effects of several human activities (e.g. oil spills, coastal habitat modification, overfishing) are now amplified by climate change, which is compromising both the resistance and the resilience of many marine organisms. During the last decades, the Northwestern Mediterranean Sea has been hit by a series of mass mortality events, which impact benthic suspensivore organisms, such as sponges, cnidarians, bivalves, bryozoans and tunicates, and associated assemblages (Cerrano & Bavestrello 2009). These mortality events coincide with thermal anomalies generally caused by unusual water warming during prolonged periods of water column stability (CIESM, 2008).

Affected species often show modifications in their physiology (Prevati *et al.* 2010), distributions, and sometimes phenology (Bavestrello *et al.* 2006), which can have unpredictable consequences on species’ interactions (Hughes 2000). Often the affected species are ecosystem engineers and their rarefaction and/or disappearance has profound consequences on the habitat architecture, such as reducing spatial complexity and decreasing biodiversity richness (Matias *et al.* 2010). In the Mediterranean Sea, several causes of these mortality events have been
identified, typically associated with environmental factors (Cerrano et al. 2000, 2005; Pèrez et al. 2009; Calvisi et al. 2003; Linares et al. 2005, 2008b; Cigliano & Gambi 2007; Previati et al. 2010) but a number of pathogens have also been implicated (Martin et al. 2002; Gay et al. 2004; Bally & Gărarrabou 2007; Vezzulli et al., 2010). Among the affected areas in the Mediterranean, perhaps the Ligurian Sea can be considered the most severely affected (Gărarrabou et al. 2009). However, in the late summer of 2008, one of these particular thermal anomalies was registered in the Marine Protected Area of Tavolara Punta Coda Cavallo (Central Western Tyrrhenian Sea) and had a dramatic effect on sea-fan (Octocorallia: Gorgonacea) populations, particularly on two rocky shoals adjacent to Tavolara Island, where presence of large numbers of the gorgonian Paramuricea clavata characterizes one of the most famous dive spots in the area.

Paramuricea clavata is known to be sensitive to high temperatures (Cigliano & Gambi 2007; Coma et al. 2009; Fava et al. 2010; Previati et al. 2010) and can show an immediate response to these events. Crucially, this species is considered an ecosystem engineer and facilitator species (Bruno & Bertness 2001; Scinto et al. 2009) within coralligenous assemblages. The aims of this work were: (i) to describe the mass mortality event that affected populations of P. clavata and (ii) to determine whether a range of environmental parameters are correlated with P. clavata mass mortality. Possible pathways for restoration and management of this species are also discussed.

Material and Methods

Study area

Tavolara Island (40°54′, 19′ N; 9°42′, 28′ E) is formed from limestone-dolomite rock. Together with the granitic Molaro, Molarotto and other minor islets, Tavolara forms a small archipelago with an epibenthic community that has been well described by Navone & Trainito (2008) and Navone et al. (1992). In the study area, the effects of the mass mortality event on the pre-coralligenous and coralligenous assemblages of two nearby sites (termed Papa 1 and Papa 2) were quantified. Papa 1 ranges in depth from 15 to 39 m, and Papa 2 from 24 to 43 m. The current direction flows in a NE–SW direction, from Papa 2 towards Papa 1. At both sites there is a dense forest of Paramuricea clavata and also Eunicella cavolinii (Calvisi et al. 2003; Bianchi et al. 2007). SCUBA diving surveys were undertaken during October 2008, December 2008 and June 2009, which corresponded to the period when mortality was first noted for P. clavata and 3 and 9 months subsequently.

Population structure and mortality dynamics: field surveys

To study population dynamics, a minimum of six quadrats (50 × 50 cm) were randomly sampled from 40 to 20 m depth every 5 m from the bottom to the top of each shoal, following standard methodology set out by similar studies (Cerrano et al. 2005; Coma et al. 2006; Linares et al. 2008a) and in relation to the geomorphology of the sites (Papa 1 from −35 to −20 m; Papa 2 from −40 to −25 m). Within each quadrat the number of colonies (converted to colony density), colony heights, colony health (defined as the percentage of colony with damaged coenenchyme: 0% was considered healthy, <25, <50, <75, <99 and 100%), and the number of fishing lines and/or nets wrapped around the colonies were recorded. Furthermore, for each colony the epibiosis level was recorded (according to methods provided by Bavestrello et al. 1997) and the epibiotic organisms were identified. On the basis of organisms that had settled on the scleraxis we defined different temporal phases: (i) denuded (when the scleraxis is visible, with tissue on scleraxis), (ii) new (covered with filamentous green and/or red algae, and/or hydrozoans), (iii) medium (possessing a thick coat of algae, and/or sponges) and (iv) old (mainly colonized by calcareous organisms such as bryozoans). To test the differences in population composition, within sites and among times, ANOVA tests were performed after verifying that data were normally distributed and there was equality of variances.

We assumed that the pre-mortality population structure was very close to that observed in October (i.e. during/just after mortality) for three reasons: (i) most colonies had only just died, with naked scleraxis and with necrotic coenenchyme portions still present on the colonies, (ii) no fragments or whole colonies were found (implying that colonies had not detached from the base) and (iii) colonies were always measured – including the denuded and epibionted parts of the colonies. The post-mortality structure of colonies was considered to be typical of that observed from December 2008.

Environmental features – laboratory analyses

To evaluate whether chemical features of seawater and/or bacterial infections could be involved in the mortality, both seawater samples and portions of colonies were collected.

Seawater temperature and water chemistry

Temperature was measured during survey dives using two types of underwater computers: (i) UWATEC (± 0.5 °C), with a system that records and memorizes automatically
water temperature during the dives every 4 s, creating a profile, and (ii) underwater computers with a punctual temperature measurement (variation of ±1°C) that divers recorded manually every 5 m during the dive ascent. Water temperature data were taken in both sites. Average values of water temperature were accomplished with both manually recorded and automatic UWATEC data, separated by depth ranges: SST (sea surface temperature) or 0, 5, 10, 15, 20, 25, 30, 35 and 40 m depth.

To determine dissolved oxygen concentrations (DOC) during the mortality event, separate seawater samples were carefully collected, avoiding air bubbles, and immediately fixed following Carpenter’s (1965) protocol. Inorganic nutrient concentrations were determined according to Hansen & Grasshoff (1983). Marine water was pre-filtered with cellulose acetate filters (0.45 μm pore diameter) and maintained at −20°C until laboratory analysis. Nitrates, nitrites, ammonia and phosphates were analyzed with SYSTEA (nutrient analyzer) and silica concentrations were quantified using a Jasco V-500 spectrophotometer.

Microbiological analysis

Top colony pieces (n = 45 in total) of about 5 cm of healthy and damaged *P. clavata* colonies were taken (20 healthy and 25 damaged, all samples from different colonies). Samples were maintained in cold seawater (4°C) until laboratory manipulation, then washed in sterile seawater to remove other bacteria or fauna that were not strictly related to *P. clavata* damage and incubated in an enriched APW (alkaline peptone water) culture broth. After 10 h, samples were plated onto thiosulfate citrate

bile salt sucrose (TCBS) agar to isolate the main morphotypes of bacteria belonging to the genus *Vibrio*. Other pieces of tissue were frozen (at −20°C) until total genomic DNA could be extracted. After DNA extraction, bacterial samples were identified on the basis of their 16S rRNA gene sequences (see Vezzulli et al., 2010 for full details of methods). To identify isolates, PCR amplification of a 798-bp region was performed using the universal primers BR1 (5′-AGAGTTTGATCCTGGCT-3′) and BR2 (5′-GGACTACCAGGTATCTAAT-3′), amplifying positions 8–806 of the *Escherichia coli* numbering of the 16S rRNA gene that include hyper-variable regions. 16S rRNA gene sequence similarity was determined with SEQMATCH (version 2) analysis of Ribosomal Database Project (RDP-II, Release 9) of the Center for Microbial Ecology, Michigan State University (http://rdp.cme.msu.edu/seqmatch). To assess the pathogenic potential of isolated strains towards *P. clavata* colonies, infection experiments were performed in aquaria at different temperatures and environmental conditions simulating those observed in the environment during the occurrence of mortality events (see Vezzulli et al., 2010 for full details of experiments).

Results

Population structure and mortality dynamics: field surveys

In total, 476 colonies were observed in 158 quadrats. Records of colony densities, height and size class distribution show how the two sites (shoals) have a different population structure, and this appears to have elicited a different response to the mortality event.
Papa 1. In this site the mean density (± SE) was 9.12 ± 2.18 colonies per m². Significant differences in densities were detected among depths (P < 0.05, Fig. 1), predominantly due to the low number of colonies in the upper limits of this species’ distribution. The mean height of *Paramuricea clavata* (± SE) was 21.03 ± 4.24 cm during the mortality event and 27.72 ± 3.12 cm during the last survey, with no significant differences detected both in mean height of the colonies on the investigated temporal scale (P > 0.05, see also Fig. 2) and between the different depths (P > 0.05). Damaged colonies of *P. clavata* were found at all depths, but at 35 m depth the percentage of damage was mainly constant and generally lower than at the other (mostly shallower) depths (Fig. 3). Between 30 and 20 m depth, mortality occurred at a high percentage of colonies, and was especially prevalent in the larger sized classes. At 25 m depth, all size classes of colonies were 100% damaged, both in October 2008 and in December 2008. In the last survey, in June 2009, more healthy colonies (compared with previous surveys) were found and the average size of the population had shifted towards smaller sized classes (i.e. 0–30 cm) (see Figs 1, 2 and 4).

Papa 2. In this site mean density (± SE) of *P. clavata* was 17.33 ± 2.13 colonies per m². No differences in density were detected both among depths and the investigated periods (P > 0.05) (Fig. 1). Mean colony height (± SE) during the mortality event was 29.72 ± 6.86 cm and 28.54 ± 2.01 cm during the last survey. The smallest colonies were found at 25 m depth (Fig. 2), while colony height elsewhere was significantly greater (P < 0.001), although there was no obvious correlation between colony height and the depth of the substrate they occupied. Damaged colonies were found at all depths during the entire period of study. At 40 m depth the percentage of damaged colonies was generally low and varied between about 20 and 40%. By contrast, at 35 and 25 m depths the frequency of mortality was higher between October...
and December, especially for the 21–30 cm size class individuals. In June, the size class distribution shifted towards the smaller size classes (i.e. there were more colonies in the range 0–30 cm) (Figs 1, 2 and 5). Overall, the mean percentage of damage of colonies indicates that damage is generally greater in the shallower parts of the shoals, in some cases up to 100% throughout the whole size class of individuals (Fig. 3).

At both sites, epibiosis on the denuded parts of the colonies followed a pattern of four temporally successive steps: (i) denuded branches, here recorded in October, (ii) newly settled organisms such as filamentous algae and hydroids, (iii) a medium stage of epizootic colonization with algae and small sponges, which was noted in December, and finally (iv) an old stage with colonization by algae, sponges, bryozoans and other calcareous organisms, which was found during the last surveys in June (Table 1).

**Environmental features: laboratory analyses**

Seawater temperature measurements confirmed the high temperature (22 ± 1 °C in September and 21 ± 0.5 °C in October) along the water column and the absence (in the investigated depth range of between 20 and 43 m) of thermocline in October, confirming a prolonged water stability over it (Fig. 6). Temperature is depth-dependent; at all depths considered, water temperature was at least a degree higher during the months of September and October 2008 than in the previous year. Data for December 2007 were not available.

Although the dissolved oxygen concentrations were always high in both the sampling sites (close to healthy and damaged colonies), water results have highlighted higher levels of nitrite, nitrate and ammonia during the mortality event, especially around the damaged colonies where tissue degradation was taking place (Table 2). In contrast, phosphate concentrations were higher next to the healthy colonies. These concentrations led to P-limitation conditions (higher N/P ratio where N is the sum of nitrite, nitrate and ammonia concentrations) next to the compromised colonies, especially during October.

Microbiological tests revealed that *Vibrio* bacteria were consistently more abundant in diseased organisms with up to a twofold higher concentration compared with those found on the healthy corals (Fig. 7). The 16S rRNA
gene sequencing of 61 Vibrio isolates associated to diseased and healthy Paramuricea clavata colonies showed a close homology of the majority of the strains with Vibrio harveyi (n = 24), Vibrio splendidus (n = 22) and Vibrio coralliilyticus (n = 15), the latter only being identified in diseased organisms.

Discussion

The main aims of MPAs, as identified in the IUCN Guidelines for Establishing Marine Protected Areas (Kelleher & Kenchington 1992), are (i) to maintain essential ecological and life-support systems, (ii) to ensure the sustainable utilization of species and ecosystems and (iii) to preserve biotic diversity. Monitoring, defined as continuous observation of conditions over time, is a crucial tool for the conservation of marine biological diversity and provides managers with important data from which they can make informed decisions about patterns and processes that affect biodiversity, and thus the functioning (or not) of an MPA. Here, we present our monitoring data to describe some of the factors associated with a mass mortality of the gorgonian Paramuricea clavata at the MPA at Tavolara Island, Italy.

The mortality event described here affected a population of octocoral that is well known and utilized by the diving tourism industry in a ‘Specially Protected Area of Mediterranean Importance’ (SPAMI). Our results represent an important baseline for future monitoring.
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Fig. 6. Temperature profile from 2008 of the months of interest in the investigated area, recorded by SCUBA operators and SST (sea surface temperature) from http://www.poseidon.ogs.it. Data from December 2007 were not available.

Table 2. Environmental features recorded for the sea-water collected next the decaying (damaged) and the control (healthy) colonies.

<table>
<thead>
<tr>
<th></th>
<th>Dissolved oxygen</th>
<th>Silicate</th>
<th>Nitrite+nitrate</th>
<th>Ammonia</th>
<th>Phosphate</th>
<th>N/P ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ml l⁻¹</td>
<td>µM</td>
<td>µM</td>
<td>µM</td>
<td>µM</td>
<td></td>
</tr>
<tr>
<td>October</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Healthy</td>
<td>7.49</td>
<td>1.15</td>
<td>2.40</td>
<td>1.63</td>
<td>0.18</td>
<td>22.9</td>
</tr>
<tr>
<td>Damaged</td>
<td>7.23</td>
<td>1.54</td>
<td>3.11</td>
<td>2.10</td>
<td>0.15</td>
<td>35.4</td>
</tr>
<tr>
<td>December</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Healthy</td>
<td>nd</td>
<td>2.42</td>
<td>0.92</td>
<td>0.96</td>
<td>0.12</td>
<td>15.2</td>
</tr>
<tr>
<td>Damaged</td>
<td>7.77</td>
<td>2.12</td>
<td>0.96</td>
<td>1.23</td>
<td>0.10</td>
<td>22.0</td>
</tr>
</tbody>
</table>

N, nitrogen; nd, not detected; P, phosphate; SD, standard deviation.

Fig. 7. Concentration of Vibrio found in the colonies (healthy and damaged) of Papa 1 and Papa 2. CFU = unity of bacteria colony formation with ± SE. This graph considers all the Vibrio species found on the Paramuricea colonies: of these V. harveyi and V. splendidus were the main components on the healthy colonies and V. corallyticus was also present on the damaged or diseased colonies.

Broadly speaking, Papa 1 is less dense and has smaller colonies than Papa 2. Mean colony height did not differ over a relatively short period of 1–3 months after the mortality episode, but there was a clear shift towards small size classes by 9 months after the mortality event. This trend was reported also in other monitoring studies on gorgonian mortality (Cerrano et al. 2005; Cupido et al. 2008, 2009; Linares et al. 2008a,b,c). This phenomenon is mainly due to the loss of the colonies from the larger size classes and also the fragmentation and/or damage to branches. Moreover, the presence of recruits caused a shift towards smaller colonies, leading to a general loss of habitat complexity. Furthermore, there was evidence that most of the colony branches with epibionts that were counted in December 2008 had either fallen off or were broken in June 2009.

From 35 m (for Papa 2) and 30 m depth (for Papa 1), up to the surface of the shoals, the larger colonies were more affected (i.e. had a higher percentage of damage) by the mortality event: deeper colonies were less affected in both sites. Colonies living at greater depths could hence constitute a reservoir for the production of planulae for future population recoveries (bottom-up and lateral supply).

In coralligenous assemblages, perhaps the most important habitats in the Mediterranean Sea (Ballesteros 2006),
gorgonians and particularly *P. clavata*, are considered key species, being important engineering and/or foundation species (*sensu* Dayton, 1972; Mistri & Ceccherelli 1994; Cupido *et al.* 2009). Mass mortality events have wide consequences for gorgonian populations (Linares & Doak 2010) and for the community that depends on them, as the loss of these species alters sedimentation, turbidity and water movement, which negatively affect the complex structure of the hard-bottom benthic communities and the local biodiversity richness (Scinto *et al.* 2009). In both September and October 2008, the position of the thermocline could not be detected down to 40 m depth during the mortality event and temperature was ~2 °C higher than during September 2007. The verified thermal anomalies and the constant warming of the Mediterranean may have important consequences for the natural biocenosis (Bianchi 2007; Coma *et al.* 2009) and may be the cause of the mass mortality events occurring in the last few years (Pérez *et al.* 2000; Pérez 2008; Coma *et al.* 2009).

In October, seawater analyses indicated altered values of ammonia, nitrite and nitrate close to damaged colonies, which were higher than usual and likely due to tissue degradation. These anomalies were not recorded in December, after the mortality episode had finished. Changes in phosphate values could have been related to the summer increase of urban sewage outflow due to high tourist density. An alteration of the nutrient concentrations was highlighted by the change of the N/P ratio values (Table 2), which may potentially favor unusual phytoplanktonic and/or bacterial species. The P-limited situation could have added an energetic constraint on the weak *P. clavata* population. These general conditions (high seawater temperature, altered N/P ratio) could have facilitated the increase of bacteria on damaged colonies. We uncovered three main groups of *Vibrio*, of which *Vibrio corallisilioticus* has been implicated as an important cause of mortality for Mediterranean *P. clavata* (Martin *et al.* 2002; Bally & Garrabou 2007) and Caribbean corals (Cervino *et al.* 2004). *Vibrio* bacteria are normally found in seawater and are thermodependent: at high temperatures (22–24 °C) *Vibrio* grows rapidly. *Vibrio corallisilioticus* showed the highest virulence toward *P. clavata* colonies and satisfied Koch postulates for pathogenicity. This bacterium appears to act as an opportunistic agent, infecting weak, thermally stressed colonies and compromising colony recovery (Vezzulli *et al.*, 2010).

Until now there have been no standardized actions to mitigate the impact of mass mortalities of *P. clavata*. Intervention strategies remain to be validated and it is important, especially where diving activity is frequent, to avoid population fragmentation that would lead to a progressive reduction in population density (Linares & Doak 2010) and a general loss of biodiversity (Cerrano & Ravestrello 2009). For this reason, monitoring is the only effective approach to plan adequate programs of intervention. Hypotheses to limit damages and/or improve recovery damaged colonies include: (i) development of an ‘early warning system’ to measure water stratification and predict mass mortalities and (ii) utilization of pruning and transplant technique protocols. For example, controlled miniaturization of larger colonies could lead to more resistant and resilient specimens that will also furnish a number of fragments for transplants to highly damaged areas to be used for restoration. Certainly, manipulation and transplant experiments need to be designed and tested before this strategy can be used routinely (see for example the pilot study of Linares *et al.* 2008c). Sites within MPAs have greater possibilities for recovery and adequate management, as the anthropogenic impacts are reduced and controlled; but as shown in this and other studies, MPA protection certainly does not prevent mass mortalities related to environmental causes.

**Conclusions**

Short-term effects of mortality events include habitat simplification and reducing the economic value due to a decrease of touristic appreciation (Trainito 2007; Navone & Trainito 2008). Evaluation of long-term consequences needs adequate monitoring programs. On the basis of previous mortality episodes described in different areas (Liguro-Provençal Basin and Tyrrenian Sea), long-term effects may vary in relation to the presence of healthy ‘pocket reservoir’ populations living below the water stability area delimiting the thermal anomalies. Their presence may represent an important larval supply to facilitate the recovery of shallow populations. High water temperature and prolonged summer conditions are among the most relevant causes of these mass mortality events (including the one reported here), reducing natural defences of colonies. In these compromised conditions, colonies are more vulnerable to infections and energetic constraints.

**Acknowledgements**

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**References**


Bally M., Garrabou J. (2007) Thermodependent bacterial pathogens and mass mortalities in temperate benthic


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Short and mid-long term effects of cockle-dredging on non-target macrobenthic species: a before-after-control-impact experiment on a tidal mudflat in the Oosterschelde (The Netherlands)

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Abstract

To study the possible environmental impact of hydraulic cockle-dredging on macrobenthic communities and the environment, a fishing experiment was executed on a tidal mudflat in the Oosterschelde (SW Netherlands) according to a BACI (before-after-control-impact) design. Following the characterization of the initial situation, a part of the mudflat was commercially fished, after which dredged and undredged areas were compared on the basis of macrofauna descriptors and sediment constitution approximately 2 months (short term) and 1 year (mid-long term) after fishing. Whereas a clear reduction of the larger Cerastoderma edule cockles (>23 mm) in the fished areas was found, no effect of dredging on total macrofauna densities or median grain size was observed. No negative effect of fishing on total macrofauna biomass was found; in contrast, an increase of the biomass of the non-target species almost compensated for the loss in weight due to the extraction of the larger cockles. No significant effect of dredging on species diversity, richness or evenness was found in the short or mid-long term, these descriptors tending to have increased rather than decreased in the dredged plots after 1 year. The selective fishing for larger cockles reduced the average cockle size, but 1 year after fishing the average size had returned to the initial values in the dredged area. However, compared to the control area, the average size might still be reduced, as the size of the cockles in the control area also increased during the year. Local environmental conditions, with their specific macrobenthic communities, seem to be crucial for the type of effects and the impact of dredging. It is therefore of eminent importance to follow a research design with pre-defined environmental conditions, rather than a comparison of different areas that are open or closed to fisheries. The present study based on a BACI approach indicates that mechanical cockle fisheries had no overall negative impact in our study area.

Introduction

Several studies have investigated the potential impact of dredging or sediment-disturbing activities on macrobenthic communities and on the non-target species in particular. Some of these show strong effects (e.g. Beukema 1995; Piersma et al. 2001; Leopold et al. 2004), but other studies show minor effects or none at all (e.g. Craeymeersch & Hummel 2004; Ens et al. 2004; Beukema & Dekker 2005). These studies differ in the severity of the
disturbances, especially the disturbance depth (Hall & Harding 1997; Kaiser et al. 2001), the season of the disturbance (Hall & Harding 1997), the frequency of disturbance (e.g. Kaiser et al. 2001), the possible selectivity of the different fishing techniques used (Ferns et al. 2000) and the methodological approach involving comparison of different areas that were fished or unfished for an extended period (Piersma et al. 2001) versus an experimental approach with exclusion of fishery in cockle beds (Craeymeersch & Hummel 2004).

The many studies on this topic differ also with respect to their research questions. They ascertain negative effects of fishing disturbances on (i) the environment as a whole (e.g. Leopold et al. 2004; Zwarts 2004), (ii) the structure of communities (Leitão & Gaspar 2007), (iii) the abundance of target species (Piersma et al. 2001), or (iv) processes as settlement, population dynamics and recolonization of selected species (Potter et al. 1997; Hiddink 2003; Beukema & Dekker 2005). These studies mostly consist of inventories after large impacts, and the next step consists of their integration in policies aiming at a mitigation of the risk that takes into account the opportunities for sustainable fisheries (Beukema & Cadée 1999). Thus an impact is expected beforehand, where the study investigates the rehabilitation potential or duration of rehabilitation of the target or non-target populations or the environmental conditions (Hall & Harding 1997).

Given that different environments have their specific communities and species assemblages, various impacts of fisheries might be expected depending on the substrate specifications (Ferns et al. 2000), tidal range and elevation or depth (Leitão & Gaspar 2007). Furthermore, different evaluations of effects can be expected according to the sampling design, ranging from ad hoc inventories in extensive areas that are either fished or protected over various time spans (e.g. Piersma et al. 2001; Beukema & Dekker 2005) to a priori elaborated experimental designs on local sites with an exact knowledge of the fishing intensity and timing (Ferns et al. 2000).

We are interested in whether dredging has a destructive effect on non-target species, which might be damaged by being lifted up from the sediment or processed through the fishing device. These effects might be visible in the short term through increased mortality resulting from injuries or from exacerbated predation by other macrobenthic species or vertebrates (Ferns et al. 2000; Hiddink 2003). This implies that the predators of the highly dredging-impacted species might profit from this disturbance. Dredging can also induce shifts in the species composition as a result of the alteration of the environmental conditions such as the sediment composition in the short and especially the mid-long term (Hiddink 2003). Comparisons between observations at short and mid-long term can show whether the effects on the species assemblages are transitory, whereas mid-long term observations are required to detect effects on species recruitment and larval settlement (Piersma et al. 2001).

In this study we specifically investigated whether the sediment characteristics (grain size) and the macrobenthic communities (including non-target species) are negatively affected by hydraulic dredging for cockles on a soft-sediment tidal flat. To account for the various sources of variation besides the direct effect of dredging, a BACI (before-after-control-impact) design was used (Smith 2002). A substantial part of a mudflat was commercially fished, and other parts were left undisturbed. In the dredged and undredged areas, 100 × 100 m plots were delimited and randomly sampled before and shortly (short term) and 1 year (mid-long term) after fishing.

This study is the first to investigate the impact of commercial cockle fisheries with suction dredgers on non-target benthic macrofauna species and communities using a BACI approach in which the sensitivity of the experimental design to detect quantitative changes is also taken into account.

Material and Methods
Study area and experimental design

The experimental research on the effects of cockle dredging was carried out on the Slikken van de Dortsmans tidal flats in the Oosterschelde, a semi-open tidal bay in the Southwest Netherlands (Fig. 1) with a salinity of above 30‰ (Coosen et al. 1994). Next to the blue mussel Mytilus edulis, the cockle Cerastoderma edule is the dominant suspension feeder in the Oosterschelde. However, nowadays, total cockle biomass is lower than it used to be during the 1980s and before. Besides the intensive fishing on the cockle populations over several years, the construction of a storm surge barrier in the mouth of the Oosterschelde (from 1976 to 1986) had a great impact on the suitability of the area for cockles. The construction of the storm surge barrier led to a 30–70% reduction in current velocities, and a 12% reduction in the tidal range, producing clearer waters, crumbling away of the elevated areas, and sedimentation at the brims of the tidal flats (Geurts van Kessel et al. 2003). The tidal range in the research area varies between 1.7 and 3.8 m.

Since the early 1990s, cockle fishery in the Oosterschelde has been subject to authorization, which is only granted in years with abundant cockle biomass. No authorization had been given since 2001 in our research area (Geurts van Kessel et al. 2003). As a consequence,
the cockle banks in the present study had been free of any dredging activity for a 5-year period before the \( t_0 \) sampling (September 2006). Nine plots of 100 × 100 m were randomly selected within the research area. Because of the expected spatial heterogeneity of habitat and living communities on the tidal flat, which is largely on a North–South gradient, it was decided to separate the nine plots into three groups that were spatially clustered (north, middle and south part of the study area). The positioning and depth of the plots are indicated in Fig. 1. Within each group, two plots were dredged and the last plot was used as an undredged/control reference. Within each of the nine plots, five sample sites were randomly selected. On 6 September 2006 \( (t_0) \), 45 macrofauna and sediment samples were taken, after which the whole area was dredged, with the exception of the three control plots. The fishing operation was performed for commercial purposes by three cockle boats equipped with hydraulic dredges. The dredging activity of the ships was recorded with a satellite tracking system (STS) that revealed, after interpolation of the 1-min interval signals, dredging tracks all over the experimental plots but not in the control plots (Fig. 1). After dredging, the tracks in the field clearly visible in the sediment were also checked, and were indeed found all over the dredged plots and not in the control plots. Fishing activity took place from 5 September until 9 November and was restricted to unsampled areas during the first day of fishing. On 9 November 2006 \( (t_1) \), all sample sites were sampled for macrofauna and sediment to detect possible short-term effects, and on 1 and 2 October 2007 \( (t_2) \), the sample sites were sampled again to detect possible mid-long term effects.

The current experiment is a standard BACI design (Smith 2002), which enables the changes observed in experimental plots to be compared with those occurring in control plots, taking into account autonomic developments during the study period.

**Sampling and measurements**

At each sample site, five macrofauna and five sediment samples were taken at each sample time. Macrofauna samples consisted of three cores \((3 \times 0.005 \text{ m}^3)\) pushed 30 cm into the sediment within a 1-m radius of the sample site, located with a GPS. The macrofauna samples were sieved over a 1-mm mesh, fixed with 4% buffered formalin and stained with Rose Bengal, after which specimens were determined to the species level, with the exception of the Oligochaeta, Actinaria and Nemertea. The numbers per species were counted and densities determined. To establish the density of species that are frequently fragmented, such as polychaetes, the number of heads was counted. When only body parts were found and no head, the number of specimens was counted as one. Small or fragmented specimens that could not be classified to species level were classified to genus level (e.g. *Cerastoderma* sp., *Spio* sp. and * Arenicola* sp.).
length of the cockles was also measured as the maximum measurable shell length to the nearest millimeter.

The total biomass (g ADW, ash-free dry-weight) of each species was determined either directly from the dried specimens (2 days at 80 °C) as the decrease in weight after 2 h scorching at 560–580 °C, or indirectly by length–weight regressions \( W = aL^b \), where \( W \) is weight in g ADW and \( L \) is length in mm. The length–weight regressions used were based on (i) specimens scorching during this study, (ii) existing data in our BIS (benthos information system) database from the same area/season, and (iii) the fresh-weight of the specimens and taxon-specific conversion factors from other monitoring campaigns in BIS.

Sediment samples were taken with a 1-cm diameter tube pushed 3 cm into the sediment. The median grain size (\( \mu m \)) of the samples was determined by laser-diffraction methodology using a Mastersizer 2000 (Malvern Instruments).

Descriptors

Plots, treatments and sample times were compared for total macrofauna and species densities and biomasses, species composition, and frequencies and diversity. The length distribution of the cockles (\textit{Cerastoderma} sp. and \textit{Cerastoderma edule} combined) was also compared between treatments. Diversity was measured as species diversity according to the Shannon index, species richness as the number of individual species and according to Margalef, and evenness according to Pielou, calculated with the software PRIMER 5.2.8 for Windows (Clarke & Warwick 2001). All total macrofauna and diversity indicators were calculated with and without taking \textit{Cerastoderma} sp. and \textit{C. edule} into account, because it is expected that these cockles are affected by dredging as the (larger) cockle is the target species. Further, top-10 lists of the most abundant individual species in chance of occurrence in samples, in densities and in biomasses were put together for each of the sample dates and treatments; 18 lists in total. Species mentioned in at least one of the lists for one of the descriptors were selected to be related in a multivariate way to time and treatment.

Differences in the sediment grain size between the treatments were also analyzed. To conform to the requirements of the parametric statistical testing regarding normality in the distribution of the data, the density and biomass data were log-transformed before analyses. The diversity indicators (Shannon, Margalef and Pielou), the median grain size and cockle length data appeared to be normally distributed in all cases (Kolmogorov–Smirnov test at \( P < 0.05 \)).

Data analysis

The comparisons between treatments were performed according to a standard BACI-ANOVA design where the effects of treatment, time and time–treatment interaction were tested at \( P < 0.05 \). As a result of a rather strong ‘plot’ effect, the individual samples can not be considered to be taken randomly (without consideration of plot origin) within the treatments. Therefore a nested design according to: ‘Change in Parameter’ = ‘Parameter average’ + ‘Treatment effect’ + ‘Plot effect within each treatment’ + ‘Unexplained variation’ where ‘Unexplained variation’, which is the Error term, equals the variation among samples within plots (Sokal & Rohlf 1995). Because of the decrease in the degree of freedom due to the nesting of plots within each treatment, the present ANOVA design is a relatively conservative test, which could fail to detect slight responses to the dredging. We are aware that data per treatment should not be gathered for testing when there are differences between plots within treatments. However, we wanted to make sure that possible negative effects of cockle-dredging, when present, do not pass unnoticed. We therefore used the more sensitive (i.e. without distinction of plot origin) Student-\( t \) test (\( P < 0.05 \)) for plain comparisons between the treatments or sampling times. Even the robustness of these more sensitive tests may be relatively low, due to the large variance among sample sites already at the start of the experiments (\( t_o \)), or due to the non-normal distributions. As we are especially interested in the developments over time for different treatments, independent of autonomous developments, we calculated the differences between \( t_j \) and \( t_o \) or \( t_j \) and \( t_0 \) and compared those per treatment using the Student-\( t \) test (\( P < 0.05 \)).

Effects on individual species were investigated with redundancy analysis (RDA), which is a linear method of canonical ordination where environmental variables are combined to build the ordination axes, locating the samples within the multivariate space defined by the species data, i.e. the log-transformed density, biomass or presence frequency data (Ter Braak & Šmilauer 1998). The analyses were restricted to the most abundant and dominant species determined as belonging to the top-10 species with respect to the descriptor to be analyzed (density, biomass or presence frequency) in at least one of the plots at one of the sample dates. The suitability of the linear response model was tested based on the value of the gradient length estimated with a detrended correspondence analysis (DCA); for a gradient length between 1.5 and 3 SD, both linear and unimodal models could be applied.

High species score (density, biomass or presence frequency) at a given location might be driven by out-of-scope factors coincidental with the treatment, which
could lead to misinterpretation based on the RDA plots. Therefore, the effect of the treatments on densities and biomasses of individual species were tested using Student t-tests at $P < 0.1$. Again, this is a rather sensitive test to avoid missing possible negative impacts. To cope with the bias introduced with the multiple $t$-testing, a Bonferroni correction according to $P \leq \alpha/n$ (Sokal & Rohlf 1995) was also applied to identify the ‘real’ significant effects on species. All statistics were executed in SYSTAT for Windows 11.

Power analyses were performed in cases of absence of significant differences to determine the robustness of the tests. The minimum difference that could possibly be detected with $P < 0.05$ was determined taking the variation between samples and the number of samples into account (Sokal & Rohlf 1995). The number of available observations and their standard deviations were tested at the level of 80% probability, assuming that the data belong to one normal distributed population of observations. The Kolmogorov–Smirnov test indicated that the values for each of the parameter $\times$ treatment $\times$ time intervals can indeed be considered to be normally distributed, except for the difference in biomass between $t_0$ and $t_2$ at the dredged sites.

Results

Initial situation ($t_0$)

Data collected at the start of the experiments ($t_0$) show distribution patterns over the research area with a clear differentiation of the three northern plots from the southern plots (Fig. 2). The three northern plots are characterized by smaller median grain sizes and lower total macrofauna densities and biomasses (and thereby higher Shannon, Margalef and Pielou diversity indices) than the southern plots (ANOVA, $P < 0.05$). The intermediate plots showed intermediate values or resembled the southern or northern plots. In all cases, as shown also in Fig. 2, the experimental plots clearly resembled the reference plots (and thus showed the same geographic N–S gradient). Therefore, at $t_0$ the averages of the reference plots for median grain size (Fig. 3A), total density (Fig. 6A), total biomass (Fig. 6C), species diversity (Fig. 7E), species richness (Fig. 7A) and evenness (Fig. 7C) are the same as for the experimental plots. The initial large variance between plots was dealt with by nesting the variance within the treatments, which then serves as the error term for the treatment–time interaction to be tested.

The smallest detectable differences with the used design, taking initial variability into account, equals 1% in median grain size, 10% in evenness, 22% in species richness, 24% in species diversity, 48% in total densities and 55% in total biomass, with a probability of 80% at $P < 0.05$, as calculated using power analyses.

Median grain size

It was expected that the median grain size would be directly influenced by dredging because of the sediment resuspension that occurs during fishing activity. However, no difference in median grain size could be detected between the control and the dredged areas at any time ($t_0$, $t_1$ or $t_2$; $t$-test, $P < 0.05$) or between sampling occasions ($t_0$–$t_1$, $t_0$–$t_2$) (Fig. 3; Table 1). The average median grain size over all samples equals 175 $\mu$m, varying locally and independently of treatment or time between 150 and 190 $\mu$m.

Cockles

The present dataset allows an estimation to be made of the impact of the fisheries on the cockle populations. Significantly lower cockle numbers were found in the dredged area compared to the control area at $t_1$ ($t$-test, $P < 0.05$), and lower cockle biomass was found in the
dredged area than in the control area at both \( t_1 \) and \( t_2 \) (\( P < 0.05 \)) (Fig. 5). The effect of fishing was more evident in the biomass changes, as it was primarily the larger cockles that were fished (Fig. 4).

The size distribution of the cockles measured in this study can be used to estimate the size selectivity of the dredging with respect to the cockles. As indicated by the average cockle length and length distribution (Fig. 5A), clear shifts are found towards small-sized individuals between \( t_0 \) and \( t_1 \) and back to the original size distribution at \( t_2 \) in the dredged areas. In the reference area, size distributions at \( t_0 \) and \( t_1 \) are quite similar, whereas there is a slight increase in size distribution mode between \( t_0 \) and \( t_2 \) (Figs 4 and 5). Distinguishing different size classes (small \( \leq 23 \) mm and large \( > 23 \) mm) of cockles could provide information about the differential effect of dredging as a function of shell size. Indeed, a 23-mm shell length is approximately the size of separation of a 15-mm grid as used by the cockle ships (Hiddink 2003). However, due to the low numbers of observations and their high variance, only differences of 82% (larger size classes) to 85% (smaller size classes) can be detected (power analysis; \( P = 80\% \), \( P < 0.05 \)). At \( t_1 \), on average, 38.3% of the cockles in the dredged area are large, whereas in the control area, this figure is 72.2% (significant at \( P < 0.1 \)). We also found a significant (\( P < 0.1 \)) decrease in larger cockles between \( t_0 \) and \( t_1 \) in the dredged area compared to the control area.

### Total macrofauna indicators

The total density of macrofauna excluding the cockles was relatively stable over time and no significant differences were found between the dredged and control areas (Fig. 6A; Table 1). Although differences in development of the densities might have been present between the two treatments, densities do not appear to have been decreased over time in the dredged plots, whereas the autonomous trend (visible in the control) shows a slight decrease (Fig. 6B). As no significant differences were observed, any differences must have been smaller than 48% at \( t_1 \) and 54% at \( t_2 \), as calculated by a power analysis.

In the total biomass, the autonomous effect of decrease over time seems to be even stronger than indicated by the numbers, and here also such a trend is absent in the dredged area (Fig. 6C,D). However, conducting BACI-ANOVA, differences in trends do not appear to be significant (\( P = 0.444 \) from \( t_0 \) to \( t_1 \) and \( P = 0.099 \) from \( t_0 \) to \( t_2 \); Table 1).

When the total biomass is calculated including the cockles, the possible difference in trends is almost
compensated by the cockle biomass. However, it is clear that on both the short and the mid-long term, with or without the cockles included, no decrease in densities or biomass is seen as a result of dredging.

Species richness and species diversity show similar patterns when comparing the two treatments over time (Fig. 7A,E). Initially the two treatments did not differ and this was still the case just after dredging. However, 1 year after dredging the indicators tended to be increased for the dredged area, whereas the control area remained unchanged. The observed trends can not be considered significantly different as shown by BACI-ANOVA.
Table 1. Test results of BACI-ANOVA for time-treatment interactions taking 'plot nested within treatment x time' [time*plot (treatment)] as error; df(time*treatment) = 1; dferror = 7; cockle data excluded.

<table>
<thead>
<tr>
<th></th>
<th>Short-term effects (t₀-t₁)</th>
<th>Mid-long term effects (t₀-t₂)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F-ratio</td>
<td>P</td>
</tr>
<tr>
<td>Median grain size</td>
<td>1.007</td>
<td>0.444</td>
</tr>
<tr>
<td>Log (density)</td>
<td>1.285</td>
<td>0.352</td>
</tr>
<tr>
<td>Log (biomass)</td>
<td>0.061</td>
<td>0.979</td>
</tr>
<tr>
<td>Margalef richness</td>
<td>0.642</td>
<td>0.612</td>
</tr>
<tr>
<td>Pielou's evenness</td>
<td>0.251</td>
<td>0.858</td>
</tr>
<tr>
<td>Shannon diversity</td>
<td>0.494</td>
<td>0.698</td>
</tr>
</tbody>
</table>

(P = 0.101 for the trends in richness and P = 0.113 for the trends in diversity between t₀ and t₂) (Table 1). However, there was definitely no negative effect of dredging on species richness and diversity. Either no effect was found on the evenness, or it must have been smaller than 10% according to a power analysis, but then, the impact of dredging seems to be positive instead of negative (Fig. 7C).

Effects on singular non-target species

Dredging could be species-selective in its impact on the macrofauna, either through direct effects on recruitment and mortality rates or, indirectly, through changes in habitat-induced shifts in species composition. Figure 8 shows the results of RDAs based on densities (Fig. 8A) and biomass (Fig. 8B) for the most abundant species. Results of the presence frequency analyses are not shown, as they are very similar to the density analyses. The graphs show the projection of the gradient axes of the species descriptor (from low to high values) together with that of the two environmental treatments (control and dredged) and sampling times (t₀, t₁ and t₂). The closeness of both projections of species and factor gradients points to a direct or indirect relationship between the species descriptors and either the dredging and/or time (autonomous trend). Species like Cerastoderma edule, Tharyx marioni and Hydrobia ulvae seem to be particularly numerous at t₀, indicating an autonomous trend, although the first two are also related to the control, which indicates a negative impact of dredging. Species found in higher numbers in the control plots at t₂, such as Nephtys hombergii and Urothoe poseidonis, might also be impacted by dredging. On the other hand, for many more species, the highest numbers were found in the dredged area at t₁ (Arenicola marina, Lanice conchilega) and, especially, at t₂. A similar trend can be found for the analyzed biomass data (Fig. 8B), although other species appear in certain corners of the graph. It should be noted that coincidental appearance of larger numbers or larger specimens (higher biomass) in certain plots at certain dates, especially for low density species, can not be discriminated from real treatment effects in RDAs. Therefore, for further detailed statistical analyses, per species t-testing would be needed.

The series of t-tests on individual species (Table 2) showed many species potentially affected by dredging, especially showing increases in densities or biomass. However, in multiple tests as performed with these t-tests, a (conservative) Bonferroni correction should be performed, after which none of the observed differences are really significant. Besides the negative effects on the cockle populations, as shown earlier (Figs 4 and 5), the t-tests on individual species (Table 2) indicated possible negative impacts of dredging compared to the autonomous trend for three other taxonomic groups. These negative trends are only detected in the short term. Whereas an autonomous increasing trend in densities is observed 6 weeks after the onset of fishing for H. ulvae and the sub-class of the Oligochaeta, both were decreased in the dredged area. Arenicola sp., which is a special group as it very likely
Short and mid-long term effects of cockle-dredging on non-target macrobenthic species

Table 2. Possible differences in density and/or biomass developments between control (C) and dredged (D) plots for the non-target macrobenthic species, from t₀ to t₁ and from t₀ to t₂, as indicated from paired t-tests without Bonferroni correction.

<table>
<thead>
<tr>
<th>species class</th>
<th>development</th>
<th>P-level</th>
</tr>
</thead>
<tbody>
<tr>
<td>density t₀–t₁</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydrobia ulvae</td>
<td>Gastropoda</td>
<td>↓D, ↓C</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>Citellata</td>
<td>↓D, ↓C</td>
</tr>
<tr>
<td>biomass t₀–t₁</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arenicola sp</td>
<td>Polychaeta</td>
<td>↑D, ↑↑C</td>
</tr>
<tr>
<td>density t₀–t₂</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anaiteis mucosa</td>
<td>Polychaeta</td>
<td>↑D, ↓C</td>
</tr>
<tr>
<td>Carcinus maenas</td>
<td>Malacostraca</td>
<td>=D, ↓C</td>
</tr>
<tr>
<td>Harmothoe lunulata</td>
<td>Polychaeta</td>
<td>↑D, ↓C</td>
</tr>
<tr>
<td>Spio sp.</td>
<td>Polychaeta</td>
<td>↓D, ↓↓C</td>
</tr>
<tr>
<td>biomass t₀–t₂</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crangon crangon</td>
<td>Malacostraca</td>
<td>↑D, ↓C</td>
</tr>
<tr>
<td>Gammarus sp.</td>
<td>Malacostraca</td>
<td>↑D, ↑↑C</td>
</tr>
<tr>
<td>Gammarus locusta</td>
<td>Malacostraca</td>
<td>↑D, ↑↑C</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>Bivalvia</td>
<td>↓D, ↓↓C</td>
</tr>
<tr>
<td>Nephtys hombergii</td>
<td>Polychaeta</td>
<td>↑D, ↓C</td>
</tr>
<tr>
<td>Platynereis dumerilii</td>
<td>Polychaeta</td>
<td>↑D, ↑↑C</td>
</tr>
<tr>
<td>Polydora ligna</td>
<td>Polychaeta</td>
<td>↑D, ↑↑C</td>
</tr>
<tr>
<td>Scoloplos armiger</td>
<td>Polychaeta</td>
<td>↑D, ↑↑C</td>
</tr>
</tbody>
</table>

↓ Decrease; ↓↓ stronger decrease than for the other treatment of the same species; ↑ increase; ↑↑ stronger increase than for the other treatment of the same species; (=) unchanged.

P-levels for significant differences after Bonferroni correction are P < 0.0001 for the dominant species only and P < 0.00002 for all observed species, which were achieved by none of the species.

Species not belonging to the 10 most dominant species in densities or biomass in one of the treatment x time combinations.

represents small individuals and body parts of A. marina, tended to increase less in the dredged area than in the control area (P < 0.1). In contrast to the three groups that might be affected negatively by dredging in the short term, there are six species showing an increase after dredging in the short term. The biomasses of A. marina, Capitella capitata, Pygospio elegans, Streblospio shrubsolii and Urothoe sp. appear to increase during the first 6 weeks after the onset of dredging, whereas the opposite or at least no increase was found in the control area. For Carcinus maenas, the autonomous decreasing trend in density was not observed in the dredged area. The difference (P < 0.1 in the t-test) between the treatments for C. maenas was still observable after 1 year.

Many more species show an increase after dredging in the mid-long term. Anaiteis mucosa, Harmothoe lunulata and Spio sp. did not show a decreasing trend or such a strong decreasing trend in density in the dredged area as in the control area after a year. Further, seven species appear to show a stronger increase in biomass in the dredged area than in the control area in the mid-long term, and the decreasing trend in Mya arenaria biomass seems to be less strong in the dredged area than in the control area. Whereas most species that tended to increase after dredging belong to the polychaetes, there are also several malacostracans as well as M. arenaria, which is a bivalve.

Discussion

Selective fisheries on large cockles

Our study demonstrates the efficiency of the fishing process with a clear reduction of the larger sized (>23 mm) cockles in the dredged areas. This observation confirms, apart from the visual observation of dredging tracks on the experimental areas, that fishing effectively took place on the dredged experimental plots. Partial recovery of the cockle population was observed after the fishing. Recruitment and growth of the cockles occurred in the dredged areas, but the average size of the cockles was still smaller after 1 year when compared to the control...
areas. No effect of dredging was detected on smaller sized cockles. The failure to detect any effect on the small-sized cockles should be considered, taking into account the low power of the test, which is insensitive to differences of less than 85%. A thorough analysis addressing the effects on smaller sized cockles would require larger sampling surfaces to reduce the variance in the data and thereby increase the discriminatory power of the test.

Whether dredging influences cockle recruitment, as suggested by Piersma et al. (2001), could not be determined, as no large settlement occurred during the experiment. Beukema & Dekker (2005) suggest that negative effects of dredging on cockle recruitment mostly occur in sediments with very low mud content, where dredging might induce a further reduction of the fine material in the sediment below values required for the cockles.

In the case of the present study area, where sediment is rather muddy, this effect is therefore not expected to be of great importance. Moreover, the present study did not find any effect of dredging on median grain size, despite the power of the tests used to detect differences being large. Natural temporal variation in median grain size might have a bigger impact than dredging in the investigated area.

Effects on the environment
As indicated above, dredging might affect the composition of the environment, and the top layer of the sediment in particular. On the other hand, sediment disturbance can also lead to an increased availability of nutrients in the top sediment layer or water layer (Kaiser et al. 2002; Warnken et al. 2003; Nayar et al. 2007), especially in areas with relatively low water turbulence and current velocities. Sediment disturbance can undo sediment compaction and increase sediment aeration or pore-water renewal (Falçâo et al. 2006). Increased nutrient availability can also lead to an oxygen decrease due to increased microbial activities (Riemann & Hoffmann 1991). The form and depth of disturbance and the type of environment are crucial for whether dredging will have a negative effect on certain macrobenthic species and whether certain macrobenthic species might profit.

Irrespective of these potential impacts, our study failed to detect an effect of dredging on median grain size, although the power to detect differences was large. This is in contrast to findings in the Wadden Sea, where changes in median grain size and silt content were reported in areas that were fished for cockles, although the role of winter storms and the vicinity of mussel beds were also considered relevant factors (Piersma et al. 2001).

Effects on communities and non-target species
In the present case, no severe environmental impact (on either density or biomass) of dredging was detected in the short-term observations. Moreover, mid-long term sampling showed a slight increase for both densities and biomass in the dredged area, leading to larger biomass compared to the control area after 1 year. This difference in biomass mostly resulted from a decrease in the control area (autonomous development), which seemingly was compensated by an increase in the dredged area. The higher biomass in the dredged areas was not due to a few dominant species that might benefit from the disturbed conditions, but to many species, as shown by the parallel increase in species richness and species diversity under steady levels of evenness.

Even in such a situation, with increasing biomass, species richness and species diversity, one can argue about whether this is a positive or negative development, as certain species might be favored above others, and some species might be reduced. Therefore we also focused on impacts on the individual species. With respect to the individual species, only three species/groups showed a reduction on the short-term, i.e. with recovery within a year. One of the negatively impacted species was the gastropod Hydrobia ulvae, in accordance with Ferns et al. (2000), who showed a depletion of the H. ulvae populations under the influence of mechanical cockle harvesting. In the present study, H. ulvae was the most numerous species, which could positively affect the diversity indices in the dredged areas. This species is also an important food source for several other species (Mendonça et al. 2007).

Previous studies have shown possible negative effects of dredging on smaller worms (Craeymeersch & Hummel 2004; Ens et al. 2004), in concordance with the reduction of oligochaetes observed in the present study under the influence of dredging. Other studies suggested the opposite response, i.e. an increase of dominance by worms as a result of sediment disturbances or increased nutrient availability in the environment (Reise 1982; Kaiser et al. 2002). The positive response of several worm species (i.e. Arenicola marina, Capitella capitata, Pygospio elegans, Streblospio shrubsolii, Nephtys hombergii, Platynereis dumerilii, Polydora ligni, Scoloplos armiger) as observed in the present experiment might indeed point to a shift towards worm dominance in the disturbed conditions after the dredging. In this respect, it is surprising that oligochaetes, which are known to be the first to colonize and dominate in deteriorated conditions (Ysebaert et al. 2003; Wijnhoven et al. 2008), showed decreased abundances in our study.

Several Malacostraca species (i.e. Carcinus maenas, Urothoe sp., Crangon crangon, Gammarus sp., Gammarus
locusta) also seem to profit in terms of numbers or biomass from the new conditions in the dredged area. These are mobile species and therefore fast colonizers of disturbed areas. Their increase might result from the following two non-exclusive processes. First, they might profit from an increased food availability, i.e. the presence of damaged and dead organisms (large macrofauna) in the dredged environment on which they can scavenge. Secondly, the increase in space availability due to the dredging (with removal of cockles) might sustain the observed increase of the malacostracans. The hypothesis of increased space availability as a result of the dredging might also explain the attenuation in the decrease (autonomous trend) of the bivalve Mya arenaria that is observed in the dredged area when compared with the control area. Our hypothesis of decreased competition and/or increased space availability for non-target species seems to be supported by the partial compensation of the fished-away cockle biomass by biomass of non-target species and the apparent slight acceleration in growth of the cockles remaining in the dredged area.

The present study did not detect any negative effect on bivalve species other than cockles, which are, however, potentially influenced by dredging, as shown by other studies. This result indicates that either dredging has no impact on those bivalves, as they mainly inhabit deeper parts of the sediment (e.g. M. arenaria), or that the bivalves are not significantly damaged after the processing through the dredge when they are returned to the sediment (e.g. Macoma balthica). The equivocal effects of the dredging on Arenicola sp. and A. marina should be interpreted as a methodological artifact, because Arenicola sp. mostly consists of juveniles and incomplete parts of A. marina, no other Arenicola species being observed in the research area.

The use of the t-test with improved sensitivity, compared with the nested ANOVA, by an increase of the degrees of freedom (no distinction between the plots) made it possible to reject the hypothesis that large-scale negative effects on macrofauna density, biomass and diversity would result from the dredging in the investigated area. Actually, only two groups (H. ulvae and the oligochaetes) showed a negative effect of dredging in the short term in this experiment, and the differences were not significant (ANOVA, P > 0.05). This also accounts for the range of species that showed positive effects of dredging on the short and mid-long term. From this, it can be concluded that there was no negative impact on the whole range of species, with the exception of the two groups just mentioned. Whether some species might have benefitted from the dredging remains unsubstantiated.

Consequences of the current design

Although the current study was able to show, or rule out, significant differences in the development of certain parameters with a reasonable statistical power, the unbalanced design is not ideal. A pairwise experimental design with as many undredged as dredged plots would increase the power of the tests and would make detection of smaller differences in development between the treatments possible without increasing the total number of plots/samples. As there is a large variation between plots and less variation within plots, the power can be increased the most by increasing the number of plots, rather than increasing the number of samples within plots.

Cockle fisheries in a broader context

Under the conditions in the present experiment, it can be concluded that the impact of dredging on non-target species and the sediment did not appear to be overly destructive in the mid-long term and therefore likely also not in the longer term. The negative effects observed for a few species in the short term were not detected in the mid-long term, even with the most sensitive tests. The results thus indicate that in the longer term, effects on non-target species of cockle fisheries such as carried out in this study are not to be expected. On the other hand, a longer term effect on the cockle populations can not be excluded. Although the cockle stock itself recovered after the dredging and individual growth was observed, a lag in the average size was still detected 1 year later in the dredged area compared with the control area. An overview of some relevant elements that can help place the present observations in a larger context is presented below.

The distance between dredged sample sites and undredged areas varied in this study between 10 and 300 m. In previous studies, showing negative effects of cockle-dredging on non-target species, this distance was larger (Hiddink 2003), and thus it might be argued that recolonization from neighboring areas in our study was easier. The extent of recolonization from undredged neighboring areas for both the recovery of the cockles and the increase in non-target species was not addressed directly in this study because the undredged experimental areas were very small compared to the total area dredged. We believe therefore that the undredged areas can only have contributed in a minor way to the recolonization in the much larger dredged area. Recolonization from within the dredged area might also have been possible, as the dredging intensity was not uniformly distributed over the dredged area. However, satellite tracking system registrations did indicate that undisturbed parts were
scarce. Therefore, we conclude that recolonization only contributed in a minor way to the absence of significant results of cockle fisheries on the zoomacrobaenthic community.

The present study deals with the impact of a single dredging event, whereas more disruptive effects on communities can be reasonably postulated by recurrent (yearly or even more frequent) dredging activities. At the more disruptive intensity level, it can be reasonably expected that dredging activities may prevent the establishment of long-living ecostructures such as mussel/oyster banks and seagrass fields, together with their associated flora and fauna (Dittmann 1990; Boström & Bonsdorff 2000; Jaramillo et al. 2007). The negative impact found by many other studies on a range of non-target species could be the result of other dredging techniques that are more destructive (Hall & Harding 1997; Ferns et al. 2000) than the hydraulic dredging used in the present case.

Local conditions of the fishing area should also be taken into account when considering the effects of fisheries on benthos. Queirós et al. (2006) and Hiddink et al. (2007) clearly point at the strong effect of habitat characteristics such as sediment and productivity in relation to the sensitivity to dredging disturbances. A common conclusion by both papers was that the degree of natural disturbance determines the degree of sensitivity to fishing activities. It is thus possible that communities of sandy substrates as in the Wadden Sea are differentially sensitive to disturbances compared with communities found on muddy sediments, as in our study. This study could explain the differences between the negative impacts of cockle fisheries found in the Wadden Sea (Piersma et al. 2001) and the absence of significant results in our area. However, the relationship with the mud content is not consistent, as effects of fisheries, as indicated by Queirós et al. (2006), were more negative on the muddier areas, whereas in our muddy area no significant effects could be found. Further studies should focus more on these aspects. Several studies also show negative effects of dredging on the bivalve recruitment (Piersma et al. 2001; Hiddink 2003). In the absence of massive bivalve recruitment in the area during the research period, no conclusion can be drawn relative to the effect of dredging on the recruitment from the present study.

From the results of our study we conclude that sustainable cockle fisheries may be possible, taking into consideration the above-mentioned aspects. The sensitivity and the recovery potential of a dredged area, amongst other factors related to the type of habitat and probably also to the period of non-disturbance, should be specified on the basis of adequate field-experiments, preferably using a BACI approach.

Acknowledgements

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References


Short and mid-term effects of cockle-dredging on non-target macrobenthic species


Charles Darwin and marine biology

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Keywords
Barnacle; Beagle; coral reefs; Darwin; Grant; Lyell; transmutation; uniformitarianism.

Abstract
In a celebration of the 200th anniversary of his birth in 1809, this short essay explores the influence of marine biology on Charles Darwin, and vice versa. Darwin made his first forays into the world of marine biology as a medical student in Edinburgh from 1825 to 1827. He came under the influence there of the Lamarckian Robert Grant, and developed an understanding of the simple organisation of the early developmental stages of marine invertebrates. Yet Darwin balked at Lamarckian transmutation. The voyage of the Beagle led to Darwin’s perceptive theory of the origin of coral reefs, an origin still mainly accepted today. This theory was steeped in the uniformitarianism of the geologist Lyell, depending on the slow, gradual growth of billions of coral polyps keeping pace with slow sinking of land to produce an atoll. From 1846 to 1854 Darwin revolutionised the understanding of barnacles, producing monographs still relevant today. His barnacle studies gave him the credibility to pronounce on the origin of species; he found great variation in morphology, and a series of related species with remarkable reproductive adaptation culminating in the presence of dwarf males. Barnacles showed him an evolutionary narrative laid out before him, and contributed greatly to his qualification and confidence to write with authority on the origin of species.
sponges, soft corals (*Alcyonium digitatum*), sea slugs (*Tritonia hombergi*), polychaetes (the sea mouse *Aphirolite aculeata*) and bryozoans (*Flustra foliacea*).

At this time Darwin came under the influence and mentorship of a man who would be key to the later development of Darwin’s ideas on evolution. Robert Edward Grant was a marine invertebrate zoologist and a fellow Plinian, living in Edinburgh on a decreasing legacy from his late father (Desmond & Moore 1991). Grant became Darwin’s unofficial tutor on marine invertebrates, teaching him to make observations and to dissect specimens. Through Grant, Darwin developed an understanding of animal development and the simple organisation of the early life-history stages of particular invertebrates. Grant was an expert on sponges recognised by his peers, as exemplified by the naming of the newly erected sponge genus *Grantia* in his honour by John Fleming in 1828; the common local sponge *Spongia compressa*, the purse sponge, became *Grantia compressa*. It was Grant who coined the name ‘Porifera’ for the sponges.

After working with Grant, Darwin (aged 18) gave a talk to the Plinian Society on 17 March 1827, showing that the larvae of the bryozoan *Flustra foliacea* use cilia for locomotion and that the black markings (sea peppercorns) on the shells of oysters are the eggs of the marine leech *Pontobdella muricata*. A triumph for a budding marine biologist but, according to Darwin’s daughter Henrietta, Darwin had been scooped 3 days earlier by Grant in a talk to the more formal (graduate) student society, the Wernerian Natural History Society – an introduction for Darwin to ‘the jealousy of scientific men’ (Browne 1995).

Grant, however, represented something more – sedition personified (Desmond & Moore 1991). Grant was a francophile who had studied anatomy and embryology in France with Geoffroy Saint-Hilaire. Correspondingly, Grant was a Lamarckian, more openly so later, for his views were still forming at this time. Lamarck (1809) used the term ‘transmutation’ for his theory that described the altering of one species into another. Lamarck did not propose common ancestry but considered that complex forms transmuted from simple forms of life created continuously by spontaneous generation. As a Lamarckian, Grant arranged life into chains, considering that the origins of animals and plants lay in the simplest forms; and that the natural ordering, simple to complex, of sponges represented the historical order of appearance of sponges. Thus Grant directly exposed Darwin to evolutionary theory, with the associated concepts of structural homology and unity of plan with similar organs present in different animals. Grant went on in 1827 to become Professor of Comparative Anatomy for life (1874) at University College, London. University College had been founded as London University in 1826, admitting students regardless of religion and gender, a secular alternative to Oxford and Cambridge. London University was clearly a more suitable venue for Grant’s seditious views than God-fearing Edinburgh.

The 2 years at Edinburgh convinced Charles Darwin that medicine was not for him, and in 1827 he left Edinburgh a disappointed man: he did not like medicine, nor the men who pursued it; he had found no qualities in professors to generate long-lasting respect (even Grant had disappointed him); and he was not ready to be a transmutationist or be labelled a radical like his grandfather, Erasmus Darwin (Browne 1995). Medicine was not for him, but he now had little choice – the family fell back on the typical safety net for second sons, the Church of England. So from 1827 to 1831, Charles Darwin found himself at Christ’s College at the University of Cambridge on the first stage of his journey to Holy Orders. There was still room for natural history, now under the influence of John Henslow, the Professor of Botany, and for geology under the influence of Adam Sedgwick, Professor of Geology.

However, there was no more immediate access to marine biology for Darwin until the portentous year of 1831. Then Henslow introduced Darwin to Robert FitzRoy, captain of HMS *Beagle*, who subsequently invited to Darwin to join a voyage around the world as a self-financing gentleman naturalist. The voyage lasted from December 1831 to October 1836. Darwin regularly sent back natural history and geology collections which gained him a scientific reputation in his absence, and the voyage changed his life for ever.

In January 1835, Darwin collected many specimens of a large intertidal gastropod mollusc on a shore in the Chonos archipelago, Chile, a collection not considered even worthy of reference in several editions of Darwin’s journal of the voyage (Darwin 1839). The mollusc concerned was a muricid gastropod, *Concholepas concholepas* (as *Conch­olepas peruviana*), the shells of which were riddled with cavities containing minute animals, no bigger than pinheads. These were to be later identified as boring barnacles, and these were also destined to affect Darwin’s future life enormously.

Before leaving on the *Beagle*, Darwin had been greatly influenced by Sir Charles Lyell, a leading geologist of the time, who had published the first edition of his *Principles of Geology* in three volumes (1830, 1832, 1833). Lyell was a believer in uniformitarianism, a philosophy claiming that geological and biological forces have always been working in the same way and at the same intensity over ages. This view of uniformitarianism was in conflict with the then-prevailing theory of catastrophism, which considered that the earth experienced major changes only as
a result of large catastrophic events. A key consideration was whether the earth was old enough to experience large-scale changes in any other way, but Lyell thought it necessary to create a vast time scale for Earth's history to vouch for fossil remains of extinct species, excluding sudden geological catastrophes. Charles Darwin shared a support for uniformitarianism.

The formation of coral reefs was a lively topic for debate at the time, and in the second volume (1832) of *Principles of Geology*, Lyell had explained the origin of coral atolls as coral reefs growing up from the crater rims of underwater volcanoes. Volume 2 was sent out to Darwin by his mentor and faithful correspondent Professor Henslow, to reach him in Montevideo in November 1832. Darwin’s observations on the *Beagle*, however, had convinced him otherwise. Darwin drafted an alternative theory for the origin of coral reefs that essentially stands today. Lyell accepted it immediately.

An essential point in coral reef formation is that reef-building corals only grow in well-lit shallow waters, supplying light to their symbiotic zooxanthellae, and could not grow up from deeper, dark depths. In Darwin’s explanation, corals form fringing reefs just below low tide along tropical coastlines, and eventually the coral reef will grow out to become a barrier reef. Darwin had seen the effects of earthquakes in Chile and knew that land could rise or fall. If the coast is sinking slowly, then the growth of coral could keep pace. If the land sinks beneath the waves an atoll is formed. His first hand observations in Keeling Atoll helped convince him of his views. Darwin could see that, although coral reefs were huge geological structures on a world scale, they were created by the slow, gradual growth of billions of tiny creatures over vast reaches of time. This was an example of Lyell’s ‘uniformitarian’ principle in action, the cumulation of small changes over a long period, to be repeated in Darwin’s studies on earthworms years later.

Later observations of cores of coral limestone to great depths (culminating in studies in Bikini Atoll in the 1950s) provided supporting evidence for land sinking at an appropriate rate — coral could simply not have grown up from these depths in the absence of light.

Darwin published *Coral Reefs* in 1842 (Darwin 1842). It showed the tight logical structure to become evident again in the *Origin of Species* to be published in 1859.

On his return from the *Beagle* in 1836, Darwin sought to place his collections with experts to identify and describe them — not altogether an easy task. The mammals were placed with Richard Owen – later to found the Natural History Museum in South Kensington and vehemently oppose Darwin’s views on evolution. He avoided Robert Brown (Keeper of Botany) at the British Museum who had been sitting on a collection of Galapagos plants, unstudied for 6 years. Robert Grant, now in London, volunteered to help, particularly with ‘lower animals’, but was turned down by Darwin who had become a competent and competing coral expert, given his interest in coral reef formation. In fact, ironically, the corals were not monographed. Nor did Darwin and Grant have anything more to do with each other (Desmond & Moore 1991).

By October 1846, Darwin thought that he had described all his *Beagle* specimens, and turned his attention to a single remaining barnacle species, the boring barnacles in the gastropod shells collected in Southern Chile in January 1835. The barnacle was clearly ‘quite new and curious’ — he called it that ‘ill-formed little monster’ — certainly aberrant and the world’s smallest barnacle. Darwin did not know how to classify it, referring to it as ‘Mr Arthrobalanus’. A new microscope was necessary, but so was a comparison with ‘more normal’ barnacles. So Darwin started borrowing the necessary specimens, and the project grew and grew as he soon appreciated the state of chaos of the knowledge of barnacles.

Why did Darwin embark on a project that was to occupy the next 8 years? Darwin had been formulating his ideas on variation and natural selection, resulting eventually in *The Origin of Species* (Darwin 1859), and he agreed with the view of his botanist friend Joseph Hooker that no-one had a right to examine the question of species who had not described many. So Darwin would earn that right. Barnacles would establish his credentials, and a thorough examination of all barnacle varieties could put him in a commanding position when discussing natural selection. In fact, as he proceeded, he began to uncover the most extraordinary proofs of his notebook speculations (Desmond & Moore 1991).

So Darwin studied barnacles (‘my beloved barnacles’) in his study at Down House in Kent from 1846 to 1854. He would go on to deliver a thorough reappraisal of both living and fossil barnacles, monographs that still command the field today (Darwin 1851a,b, 1854a,b).

So what are barnacles? Zoological folklore has it that Louis Agassiz described a barnacle as ‘nothing more than a little shrimp-like animal, standing on its head in a limestone house and kicking food into its mouth’.

Barnacles are indeed crustaceans, crustaceans that lack an abdomen and with a head enormously developed as a stalk or, as in the sessile barnacles, that limestone house of overcalcified cuticle. Darwin (1851a) drew a diagram (Fig. 1) of the relationship between the anatomy of a stalked barnacle (*Lepas*) and a decapod crustacean (*Lucifer*) discussing similarities or differences in terms of the homologies of the body parts, a conceptual way of thinking with which he was clearly happy. Typically we
Rainbow Charles Darwin and marine biology

Fig. 1. The diagram drawn by Darwin (1851a) of the relationship between the anatomy of a stalked barnacle (Lepas) and a planktonic decapod crustacean (Lucifer) to show the homologies of the external parts (m, mouth).

Table 1. Barnacles and their relatives are members of the class Maxillopoda, together with the likes of tuntulocarids, branchiurans, pentastomids, mystacocarids and copepods (Martin & Davis 2001).

<table>
<thead>
<tr>
<th>Subclass</th>
<th>Infraclass Facetotecta</th>
<th>Infraclass Ascothoracida</th>
<th>Infraclass Cirripedia</th>
<th>Superorder Acrothoracica</th>
<th>Superorder Rhizocephala</th>
<th>Superorder Thoracica</th>
<th>Order Pedunculata</th>
<th>Order Sessilia</th>
</tr>
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recognize three groups of cirripede barnacles today (Acrothoracica, Rhizocephala, Thoracica), closely related to two other taxa, the Ascothoracida and Facetotecta (Table 1, after Martin & Davis 2001).

So what was that ‘ill-formed little monster’ ‘Mr Arthropbalanus’ found boring into the shells of Concholepas concholepas, collected in southern Chile in January 1835? In 1849, Hancock described a boring barnacle from the columnella of whelk shells, Buccinum undatum, occupied by the hermit crab Pagurus bernhardus – Alcippe (now Trypetes) lampas (Hancock 1849). ‘Mr Arthropbalanus’ turned out to be a close relative. Darwin (1854a) described it as Cryptophialus minutus, and placed both species in a new order, the Abdominalia. The order was renamed the Acrothoracica by Grivel (1905) because these burrowing barnacles lack an abdomen, the taxon featuring as a superorder in Table 1. Acrothoracicans live in burrows in calcareous rocks and shells, and have a body and cirri not dissimilar to that of the more common thoracicans.

Darwin discovered reproductive modes in some barnacles that astounded him. Most barnacles are hermaphrodite, but not all. Darwin (1851a) discovered that different species of the stalked barnacle genus Scalpellum showed a gradient from complete hermaphroditism to hermaphrodites with small complemental ‘dwarf’ males with the larger ‘hermaphrodite’ acting as a female (e.g. Scalpellum scalpellum). Was this an example of what transmutation might look like? Darwin (1851a) also discovered that the stalked barnacle Ibla cunningii also has large females with small complemental males. The dwarf male shows great reduction in form as it becomes specialised for reproduction only. Transmutation?

The study of barnacles indeed provided Charles Darwin with many of the facts that he needed to support his ideas on evolution – both through comparative anatomy and through the study of fossils. What Darwin found in his barnacles (Stott 2003) was variation beyond his wildest imaginations, and reproductive modes that took his breath away, with the development of complemental males living parasitically on the female, no more than reproductive sacs of sperm, with no heads, stomachs or digestive systems. Barnacles had adapted to their environments and an evolutionary narrative branched out before his eyes (Stott 2003). Darwin’s barnacles showed him what transmutation could look like. Bit by bit, each apparently trivial adaptation in living structure accumulated, one after another, until animals became so distinct from their parents and cousins that they could be called a different species (Browne 1995).

While Darwin made fundamental contributions to the study of coral reefs and barnacles, clearly in return, marine biology contributed much to Darwin’s development of evolutionary thinking. The interaction of marine biology and the intellect of Darwin was key to the development of his supreme contribution to biology – the mechanism of natural selection acting on natural variation to explain the origin of species and the evolution of organisms.

Acknowledgements

This essay results from an invited lecture given at the 44th European Marine Biology Symposium in Liverpool in 2009 in acknowledgement of the 200th anniversary of the birth of Charles Darwin. The lecture attempted to bring Darwin’s specific contributions in marine biology to a wide audience of marine biologists, perhaps understandably only aware of Darwin’s hugely significant contribution of natural selection as a mechanism underpinning evolution. I am indebted to Professor Chris Frid for the invitation. It will come as no surprise to readers that this is not a paper of original scholarship, but simply a secondary compilation from excellent works of real biographical scholarship published on Charles Darwin.
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Darwin. I have leant heavily on the outstanding biographies by Janet Browne (1995, 2002) and by Adrian Desmond and James Moore (1991), to whom interested readers are referred. Rebecca Stott (2003) has produced a fascinating account of the barnacle years which dominated the life of Darwin and his family at Down House from 1846 to 1854.

References