ORIGINAL ARTICLE

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Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002

Abstract Changes in the presence and absence of invertebrates as well as in species conspicuousness were documented in a rocky intertidal community based on surveys in 1984 and 2002. In 2002 six vertically and/or morphologically different stations of an intertidal platform were sampled. Five of these six habitats had already been surveyed in 1984. Replicating precisely the method of the first assessment, presence/absence changes as well as changes in species conspicuousness of 83 invertebrate species were documented, indicating that this intertidal community changed considerably during the 18-year interval. Compared with the study in 1984, 27 species newly appeared, whereas 32 species disappeared. Furthermore, 16 species increased in conspicuousness, whereas eight invertebrates decreased. The total number of species in 2002 was 154 versus 158 in 1984. Although algal species were not recorded as thoroughly as invertebrates, a massive decline in cover of *Halidrys siliquosa* was noted. Conversely, two invasive algal species became established after 1984, *Sargassum muticum* (since 1988), a cosmopolitan fucoid alga that prefers shallow subtidal areas for colonization, and *Mastocarpus stellatus* (introduction in the 1980s) that particularly colonized areas in the mid intertidal. In 1984 the mid intertidal zone was dominated by the brown alga *Fucus serratus*, whereas in 2002 the blue mussel *Mytilus edulis* and the periwinkle *Littorina littorea* were the most conspicuous organisms. Annual mean sea surface temperature (BAH measurements) warmed by 1.1°C over

the past four decades. Range-related community shifts, introductions of non-indigenous species and the input of pollutants, are considered to explain long-term ecological changes in the invertebrate community at Helgoland.

Introduction

Intertidal communities are plastic systems as they change continuously in composition and abundance of organisms at several spatial and temporal scales (Dye 1998; Menconi et al. 1999). The exceptionally spatial and temporal variability in rocky shore communities arises from a combination of abiotic and biotic factors (Menge 1976, 1991; Lubchenco and Menge 1978; Underwood 1985; Menge and Sutherland 1987). Many studies have shown that intertidal communities are structured along gradients of abiotic factors, such as exposure to wave action and vertical tide level (e.g. Stephenson and Stephenson 1949, 1972; Southward 1958; Lewis 1978). To elucidate biotic influences, particularly manipulative experiments have led to an appreciation of the importance of species interactions, such as grazing, predation and competition, in spatial structuring of rocky shore communities (e.g. Dayton 1971; Paine 1974; Hawkins and Hartnoll 1985; Janke 1990; Jenkins et al. 1999; Leonard et al. 1999). Some studies have also shown that spatial and temporal variability in settlement and recruitment is important in establishing the mosaics associated with such communities (e.g. Harms and Anger 1983; Caffey 1985; Jenkins et al. 2000, 2001).

Although short-term, i.e. interannual to intra-decadal studies are indispensable to understand rocky shore community interactions, they mainly reflect the natural variability of parameters relevant to population dynamics. However, long-term investigations spanning

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several decades, are a prerequisite to analyse anthropogenic impacts on communities, and to differentiate these from short-term as well as long-term natural fluctuations in populations or communities at a specific site (Chiappone and Sullivan 1994). For example, changes in the abundance of macrobenthic species were related to predicted effects of recent climate warming (Beukema 1992; Barry et al. 1995; Southward et al. 1995; Sagarin et al. 1999). Furthermore, changes in the European littoral communities appear to coincide with the anthropogenic introduction of the Pacific oyster *Crassostrea gigas* during recent decades (de Kluijver 1997; Reise 1998; Wolff and Reise 2002).

Rocky shore communities are well suited for long-term ecological studies and are appropriate indicators for the status of the whole community or ecosystem. The limited locomotory potential, or fully sessile lifestyle, prevents the organisms to avoid short-term disturbances in the marine environment such as toxic algal blooms or long-term changes such as input and accumulation of harmful substances and nutrients, the introduction of alien species and climate change. Furthermore, rocky shore communities are usually well accessible, are clearly structured due to their overall two-dimensional nature and present lesser taxonomic problems than other ecosystems (Lewis 1976; Hartnoll and Hawkins 1980).

At Helgoland hard-bottom communities have been studied for more than a century (Harms 1993). Due to the relatively small extent of the Helgoland rocky littoral, covering about 35 km^2, species composition as well as their spatial and temporal variability is relatively well recorded. At the same time, the rocky littoral of Helgoland is a marine protected area since 1981. Despite these facts, a comprehensive review of the invertebrate communities in the intertidal of Helgoland was only carried out by Janke (1986) and was not repeated since then. He documented species abundance, vertical zonation and its dynamics at a particular intertidal site during spring and summer of 1984. The present study follows precisely the investigation by Janke (1986) and aims at a detailed comparison in order to reveal possible changes in the composition of invertebrate species over the past two decades. Furthermore, our study was intended to form a basis for a regular sampling scheme on a long-term schedule.

Methods

Study site

An intertidal site at Helgoland, German Bight, North Sea (54°11′N, 7°55′E), previously sampled by Janke (1986), was re-surveyed. This site is located on a rocky abrasion platform in the north-eastern part of the island, known as "Nordostwatt" (Fig. 1). The area surrounding the "Nordostwatt" is described in Janke (1986) and detailed information about the surface morphology of the study site is given in Hagmeier (1930) and Janke

(1986). Janke (1986) described the algal and faunal community of the "Nordostwatt" as very sheltered with a typical pattern of distinct vertical zonation. Horizontal belts are described as the *Enteromorpha*-, the *Mytilus*-, the *Fucus serratus*- and the *Laminaria*-zone (Janke 1986, 1990; see Fig. 2). The "Nordostwatt" also includes several shallow subtidal channels, which extend in the northwest direction towards the open sea. The location features of each habitat and the dominant algal species are listed in Table 1. For a more detailed description of the algae biotopes on the abrasion platform see Bartsch and Tittley (2004).

Survey methods

Changes in the invertebrate community at the "Nordostwatt" were determined by comparing estimates of species abundance within the set of samples first surveyed by Janke in 1984 with estimates of abundance from the same set of samples re-surveyed in 2002. The original set of samples in 1984 is composed of nine different habitats which were reduced to five in 2002. The selected habitats were unchanged in their structure since 1984, whereas the excluded ones were influenced by rocks, which occasionally fall from the vertical cliffs above.

These five habitats were the (1) *Enteromorpha*-, the (2) *F. serratus*-zone, the (3) channels, the (4) *Laminaria*-zone and individuals of (5) *Laminaria digitata*. As an additional habitat the *Mytilus*-zone was sampled in 2002. The *Mytilus*-zone had clearly dissociated as a separate zone from the *F. serratus*-zone, while in 1984 the *Mytilus*-beds were still inside the *F. serratus*-zone and were sampled as part of this zone.

The invertebrates within the six habitats were sampled every month from April until September 2002 using the techniques of data collection described by Janke (1986). The different structures within each habitat (e.g. rock pools, areas covered by sediment, visually dominant macroalgae) were sampled using different procedures. Rock pools and channels were sampled with a fine meshed hand net over a period of about 10 min. Two litres of sediment as well as small pieces of rock were taken. Furthermore, 1 l of smaller algal species (e.g. *Enteromorpha* species, *Chondrus crispus*) and 10 l of large brown algae (e.g. *F. serratus*, *Sargassum muticum*) were collected. These samples were examined at the laboratory and the abundance of the invertebrates was estimated in the same way as species that could be readily identified with the unaided eye in the field.

The method of abundance estimation of the invertebrates in categories was taken from Janke (1986; see Table 2). The categorization of the invertebrates according to conspicuousness is subjective to a certain extent. In order to reduce the subjectivity, an on-site comparison of the categorization of the species was performed over 2 days with Dr. Janke in person until a close match in results was achieved.
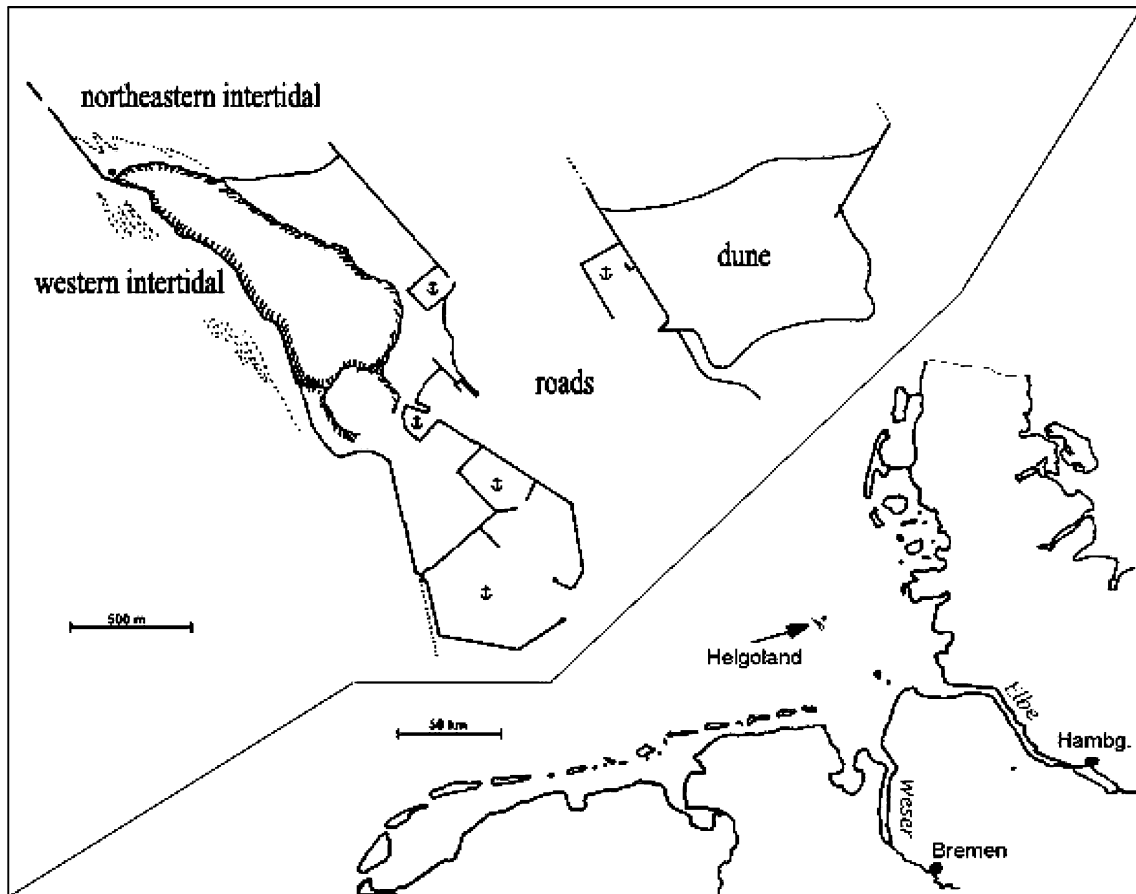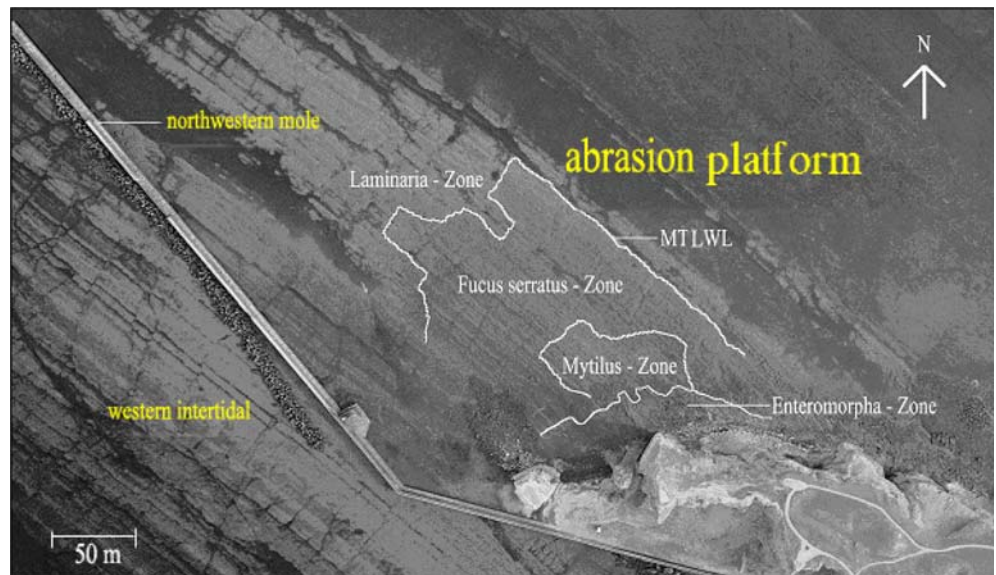
Fig. 1 The study site in the north-eastern part of Helgoland, and the island's location in the North Sea (according to Benoit 1996, unpublished)

Fig. 2 Aerial picture of the abrasion platform of the "Nordostwatt" of Helgoland (land survey office of Schleswig–Holstein). The investigated zones are marked

Although Janke did not quantify algal cover, he provided qualitative accounts of conspicuous algae which were also qualitatively sampled within each habitat in 2002.

Data analysis

Some of the species names, which were identified in Janke's study, were updated based on subsequent taxo-

Table 1 The location features (mean period of emersion during one tide in hours; parallel and perpendicular extension to the coastline in metres) and dominating algal species of the six habitats of the abrasion platform

Vertical belt	Location features				Dominant algal species
	Zone	Mean period of emersion	Parallel extension	Perpendicular extension	
Enteromorpha-zone	High intertidal	ca. 6	ca. 15–40	ca. 50–60	*Enteromorpha* spp., *Ulva* spp., *Ulothrix/Urospora* spp., *Fucus serratus*
Mytilus edulis-zone	Mid intertidal	ca. 4	ca. 35-80	ca. 60–70	Seasonal species (e.g. *Cladophora* sericea, *Monostroma* spp., *Rhizoclonium tortuosum*, *Dumontia contorta*), *F. serratus*, *Fucus vesiculosus*, *Ralfsia verrucosa*, *Chondrus crispus*, *Mastocarpus stellatus*, *Phymatholithon* spp.
Fucus serratus-zone	Low intertidal	ca. 2.5	ca. 100-210	ca. 60–150	*Cladophora rupestris*, *F. serratus*, *C. crispus*, *Corallina officinalis*, *Phymatholithon* spp.
Channels	Shallow subtidal	Permanently submerged except for short times during extreme spring tides	–	ca. 3–5	*Ulva* spp., seasonal species (e.g. *Cladophora* spp., *Rhizoclonium tortuosum*), *Sargassum muticum*, *Laminaria digitata*, *F. serratus*, *C. officinalis*, *C. crispus*, *Phymatholithon* spp.
Laminaria-zone	Subtidal	(see channels)	From ca. 230	–	*Ulva* spp., *C. rupestris*, *L. digitata*, *F. serratus*, *C. officinalis*, *C. crispus*, *Phymatholithon* spp.

nomic revisions. In a few cases, taxonomic changes required unification of recent species. For example, the abundance of the sponge *Sycon ciliatum* in the investigation of 2002 was compared to those of *S. coronatum* in Janke's study. The two species are united as *S. ciliatum* (van Soest 2001).

Species of which the taxonomic position is tentative were combined to a complex. An example is the mussel *Hiatella rugosa* which was regarded as a complex with *H. arctica* by Willmann (1989). Furthermore, some species were combined into a complex if the morphological distinctions between two species were difficult to quantify or too time consuming to investigate. For example, the definite taxonomic differentiation between

the bryozoans *Alcyonidium gelatinosum* and *A. mytili* involves electrophoresis, and between the periwinkle *Littorina mariae* and *L. obtusata* requires preparation of the penis (Hayward 1985; Willmann 1989).

Due to taxonomic ambiguities, three species (*Didemnum* spec. ('84 and '02), *Sagartiogeton* spp. ('02), *Schizoporella* spp. ('02) and ('84) were eliminated from further analysis. The hydrozoans *Clytia hemisphaerica* and *Kirchenpaueria pinnata* were excluded from the comparison because these two species occurred only on the introduced Japanese seaweed *S. muticum* that was selected as an additional sample in 2002 (see above).

Presence and absence of species as well as species conspicuousness were compared between the investigations. For all taxonomic groups, the proportion of species additions (species present only in the latter study) and losses (present only in the former study) as well as the proportion of increases (species conspicuousness higher in the latter study) and decreases (lower in the latter study) were compared, except for cases of taxonomic ambiguities.

For multivariate analysis the PRIMER software package from Plymouth Marine Laboratory (PML), UK was used. Cluster analysis and multi-dimensional scaling was carried out on the semi-quantitative data (categories of conspicuousness; Table 2) of all invertebrates (except for eliminated species; see above). The classification and ordination technique based on non-transformed data using the Bray–Curtis index and the average linkage method for clustering was applied. The mean species abundances of the sampling months were considered, so that the data matrix consists of 186 invertebrates and 11 samples (five habitats in both sampling years plus *Mytilus*-zone surveyed only in

Table 2 Categories of species conspicuousness

Category of conspicuousness	Definition
Absence (0)	No specimens found
Occasional (1)	Only 1 or 2 specimens found
Rare (2)	A few (3–5) specimens found, widely scattered over the study area
Regular (3)	Specimens occurring regularly (6–20) at short-distances without forming colonies or aggregations
Conspicuous (4)	Specimens in all samples, forming small or medium size colonies or aggregations
Very conspicuous (5)	Specimens in all samples, conspicuous at first glance, forming large colonies or aggregations
Dominant (6)	Sessile specimens dominating the area and displacing most other species from it

Table 3 Changes in 186 species used for semi-quantitative comparison between 1984 and 2002 (average conspicuousness is calculated over the sampled habitats and months of the respective year; for definition of categories, see Table 2)

Species	Average conspicuousness	
	1984	2002
Porifera		
Halichondria panicea	3	3
Halisarca dujardini	1	2
Leucosolenia botryoides	1	2
Sycon ciliatum	1	1
Cnidaria		
Actinia equina	1	1
Aurelia aurita	1	1
Clava multicornis	2	1
Coryne pusilla	1	1
Craterolophus convolvulus	1	1
Dynamena pumila	3	3
Eudendrium rameum	1	1
Halecium tenellum	0	1
Haliclystus auricula	0	1
Hartlaubella gelatinosa	1	1
Hydrallmania falcata	1	1
Laomedea flexuosa	2	2
Metridium senile	1	1
Obelia geniculata	1	1
Plumularia setacea	0	1
Sagartia elegans	1	1
Sagartia troglodytes	1	1
Sagartiogeton laceratus	1	0
Sagartiogeton undatus	1	1
Sertularia cupressina	1	1
Urticina felina	1	1
Nemertea		
Amphiporus lactifloreus	1	0
Cephalothrix rurifrons	1	1
Emplectonema gracile	1	0
Lineus bilineatus	1	1
Lineus ruber	2	1
Lineus viridis	1	0
Micrura fasciolata	1	0
Oerstedia dorsalis	1	1
Procephalothrix filiformis	1	0
Tetrastemma candidum	1	1
Tetrastemma vermiculus	1	1
Polyplacophora		
Lepidochitona cinerea	2	1
Lepidochiton asellus	1	0
Gastropoda		
Acanthodoris pilosa	1	1
Acmaea virginea	1	0
Aeolidia papillosa	1	0
Archidoris pseudoargus	1	0
Buccinum undatum	1	1
Calliostoma zizyphinum	1	0
Cuthona foliata	0	1
Dendronotus frondosus	1	0
Doto coronata	1	0
Elysia viridis	0	1
Epitonium clathrus	0	1
Facelina auriculata	1	1
Flabellina pedata	1	0
Flabellina verrucosa	1	1
Gibbula cineraria	3	4
Hydrobia ulvae	2	2

Table 3 (Contd.)

Species	Average conspicuousness	
	1984	2002
Lacuna pallidula	2	3
Lacuna vincta	2	2
Lamellaria perspicua	0	1
Limapontia capitata	0	1
Limapontia senestra	0	1
Littorina littorea	2	2
Littorina mariae/L. obtusata (complex)	2	4
Littorina saxatilis	1	1
Nucella lapillus	1	0
Onchidoris muricata	1	0
Onoba aculeus	2	1
Polycera quadrilineata	1	1
Pusillina inconspicua	1	1
Raphitoma linearis	0	1
Retusa truncatula	1	0
Rissoa parva	1	1
Skeneopsis planorbis	1	0
Bivalvia		
Anomia ephippium	1	1
Hiatella arctica/H. rugosa (complex)	2	1
Mytilus edulis	2	2
Pholas dactylus	0	1
Venerupis pullastra	1	1
Sipuncula		
Golfingia minuta	1	1
Kamptozoa		
Pedicellina cernua	1	0
Annelida (Polychaeta and Oligochaeta)		
Aphelochaeta multibranchiis	1	1
Autolytus prolifera	1	1
Capitella giardi	0	1
Circeis spirillum	1	1
Dodecaceria concharum	0	1
Eulalia viridis	1	1
Eumida sanguinea	1	0
Fabricia sabella	4	4
Gattyana cirrosa	1	0
Harmothoe imbricata	1	0
Harmothoe impar	1	1
Janua pagenstecheri	2	3
Lanice conchilega	1	1
Lepidonotus squamatus	1	1
Malacoceros fuliginosus	1	1
Microphthalmus sczelkowii	1	0
Neoamphitrite figulus	1	1
Nereis diversicolor	1	0
Nereis pelagica	2	1
Nereis virens	1	0
Nicolea zostericola	0	1
Ophryotrocha gracilis	1	1
Paranais litoralis	1	0
Phyllodoce maculata	1	1
Polydora ciliata	4	4
Pomatocerus triqueter	2	2
Sabellaria spinulosa	1	1
Scolelepis squamata	1	1
Spirorbis corallinae	0	1
Spirorbis spirorbis	2	3
Spirorbis tridentatus	3	3
Sthenelais boa	1	1
Syllides articulocirratus	1	0
Syllis gracilis	0	1

Table 3 (Contd.)

Species	Average conspicuousness	
	1984	2002
Tubificoides benedii	0	1
Typosyllis armillaris	1	1
Pantopoda		
Achelia hispida	1	1
Anoplodactylus angulatus	1	0
Nymphon rubrum	1	0
Phoxichilidium femoratum	1	1
Pycnogonum littorale	1	1
Crustacea		
Aora typica	0	1
Apherusa bispinosa	1	1
Apherusa jurenei	1	1
Athanas nitescens	0	1
Balanus balanus	1	1
Balanus crenatus	2	2
Bodotria scorpioides	1	1
Calliopius laeviusculus	1	2
Cancer pagurus	1	1
Caprella linearis	1	1
Carcinus maenas	3	3
Chaetogammarus marinus	1	2
Cheirocratus sundevallii	1	1
Corophium insidiosum	2	1
Crangon allmanii/C. crangon (complex)	1	1
Dexamine spinosa	1	2
Dexamine thea	1	1
Elminius modestus	1	2
Galathea squamifera	1	1
Gammarellus homari	0	1
Gammarus locusta	0	1
Hyale nilssoni	1	1
Hyas araneus	1	1
Idotea baltica	0	1
Idotea chelipes	0	1
Idotea granulosa	2	3
Jaera albifrons	2	1
Jassa falcata	3	3
Jassa marmorata	0	1
Ligia oceanica	0	1
Liocarcinus holsatus	1	1
Melita palmata	1	1
Pagurus bernhardus	2	2
Palaemon elegans	0	1
Pandalina brevirostris	1	0
Pilumnus hirtellus	2	1
Pisidia longicornis	1	1
Semibalanus balanoides	1	1
Verruca stroemia	2	3
Insecta		
Anurida maritima	1	1
Clunio marinus	1	1
Petrobius brevistylis	1	0
Bryozoa		
Alcyonidium mytili/A. gelatinosum (complex)	2	2
Bowerbankia gracilis	1	1
Bowerbankia imbricata	0	1
Bowerbankia pustulosa	1	1
Callopora lineata	1	1
Celleporella hyalina	1	1
Cibrilina punctata	1	0
Conopeum reticulum	1	1
Cryptosula pallasiana	2	2

Table 3 (Contd.)

Species	Average conspicuousness	
	1984	2002
Electra pilosa	3	3
Escharella immersa	1	1
Escharella variolosa	1	1
Flustrellidra hispida	2	2
Membranipora membranacea	1	1
Schizoporella errata	1	1
Walkeria uva	1	1
Echinodermata		
Amphipholis squamata	2	2
Asterias rubens	1	1
Psammechinus miliaris	1	1
Ascidiae		
Botrylloides leachi	1	1
Botryllus schlosseri	2	3
Clavelina lepadiformis	1	2
Molgula citrina/M. complanata (complex)	1	1
Polyclinum aurantium	0	1
Sidnyum turbinatum	2	3

2002). Two arbitrary similarity values were chosen at a spread of hierarchical levels to determine particular groupings of samples.

## Results

Changes in presence and absence

A total of 154 species in 24 taxonomic groups were found in 2002. Janke, by contrast, found 158 species in 25 taxonomic groups in the same habitats. 126 species appeared in both studies. 28 species were only found in 2002, whereas 32 species were recorded only in the former study (Table 3; Fig. 3).

Within the gastropod molluscs (22 species in 2002; 26 species in 1984) the proportion of species lost and added was particularly high with 54.5% between both years. Of 33 gastropod species compared seven species were newly recorded in 2002 and eleven had disappeared. The polychaetes and oligochaetes (29 species in 2002; 31 species in 1984) showed conspicuous changes in the proportion of species lost and added. A change of 36.8% was noted. Six of 38 annelids newly occured in 2002, and eight species were not found any more. The annelids were followed by crustaceans (25.6%) which was the group with the highest number of species in 2002 (38 species in 2002; 30 species in 1984). Nine of 38 crustacean species newly appeared during the present study, and only one was missing between surveys. The taxonomic group of the kamptozoans was not found during 2002.

Changes in species conspicuousness

A considerable change in species conspicuousness was recorded in the group of crustaceans (Table 3). About

Fig. 3 Macrofauna of the rocky intertidal of Helgoland: changes in presence/absence of all species recorded in 1984 and/or 2002 in the sampling area. "Both studies" are species recorded in 2002 and 1984. "Additions" are species recorded in the present study, but not in 1984. "Losses" are species recorded in the latter study, but not in 2002
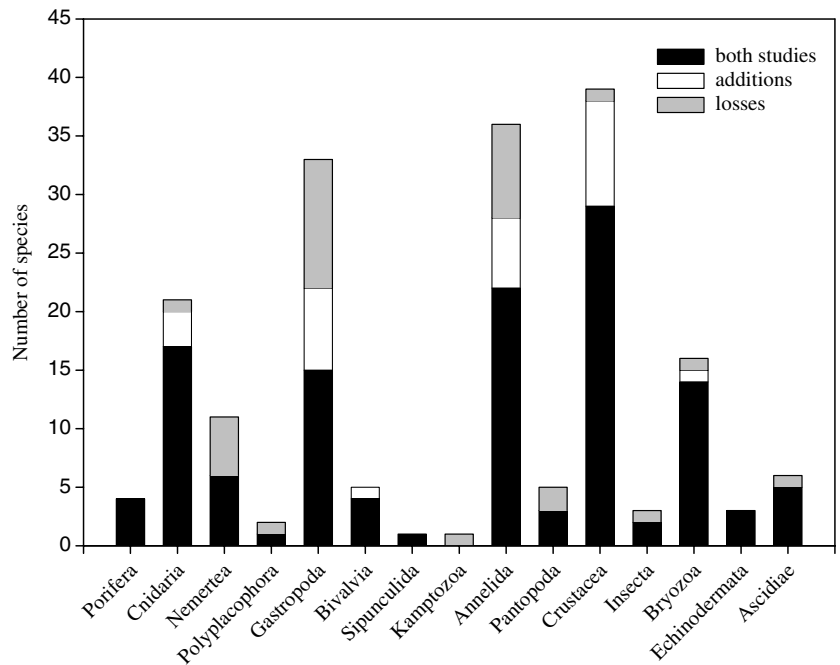
20.7% increased in conspicuousness, and 10.3% decreased between surveys. The crustaceans were followed by gastropods with 20% increase and 6.7% decrease in conspicuousness. None of the ascidian species decreased in conspicuousness between 1984 and 2002, but three out of five ascidian species increased.

Multivariate analysis

In the dendrogram three main groups can be distinguished at the 50% similarity level (Fig. 4). These groups (A–C) show different zones which are grouped together due to fundamentally different communities at different tidal heights. The first group (A) consists of samples gathered in the lower intertidal zones (*F. serratus*-, *Laminaria*-zone, channels, *L. digitata*) over the whole sampling period in 1984 and 2002. The second group (B) is represented by the mid intertidal (*Mytilus*-zone) sampled in 2002, and the third group (C) combines samples gathered in the high intertidal zone (*Enteromorpha*-zone) during both study periods.

At the 70% similarity level four sub-groups within group A, and two sub-groups within group C are formed (Fig. 4). These sub-groups show a splitting according to the two sampling years. Groups which are combined

Fig. 4 Dendrogram of the five habitats surveyed in 1984 and 2002, plus the *Mytilus*-zone sampled only in 2002, using group-average clustering from Bray–Curtis similarity on non-transformed data. The groups distinguished at the 50% similarity threshold (*continuous line*) are marked A–C, and the sub-groups distinguished at the 70% similarity threshold (*dashed line*) are marked 1A–4A, 1C and 2C. (*Ent Enteromorpha*-, *Myt Mytilus edulis*-, *Fuc Fucus serratus*-zone, *chan* channels, *L. dig Laminaria digitata*, *Lam Laminaria*-zone)
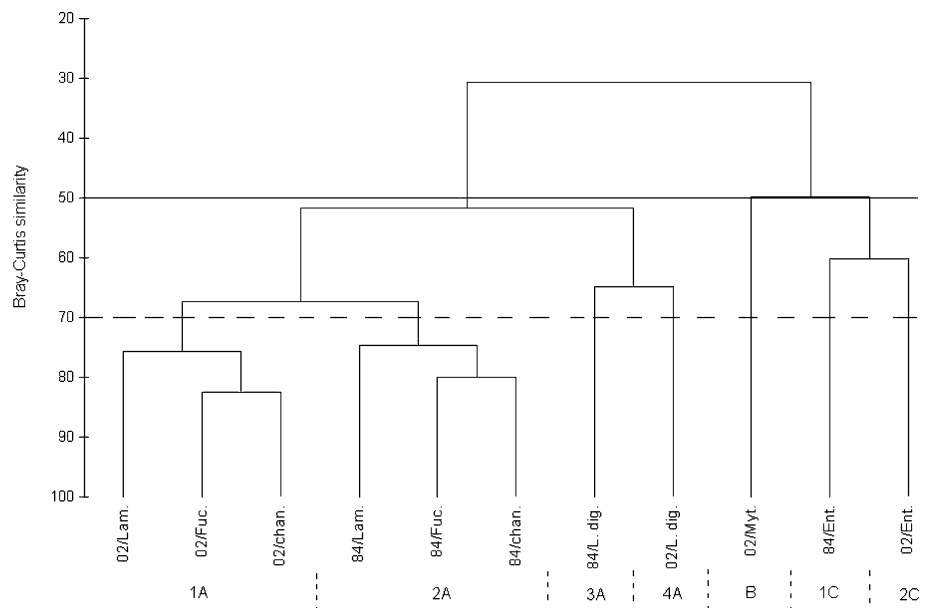
owing to different communities in 2002 and 1984 are clear in 1A (lower intertidal zones in 2002) and 2A (lower intertidal zones in 1984) where the *F. serratus*-, *L. digitata*-zone and channels of 1 year can be regarded as replicates and are more similar to each other than one particular zone of the lower intertidal over both study years. These two sets of groupings are superimposed on the MDS ordination (stress value: 0.05; results not shown).

Changes in algal cover

In the present study the brown alga *S. muticum* dominated in biomass in the channels, forming conspicuous floating fields. The red alga *Mastocarpus stellatus* was a prominent species in the *Mytilus*-zone. None of these species were present in 1984.

In contrast, the brown algae *F. serratus* which dominated the mid and lower intertidal zone in 1984 did not form abundant stands in the *Mytilus*-zone of the abrasion platform in 2002. *Halidrys siliquosa*, which was sampled in the *Laminaria*-zone in 1984, did not form stands during the whole investigation in 2002 any more. Only single scattered specimens were found.

Discussion

The temporal comparison revealed the most pronounced changes within the molluscs, the annelids and the crustaceans (Table 3; Fig. 3). The numerical changes in these three taxonomic groups were to be expected as those groups contained the highest number of species. On closer examination of species within the taxonomic groups it appeared that species, which occurred only in one year, were species which were classified as "occasional" in average conspicuousness. However, some species with low abundance were those which live near their limit of distribution and were subjected to strongly variable environmental conditions, e.g. in temperature. Accordingly, those species should not be neglected when compared to abundant ones, although there is a necessity for critical consideration of rare species which are easily overlooked, particularly when species are small and inconspicuous.

The cluster analysis showed spatial as well as temporal differences in the invertebrate communities of the abrasion platform. During the recent decades many investigations demonstrated a distinct pattern of vertical zonation due to fundamentally different composition of species in the high, mid and low intertidal zone in rocky shore communities (e.g. Stephenson and Stephenson 1949, 1972; Crisp and Southward 1958; Southward 1958; Menge 1976; Lewis 1978). Accordingly, a grouping of different zones with different invertebrate assemblages at different intertidal heights was to be expected (Fig. 4).

More interesting were the differences in the invertebrate communities between Janke's study in 1984 and the present one in 2002. Here, the most obvious changes occurred in the lower intertidal (Fig. 4). This is important because the lower intertidal spans about three-quarters of the area sampled (Table 1; Fig. 2). In the following discussion, changes in the communities of the lower intertidal between the sampling years are described on the basis of examples and linked to temperature change, introduction of non-indigenous species and the effects of pollutants. In this context, massive changes in the composition of macroalgae assemblages found on the abrasion platform are also discussed.

A warming trend of the North Sea was first indicated by Becker and Pauly (1996). A precise record is the Helgoland Roads time series, which showed an annual mean sea surface temperature increase of 1.13°C for the 40 years since 1962 (Wiltshire and Manley 2004).

The presence and absence of gastropod molluscs changed markedly between both years. Especially some sea slugs, such as *Aeolidia papillosa* and *Dendronotus frondosus*, were absent in the present study. These species normally live permanently submerged (Thompson 1988), and are thus limited in occurrence in a tidal area. Furthermore, Meyer (1971) reported that nudibranchs (e.g. *A. papillosa* and *D. frondosus*) of the Atlantic coast of North America are cold stenotherms with regard to their reproductive phase. In spring 1984 as well as in the summer months these sea slugs were found in shallow subtidal areas at the study site. In contrast, in 2002 these species were observed only in deeper subtidal areas around Helgoland. However, in dredge samples from the Tiefe Rinne (deep channel, maximum 60 m) immediately south of Helgoland, these sea slugs were numerous (Schubert personal communication). This may indicate that the appearance of the sea slugs is limited by high temperatures which frequently predominate in intertidal sites. Furthermore, we recorded the warm adapted sea slug *Elysia viridis* for the first time in the intertidal and its appearance may be related to recent climate anomalies (Franke and Gutow 2004).

The increased conspicuousness of the "southern" sea squirt *Botryllus schlosseri* in the present study may also be related to the current increase in mean water temperatures. As a matter of fact, in a former survey carried out at Helgoland harbour, low resistance to low winter temperatures was detected in this species (Harms and Anger 1983). Generally, the mild winter temperatures in the last decade seem to be one of the decisive factors that favour species immigration from milder areas of the Atlantic Ocean to the North Sea. Such a northward shift of southern species and/or a retreat northwards of northern species is one factor, which causes changes in the distribution and abundance of species (e.g. Beukema 1992; Southward et al. 1995; Edwards et al. 1999; Franke and Gutow 2004; Hiscock et al. 2004).

Another factor is the anthropogenic introduction of alien species whose settlement and recruitment success may be enhanced by temperature increases. There are well known examples of alien species, which profit from climate change and often cause abundance changes in

the native community (e.g. Franke et al. 1999; Walther et al. 2002; Drinkwaard 1999; Diederich et al. 2004).

An example for the intertidal of Helgoland are two space competitors, the indigenous barnacle *Semibalanus balanoides* and the alien *Elminius modestus*, which was first recorded at Helgoland in 1954 (Den Hartog 1959). Their interaction is strongly influenced by physical factors, especially temperature, which affects the breeding period, settlement, recruitment and mortality rate and change in the abundance of the two competitors is the consequence (Crisp 1964; Moyse and Nelson-Smith 1964; Southward et al. 1995; Franke and Gutow 2004). Such change in abundance also appeared in the present study. *E. modestus* increased in conspicuousness, whereas *S. balanoides* did not change. Currently, *E. modestus* dominates the barnacle community in the upper zones of the northeastern intertidal of Helgoland (Wendt personal communication).

Exotic species appear to particularly profit from climate induced effects causing changes in the distribution and abundance of the rocky shore community. However, some changes recorded here may also be indicative of pollutant influences. During the study in 1984, *Nucella lapillus* appeared in small numbers (Janke 1986). In 2002, only two individuals of *N. lapillus* were found outside the routine sampling area. The prosobranch *N. lapillus* is generally regarded as one of the most sensitive species, which becomes sterile at even low TBT-concentrations (Gibbs et al. 1988; Birchenough et al. 2002). It is known that the TBT contaminations of the surface water around Helgoland did not change considerably between the application ban of the use of anti-fouling paints for small vessels and the end of the 1990s (Watermann 1993; Kalbfus 1997). Therefore, it may be possible that the prevailing TBT concentrations are responsible for the decrease of *N. lapillus* at Helgoland between the study in 1984 and 2002.

Although neither study did consider algal species as thoroughly as invertebrates, massive changes in the composition of macroalgae were obvious. Conspicuous and major changes which took place after 1984 are the extensive settlement of the marine benthic macroalgae *S. muticum* and *M. stellatus* as well as the decrease of *F. serratus* in the *Mytilus*-zone (see Fig. 2). Less conspicuous though substantial is the decrease in the alga *H. siliquosa* in the upper *Laminaria*-zone.

The first record, the spread and the present occurrence of *S. muticum* and *M. stellatus* around Helgoland were reported by Kornmann and Sahling (1994), Bartsch and Kuhlenkamp (2000) and Bartsch and Tittley (2004). The reduction of *H. siliquosa* to scattered singular stands in the present study may be related to a replacement by *S. muticum* in submerged areas of the platform. That *S. muticum* competes with seaweeds and causes a significant decrease in the settlement of slowly growing and several year old algae, particularly in *H. siliquosa*, was shown by Stæhr et al. (2000).

The decrease of the brown alga *F. serratus* in the *Mytilus*-zone which happened between winter 1984/1985 and 1985/1986 (Janke 1986, 1990) may have been caused by a series of cold winters in the mid 1980s and particularly by freezing and following detachment of *F. serratus* blades by tidal currents and wave action. The recovery of dense *F. serratus* stands was probably prevented by biotic factors such as increased grazing of littorinids which may have prevented a settlement of *Fucus* species. Furthermore, an inhibited pressure of predation by *N. lapillus* may have led to an increased abundance of mussels, which in turn compete with brown algae. Such effects could be shown in several studies on population dynamics in rocky shore communities (e.g. Menge 1976; Menge and Sutherland 1976; Lubchenco 1983). However, to assess the natural variation of *F. serratus* stands in the *Mytilus*-zone due to a combination of physical and biotic factors a long-term study would be needed at Helgoland.

Finally, this study clearly shows that snapshots at two points in time can be used to indicate changes which may essentially be anthropogenic. However, it is difficult to obtain clear evidence that such medium-term change is dependent on man-induced factors and does not reflect natural cycles with a periodicity of decades. Particularly in the observation and understanding of non-seasonal cycles, due to complex interactions of abiotic and biotic factors in many cases, it is important to differentiate these from man-induced fluctuations in communities. To detect natural variation in seasonal cycles from year to year and to relate the medium-term changes to possible a-seasonal cycles, continued monitoring is necessary (Hartnoll and Hawkins 1980; Hawkins and Hartnoll 1983; Southward 1995). The current study was intended to help to create a baseline for further regular sampling using accepted quantitative methods. These studies may support appropriate measures in the management of the rocky shore communities around Helgoland in view of the area being a marine protected area and a reference site for European ecological comparisons.

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