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Long-term changes in the macrozoobenthos around the rocky island of Helgoland (German Bight, North Sea)

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Abstract The paper briefly summarizes what is known about long-term changes (facts, causes, consequences) in the macrozoobenthos of intertidal and subtidal hard-bottom communities around the island of Helgoland (German Bight, North Sea). There is increasing observational evidence that these communities (spectrum and abundances of species) are changing on a long-term temporal scale. The reasons are diverse and mainly anthropogenic. A shift in North Sea climate towards more oceanic conditions may be among the most important factors driving the recent changes in species spectrum. Many of the species which have been recorded as new to the Helgoland area during the past decade are southern (oceanic) species which may be considered as indicators of a warming trend.

Keywords Long-term changes · Hard-bottom communities · Macrofauna · Helgoland · North Sea

Introduction

The surroundings of the island of Helgoland represent a geologically and ecologically unique locality in the south-east part of the North Sea: a rocky intertidal and subtidal area covering about 35 km², which has been designated as a nature reserve since 1981. Helgoland is geographically and ecologically isolated from similar hard-bottom areas in Norway and Britain by some hundred kilometres of sandy or muddy soft bottoms. Little is known as to the extent to which animal popu-

lations associated with the hard bottoms at Helgoland are genetically isolated from neighbouring populations on the British and Norwegian coasts. The degree of isolation has so far only been analysed for the lobster *Homarus gammarus*: its local population at Helgoland was found to be largely isolated from other European stocks (Ulrich et al. 2001), and this may also apply to other species with restricted dispersal capacities.

Due to the relatively small extent, and the distinct isolation, of the Helgoland hard-bottom area, the associated macrozoobenthos shows considerable short-term variability in abundance and composition of species. The gastropod *Nucella lapillus*, for instance, was a regular and abundant component of the Helgoland shore fauna up to the 1980s, then became rare, went extinct at this locality for a number of years in the early and mid-1990s, but ultimately reappeared in the late 1990s (personal observation). To distinguish mere short-term (interannual to intra-decadal) variability from true long-term trends, continued monitoring spanning decades is indispensable. Although there is a more than 100-year tradition in the study of hard-bottom communities around Helgoland (Harms 1993), the macrozoobenthos has never been monitored continuously long-term. Most studies have been mere snapshots, documenting the situation in a particular location over a relatively short period of time (usually less than one annual cycle). A comparison of such snapshots taken at large intervals can only give some indications, but no conclusive evidence, of long-term trends in the dynamic of populations.

Harms (1993) provided a checklist of species from the Helgoland area, extracted from publications available at that time. Since 1993, however, an increasing number of species have been found which seem to be new to the area. Though some species might have escaped the notice of former investigators and some might have been misclassified, the findings clearly suggest that we are witnessing a significant change in the species composition of the Helgoland area. This corresponds with an increasing bulk of data from the past two decades

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indicating a recent shift in North Sea physical and biological parameters (e.g. Greve et al. 1996; Kröncke et al. 1998; Edwards et al. 1999; Reid and Edwards 2002; Stebbing et al. 2002; Lozán et al. 2003) which seems to be more profound and persistent than shifts recorded for earlier decades (e.g. Radach et al. 1990; Austen et al. 1991; Evans and Edwards 1993).

The arrival of species new to a locality can be attributed to two alternative processes.

1. Introduction: as a result of worldwide human activities a growing number of species can overcome natural barriers to dispersal, spreading as non-indigenous (exotic or alien) species into areas where they have not been present so far (biological globalization).
2. Range extension: when the ecological conditions in an area are changing on a long-term basis, species from neighbouring areas may get a chance to extend their range of distribution permanently into those areas by their natural means of dispersal. Due to their usually short life-cycles and superior dispersal capacities, pelagic species (which are beyond the scope of this paper) can respond more quickly than benthic species to changes in environmental conditions; their ranges thus fluctuate markedly on a short-term temporal scale (see e.g. Southward et al. 1995). Benthic species (especially those with short-lived larvae or direct development) are much less influenced by short-term factors; thus long-term trends superimposed on the background noise of high- and intermediate-frequency fluctuations can usually be detected more rapidly and reliably in benthic species than in those following a pelagic lifestyle.

In 1988 we started a long-term monitoring programme on species (particularly isopods and amphipods) associated with uprooted, surface-floating seaweed that accumulates around Helgoland. As algal rafting is an important means for small benthic species without long-lived larvae to disperse over long distances and colonize new areas (e.g. Johannesson 1988; Ingólfsson 1992; Thiel and Gutow 2004), this study aimed at to identify at an early stage species which might get a chance in the near future to establish themselves as new members of the local benthic communities.

The present paper briefly summarizes what is known about long-term changes, and their possible causes and consequences, in the macro-zoobenthos around the island of Helgoland over the past decades.

The decline of economically important species: lobsters and oysters

The subtidal cliffs of Helgoland harbour an isolated population of the European lobster *Homarus gammarus* (Ulrich et al. 2001). During the 1930s, at the height of the Helgoland lobster fishery, up to 87,000 specimens (41 t) per year were landed by local fishermen. After a

dramatic decrease in stocks, the number of lobsters caught per year has been fluctuating since the late 1960s at a constant, extremely low level of only a few hundred specimens (Goemann 1990). Measures undertaken from the 1960s to the 1990s by the Biologische Anstalt Helgoland (BAH) to restock the local population did not produce any positive result.

Diverse anthropogenic factors (over-exploitation, habitat destruction, pollution) may have contributed to the breakdown of the lobster population after World War II as well as to the apparent lack of subsequent recuperation, yet detailed knowledge on causal relationships are missing. While lobsters became rare, the edible crab *Cancer pagurus* apparently increased in abundance. This was probably due, at least in part, to competitive release as these two species compete severely for space (shelter) and food and show aggressive interference to the point of mutual predation (Finsterle 1996). Local fishermen agree with each other that numbers (and body size) of *C. pagurus* at Helgoland are greater now than at any other time over the past few decades. The crab appears to have taken over the niche formerly dominated by the lobster, and this shift may be a serious obstacle to a rapid recovery of the lobster population.

In 2000 a new project was started at the BAH with the intention of getting more detailed insights into the biology and ecophysiology of the local lobster population as a basis to optimize future restocking efforts. This project includes the breeding of lobsters in the laboratory, and the release of several thousands of laboratory-bred and tagged 1-year-old juvenile lobsters into their natural habitat.

The Helgoland “oyster bank” was as a small (0.8 km²) species-rich area south-east of the island (beyond today’s nature reserve) at about 25 m depth, with a sediment made up of coarse shell gravel (Caspers 1950). As a thriving oyster (*Ostrea edulis*) bed, the area was extensively exploited by the oyster fishery especially during the last quarter of the 19th century, when up to half a million oysters were harvested in a single season. Over-fishing and, ultimately, climate anomalies and/or the outbreak of diseases resulted in a virtually complete local extinction of the species during the 1920s. In 1938, a quantitative study of the macrofauna of the oyster bank was performed by Caspers (1950). The community then proved to be still remarkably little affected by the loss, about 15 years previously, of its most important species, with a single exception: the bivalve *Nucula nucleus* L., possibly released from competition for food, had increased significantly in number and had become the most abundant species in the community. The most recent (2003) revisit to this area, 65 years after Caspers’ comprehensive study, revealed that the formerly rich community no longer exists, probably destroyed over recent decades by the extensive bottom-trawl fishery.

Natural beds of *O. edulis* have also declined elsewhere in Europe. To replace the lost native species, the Pacific oyster *Crassostrea gigas* has been introduced to various

localities on the North Sea coast for commercial breeding during recent decades (e.g. Rhine delta, 1965; north Frisian Wadden Sea/island of Sylt, 1985). Contrary to all expectations, the foreign oyster species successfully reproduced and recruited outside the culture plots on intertidal mussel beds (*Mytilus edulis*) and artificial hard substrata. Probably favoured by warm summers, *Crassostrea* spread over the west, north and, most recently, east Frisian Wadden Sea and appears to have established itself as a permanent member of the Wadden Sea biotic community (Reise 1998; Wehrmann et al. 2000). Compared to the native *O. edulis*, the life strategy of *C. gigas* is more opportunistic (more eggs per female and year, extended pelagic phase). Thus, it was just a matter of time until the species would arrive at the rocky shore of Helgoland, probably through larval dispersal from the East Frisian Wadden Sea. And in fact, in spring 2003 juvenile Pacific oysters were found for the first time at Helgoland. The species' future status and possible effects on local biotic assemblages at Helgoland will be carefully studied in the years to come.

Intertidal macrofauna

The first comprehensive, semi-quantitative study of the macrofauna and its spatial distribution in the rocky intertidal was performed in 1984 (March to September) by Janke (1986). This study was repeated 18 years later in 2002 (Reichert 2003). A total of 172 (1984) and 161 (2002) macrofaunal species were found. The species spectra in 1984 and 2002, however, differed significantly. Not considering species which were recorded only occasionally during the studies, 94 species were found in

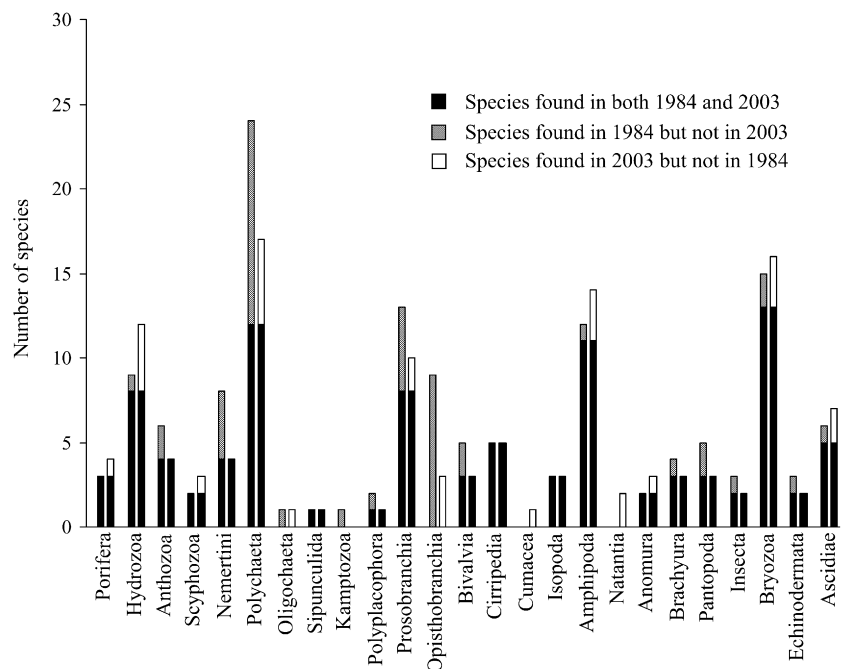
both 1984 and 2002, while 44 species were found only in 1984 and 29 in only 2002. Most obvious qualitative changes were observed in polychaetes, nemertines and gastropods (Fig. 1). Though some species might not have been noticed or might have been misclassified in the first or the second study, the data clearly point to a surprisingly high degree of change in the species composition of the studied intertidal community between 1984 and 2002.

Intertidal communities are strongly exposed to short-term (intra- and interannual) variability, e.g. in climate, and thus may be expected to undergo marked year-to-year fluctuations in biological parameters. Consequently, much of the difference between the species inventories recorded in 1984 and 2002 may simply reflect inter-annual fluctuations in ecological conditions, rather than true long-term trends. This is supported further by the fact that no obvious common ecological traits could be attributed to either the species missed in 2002, or to those which were new in 2002 (Reichert 2003).

Two exotic algal species, the red alga *Mastocarpus stellatus* (since 1983) and the brown alga *Sargassum muticum* (since 1988) have become very common at Helgoland and are still extending their range around the island (Bartsch and Kuhlenkamp 2000; Reichert 2003). This substantial change in the algal cover of the rocky intertidal and shallow subtidal biotopes will certainly affect the native macroalgal community and the associated macrofauna. So far, however, detailed information is not yet available.

The barnacle *Elminius modestus* Darwin is the only exotic macrofaunal species with some ecological significance in the rocky intertidal of Helgoland. The species was introduced to the southern British coast during the

Fig. 1 Macrofauna of the rocky intertidal of Helgoland: a comparison of species spectra recorded in 1984 (right columns) and 2002 (left columns) (modified after Reichert 2003)



1940s, probably as a fouling organism on ships from Australia, then rapidly spread over north-west European coasts and was first recorded at Helgoland in 1954 (Crisp 1958; Den Hartog 1959; Kühl 1963). Here, *E. modestus* has become a prominent member of the intertidal community, at least partly at the expense of the native *Semibalanus balanoides* (L.). Although the two species compete for space, neither has been driven to extinction so far. *E. modestus* is much less resistant to low winter temperatures than the native *S. balanoides* (Harms and Anger 1989; Harms 1999). The continuing coexistence of the two competitors probably results from natural selection fluctuating in favour of *E. modestus* during mild winters, and in favour of *S. balanoides* during severe winters. After the severe winter of 1995/1996, 85% of barnacles in the north-east intertidal of Helgoland were *S. balanoides*. Over subsequent years, characterized by mild winters, *E. modestus* gradually increased in abundance compared to *S. balanoides*, and by spring 2003 seems to be about to marginalize the latter (less than 5% *S. balanoides*; unpublished data).

The American slipper limpet *Crepidula fornicata* (L.), accidentally introduced to Europe in the 1870s (Minchin et al. 1995), has been encountered occasionally in small numbers over the last decade in the lower intertidal and shallow subtidal of Helgoland (personal observations). However, in contrast to *E. modestus*, it does not seem that the species might ever play a significant ecological role at Helgoland. As the species' northern occurrence seems to be limited by its sensitivity to low winter temperatures (Thieltges et al. 2003), it may be more than a mere coincidence that the only records at Helgoland date from a prolonged period of mild winters.

Subtidal macrofauna

Our knowledge on long-term changes in subtidal communities is as limited as that on changes in the intertidal. In contrast to intertidal systems, subtidal communities are much less influenced by short-term factors, are ecologically more stable and thus may be expected to reveal true long-term trends in ecological parameters earlier and more reliably.

Species composition, abundance and biomass of the "Tiefe Rinne" (a depression of the seafloor down to almost 60 m, about 2.5 nautical miles south of Helgoland, with a sediment dominated by coarse shell gravel) was studied in 1988/1989 (Berberich 1989) and compared with the situation found about 50 years before (Caspers 1939). Although a number of obvious changes could be recorded (some species such as *N. nucleus* and *Amphiura filiformis* had decreased remarkably in number, others such as *Amphipholis squamata* and *Galathea intermedia* had increased; some species were recorded only in 1939, some others only in 1989), the snapshot character of the studies does not allow the inference of long-term trends or causes of the observed changes. A systematic sampling programme for the "Tiefe Rinne"

would be most informative with respect to the impacts of recent changes in North Sea climate.

Swimming crabs (Portunidae) are an important element of the macrofauna of both hard and soft bottoms around the island of Helgoland. A semi-quantitative sampling programme in 2002 revealed an unexpected high diversity of species (Fig. 2). Most surprisingly, about one third of all swimming crabs belonged to *Liocarcinus depurator* (L.), a species which is conspicuous in colour and body shape but had never been reported previously from the Helgoland area. Special attention was paid to a possible occurrence of *L. vernalis* (Risso, 1827). This Mediterranean-Lusitanian species, sensitive to low water temperatures, is probably about to expand its range northwards (d'Udekem d'Acoz and Rappé 1991; Ingle and Clark 1998). It seems to have been only recently, in the 1990s, that the species has established populations on the south-western coast of England as well as on the Belgian and Dutch coasts. While *L. vernalis* seems to still be absent from Helgoland, the sampling programme revealed the occurrence of the hermit crab *Diogenes pugilator*. This predominantly Mediterranean species is also common at the south and west coasts of the British Isles but has never been reported before from the North Sea.

In 2002 (April to December) the opisthobranchs (Gastropoda) of the shallow sublittoral of Helgoland were studied qualitatively (Schubert 2003). A total of 34 species was found, of which 14 species were recorded for the first time from this area. On the other hand, of those species which had been mentioned in previous studies, nine could not be found again. Although no definite conclusions can be drawn from these findings, there are some indications that the occurrence of at least two new species (*Elysia viridis* and *Gleitodoris planata*) may be related to the recent climate anomalies. *G.* (= *Discodoris*) *planata* has only been recorded from the south and west coasts of the British Isles, and it is difficult to see how it could have spread to Helgoland.

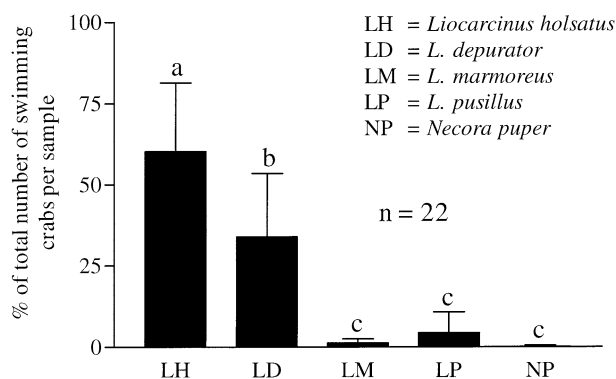


Fig. 2 Relative abundances (mean and SD) of swimming crab species (Portunidae) at Helgoland (data calculated from a total of 1,187 specimens collected from 22 samples taken between March and August 2002). Different letters indicate statistically significant differences in relative abundance

The macrofauna on floating objects

Surface-floating objects (mainly uprooted seaweed, but also persistent anthropogenic debris such as plastic) offer species an opportunity for long-distance dispersal and invasion of new habitats (e.g. Highsmith 1985; Ingólfsson 1995; Hobday 2000; Barnes 2002). By utilizing floating objects as vehicles, benthic species with no long-lived planktonic larvae can compensate to a certain degree for their own restricted dispersal capacities.

Since 1988, floating macroalgae which accumulate around Helgoland have been studied regularly during summer periods in order to identify potential newcomers for local benthic assemblages (Franke et al. 1999). The algal rafts have consisted mainly of detached thalli of the large brown algae *Ascophyllum nodosum* and *Himantalia elongata* which can survive for months while being carried along with surface currents over long distances (e.g. from the English Channel to the German Bight). The associated macrofauna was found to be dominated by isopods (various species of the genus *Idotea*) and amphipods, i.e. by brooding species with direct development. However, it is not only animal species which can use floating seaweed as a vector for dispersal and invasion of new habitats: Kuhlenskamp (unpublished) studied the macroalgae attached to floating *Himantalia* thalli at Helgoland in summer 1999, and found 10 species among them which have never been reported as indigenous for this part of the North Sea.

Among the high diversity of subtidal amphipod species found among floating seaweed around Helgoland during the sampling period 1988 to 2000, there were seven species which are characterized in the literature as southern species extending northwards to the south and west coasts of the British Isles and into the English Channel, but not further into the North Sea (Lincoln 1979; Hayward and Ryland 1990). Records of these species were most frequent in the second half of the 1990s (Table 1). It seems that none of these species has succeeded in establishing permanent populations in the subtidal communities around Helgoland so far, yet it may be promising to look for them carefully as potential newcomers in future sampling programmes.

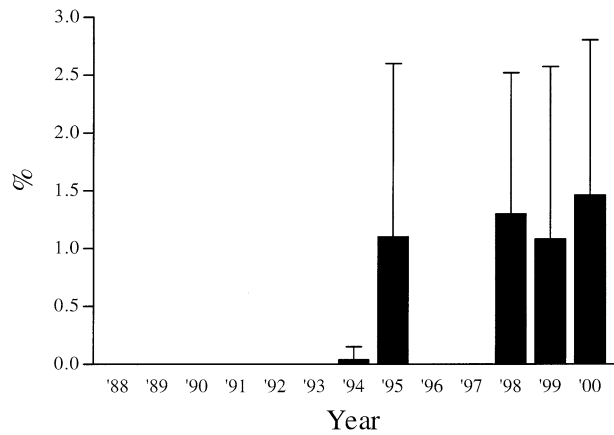


Fig. 3 *Idotea metallica* (Crustacea, Isopoda) on samples of floating seaweed collected off Helgoland over the period 1988 to 2000; percentage (mean and SD) of all individuals of the genus *Idotea*

Special attention was paid to the neustonic isopod *Idotea metallica*. This species was definitely absent from algal rafts at Helgoland until summer 1994, when it was recorded here for the first time in the south-eastern part of the North Sea (Franke et al. 1999). The species was also present here in increased numbers, including all developmental stages, in summer 1995, but was missing after the severe winter of 1995/1996, and in summer 1996 and 1997. Thereafter, the species reappeared and can now be found regularly during the summer, making up 1–2% of the total number of isopods (genus *Idotea*) associated with floating seaweed (Fig. 3). The temporal pattern of the species' appearance, disappearance and re-appearance strongly suggests a close relationship with the recent anomalies in North Sea climate. Persistent populations of *I. metallica* occur in subtropical waters in the Mediterranean and off the east coast of North America. In the North Sea, however, the species is unable to over-winter, and even a continuing warming trend will not change this situation in the near future (Gutow and Franke 2001). Originating probably from a persistent North Atlantic metapopulation network, small numbers of *I. metallica* are more or less continuously introduced into the North Sea on floating material (Gutow and Franke 2003). The recent occurrence of

Table 1 Records of "southern" amphipod species on floating seaweed at Helgoland (1988–2000)

	Records in												
	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
<i>Apherusa ovalipes</i> Norman & Scott	-	+	-	-	+	-	+	+	-	+	+	-	+
<i>Atylus guttatus</i> (Costa)	-	-	-	-	-	-	+	+	-	-	+	+	-
<i>Corophium acherusicum</i> (Costa)	-	-	-	-	-	+	-	+	-	-	+	+	+
<i>Dexamine thea</i> Boeck	-	-	-	-	-	-	-	-	-	-	+	+	-
<i>Elasmopus rapax</i> Costa	+	-	-	+	-	-	-	+	-	+	-	+	+
<i>Liljeborgia pallida</i> (Bate)	-	-	-	-	+	-	-	-	+	+	+	+	+
<i>Stenothoe valida</i> Dana	-	-	-	-	-	-	-	-	-	-	+	+	+
Total no. species	1	1	0	1	2	1	2	4	1	3	6	6	5

conspicuous summer populations of *I. metallica* in the North Sea is probably favoured by two climate-related phenomena (see Discussion): (1) an increased influx of Atlantic waters (and thus floating material) into the North Sea; and (2) a general warming of the North Sea which enables the introduced *I. metallica* to reproduce here over a longer period and thus to build up an abundant population.

On floating seaweed near to the coast, *I. metallica* experiences severe interference competition from its congener *I. baltica* which is the most abundant isopod species in these patchy habitats. Laboratory experiments have indicated that *I. baltica* is the dominant competitor on floating macroalgae and probably will not become displaced from there by the newcomer *I. metallica*. *I. metallica* is likely to remain restricted to abiotic floating material at some distance from the coast. As an omnivorous species with a clear tendency to feed on zooplankton, it is much better adapted than *I. baltica* to cope with a limited supply of plant food and with periods of starvation (Gutow 2003a, 2003b; Leidenberger 2004).

Discussion

While short-term fluctuations in biotic communities mainly reflect the natural variability of parameters relevant to population dynamics, the long-term changes observed over recent decades may be essentially anthropogenic. The causes of long-term ecological changes in marine biotic communities are diverse and include: (1) fisheries and other kinds of exploitation of marine resources by man; (2) the intentional or accidental introduction of alien (non-indigenous) species by man; (3) input and accumulation of pollutants and nutrients; and (4) climate change.

In most cases it is still difficult to definitely attribute the long-term change in the abundance of a particular species to one (or a combination) of these factors. The main reason is that our knowledge of the species' niches in a broad sense, i.e. knowledge of their autecology (e.g. thermal niche) as well as their interspecific relationships, is extremely limited.

Having been a nature reserve since 1981, the Helgoland hard-bottom communities are actually now relatively little affected by fisheries. As to exotic species, it is particularly coastal environments (Wadden Sea, river estuaries) which have been extensively invaded by those species over the last few decades (Nehring and Leuchs 1999; Reise et al. 1999; Wolff 1999; Lenz et al. 2000) while the offshore hard-bottom macrofauna around Helgoland has so far been relatively unaffected. This situation, however, might change rapidly with the arrival of another exotic species, e.g. the recent arrival of the Pacific oyster *C. gigas*. Due to its distinct offshore character, the Helgoland area seems to be less affected by pollutants and eutrophication than more coastal communities. On the other hand, there is increasing

observational evidence that most recent changes in the abundances and the spectrum of species associated with the hard bottoms around Helgoland are (directly or indirectly) ecological responses to the recent climate anomalies. Many of the species which have been recorded as new to this area during the past decade represent southern (warm-water) species which may be considered indicators of a warming trend.

There is ample evidence that the North Atlantic Oscillation (NAO) governs climate variability in north-west Europe, particularly during winter, and thus has a wide range of ecological impacts. Superimposed on its natural high- and intermediate-frequency variability, the NAO index has shown a prolonged upward trend over the past 3–4 decades, resulting in unusually high surface temperatures over the northern hemisphere (Hurrell et al. 2003). The North Sea climate has been changing in particular since the mid 1980s, largely due to an increase in the frequency and strength of westerly winds during winter, which in turn increases the influx of warm and salty waters from the Atlantic. Annual mean sea surface temperature at Helgoland has increased by 1.1°C and salinity by 1‰ over the past four decades (Wiltshire and Manley, 2004), indicating a clear trend towards “oceanic conditions” and a decrease in continental influences. The increase in surface water temperature is particularly evident during winter: the 1990s were characterized by a sequence of remarkably mild winters, with the single exception of 1995/1996 (Franke et al. 1999).

Temperature is one of the most important ecological factors: small changes in extremes, annual means and/or pattern of monthly means often cause large changes in distribution, abundance and seasonal dynamics of marine species (e.g. Hengeveld 1990). Low winter water temperatures, and reduced and variable salinities, are the crucial factors responsible for the absence of true oceanic species from the North Sea. A continuing upward trend in the NAO index would certainly change this situation, offering more and more oceanic species a chance to extend their range into the North Sea. On the other hand, a number of established species (species near their southern limits, e.g. cod, or species competitively inferior to immigrants) may be expected to disappear from this area as a result of continued warming. However, while the immigration of new species is relatively easy to recognize, it is extremely difficult to demonstrate conclusively a species' complete local disappearance. In fact, in contrast to the increasing number of species apparently new to the area, we do not know of any macrofaunal benthic species that has definitely gone extinct here during recent decades.

A comparison of marine communities and species diversity in the English Channel and the North Sea suggests that a continuing shift in North Sea climate towards more oceanic conditions (higher mean winter water temperature, higher and more constant salinities) would result in an extensive restructuring of communities, with an increase in total number of species in this area (e.g. Beukema 1992). During progressive latitudinal

shifts in species distribution, however, serious problems may be expected to occur in biotic communities when species which are intimately connected to each other by trophic, competitive or other kinds of relationships do not respond simultaneously to a changing climate, thus giving rise to some kind of spatial and/or temporal mismatch among one another (e.g. Olive 1995).

Future studies of long-term changes in biotic communities should consider these simple facts.

- 1 It is only continued monitoring (i.e. regular and frequent sampling over decades), and not snapshots at large intervals, which can definitely demonstrate long-term trends in biotic communities.
- 2 High sensitivity to short-term factors complicates the detection of long-term trends. Consequently, trends may be revealed more rapidly and reliably in benthic than in pelagic communities, and in subtidal than in intertidal communities.
- 3 A well-founded analysis of the causes and consequences of observed long-term changes in biotic communities requires a detailed knowledge of the niches of the involved species, i.e. knowledge of the key factors that restrict the distribution and abundance of species. Only this knowledge will allow us to advance from mere correlations towards a causal understanding of the observed phenomena.

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