TEMPORAL AND SPATIAL SCALES IN SPECIES ASSEMBLAGES OF THE ROCKY INTERTIDAL AT HELGOLAND (GERMAN BIGHT, NORTH SEA)

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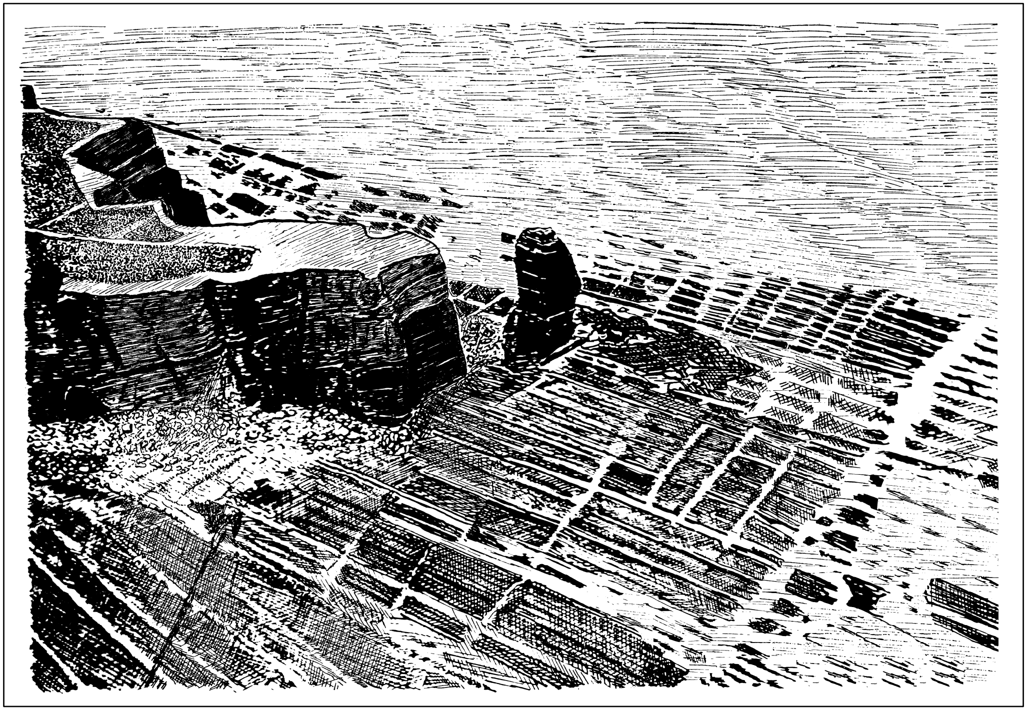

Modified after Hagmeier, 1930

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GENERAL INTRODUCTION

A central objective in ecology is to understand the patterns of distribution and abundance of plant and animal individuals, populations and communities. As a first step, the knowledge of patterns of spatial and temporal variation helps to identify and interpret the effects of ecological processes influencing distribution. The present body of theory shows that ecological processes shaping the patterns operate at several temporal and spatial scales. For instance, considering time there are processes ranging from every-day to geological scales, including those that involve climate change. There is now ample evidence that the recent climatic changes have affected the range and distribution of species, and the composition and dynamics of benthic communities (Hiscock et al., 2004; Walther et al., 2002). However, the relevant temporal scales of most ecological investigations are often short-term, and thus a clear understanding of the role of short-term versus long-term environmental processes in community dynamics is lacking. Only a long-term monitoring programme, i.e. a survey systematically undertaken to provide an observation series spanning several decades, allows the detection of changes on large temporal scales which may partly be due to human activities against changes on smaller temporal scales which mostly reflect natural variation.

Rocky shores may be considered as a suitable medium for such ecological research, mainly due to the simplicity of studying rocky shores compared to terrestrial ecosystems or offshore marine systems (Raffaelli & Hawkins, 1996). Rocky shores are usually well accessible, are clearly arranged as a consequence of their overall two-dimensional nature and are characterized by steep environmental gradients (Fig. 1). Plants and animals at rocky shores mostly have a sessile lifestyle and even those with potential mobility are generally slow moving. Furthermore, the often typically large and conspicuous algae and invertebrates usually exhibit lesser taxonomic problems than organisms of other ecosystems. Therefore, patterns of distribution and abundance of algae and invertebrates can be easily and non-destructively sampled in sets of fixed sampling units (at small to larger spatial scales) allowing the identification of processes and their associated scales which influence the distribution patterns.

Spatial and temporal scales in intertidal species assemblages

In general, variation in distribution and abundance of intertidal algae and invertebrates is studied at a range of spatial scales spanning centimetres to hundreds of kilometres (e.g. Benedetti-Cecchi, 2001; Fraschetti et al., 2005; Underwood & Chapman, 1996).

At large spatial scales, i.e. hundreds of metres to kilometres, intertidal assemblages vary among shores which are frequently subjected to variation in wave exposure. The wave exposure gradient influences intertidal algal and invertebrates in various ways and is therefore difficult to define. For instance, wave exposure directly and positively affects species, such as suspension feeding mussels and sessile predator anemones, by generating fluxes of nutrients (Bertness et al., 1992). On the other hand, physical forcing and sedimentation can directly and negatively influence seaweeds and invertebrates (e.g. Airoldi & Cinelli, 1997; Vadas et al., 1990). To cope with physical disturbance by exposure to wave action, intertidal species have developed firm attachments, thickened shells, low profiles and flexibility in structure (Raffaelli & Hawkins, 1996).

Figure 1 A rocky shore of the island of Helgoland in the German Bight, North Sea at low tide.

Besides variation in rocky shore assemblages at large spatial scales, there is also considerable variability at spatial scales of metres to hundreds of metres. Variation at these scales is mainly caused by emersion, i.e. the time spent out of the water. The higher on the shore marine organisms live the longer the periods of time spent in the air. Whether it is desiccation, extremes of temperature and salinity or lack of nutrients and food caused by emersion, the shore represents an essentially unidirectional stress for most marine organisms along the vertical gradient.

Species assemblages are structured along this vertical gradient according to their different abilities to avoid or endure physical forcing. This structuring into spatial zonation patterns, as distinct horizontal bands of specific marine organisms, is most obvious along the intertidal gradient in many parts of the world (Lewis, 1964; Southward, 1958; Stephenson & Stephenson, 1972; see Fig. 1). However, variation in abundance of intertidal species according to height on the shore is not only attributable to physiological stresses, but also to biological interactions such as competition (e.g. Connell, 1961; Dayton, 1971; Hawkins & Hartnoll, 1985), grazing (e.g. Hawkins & Hartnoll, 1983; Jenkins et al., 1999a, b; Lubchenco, 1982) and predation (e.g. Dayton, 1971; Lubchenco & Menge, 1978; Paine, 1974). These may be equally important in influencing the upper and/or lower limits of distribution of individual species on rocky shores.

In recent years, it has been realized that most intertidal algae and invertebrates are distributed in extremely patchy patterns at small spatial scales (centimetres to metres) within any height on rocky shores (Aberg & Pavia, 1997; Benedetti-Cecchi, 2001; Chapman, 2002; Fraschetti et al., 2005). Small-scale variation in distribution patterns of species assemblages may be related to small-scale changes in behavioural responses (e.g. Chapman & Underwood, 1994; Underwood & Chapman, 1989), recruitment (e.g. Chapman & Underwood, 1998), patchy distributions of microhabitats (Underwood & Chapman, 1996) and interactive effects of abiotic and biotic factors (Benedetti-Cecchi et al., 2000a). For instance, interactions of such processes maintaining differences in assemblages may be caused by microhabitats across a rocky shore (e.g. pools, crevices, cracks) which result in diverse small-scale variation in physical conditions (e.g. micro-hydrodynamic or micro-climate changes), and therefore in small-scale variation of behavioural responses of species, such as snails.

Next to spatial heterogeneity of rocky shore communities, the composition and abundance of assemblages is also inherently variable through time. Temporal variation in intertidal communities may be short-term (interannual to intra-decadal trends) or long-term (trends spanning several decades). Short-term variation in intertidal communities mostly reflects the seasonal fluctuation of physical and biological parametres which constrain population dynamics, such as mortality, recruitment, growth and behavioural responses (e.g. Benedetti-

Cecchi et al., 2000b; Foster et al., 2003; Jenkins et al., 2000, 2001). However, these seasonal cycles also vary frequently inter-annually in their amplitude and/or timing, caused by environmental changes between the years or by superposition of a longer term trend upon the annual cycle. While seasonal cycles operate generally over the whole shore and change the overall community structure, inter-annual variation in seasonal cycles mainly influences community components (Hartnoll & Hawkins, 1980). Processes generating inter-annual variation in species assemblages are mainly prompted by changes in the outcome of biological interaction due to variation of environmental conditions such as wind force and direction or temperature extremes (e.g. Beukema et al., 2001; Crisp, 1964; McCook & Chapman, 1997).

In contrast, long-term changes in intertidal communities are often related to anthropogenic impacts on rocky shore communities such as the input and accumulation of harmful substances and nutrients (e.g. Baeck et al., 2002; Worm & Lotze, 2006), the introduction of alien species (e.g. de Kluijver, 1997; Reichert & Buchholz, 2006) and finally climate change (e.g. Hiscock et al., 2004; Sagarin et al., 1999; Southward et al., 1995). However, long-term variation in intertidal communities may also show temporal fluctuation with a periodicity of decades due to natural and thus gentler climatic variations as well as changes in biological interaction (e.g. changes in predator or prey abundances, changes in habitat structure, e.g. decrease of algal cover; Hiscock et al., 2004; Sagarin et al., 1999).

To separate man-induced variations from natural trends, it is necessary to gain knowledge about natural temporal variation in the distribution and abundance of communities as a basis for impact-detection studies or ecological observation programmes. The spatial and temporal heterogeneity of rocky shore communities have important implications for monitoring programmes, regarding the sampling design and frequency (Benedetti-Cecchi et al., 2003; Hartnoll & Hawkins, 1980; Underwood, 2000; Underwood & Chapman, 2003).

Sampling rocky shore communities

Basic knowledge about natural short-term variation of communities is usually obtained by sampling several times throughout the year and over a number of successive years (usually 3-5 years). Particular attention should be paid to avoid frequent sampling, as it will itself modify the community structure (Hartnoll & Hawkins, 1980). Furthermore, it is possible to increase the effectiveness of monitoring by concentrating upon species assemblages which display the least natural variation in time. To gain insight into long-term variation of communities and their causes, natural or anthropogenic, a sampling programme needs to span at least one decade (Franke & Gutow, 2004; Hartnoll & Hawkins, 1980; Southward, 1995).

An effective sampling design should consist of (1) quantitative survey methods, (2) representative sampling areas, (3) an appropiate size and number of sample units and (4) a suitable arrangement of these sample units to each other.

The use of a quantitative survey method (e.g. percentage cover) contributes essentially to minimise the subjectivity of the investigator, particularly for long-term observations where often several observers are involved. Moreover, quantitative data sets can be subjected to statistical analysis and may be used in comparative meta-analysis.

Representative sampling areas should include algal and invertebrate assemblages which are characteristic for the study location, and thus represent the community as a whole. Therefore, an exhaustive description of assemblages at the specific sampling location is a prerequisite. With such a community description, representative sampling areas which are constant for the duration of the monitoring programme can be established. When conducting long-term observations, permanent sampling areas are superior to areas which are newly relocated at each survey; they facilitate the sampling process, eliminate the variation from microhabitat change and provide records of sequences of change in these sampling areas (Hartnoll & Hawkins, 1980).

Furthermore, each algal and invertebrate assemblage which has to be characteristic for the study location should be sampled with an appropriate number of replicates at fixed size (e.g. by 0.25 m^2 sampling square). The number of necessary replicates can be calculated as the minimum sampling area which is just large enough to give an accurate account of the quantitative composition of each species assemblage (Weinberg, 1978).

When species assemblages are described and minimum sampling areas are calculated, the set of sampling areas can be established. To simultaneously assess spatial variation at several scales, a nested sampling design is a powerful tool; here, sets of sampling units at small spatial intervals repeated at sites, locations, etc., that are different distances apart, are established (Fraschetti et al., 2005; Underwood, 2000). A nested sampling design, in association with appropriate analytical procedures (e.g. hierarchical analysis of variance, correlation and regression models), is a suitable starting point from which hypotheses for manipulative experiments may arise. Such experiments then aim to identify the natural processes or man-induced disturbances underlying the observed patterns.

The rocky shore communities of Helgoland and their implications for ecological monitoring

The rocky shore communities of Helgoland (German Bight, North Sea; see Fig. 2) are situated in a central position for ecological monitoring. The island is located in the south-eastern North Sea, whose climate is currently shifting towards more oceanic conditions; in particular, there is increasing evidence suggesting that the benthic community composition around the island of Helgoland is changing (e.g. Franke & Gutow, 2004; Reichert & Buchholz, 2006; Wiltshire & Manly, 2004). This shift in North Sea climate may be an important factor driving recent changes in species composition. Many species which newly appeared at the island of Helgoland during the past decade are oceanic (southern) species which may be considered as indicators of a warming trend.

The intertidal communities of Helgoland are geographically isolated from other hard-bottom communities located in the North Sea by surrounding soft sediments so that processes of change occur in a focused way. At the same time, the rocky littoral of Helgoland has been a marine protected area since 1981, and is a reference site for European ecological comparisons.

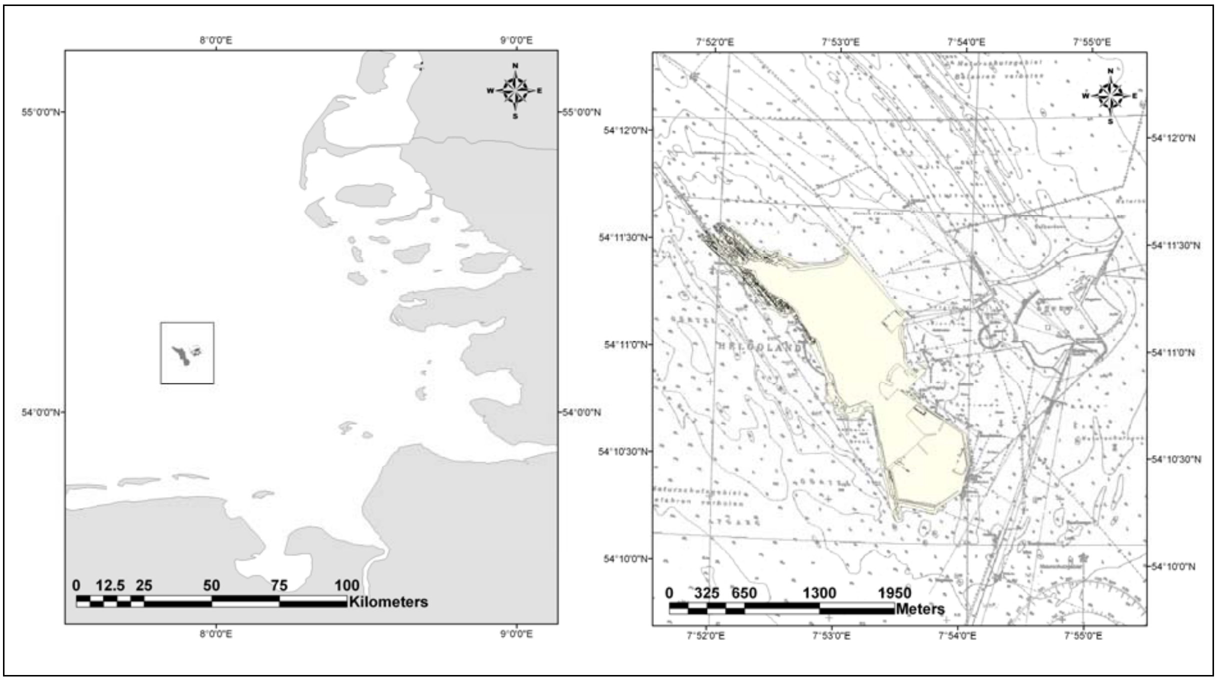

Figure 2 Geographic location of the island of Helgoland in the German Bight, North Sea.

Algal and invertebrate assemblages of the relatively small Helgoland rocky littoral, covering about 35 km², have been studied for more than a century (Harms, 1993). However, there are only a few intertidal studies which describe distribution patterns and reveal possible temporal variation in the composition of algae (Bartsch & Tittley, 2004) or invertebrates (Janke, 1986, 1990) at specific locations; a comprehensive review of the intertidal communities at Helgoland had not yet been carried out. To date, all intertidal studies deal with only one particular taxonomic group or are semi-quantitative. All told, there is no thorough quantitative description of communities as a whole, including both algal and invertebrate species. Moreover, spatial patterns of algal and invertebrate communities in rocky intertidal locations at Helgoland have only been scarcely defined, and no evidence is available to date that determines wether spatial patterns of the hard-bottom assemblages are dependent on the scale of measurement, and if processes creating patterns operate at different spatial scales.

Thus, the current rapid change of the North Sea climate, the rocky littoral at Helgoland as a marine protected area and a reference site for European ecological comparisons, as well as the limited knowledge of distribution patterns and temporal changes in species assemblages ask for a thorough analysis of the status of the rocky shore communities at Helgoland.

Objectives

The main objective of this thesis was to give a thorough quantitative assessment of the intertidal communities of the island of Helgoland as a whole, including both algae and invertebrates. My specific objectives were (1) to assess the variation in species assemblages at two points in time and at a short-time scale from 2004 to 2006, (2) to determine characteristic communities, their abundance and distribution patterns, (3) to evaluate the patterns of variations in species assemblages at defined spatial scales and (4) to explore relationships between environmental variables and the occurrence of species or assemblages. With the knowledge gained about variation in these assemblages a baseline for further regular sampling was to be developed to monitor the rocky shore communities of Helgoland on a long-term basis.

Outline of this thesis

The results of this study are presented and discussed in the form of four manuscripts for publication in appropriate scientific journals. Finally, as an overview, the establishment and application of a new approach in monitoring marine biodiversity at Helgoland are summarized in the last chapter of this thesis.

In Manuscript I, the invertebrate community of a rocky intertidal location of Helgoland is compared to a previous study (Janke, 1986), aiming at revealing possible changes in the composition of invertebrates over the past two decades. The results demonstrate considerable changes in presence/absence and abundance categories of invertebrates between both surveys. Potential factors that could have caused these changes are discussed and an assessment is given as to what extent such single surveys at two points in time and a semi-quantitative approach are suitable for indication of long-term trends in rocky shore communities.

Manuscript II quantitatively describes the benthic communities as a whole, including algae and invertebrates, of the rocky intertidal of Helgoland. The results reveal six communities which differ in species composition and in their spatial distribution. Wave exposure and elevation are discussed as potential explanatory variables for the observed variation in communities and a suggestion is provided for a nested sampling design at different spatial scales.

Manuscript III evaluates scale-dependent patterns of variability in the intertidal community structure of Helgoland, and determines the relative importance of elevation as a potential factor to explain the observed variability in the community. The highest variability in community structure occurs at smaller scales; for macroalgae, the scale-dependent patterns of variability depend on whether species are rare or common. Possible ecological processes that influence the observed scale-dependent patterns of community structure, particularly patterns associated with changes in elevation, are discussed.

In Manuscript IV, scale-dependent patterns in typical algae and invertebrates of the communities at Helgoland and the relative importance of elevation are studied. Variation in the cover of individual species is most important at smaller spatial scales, as it is the case for total abundance of the community (Manuscript III), and macroalgae at both locations are more consistent over time than invertebrate species. Our results suggest that the relevant processes shaping the individual macroalgae and invertebrates at the Helgoland intertidal vary between locations and the specific species. The potential causes of variation in macroalgal and invertebrate species at different spatial scales are discussed, and further suggestions for a future monitoring programme are given.

For the first time at Helgoland, this study deals with the quantitative assessment of communities as a whole, including both algae and invertebrates. The description of the community structure as well as the analyses of spatial and temporal variation of species assemblages at the rocky intertidal served as the basis for regression models. These models have shown conspicuous relationships between environmental variables and spatial patterns of species assemblages. Finally, based on the results of this study, recommendations were established for further regular sampling of the rocky shore communities of Helgoland in view of the area being a marine protected area and a reference site for European ecological comparisons.

GENERAL MATERIAL AND METHODS

Study locations

The surveys were conducted at one intertidal location from spring until autumn 2002 (Manuscript I), at three intertidal locations in summer 2004 (Manuscript II) and at two intertidal locations from summer 2004 until spring 2006 at the island of Helgoland, German Bight, North Sea (54° 11´N, 7° 53´E). The locations were in the northern, western and southern part of the island and were named after their geographic position (see Fig. 1). These locations differed in wave exposure. De Kluijver (1991), used standardized gypsum blocks and took their rate of erosion as a measure for exposure, showed that total amount of water movement was higher at the west site of Helgoland (0.14-0.16 $g \cdot h^{-1}$) than at the northeastern site (0.14 $g \cdot h^{-1}$) and at the southern site (0.10 $g \cdot h^{-1}$; de Kluijver, 1991). In shallow places at the west side the erosion rates reaches 0.28 $g \cdot h^{-1}$ during westerly winds (force 4-5). The prevailing winds around Helgoland are westerly (de Kluijver, 1991). Therefore, the western intertidal was defined as exposed, the northern intertidal as semi-exposed and the southern intertidal as sheltered location (Fig. 1).

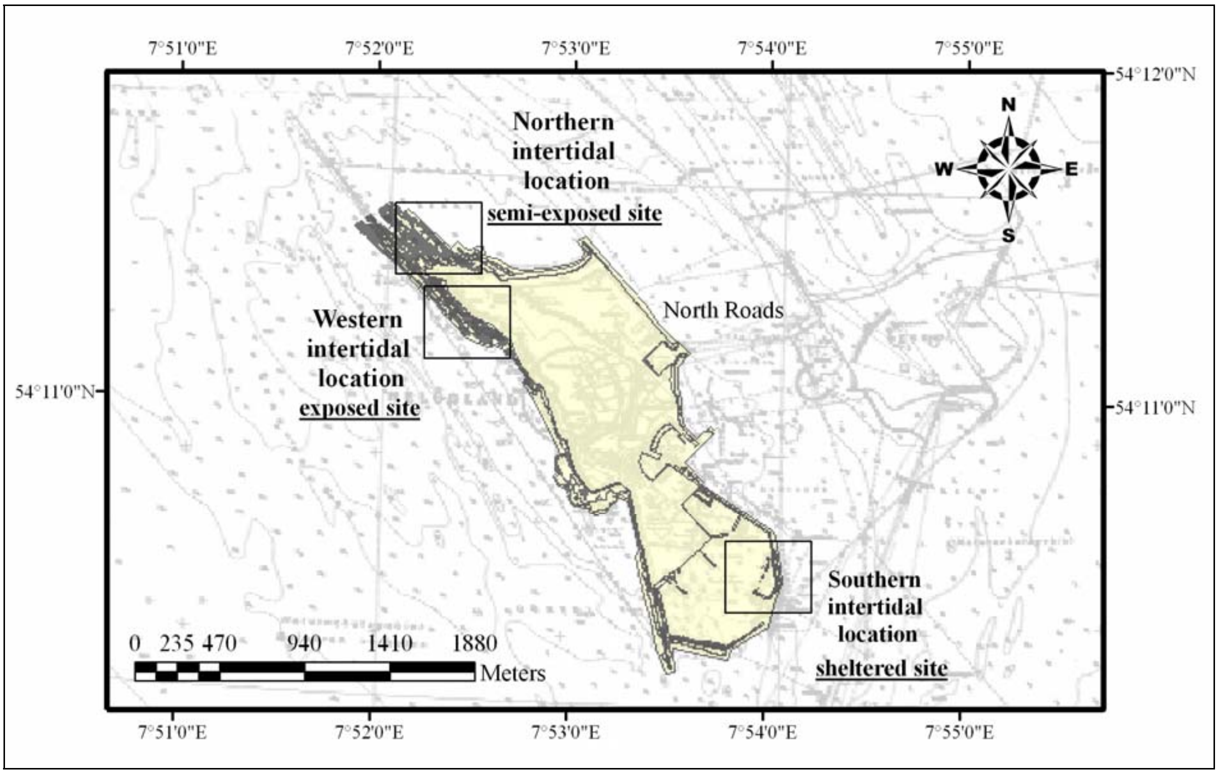

Figure 1 Helgoland with the western, northern and southern intertidal study location differ in wave action.

The northern and western intertidal location also differed in the geo-morphological structures of the rock-platform. The surface geomorphology of the northern location is characterized by a series of channels (mean height: ca. -1.00 m refer to the height Normal Null (NN) of the German height reference system; width: ca. 3-5 m) extending to the northwest towards the open sea, and are separated by ridges (mean height to NN: ca. -0.60 m; width: ca. 5-15 m). The ridges and channels showed an alternating pattern along the shore. The western location shows similar heights and widths of channels (mean height to NN: ca. -1.50 m; width: ca. 2-20 m) and ridges (mean height to NN: ca. -1.00 m; width: ca. 5-25 m) as the northern location, but the geo-morphological features are more irregular. The ridges form rather discrete patches enclosed by channels which also submerged during low tide. The southern location resulted from the construction of piers of the southern harbour in 1936. The pier consists of vertical areas and stepwise sloping horizontal sites. The southern location was made of concrete, whereas in the northern and western location the substratum was mostly made up of relatively soft natural red sandstone.

The specific geomorphology of the northern location favours a mosaic of microhabitats (Hagmeier, 1930; Janke, 1986; see Fig. 2), and there is a description of distinct vertical zones named after the most conspicuous algae or invertebrates: the *Enteromorpha*-, the *Mytilus*-, the *Fucus serratus*- and the *Laminaria*-zone (Bartsch & Tittley, 2004; Janke, 1986, 1990). The location features of each zone and dominating algal species are listed in Table 1 (see also Reichert & Buchholz, 2006). At the southern location, vertical zones also occur, whereas at the western location such conspicuous vertical bands do not occur (see Manuscript II). Due to the seawall along the western part of the island high- and mid-shore assemblages were basically non-existent in the western study location. For the lower intertidal, the northern and western shore harboured qualitatively similar algal and invertebrate assemblages, while the southern study location differed in the species assemblages (see Manuscript II).

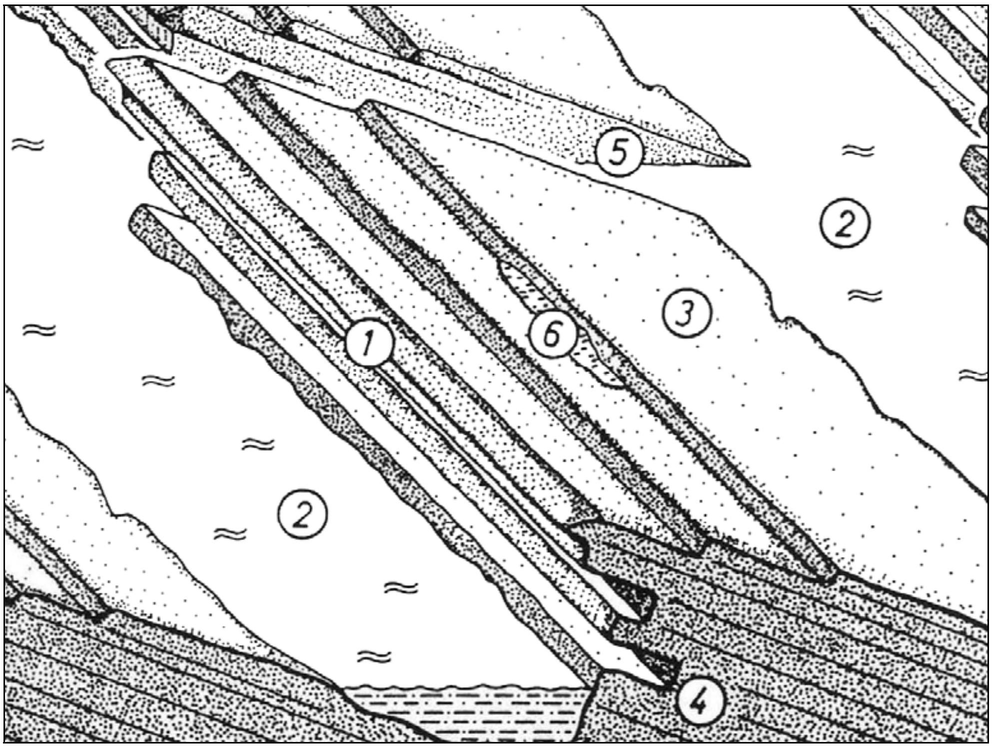

Figure 2 Schematic depiction of the surface geomorphology of the northern intertidal location. Numbers in circles indicate microhabitats: 1: head of sandstone layer; 2: channel; 3: sandstone layer; 4: crevice; 5: fault; 6: sediment (modified after Hagmeier, 1930).

Sampling design and survey methods

A set of habitats surveyed by Janke (1986) were re-sampled in 2002 (Manuscript I). From nine habitats in total (Janke, 1986), four habitats were excluded due to the endangerment caused by rocks which occasionally fall from the vertical cliffs above. The sampled habitats were the (1) *Enteromorpha*-, (2) *Fucus serratus*-zone, (3) channels, (4) *Laminaria*-zone and individuals of (5) *Laminaria digitata*. As an additional habitat the *Mytilus*-zone was sampled in 2002, having clearly dissociated as a separate zone from the *F. serratus*-zone; 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 applying the techniques of data collection given by Janke (1986). In addition, dominant macroalgae were noted. The different structures within each habitat (e.g. rock pool, visually dominant macroalgae) were sampled using different procedures. Rock pools and channels were sampled with a fine mesh hand net over a period of about 10 min. Two litres of sediment and small pieces of rock were taken. Furthermore, 1 litre of smaller algal species (e.g. *Enteromorpha* species) and 10 litre of large brown algae (e.g. *F. serratus*) were collected. The samples were examined at the laboratory, and the invertebrate abundance was estimated in the same way as species that could be readily identified with the unaided eye in the field. The abundance estimation of the invertebrates according to categories was taken from Janke (1986; see Table 2). In order to reduce the subjectivity of the categorization of the invertebrates, an on-site comparison of the categorization of the species was performed with Dr. Janke in person until a close match in results was achieved.

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 (Reichert & Buchholz, 2006).

Vertical belt	Location features				Dominant algal species
	Zone	Mean time of emersion (h)	Parallel extension (m)	Perpendicular extension (m)	
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*, *Phymatolithon* spp.
Fucus serratus-zone	Low intertidal	ca. 2.5	ca. 100-210	ca. 60-150	*Cladophora rupestris*, *F. serratus*, *C. crispus*, *Corallina officinalis*, *Phymatolithon* 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., *R. tortuosum*), *Sargassum muticum*, *Laminaria digitata*, *F. serratus, C. officinalis*, *C. crispus*, *Phymatolithon* spp.
Laminaria-zone	Subtidal	(see channels)	From ca. 230	-	*Ulva* spp., *C. rupestris*, *L. digitata*, *F. serratus, C. officinalis*, *C. crispus*, *Phymatolithon* spp.

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

To determine characteristic communities at the Helgoland intertidal two line transects were established at the northern and western location in summer 2004 (Fig. 3a, b; Manuscript II). At the southern location, only one line transect was sampled as this location was smaller than the other two location (Fig. 3c). Each line transect per location - comparable in terms of type and slope of the substratum - was selected at random from a set of possible line transects. At the northern location, one line transect was 120 metres, the other 40 m long. At the western location, the lengths of the line transects were 20 and 6 metres respectively. The line transect at the southern location was 5 metres long. The length of the line transects selected limited by the extension of each location and the exposure to wave action. Each transect was sampled in total length by adjoining 0.25 m² quadrats. The position of every fifth quadrat along the transects was recorded using a differential global positioning system (Geo XT, Trimble, Germany) with an accuracy of 1-2 m in the field. The positions of the remaining replicates were determined by recording their distance in situ, in *x* and *y* spatial coordinates, from the georeferenced replicates. The prevailing coordinates were processed with the programme ArcGIS 9.0 (ESRI).

To evaluate the patterns of variations in species assemblages at defined spatial scales a part of the transects at the northern and western location established in 2004 were sampled at 3-month intervals over 2 years, from summer 2004 to spring 2006 (Fig. 4a, b; Manuscript III, IV). At the semi-exposed northern location, one transect was sampled at high-shore, and the other at low-shore, and thus the distance between transects, measured perpendicular to the island`s shoreline, could be ca. 65 metres. The length of transects ranged between 25 and 40 metres. Along each transect, six and five plots respectively (separated by 5 - 40 metres) were chosen at random from a larger pool of plots, which were examined in the sampling in summer 2004 with reference to the community structure. Thus, for each plot the species assemblage was well-known by the results of a previous community analysis (Manuscript II). Five replicated quadrats, separated by about one metre, were selected randomly at each plot. At the exposed western location, both transects were sampled across the vertical axes at low-shore. The transects were separated by ca. 45 metres and the length of the transects ranged between 7 and 10 metres. As for the northern location, along each transect, plots were selected at random (three and two plots respectively, separated by 4 - 10 metres) from a larger pool of plots and five replicated quadrats (separated by about one metre) were sampled randomly at each plot.

Since summer 2004, the algal and invertebrate assemblages were quantitatively sampled (Manuscript II, III, IV). In general, the species assemblages comprised three different structural layers: top, middle and encrusting layer. The top layer (TL) usually consisted of thalli of large brown algae (e.g. *Fucus* spp., *Laminaria* spp.). The middle layer (ML) was represented by epiphytic, epizoic and endozoic species growing erect from the substrate, but not reaching the top layer (e.g. hydrozoans, mussels, tube-building polychaetes). The encrusting layer (EL) was formed by epilithic organisms adhering directly to the substratum, such as bryozoans or encrusting algae of the genus *Phymatolithon* or *Ralfsia* (see also de Kluijver, 1991, 1993, 1997). In each structural layer the percentage cover of the vertical projection of sessile, slow moving invertebrates and algae was estimated, using a 0.25 m^2 quadrat.

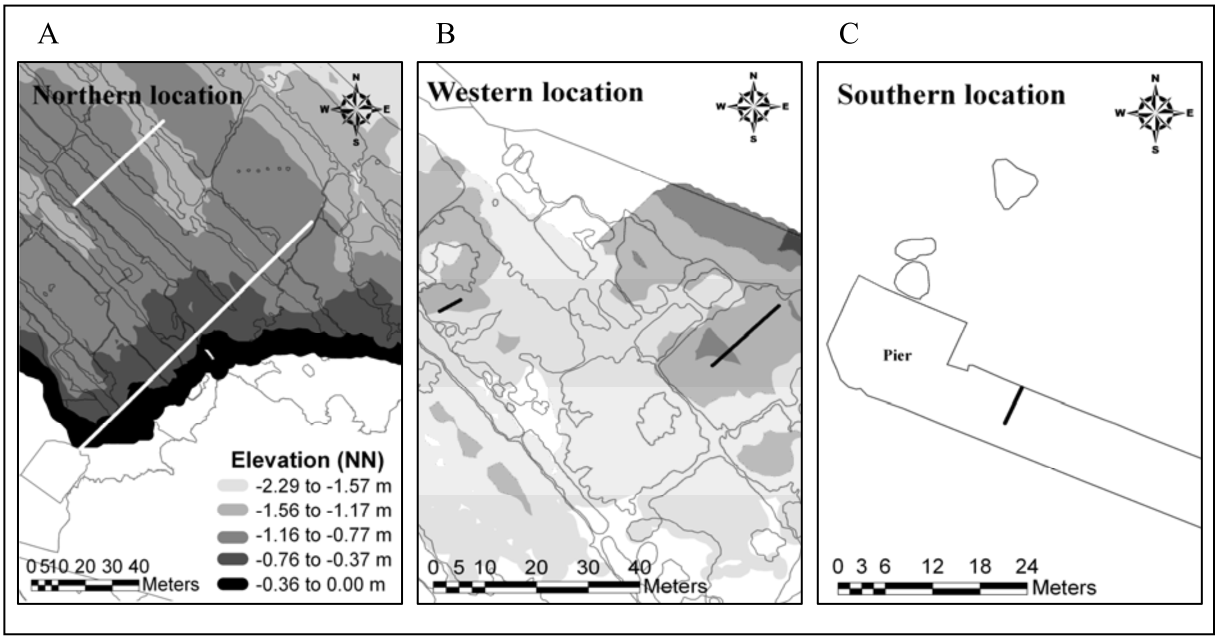

Figure 3 The line transects at the (A) northern, (B) western and (C) southern location; the northern and western location are shown with the drawn contours of the surface morphology and the elevation in metres refers to the height Normal Null (NN) of the German height reference system.

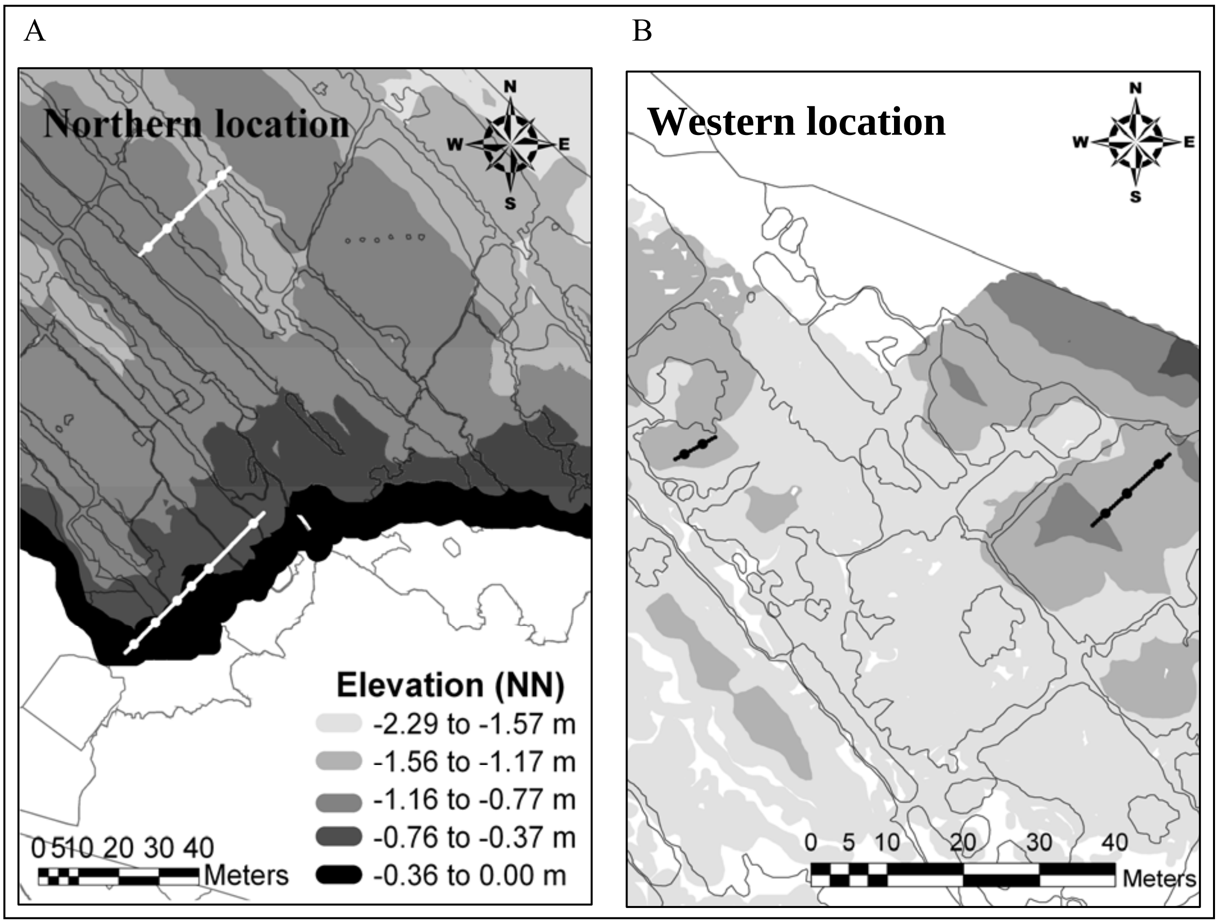

Figure 4 The sampling scales, i.e. the transects (lines) and plots (points) at the (A) northern and (B) western location; the locations are shown with the drawn contours of the surface morphology and the elevation in metres refers to the height Normal Null (NN) of the German height reference system.

In all four Manuscripts, organisms were identified in situ whenever possible. In case of taxonomic uncertainty the specimen was collected and identified in the laboratory. When possible, organisms were identified to species level; some species were combined into a complex if the taxonomic position was tentative or if the morphological distinctions between two species were difficult to quantify (see details in Manuscript I). The identification of organisms was based on the literature which is listed in Table 3.

Table 3 Literature for identification of organisms ordered by taxonomic groups.

Taxonomic group	Literature for identification
Chlorophyta	Kornmann & Sahling (1977); Burrows (1991)
Phaeophyta	Fletcher (1987); Kornmann & Sahling (1977)
Rhodophyta	Dixon & Irvine (1977); Kornmann & Sahling (1977); Irvine (1983); Maggs & Hommersand (1993); Irvine & Chamberlain (1994)
Porifera	Hayward & Ryland (1995)
Cnidaria	Manuel (1988); Cornelius (1995a, b); Hayward & Ryland (1995)
Nemertea	Gibson (1982)
Mollusca	Ankel (1936); Ziegelmeier (1957, 1966); Tebble (1966); Nordsieck (1982); Graham (1988), Thompson (1988); Hayward & Ryland (1995)
Sipuncula	Gibbs (1977)
Annelida	Fauchald (1977); Gillandt (1979); Brinkhurst (1982); Hartmann-Schröder (1996)
Arthropoda	Schellenberg (1942); Naylor (1972); King (1974); Cheng (1976); Jones (1976); Lincoln (1979); Smaldon (1979); Ingle (1983); Luther (1987); Hayward & Ryland (1995)
Bryozoa	Ryland & Hayward (1977); Hayward & Ryland (1979); Hayward (1985)
Echinodermata	Hayward & Ryland (1995)
Chordata (Ascidiae)	Hayward & Ryland (1995) and Rietdorf (2001)

Data analyses

In the following various stages of community analysis (community structure, spatial and temporal variation, relationship between variables), used in the four manuscripts, are described with a focus on the precision and benefit of the contributions of the methods used. First, a short outline of the different stages of the community analysis is given. Finally, the various univariate and multivariate methods used at these stages are described.

Description of species assemblages

The first step to further analysis of species assemblages is a simple description, rather than an explanation or testing of hypotheses (Clark & Warwick, 2001). The emphasis is on reducing the complexity of the multivariate information by univariate or multivariate methods. In the present study, only multivariate methods were applied for presenting the community structure. Multivariate methods are characterised by the fact that they base their comparison of two or more samples on the extent to which these samples share particular species at comparable levels of abundance. All multivariate methods are based on such measures of association being calculated between every pair of samples or variables (e.g. species). The calculated measure of association then facilitates a clustering of samples into groups which are mutually similar, or an ordination plot in which, for example, the samples are mapped in such a way that the distances between pairs of samples reflect their relative dissimilarity in species composition. In the present study only multivariate methods, clustering and ordination techniques, were applied for representing the community structure. For multivariate analysis, PRIMER 5 (PRIMER-E, 2000) and a FORTRAN computer program (Anderson, 2003) was used. In the following section, measures of association and transformations are described as a basis for the discussion of clustering and ordination techniques.

Measures of association

There is a wide range of measures of association (see for examples Legendre & Legendre, 1998), and whichever measure is used will strongly affect the outcome of the analysis. It is particularly important to know how a chosen technique treats species that have blank values for both samples (double zeros) as well as those that have large values.

Two characteristics of ecological community data are that (1) the relationships between the species or samples are typically non-linear and (2) there are many zeros in the data matrix. Due to these problems a measure of association should be chosen which (1) measures no linear relationships because it is based on a (dis-)similarity coefficient and (2) ignore double zeros. The Bray-Curtis coefficient (Bray & Curtis, 1957) complies with these prerequisites, and thus has become particularly common in ecological studies (Legendre & Legendre, 1998; Quinn & Keough, 2002). The data of the present study showed the characteristics of ecological community data, and thus the Bray-Curtis coefficient was applied.

Transformation

Transformations are used in order to reduce the influence of variables with high values, i.e. very abundant species (Digby & Kempton, 1987; Field et al., 1982). There are several strategies available for choosing the most appropriate transformation. In the present study, a graphical data exploration technique - scatterplots - was applied (Zuur et al., 2007); the standard deviation was plotted against the mean of the samples. If the data points in the scatterplot showed a more or less linear function a logarithmic transformation was chosen, while a non-linear function led to a square root transformation.

For the further analyses in Manuscript II, III and IV, square root-transformed data for macroalgae and logarithmically-transformed data for invertebrates were chosen. An exception was the estimations of variance components; here, untransformed data for all analyses were used to provide variance components comparable across all data (Fraschetti et al., 2005). In Manuscript I, the multivariate methods were done with non-transformed data due to the semi-quantitative sampling method which generated abundance data of species assigned to categories; thus, a possible influence of abundant species was already balanced and a further transformation was not necessary.

Cluster analysis

Hierarchical clustering joins samples consecutively to produce groups that simultaneously maximise the similarity within the groups and the distinction between the groups. The clustering results in a dendrogram, and how the samples are grouped together differ largely between the clustering procedures. Out of the large number of procedures described, the group-average linkage is the preferred standard procedure (Clifford & Stephenson, 1975; Legendre & Legendre, 1998) which was applied in the present study. It joins two groups by evaluating the mean similarity between the samples of both groups. The group-average linking does not tend to be susceptible to a chain-effect such as the single linkage or to an artificial formation of clusters such as the complete linkage (Field et al., 1982). Clustering was applied in Manuscript I and II.

Inverse analysis

Based on the results of the clustering, an inverse analysis was performed in Manuscript II to procure information about the species composition of the clustered groups (see also Kaandorp, 1986; de Kuijver, 1991, 1993; de Kluijver & Leewis, 1994). The distribution of quantities of species over the clustered groups was calculated, and thus communities were described. Characteristic and dominant species were distinguished; characteristic species were defined as those (1) present in at least 67 % of the quadrats sampled in the community and (2) occurred in just one community with 4 % cover or more. Dominant species were defined as those that were also present in at least 67 % of the quadrats sampled in the community, but occurred in more than one community with 4 % cover or more.

Ordination techniques

The aim of ordination techniques is twofold: (1) to reduce a large number of variables to a smaller number of easier-to-interpret variables and (2) to reveal patterns in multivariate data that would not be identified in univariate analyses. In the present study, non-metric multidimensional scaling (nMDS) and principal coordinate analysis (PCoA) were applied.

Multidimensional scaling (MDS)

Non-metric multidimensional scaling (Kruskal, 1964; Shepard, 1962) is generally used to visualise the similarity matrix in a two dimensional plot. The similarity coefficients for each pair of samples are ranked, and this ranking is represented as closely as possible in the nMDS plot. The stress-value indicates the quality of the plots (Kruskal, 1964). A low stress-value implies that the samples contain a clear structure (Rumohr et al., 2001).

In Manuscript I, nMDS followed the clustering to check the adequacy and mutual consistency of both representations. In Manuscript II, nMDS was neglected due to application of inverse analysis followed by the clustering. A disadvantage of nMDS is that for larger datasets the calculations tend to become time consuming due to the method on which nMDS is based on (numerical optimisation methods vs. eigenvalue equation; Zuur et al., 2007). Thus, for relatively small data set the nMDS method was used (Manuscript I), while for the larger data set the PCoA was chosen (Manuscript IV).

Principal coordinate analysis (PCoA)

PCoA is generally used to calculate an association matrix and to produce a graphical plot in a low dimensional space. However, in the PCoA plot it is not the ranking of a certain association measure for each pair of observations (e.g. replicates) or variables (e.g. species) as in nMDS, but the absolute association measure of the original matrix that is represented as closely as possible in the PCoA plot. The quality of the PCoA plot is measured by eigenvalues that represent the amount of variance explained by each axis, and is often expressed as cumulative percentage of the total variance. The higher the first eigenvalues, represented as axes (eigenvectors) in the PCoA plot, the better the representation.

In the present study, a statement on dissimilarity between replicates in the PCoA plot was irrelevant. The aim was to correlate the result of the PCoA (variance per replicate explained by the first two axes) with species abundances per replicate to select species best correlated with the first two principal axes. The correlation results were plotted in the existing PCoA plot, and thus a biplot was shown with (1) the replicates as points and (2) the species most correlated with the first two principal axes as lines. Those species shown in the PCoA were used for further statistical analyses.

Scale-dependent pattern of variation

Subsequent to the descriptive multivariate methods, the second stage of community analysis was to investigate the variation in the intertidal benthic community structure at several spatial scales. To determine relevant scales, e.g. scales on which important variation in total abundances of the community occur, several approaches of sampling can be applied (e.g. Andrew & Mapstone, 1987). One useful method is a nested hierarchical sampling design (e.g. Morrisey et al., 1992) which was applied in the present study; samples were taken at a series of nested spatial scales with all factors random. In the design, plots were nested in transects. Such a sampling design is necessary to separate the different spatial scales so that variation in the measurement of interest (e.g. total abundance) can be determined independently at each of the chosen scales. Estimation of the components of variation at each scale therefore directly translated to the estimation of spatial variation at each spatial scale.

A well known, easy-to-use and robust method for estimating components of variation uses the observed mean squares in the analysis of variance (ANOVA) to estimate terms identified in the expected mean squares (Searle et al., 1992; Winer et al., 1991). For balanced designs, this method is simple to apply. However, in the present study an unbalanced design was used with unequal numbers of a nested factor (here: plots) within a higher factor (here: transects).

Therefore, the restricted maximum likelihood method (the REML method), and also a two-way nested ANOVA with the Satterthwaite approximation (Sokal & Rohlf, 1995) were applied. The REML method has been generally accepted as having good properties for balanced and unbalanced designs (Robinson, 1987; Searle, 1995). The variance components were estimated for each source of variation in REMLs by using the Newton-Raphson iteration (Searle et al., 1992). For the REML method the significance of random factors was tested using an asymptotic significance test, whereas for the ANOVA method F-ratio testing was produced by the STATISTICA output (StatSoft, 2001). The validity of likelihood ratio tests however has been called into question because they rely on large sample approximations (Searle, 1987; Singer, 1998). Since the samples (n) in the present study were relatively small the significance test tended to be too conservative, and thus the power of detecting a significant variance component would be reduced. Therefore, (1) the REML method was used to estimate the components and checked against the ANOVA method: both methods gave approximately the same results. Then, (2) the ANOVA approach was used for hypothesis testing.

An disadvantage of the ANOVA-based method is the possibility of negative estimates for one or more of the variance components (Fletcher & Underwood, 2002). Negative estimates of variance components may occur if the variation between replicates varies markedly from location to location. In the present study, negative estimates of variance components from ANOVA testing were set to zero, removed from the model and the estimates for the remaining factors re-calculated (Fletcher & Underwood, 2002).

Relationship between variables

The last stage of community analysis in the present study was to analyse the relationship between variables. Simple correlation or linear regression analysis are the most widely applied statistical techniques to describe relationships between variables. For those statistical techniques the STATISTICA software package (StatSoft, 2001) was used. In Manuscript III and IV, several regression models were applied to analyse the relationship between elevation and community parametres since a response (e.g. species richness) and a predictor variable (elevation) can be clearly specified.

Analysis of linear and non-linear models

The aim of linear regression models is (1) to describe the relationship between the response and predictor variable, (2) to determine how much of the variation (uncertainty) in the response variable can be explained by the linear relationship with the predictor variable and how much of this variation remains unexplained, and (3) to predict new values of the response variable from new values of the predictor variable (Quinn & Keough, 2002). In the present study (Manuscript III), linear regression models were applied to aim at the first two points rather than to use the analysis for prediction. The simple linear regression model was:

$$y_i = ß_0 + ß_1 x_i + \varepsilon_I \qquad \text{(equation 1)}$$

where y_i = number of species for the ith sample when elevation is x_i.
$ß_0$ = mean number of species with elevation equal zero (intercept).
$ß_1$ = change in the number of species for a unit (e.g. cm) change in elevation (slope).
ε_i = differences between each observed value for number of species and the true mean of number of species at each possible elevation (error).

The aim of regression analysis is to estimate $ß_0$, $ß_1$ and ε_i based on n observations with fixed x-values (e.g. elevation) and random y-values (e.g. number of species). In the present study, this estimation procedure was done with ordinary least squares (OLS).

Then, the null hypothesis, that the there is no linear relationship between single species indices (e.g. species richness, total abundances) and elevation, was tested with an ANOVA F-ratio test. To meet the assumptions of linear regression analysis (e.g. normality, homogeneity of variance, independence) the variables were transformed.

As a descriptive measure of association between the response variable y (e.g. total abundances) and the predictor variable x (e.g. elevation) r, the Pearson product moment correlation (called Pearson's correlation for short) was applied in the present study. Pearson's correlation measures the “strength” of the linear relationship between the response and predictor variable. R ranges from +1 to -1. For example, r = +1 means that there is a perfect positive linear relationship between variables.

In addition to linear relationships, nonlinear relationships between the response and the predictor variable occurred, and transformation of the variables did not improve the linearity. Here, regression models were fitted which were nonlinear in their parametres. The null hypothesis was that there was no relationship among the variables. However, for the nonlinear regressions applied in the present study the null hypothesis has not necessarily been named due to the primary interest to find an empirical function that explains the variables (and not to test a particular theoretical model that is expressed in terms of a particular function). A nonlinear regression function with two parametres was applied. For the estimation procedure of the parametres, OLS was used (see linear models). To evaluate the fit of the model, an ANOVA F-ratio test was applied and Pearson's correlation measured the association between the response and the predictor variable. As Pearson's correlation measures linear relationships, a strong nonlinear relationship between two variables normally has a small Pearson's correlation.

LIST OF MANUSCRIPTS

This cumulative thesis is composed of four manuscripts which are already published (Manuscript I), under review (Manuscript II, III), or prepared for submission (Manuscript IV). Below, the manuscripts are listed by numbers and the contribution of all authors is specified.

I. Reichert, K. & Buchholz, F., 2006. Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002. *Helgoland Marine Research*, **60**, 213-223.

The scientific idea of this study was developed together with the second author. I carried out the sampling and performed the analyses. The manuscript was prepared by myself with contributions by Prof. Dr. F. Buchholz.

II. Reichert, K., Buchholz, F. & Giménez, L., 2007. Community composition of the rocky intertidal at Helgoland (German Bight, North Sea). In revision by *Aquatic Biology*.

I developed the concept of this study. The sampling, the statistical analysis and the interpretation of the data was conducted by myself. I prepared the manuscript with scientific and editorial advice by both co-authors.

III. Reichert, K., Buchholz, F., Bartsch, I., Kersten, T. & Giménez, L., 2007. Scale-dependent patterns of variability in species assemblages of the rocky intertidal at Helgoland (German Bight, North Sea). In revision by *Journal of the Marine Biological Association of the United Kingdom*.

I developed the concept of this study and carried out the sampling. Dr. I. Bartsch and Prof. T. Kersten provided the digital elevation model. The statistical analysis and interpretation of the data were done in cooperation with the last author. I wrote the manuscript which was improved in cooperation with all co-authors.

IV. Reichert, K., Buchholz, F. & Giménez, L. (to be submitted). Scale-dependent patterns of variability in the abundance of macroalgae and invertebrates of the rocky intertidal at Helgoland (German Bight, North Sea). To be submitted to *Journal of the Marine Biological Association of the United Kingdom*.

I developed the concept of this study and carried out the sampling. The statistical analysis and interpretation of the data were done in cooperation with the last author. I wrote the manuscript which was improved in cooperation with both co-authors.

The development of the general concept was done by myself and Prof. Dr. Friedrich Buchholz. The sampling design was developed with the help of Dr. Mario de Kluijver (Manuscript II-IV). Assistance in the field was given by Anja Röw (Manuscript III, IV).

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

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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.

Keywords

Indications of change · Invertebrate communities · Rocky intertidal · Helgoland · North Sea

INTRODUCTION

Intertidal communities are plastic systems as they change continuously in composition and abundance of organisms at several spatial and temporal scales (Dye, 1998; Meconi, et al. 1999). The exceptionally spatial and temporal variability in rocky shore communities arises from a combination of abiotic and biotic factors (Lubchenco & Menge, 1978; Menge, 1976, 1991; Menge & Sutherland, 1987; Underwood, 1985). 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. Lewis, 1978; Southward, 1958; Stephenson & Stephenson, 1949, 1972). 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; Hawkins & Hartnoll, 1985; Janke, 1990; Jenkins et al., 1999; Leonard et al., 1999; Paine, 1974). 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. Caffey, 1985; Harms & Anger, 1983; 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 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 & Sullivan, 1994). For example, changes in the abundance of macrobenthic species were related to predicted effects of recent climate warming (Barry et al., 1995; Beukema, 1992; Sagarin et al., 1999; Southward et al., 1995). 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 & 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 (Hartnoll & Hawkins, 1980; Lewis, 1976).

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 km², species composition as well as their spatial and temporal variability is relatively well recorded. At the same time, the rocky littoral of Helgoland has been 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 & Tittley (2004).

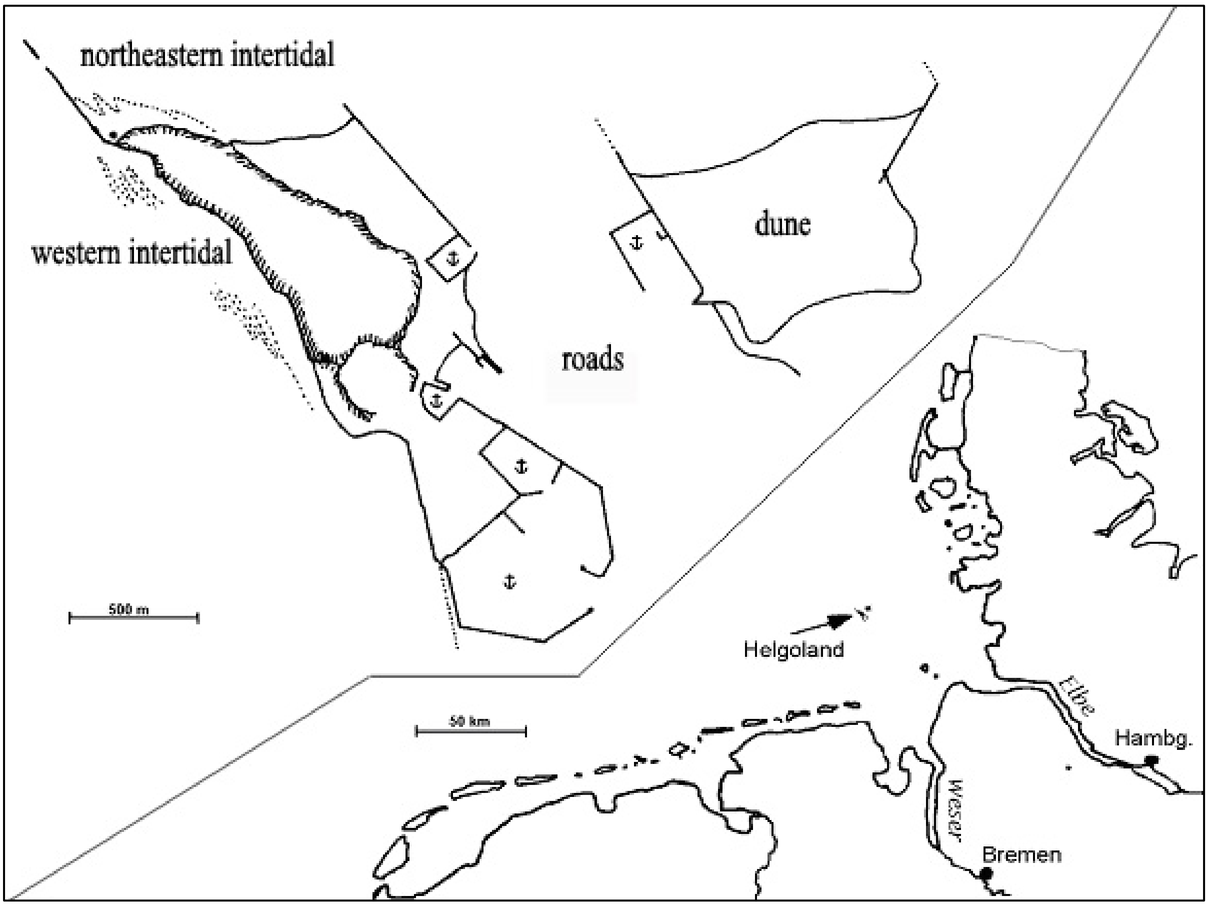

Figure 1 The study site in the north-eastern part of Helgoland, and the island`s location in the North Sea (according to Benoit, 1996, unpublished).

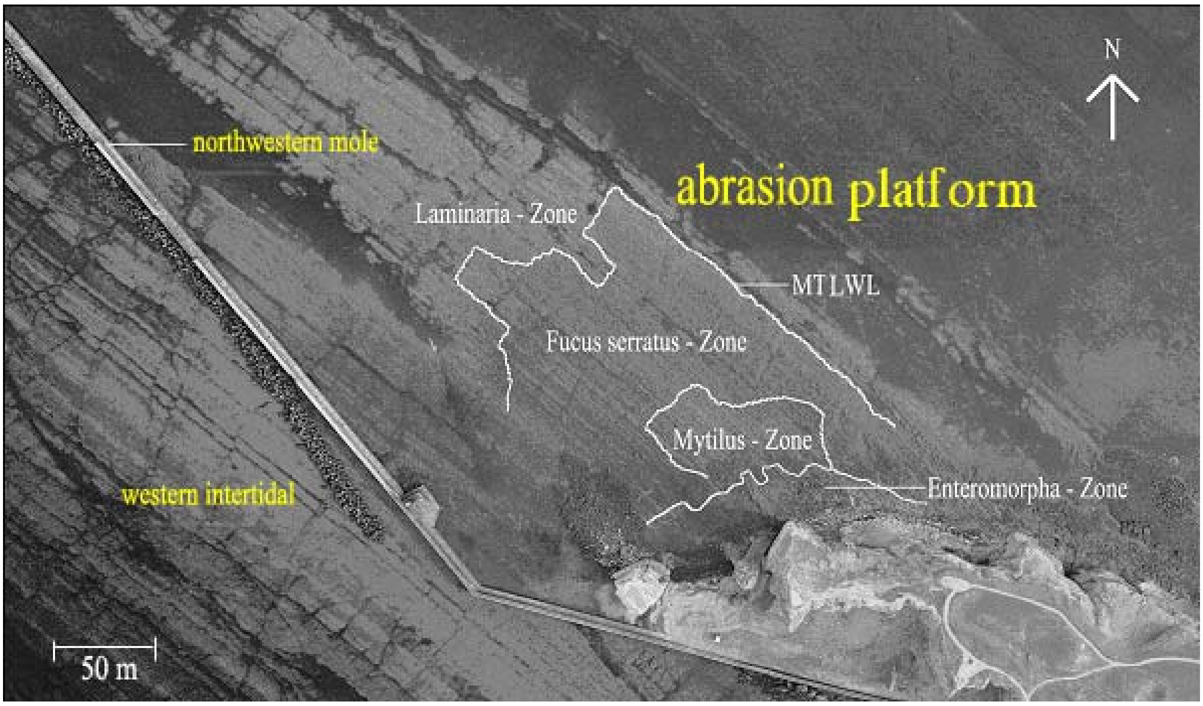

Figure 2 Aerial picture of the abrasion platform of the "Nordostwatt" of Helgoland (land survey office of Schleswig-Holstein). The investigated zones are marked.

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*, *Phymatolithon* spp.
Fucus serratus-zone	Low intertidal	ca. 2.5	ca. 100-210	ca. 60-150	*Cladophora rupestris*, *F. serratus*, *C. crispus*, *Corallina officinalis*, *Phymatolithon* 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., *R. tortuosum*), *Sargassum muticum*, *Laminaria digitata*, *F. serratus, C. officinalis*, *C. crispus*, *Phymatolithon* spp.
Laminaria-zone	Subtidal	(see channels)	From ca. 230	-	*Ulva* spp., *C. rupestris*, *L. digitata*, *F. serratus, C. officinalis*, *C. crispus*, *Phymatolithon* spp.

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) *Fucus 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 pool, 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.

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

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

Data analysis

Some of the species names, which were identified in Janke`s study, were updated based on subsequent taxonomic 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 *Sargassum 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 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 qualitatively 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 occur 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 39 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). 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.

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).

	Average conspicuousness	
Species	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

Table 3 *(contd.)*

	Average conspicuousness	
Species	1984	2002
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
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

Table 3 *(contd.)*

	Average conspicuousness	
Species	1984	2002
Sipuncula		
Golfingia minuta	1	1
Kamptozoa		
Pedicellina cernua	1	0
Annelida (Polychaeta & 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
Tubificoides benedii	0	1
Typosyllis armillaris	1	1

Table 3 *(contd.)*

Species	Average conspicuousness	
	1984	2002
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

Table 3 *(contd.)*

Species	Average conspicuousness 1984	2002
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
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

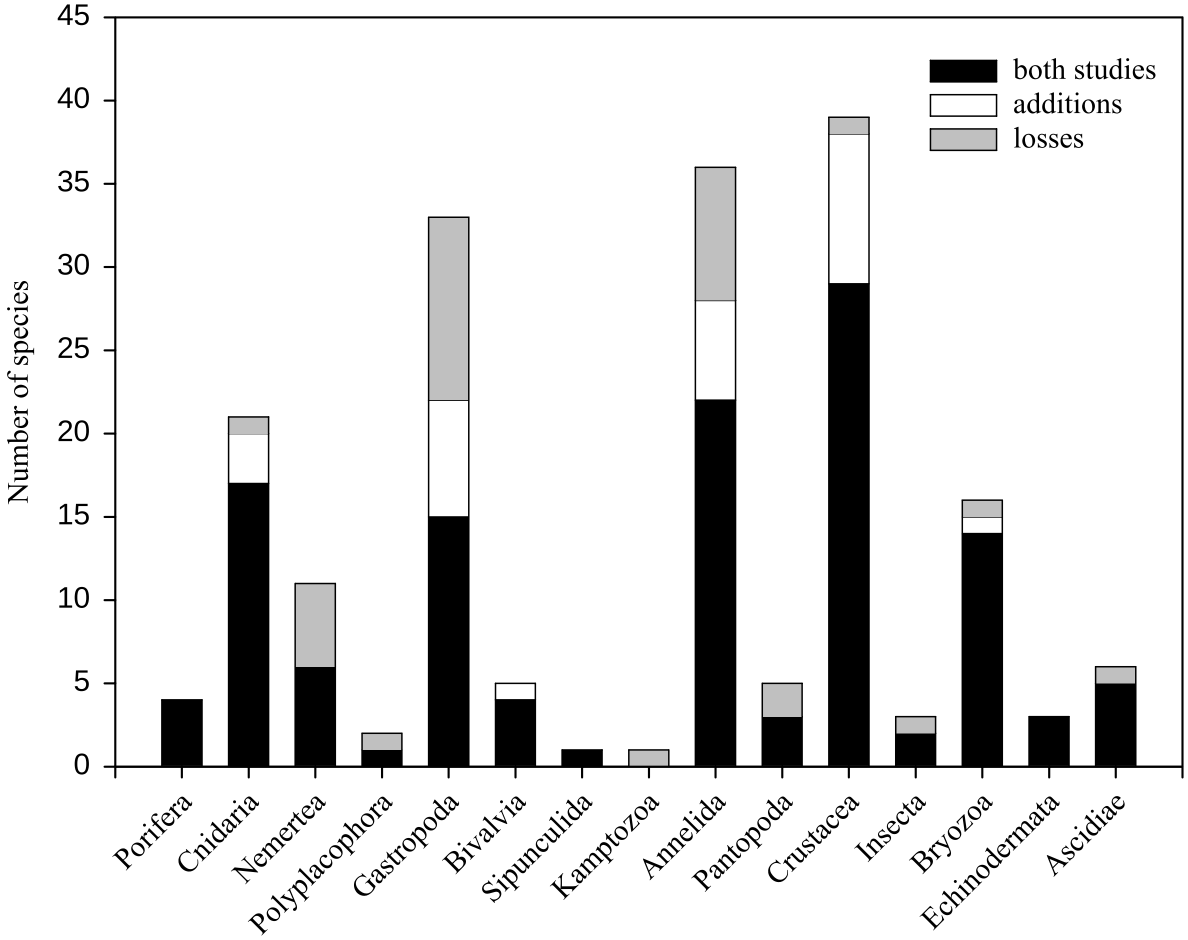

Figure 3 Macrofauna of the rocky intertidal of Helgoland: changes in presence/absence of all species recorded in 1984 and/or 2002 in the sampling area. "Both studies" are species recorded in 2002 and 1984. "Additions" are species recorded in the present study, but not in 1984. "Losses" are species recorded in the latter study, but not in 2002.

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 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).

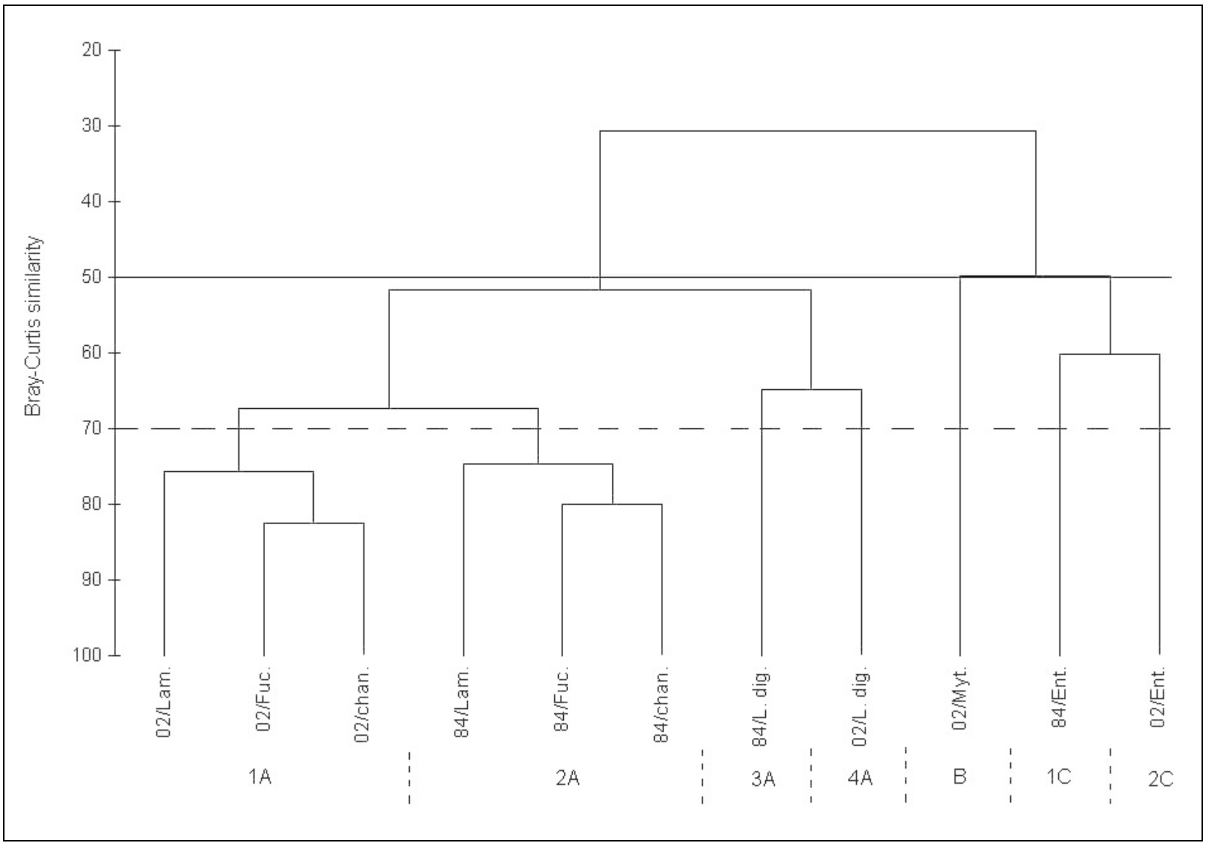

Figure 4 Dendrogram of the five habitats surveyed in 1984 and 2002, plus the *Mytilus*-zone sampled only in 2002, using group-average clustering from Bray-Curtis similarity on non-transformed data. The groups distinguished at the 50 % similarity threshold (*continuous line*) are marked A-C, and the sub-groups 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).

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 strong 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. Lewis, 1978; Menge, 1976; Crisp & Southward, 1958; Southward, 1958; Stephenson & Stephenson, 1949, 1972). 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-quaters 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 & 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 & 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 & 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 & 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; Edwards et al., 1999; Franke & Gutow, 2004; Hiscock et al., 2004; Southward et al., 1995).

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. Diederich et al., 2004; Drinkwaard, 1999; Franke et al., 1999; Walther et al., 2002).

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; Franke & Gutow, 2004; Moyse & Nelson-Smith, 1964; Southward et al., 1995). 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 (Birchenough et al., 2002; Gibbs et al., 1988). 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 (Kalbfus, 1997; Watermann, 1993). Therefore, it may 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 & Sahling (1994), Bartsch & Kuhlenkamp (2000) and Bartsch & 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; Janke, 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 been prevented a settlement of *Fucus* species. Furthermore, an inhibited pressure of predation by *N. lapillus* may have been 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. Lubchenco, 1983; Menge, 1976; Menge & Sutherland, 1976). 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 the observation and understanding of non-seasonal cycles, due to complex interactions of abiotic and biotic factors in many cases, 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 & Hawkins, 1980; Hawkins & 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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REFERENCES

Barry, J.P., Baxter, C.H., Sagarin, R.D. & Gilman, S.E., 1995. Climate-related, long-term faunal change in a California rocky intertidal community. *Science*, **267**, 672-675.

Bartsch, I. & Kuhlenkamp, R., 2000. The marine macroalgae of Helgoland (North Sea): an annotated list of records between 1845 and 1999. *Helgoland Marine Research*, **54**, 160-189.

Bartsch, I. & Tittley, I., 2004. The rocky intertidal biotopes of Helgoland: present and past. *Helgoland Marine Research*, **58**, 289-302.

Becker, G.A. & Pauly, M., 1996. Sea surface temperature changes in the North Sea and their causes. *ICES Journal of Marine Science*, **53**, 887-898.

Beukema, J.J., 1992. Expected changes in the Wadden Sea benthos in a warmer world: Lessons from periods with mild winters. *Netherlands Journal of Sea Research*, **30**, 73-79.

Birchenough, A.C., Evans, S.M., Moss, C. & Welch, R., 2002. Re-colonisation and recovery of populations of dogwhelks *Nucella lapillus* (L.) on shores formerly subject to severe TBT contamination. *Marine Pollution Bulletin*, **44**, 652-659.

Bowman, R.S. & Lewis, J.R., 1977. Annual fluctuations in the recruitment of *Patella vulgata* L. *Journal of the Marine Biological Association of the United Kingdom*, **57**, 793-815.

Caffey, H.M., 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs*, **55**, 313-332.

Chiappone, M. & Sullivan, K.M., 1994. Ecological structure and dynamics of nearshore hard-bottom communities in the Florida Keys. *Bulletin of Marine Science*, **54**, 747-756.

Crisp, D.J., 1964. Mortalities in marine life in North Wales during the winter of 1962-63. In Crisp DJ (ed) The effects of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*, **33**, 190-197.

Crisp, D.J. & Southward, A.J., 1958. The distribution of intertidal organisms along the coasts of the English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **37**, 157-208.

Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, **41**, 351-389.

De Kluijver, M.J., 1997. *Sublittoral communities of North Sea hard-substrata*. PhD thesis, University of Amsterdam, Netherlands.

Den Hartog, C., 1959. Die Seepocke *Elminius modestus* auf Helgoland. *Beaufortia*, **7**, 207-209.

Diederich, S., Nehls, G., von Beusekom, J.E.E. & Reise, K., 2004. Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? *Helgoland Marine Research*, **59**, 97-106

Drinkwaard, A.C., 1999. Introductions and developments of oysters in the North Sea area: a review. *Helgoländer Meeresuntersuchungen*, **52**, 301-308.

Dye, A.H., 1998. Dynamics of rocky intertidal communities: analyses of long time series from South African shores. *Estuarine, Coastal and Shelf Science*, **46**, 287-305.

Edwards, M., John, A.W.G., Hunt, H.G. & Lindley, J.A., 1999. Exceptional influx of oceanic species into the North Sea late 1997. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 737-739.

Franke, H.D., Gutow, L. & Janke, M., 1999. The recent arrival of the oceanic isopod *Idotea metallica* Bosc off Helgoland (German Bight, North Sea): an indication of a warming trend in the North Sea? *Helgoländer Meeresuntersuchungen*, **52**, 347-357.

Franke, H.D. & Gutow, L., 2004. Long-term changes in the macro-zoobenthos around the rocky island of Helgoland (German Bight, North Sea). *Helgoland Marine Research*, **58**, 303-310.

Gibbs, P.E., Pascoe, P.L. & Burt, G.R., 1988. Sex change in the female dog-whelk, *Nucella lapillus*, induced by tributyltin from antifouling paints. *Journal of the Marine Biological Association of the United Kingdom*, **68**, 715-731.

Hagmeier, A., 1930. Die Besiedlung des Felsstrandes und der Klippen von Helgoland. I. Der Lebensraum. *Wissenschaftliche Meeresuntersuchungen*, **15**, 1-35.

Harms, J., 1993. Check list of species (algae, invertebrates and vertebrates) found in the vicinity of the island of Helgoland (North Sea, German Bight) – a review of recent records. *Helgoländer Meeresuntersuchungen*, **47**, 1-34.

Harms, J. & Anger, K., 1983. Seasonal, annual, and spatial variation in the development of hard bottom communities. *Helgoländer Meeresuntersuchungen*, **36**, 137-150.

Hartnoll, R.G. & Hawkins, S.J., 1980. Monitoring rocky-shore communities: a critical look at spatial and temporal variation. *Helgoländer Meeresuntersuchungen*, **33**, 484-494.

Hawkins, S.J. & Hartnoll, R.G., 1983. Changes in a rocky shore community: an evaluation of monitoring. *Marine Environmental Research*, **9**, 131-181.

Hawkins, S.J. & Hartnoll, R.G., 1985. Factors determining the upper limits of intertidal canopy-forming algae. *Marine Ecology Progress Series*, **20**, 265-271.

Hayward, P.J., 1985. Ctenostome bryozoans. In: *Synopses of the British fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-169. London: E.J. Brill & Dr W. Backhuys. [New Series, no. 33].

Hiscock, K., Southward, A., Tittley, I. & Hawkins, S., 2004. Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation*, **14**, 333-362.

Janke, K., 1986. Die Makrofauna und ihre Verteilung im Nordost-Felswatt von Helgoland. *Helgoländer Meeresuntersuchungen*, **40**, 1-55.

Janke, K., 1990. Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). *Helgoländer Meeresuntersuchungen*, **44**, 219-263.

Jenkins, S.R., Hawkins, S.J. & Norton, T.A., 1999. Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community. *Journal of Experimental Marine Biology and Ecology*, **233**, 41-63.

Jenkins, S.R., Aeberg, P., Cervin, G., Coleman, R.A., Delany, J., Della Santina, P., Hawkins, S.J., LaCroix E., Myers, A.A., Lindegarth, M., Power, A.M., Roberts, M.F. & Hartnoll, R.G., 2000. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology*, **243**, 209-225.

Jenkins, S.R., Aberg, P., Cervin, G., Coleman, R.A., Delany, J., Hawkins, S.J., Hyder, K., Myers, A.A., Paula, J., Power, A.M., Range, P. & Hartnoll, R.G., 2001. Population dynamics of the intertidal barnacle *Semibalanus balanoides* at three European locations: Spatial scales of variability. *Marine Ecology Progress Series*, **217**, 207-217.

Kalbfus, W., 1997. Butylzinnverbindungen in Nord- und Ostssee. *Deutsche Hydrographische Zeitschrift. Supplement*, **7**, 75.

Kornmann, P. & Sahling, P.H., 1994. Marine algae of Helgoland: second supplement. *Helgoländer Meeresuntersuchungen*, **48**, 365-406.

Leonard, G.H., Ewanchuk, P.J. & Bertness, M.D., 1999. How recruitment, intraspecific interactions, and predation control species borders in a tidal estuary. *Oecologia*, **118**, 492-502.

Lewis, J.R., 1976. Long-term ecological surveillance: practical realities in the rocky littoral. *Oceanography and Marine Biology. An Annual Review*, **14**, 371-390.

Lewis, J.R., 1978. *The ecology of rocky shores*. London: Hodder and Stoughton.

Lubchenco, J., 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology*, **64**, 1116-1123.

Lubchenco, J. & Menge, B.A., 1978. Community development and persistance in a low rocky intertidal zone. *Ecological Monographs*, **48**, 67-94.

Menconi, M., Benedetti-Cecchi, L. & Cinelli, F., 1999. Spatial and temporal variability in the distribution of algae and invertebrates on rocky shores in the Northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, **233**, 1-23.

Menge, B.A., 1976. Organization of the new England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs*, **46**, 355-393.

Menge, B.A., 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology*, **146**, 69-100.

Menge, B.A. & Sutherland, J.P., 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *The American Naturalist*, **110**, 351-369.

Menge, B.A. & Sutherland, J.P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*, **130**, 730-757.

Meyer, K.B., 1971. Distribution and zoogeography of fourteen species of nudibranchs of Northern New England and Nova Scotia. *Veliger*, **14**, 137-152.

Moyse, J. & Nelson-Smith, A., 1964. Effects of the severe cold of 1962-63 upon shore animals in South Wales. In: Crisp DJ (ed) The effects of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*, 33, 183-190.

Paine, R.T., 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, **15**, 93-120.

Reise, K., 1998. Pacific oysters invade mussel beds in the European Wadden Sea. *Senckenbergiana Maritima*, **28**, 167-175.

Sagarin, R.D., Barry, J.P., Gilman, S.E. & Baxter, C.H., 1999. Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs*, **69**, 465-490.

Southward, A.J., 1958. The zonation of plants and animals on rocky sea shores. *Biological Reviews*, **33**, 137-177.

Southward, A.J., 1995. The importance of long time-series in understanding the variability of natural systems. *Helgoländer Meeresuntersuchungen*, **49**, 329-333.

Southward, A.J., Hawkins, S.J. & Burrows, M.T., 1995. Seventy years` observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology*, **20**, 127-155.

Stæhr, P.A., Pedersen, M.F., Thomsen, M.S., Wernberg, T. &, Krause-Jensen, D., 2000. Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. *Marine Ecology Progress Series*, **207**, 79-88.

Stephenson, T.A. & Stephenson, A., 1949. The universal features of zonation between tidemarks on rocky coasts. *Journal of Ecology*, **37**, 289-305.

Stephenson, T.A. & Stephenson, A., 1972. *Life between tidemarks on rocky shores*. San Francisco: Freeman.

Thompson, T.E., 1988. Molluscs: benthic opisthobranchs. In *Synopses of the British Fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-356. Leiden: E.J. Brill & Dr W. Backhuys. [New Series, no. 8].

Underwood, A.J., 1985. Physical factors and biological interactions: the necessity and nature of ecological experiments. In: *The ecology of rocky coasts* (eds. P.G. Moore & R. Seed), pp. 372-390. London: Hodder and Stoughton.

Van Soest, R., 2001. Porifera. In: *European register of marine species - A check-list of the marine species in Europe and a bibliography of guides to their identification* (eds. M.J. Costello, C.S. Emblow & R. White), vol. 50, pp. 85-103. Paris: Collection Patrimoines Naturels.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F., 2002. Ecological responses to recent climate change. *Nature*, **416**, 389-395.

Watermann, B., 1993. Antifoulingrückstände in Wasser und Sediment. *Schriftenreihe der Schuetzgemeinschaft Deutsche Nordseekueste e.V. Wilhelmshaven*, **2**, 47-57.

Willmann, R., 1989. *Muscheln und Schnecken der Nord- und Ostsee*. Melsungen: Neumann-Neudamm.

Wiltshire, K.H. & Manly, B.F.J., 2004. The warming trend at Helgoland Roads, North Sea: phytoplankton response. *Helgoland Marine Research*, **58**, 269-273.

Wolff, W.J. & Reise, K., 2002. Oyster imports as a vector for the introduction of alien species into northern and western European coastal waters. In: *Invasive aquatic species of Europe: distribution, impacts and management* (eds. E. Leppakoski, S. Gollasch & S. Olenin), pp. 193-205. Dordrecht: Kluwer Academic Publishers.

Community composition of the rocky intertidal at Helgoland

(German Bight, North Sea)

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ABSTRACT

At the rocky island of Helgoland (North Sea) the distribution and abundances of intertidal communities was assessed and the effect of wave exposure and tidal height on spatial distribution patterns of the communities was evaluated. Macroalgae and invertebrates were sampled quantitatively along line transects which were established in three intertidal locations, a semi-exposed, an exposed and a sheltered one.

The semi-exposed location was characterised by: (1) *Ulva* spp. at the high intertidal (*Ulva*-community), (2) mussels and periwinkles at the mid intertidal (*Mytilus*-community), (3) *Corallina officinalis* and mainly dominated by the large brown alga *Fucus serratus* at the low intertidal (*Fucus*-community). The exposed location encompassed the mid and low intertidal; at both zones the *Fucus*-community occurred. The sheltered location was characterised by: (1) barnacles (*Balanus*-community), (2) bryozoans and hydrozoans, and was dominated by the large brown alga *Ascophyllum nodosum* (*Ascophyllum*-community). At the semi-exposed location the communities were clearly related to variations in tidal height, whereas at the exposed location the community did not change with intertidal position. A relationship between wave exposure and the occurrence of specific communities was shown for the sheltered location; in contrast, communities of the semi-exposed and exposed location appear little influenced by wave exposure directly.

The community concept and the potential causes of distribution patterns of the defined communities are discussed and suggestions for a future monitoring are given. Variations in the communities at different spatial scales speak in favour of a multiple scale sampling design for monitoring change in the intertidal communities at Helgoland.

Keywords

Benthic communities · Rocky intertidal · Helgoland · Tidal height · Wave exposure

INTRODUCTION

Currently, a considerable research effort is aiming at using rocky shore communities for ecological monitoring (e.g. Franke & Gutow, 2004; Hiscock et al., 2004; Reichert & Buchholz, 2006; Sánchez et al., 2005). The objective of ecological monitoring is generally to collect and analyse information about the state of a system and its significant change in time and space related to natural fluctuations or man-induced impacts on the system. The species composition is a well suited medium for ecological monitoring and is an appropriate indicator for the status of the whole rocky shore community or ecosystem (e.g. de Kluijver, 1993; Hartnoll & Hawkins, 1980; Lewis, 1976). The limited locomotory potential, or fully sessile lifestyle, prevents the organisms to avoid short-term disturbances (e.g. desiccation, frost and toxic algal blooms) or long-term changes in the marine environment related to climate change. Furthermore, rocky shore communities are usually well accessible, are clearly arranged due to their overall two-dimensional nature, and exhibit lesser taxonomic problems than other ecosystems.

In order to use rocky shore communities for ecological monitoring at a specific site, an exhaustive description of communities is a prerequisite (e.g. Boaventura et al. 2002; Hansen & Ingólfson, 1993; Meijer & Waardenburg, 1994). To describe communities as a whole, including both algae and invertebrates, and evaluate the abundance of species in those communities in a reproducible way, cluster analysis in combination with inverse analysis is a powerful tool (de Kluijver, 1991, 1993; de Kluijver & Leewis, 1994; Kaandorp, 1986). With this analysis it is possible to distinguish communities, based on species composition, which is required to identify environmental factors which determine the communities and their distribution. The intertidal communities around Helgoland are located in a pivotal position for ecological monitoring. The island is located in the south-eastern North Sea, where the climate is shifting towards more oceanic conditions generally; in particular there is evidence suggesting that the benthic community composition around the island of Helgoland (German Bight, North Sea) is changing considerably (e.g. Franke & Gutow, 2004; Wiltshire & Manly, 2004). This shift in North Sea climate may be an important factor driving recent changes in species composition. Many species which newly appeared at the island of Helgoland during the past decade are oceanic (southern) species which may be considered as indicators of a warming trend. The rocky shore communities of Helgoland are geographically isolated from other hard-bottom communities located in the North Sea by surrounding soft sediments so that processes of change occur in a focussed way. Species assemblages of the relatively small Helgoland rocky littoral have been studied for more than a century (Harms, 1993). However, all intertidal studies deal with only one particular taxonomic group or are semi-quantitatively described. For instance, a comprehensive review of invertebrate communities in the intertidal of Helgoland was carried out by Janke (1986) and repeated by Reichert & Buchholz (2006), whereas the composition of algae over the past decades was described by Bartsch & Tittley (2004). However, there is no quantitative assessment of communities as a whole, including both algae and invertebrates, at the rocky intertidal of Helgoland.

Accordingly, the specific aim of this work was to quantitatively describe the rocky shore communities at Helgoland. For this purpose, we established line transects in three rocky intertidal locations. By means of cluster and inverse analysis we determined the communities; the distribution patterns of communities were recorded using a differential global positioning system. We used quantitative sampling along line transects (1) to assess the distribution and abundances of the communities and (2) to evaluate the effect of wave exposure as well as tidal height on spatial distribution patterns of these communities at the intertidal locations. With this work we provide recommendations for a monitoring programme of the rocky shore communities at Helgoland.

MATERIAL AND METHODS

Study location and sampling design

The survey was conducted in three intertidal locations at the island of Helgoland, German Bight, North Sea (54° 11´N, 7° 53´E) in summer 2004. The locations were in the northern, western and southern part of the island and were named after their direction. These locations differed in wave exposure. De Kluijver (1991), used standardized gypsum blocks and took their rate of erosion as a measure for exposure, showed that the total amount of water movement was higher at the west site of Helgoland (0.14-0.16 $g \cdot h^{-1}$) than at the north-eastern site (0.14 $g \cdot h^{-1}$) and at the southern site (0.10 $g \cdot h^{-1}$). In shallow places at the west site the erosion rates reached 0.28 $g \cdot h^{-1}$ during westerly winds (force 4-5). The prevailing winds around Helgoland are westerly (de Kluijver, 1991; see Fig. 1). Therefore, we defined the western intertidal as exposed, the northern intertidal as semi-exposed and the southern intertidal as sheltered location. The geo-morphological structure of the northern location is characterized by a series of channels (mean height: ca. -1.00 m refer to the height Normal Null (NN) of the German height reference system; width: ca. 3-5 m) which extend to the northwest towards the open sea, and are separated by ridges (mean height to NN: ca. -0.60 m; width: ca. 5-15 m). The ridges and channels showed an alternating pattern along the shore.

The western location shows similar heights and widths of channels (mean height to NN: ca. -1.50 m; width: ca. 2-20 m) and ridges (mean height to NN: ca. -1.00 m; width: ca. 5-25 m) as the northern location, but the geo-morphological features are more irregular. The ridges form rather discrete patches enclosed by channels which also submerged during low tide. The southern location resulted from the construction of piers of the southern harbour in 1936. The southern location was made of concrete, whereas in the northern and western location natural red sandstone prevails.

At the northern and western location two line transects were established, whereas at the southern location only one line transect was sampled as this location was smaller than the other two location (see Fig. 1). Each line transect per location - comparable in terms of type and slope of the substratum - was selected at random from a set of possible line transects. At the northern location, one line transect was 120 metres, the other 40 m long. At the western location, the length of the line transects were 20 and 6 metres respectively. The line transect at the southern location was 5 metres long. The length of the line transects selected depended on the extension and exposure to wave action at each location. Each line transect was sampled in total length by adjoining 0.25 m² quadrats. The characteristic geo-morphological structures, present at each location, were represented by the line transects established.

The position of every fifth quadrat was recorded using a differential global positioning system (Geo XT, Trimble, Germany) with a mean accuracy of 1-2 m in the field (Hennig, 2004). The positions of the remaining quadrats were determined by recording their distance in situ, *x* and *y* spatial coordinates, in relation to the georeferenced quadrat. The coordinates taken were processed with the programme ArcGIS 9.0 (ESRI).

Site Map

Figure 1 was created on the basis of georeferenced black & white (b/w) orthophotos supplied by the Department of Geomatics of the HafenCity University Hamburg, Germany. The orthophotos were generated on a digital photogrammetric workstation DPW770 from BAE Systems (using SOCET Set software) with a ground sampling distance of 10 cm per pixel using aerial images with a photo scale of 1: 7000 which were acquired on May 26th, 2001 by WESER Bildmessflug GmbH in Bremerhaven, Germany for the Landesvermessungsamt Schleswig-Holstein in Kiel, Germany. The digital aerial images were scanned with a resolution of 14 micron which corresponds to a pixel size of 10 cm on the ground, by the Landesvermessungsamt using a geometrically stable photogrammetric scanner SCAI from Zeiss. Subsequently, the images were transformed from central projection into orthogonal projection by differential rectification using the orientation data of each related image and a digital elevation model (DEM) which covers the northern and western intertidal location according to the methods described in Kersten & O'Sullivan (1996).

The DEM of the b/w 1:7000 aerial images was generated by automatic digital image correlation on the DPW770 with grid spacing of 50 cm for the northern and western intertidal location, but not for the southern location. The image correlation algorithm used is described by Zhang & Miller (1997). Empirical accuracy investigations of the automatically generated intertidal DEM showed that the height points of the DEM have a standard deviation of ±18 cm compared to 180 check points which were measured by geodetic methods using a Leica total station TCRA 1105. The maximum and minimum values of the height differences were 40 cm and -79 cm compared to the reference values (Lehmann, 2006). The DEM refers to the height Normal Null (NN) of the German height reference system (DHHN).

Survey methods

In general, the communities comprised three different structural layers: top, middle and encrusting layer. The top layer (TL) usually consisted of thalli of large brown algae (e.g. *Fucus* spp., *Laminaria* spp.). The middle layer (ML) was represented by epiphytic, epizoic and endozoic species growing erect from the substrate, but not reaching the top layer (e.g. hydrozoans, mussels, tube-building polychaetes). The encrusting layer (EL) was formed by epilithic organisms adhering directly to the substratum, such as bryozoans or encrusting algae of the genus *Phymatolithon* or *Ralfsia* (see also de Kluijver, 1991, 1993, 1997).

In each structural layer the abundance of all sessile and slow moving invertebrates as well as algae were assessed by percentage cover of the vertical projection of all species. Species of which the taxonomic position is tentative, were combined to a complex. 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 (see Reichert & Buchholz, 2006 for some examples).

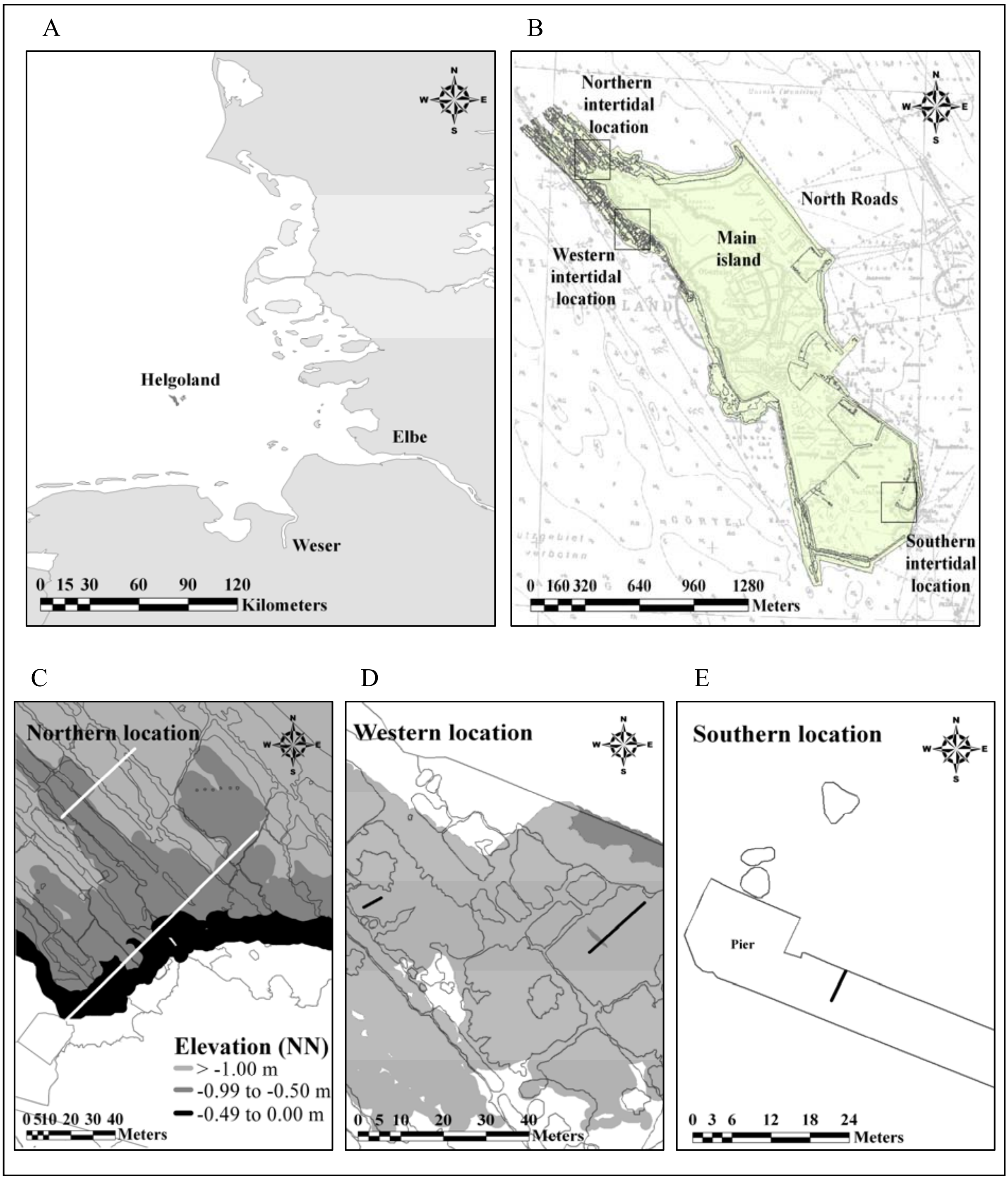

Figure 1 (A) Location of Helgoland in the German Bight, North Sea; (B) the island with the northern, western and southern intertidal location; the line transects at the (C) northern location, (D) western location and (E) southern location. The northern and western location is shown with contours of the surface morphology and the elevation in metres refers to the height Normal Null (NN) of the German height reference system.

Data analyses

Community analysis

First, we used cluster analysis to define communities in the three intertidal locations. This analysis was carried out on the abundance of all sessile and hemi-sessile algae and invertebrates of the sampled quadrats; in total 94 variables and 377 cases were analysed. The classification method based on logarithmically transformed data used the Bray-Curtis similarity index and the average linkage method for clustering was applied. For the distinction of communities, the variable stopping rule was used, as it allowed differences in the mosaic species composition in different communities (de Kluijver, 1997). For cluster analysis the programme PRIMER 5 was used.

Subsequently, we used inverse analysis to obtain information on the species composition of the communities. The abundance distribution of species over the communities was calculated. We distinguished between characteristic and dominant species; characteristic species were defined as those (1) present in at least 67 % of the quadrats sampled in the community and (2) occurred in just one community with 4 % cover or more. Dominant species were defined as those present in at least 67 % of the quadrats sampled in the community, but occurred in more than one community with 4 % cover or more.

Characteristic and dominant species as well as species which did not met our definition of characteristic and dominant species, but also occur in one or more communities, were listed in Table 1. The sequence of species in Table 1 based on the dendrogram (Fig. 2): (1) The community which combined with the remaining communities at the lowest similarity (community-X) was considered first, followed by that community combined at the second-lowest similarity with the remaining communities (community-XX), etc. (2) Those species occurred in community-X and at least one other community were listed first, followed by those species restricted to community-X; then, those species that occurred in community-XX and at least one other community were listed, followed by those species restricted to community-XX, etc.

Communities related to environmental factors

We evaluated if wave exposure as well as tidal height constrained the occurrence of communities at the locations. For the relationship between wave exposure and distribution of communities we calculated and compared the relative occurrence of communities at the semi-exposed northern, exposed western and sheltered southern location.

For the relationship between tidal height and species composition of communities we calculated the relative occurrence of communities per tidal height at the northern and western location. We extracted the tidal height for each georeferenced quadrat at the northern and western location from the prevailing intertidal digital elevation model with the programme ArcGIS 9.0 (ESRI). Thereafter, we assigned the community of each quadrat to one of three categories of tidal height: (1) 0 to -0.49 cm, (2) -0.5 to -0.99 cm and (3) -1 to -1.49 cm refer to the height Normal Null (NN) of the German height reference system. We defined the categories as the high, mid and low intertidal, respectively. For the quadrats in the southern location no intertidal digital elevation model was available and consequently, those communities could not be assigned to any categories of tidal height.

Classification of communities

Based on the community analysis and the relationship between the community patterns and the patterns of the environmental factors, we classified the communities by names, which were labelled with roman numerals up to this point. For the classification we combined species composition of the communities and the environmental factors which may be determined their distribution (wave exposure, tidal height on the shore, substratum type). We used (1) characteristic and (2) dominant species restricted to a specific community, except of species which occurred visually abundant less than two sampling seasons due to strong seasonality. Community-III was a further exception; here, we added additionally one dominant species which was not restricted to this community. The short names of the communities were defined by one of those species. The selected species was conspicuous at first glance due to its size and/or its non-patchy distribution pattern.

RESULTS

In the dendrogram six main clusters of quadrats were distinguished (Fig. 2). The first three clusters (I, II, III) consisted of 88 (cluster I) up to 144 sampled quadrats (cluster III), whereas cluster IV, V and VI related to eleven quadrats (cluster V) or less. Cluster VI already combined at a similarity of about 10 % with the other clusters, followed by cluster I which was combined with the remaining clusters (II – V) at 20 % similarity. Cluster II and III showed a similarity of about 50 %. The six meaningful clusters were regarded as intertidal communities which are described in the following.

Species composition of communities

First, species were mentioned which were dominant in several communities. Then, communities were described on the basis of (1) characteristic species and (2) dominant species restricted to a specific community.

Species, dominant in several communities, were the brown alga *Fucus serratus*, the red algae *Phymatolithon lenormandii* and *Chondrus crispus* as well as the green alga *Cladophora rupestris* (Tab. 1). *F. serratus*, *P. lenormandii* and *C. crispus* were dominant in community-II to -V, while in community-IV and -V *C. rupestris* occurred as dominant species.

Community-VI was characterised by species of Thoracica, the green alga *Blidingia minima*, the brown alga *Fucus spiralis* and species of the genus *Porphyra* (Tab. 1). In community-I species of the genus *Ulva* were characteristic. In community-V the red alga *Rhodothamniella floridula*, the seasonal green alga *Spongomorpha arcta* and tube-building polychaetes were characteristic and the green alga *Ulva lactuca* was only dominant in community-V. Community-IV was characterised by the encrusting bryozoan *Cryptosula pallasiana* and the hydrozoan *Dynamena pumila*; the large brown alga *Ascophyllum nodosum* was the dominant species restricted to community-IV. For community-III, the red alga *Corallina officinalis* was the characteristic species. Community-II was characterised by the seasonal green algae *Rhizoclonium tortuosum*, the blue mussel *Mytilus edulis* and the periwinkle *Littorina littorea*; the dominant species restricted to community-II was the encrusting brown alga *Ralfsia verrucosa*.

The highest mean percentage cover of bare substrate occurred with about 33 % in community-I and only 2.6 % of the substrate was un-colonized in community-IV. The total number of species was highest in community-III (21 algae and 39 invertebrates), whereas in community-VI only 11 species appeared (Tab. 1).

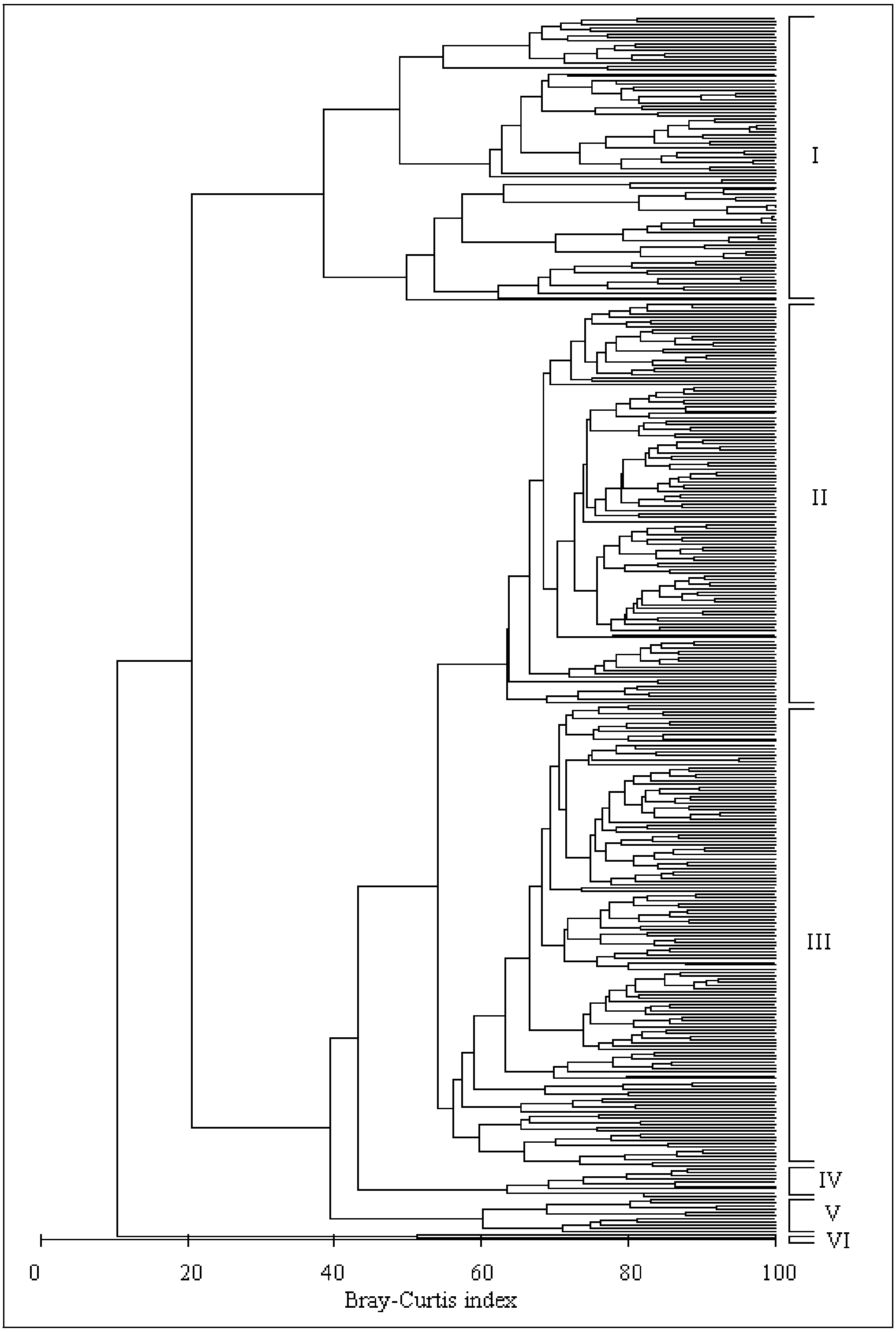

Figure 2 Dendrogram of line transects surveyed in the northern, western and southern location which resulted from cluster analysis. Clusters distinguished are marked I-VI.

Table 1 Values show mean percentage cover of species within community-I to -VI. Bold printed values indicate a presence level of at least 67 % of a certain species within the community. Characteristic species and dominant species restricted to a certain community are grey underlay. Mean percentage cover of bare rock in community-I to -VI and total species richness is additionally shown. Species above the double line show characteristic or dominant species; species below the double line are species do not meet our definition of characteristic and dominant species, but also occur in one or more communities.

Abbreviations in front of species names indicate as follows: EL: encrusting layer; TL: top layer. Abbreviations in brackets indicate higher taxonomic groups as follows: Ch: Chlorophyceae; Ph: Phaeophyceae; Rh: Rhodophyceae; Sp: sponges; Cn: cnidarians; Po: polyplacophorans; Ga: gastropods; Bi: bivalves; An: annelids; Cr: crustaceans; Br: bryozoans; Ec: echinoderms; Tu: tunicates.

	I	II	III	IV	V	VI
Thoracica (Cr)	0.01	**0.75**	0.29	**0.86**	0.00	**20.00**
Blidingia minima (Ch)	0.00	0.00	0.00	0.00	0.00	**17.00**
Fucus spiralis (Ph)	0.86	0.26	0.00	1.43	0.00	**15.00**
Porphyra spp. (Rh)	0.01	0.00	0.00	0.00	0.00	**5.25**
Ulva spp. (Chloro)	**59.24**	0.58	0.02	0.14	**3.77**	**1.25**
Fucus serratus (Ph)	14.03	**34.90**	**79.67**	**79.71**	**26.36**	0.00
EL-*Phymatolithon lenormandii* (Rh)	0.60	**24.28**	**34.06**	**40.71**	**9.32**	0.00
Chondrus crispus (Rh)	0.53	**20.13**	**15.59**	**6.36**	**13.00**	0.00
Cladophora rupestris (Ch)	0.08	0.58	**2.92**	**26.71**	**16.59**	20.00
Rhodothamniella floridula (Rh)	0.03	0.01	0.00	**2.79**	**16.55**	2.50
Spongomorpha arcta (Ch)	0.05	0.00	0.00	0.00	**10.27**	0.00
tubicolous organisms (An/Cr)	**0.80**	**0.56**	**0.54**	0.29	**4.91**	0.00
Ulva lactuca (Ch)	4.06	0.35	2.38	0.14	**27.18**	0.00
EL-*Cryptosula pallasiana* (Br)	0.00	0.01	0.26	**15.86**	0.00	0.00
Dynamena pumila (Cn)	0.00	0.08	**0.66**	**4.14**	0.18	1.00
Ascophyllum nodosum (Ph)	0.00	0.00	0.00	**44.93**	0.00	30.00
Corallina officinalis (Rh)	0.01	0.56	**7.67**	0.00	3.67	0.00
Rhizoclonium tortuosum (Ch)	0.22	**21.50**	0.73	0.00	0.00	0.00
Mytilus edulis (Bi)	0.04	**5.91**	1.20	0.14	0.05	0.00
Littorina littorea (Ga)	0.19	**5.68**	**0.97**	0.00	0.09	0.00
EL-*Ralfsia verrucosa* (Ph)	4.03	**16.85**	1.00	0.00	0.05	0.00
Sphacelaria radicans/rigidula complex (Ph)	0.26	0.00	0.00	0.00	0.45	2.50
Aglaothamnion hookeri (Rh)	0.00	0.00	0.00	0.00	0.00	7.50
Spirorbidae (An)	0.01	**0.42**	**1.87**	**0.50**	**0.32**	0.00
Littorina mariae/obtusata complex (Ga)	0.20	**0.50**	**0.53**	0.14	0.27	0.00
Cladophora sericea (Ch)	0.13	**3.94**	0.19	0.00	0.00	0.00
Gibbula cineraria (Ga)	0.02	0.35	**0.51**	0.00	0.18	0.00
Actiniaria (Cn)	0.07	0.28	0.25	**0.43**	0.00	0.00
Cladostephus spongiosus (Ph)	0.07	0.08	0.00	0.29	**1.59**	0.00
Mastocarpus stellatus (Rh)	0.06	4.32	4.06	0.00	1.36	0.00
Fucus vesiculosus (Ph)	1.32	5.68	0.54	3.57	0.00	0.00
Lepidochitona cinerea (Po)	0.01	0.04	0.01	0.00	0.00	0.00
Ectocarpaceae (Ph)	0.23	0.00	0.02	0.00	0.00	0.00
Lacuna vincta (Ga)	0.02	0.13	0.21	0.00	0.05	0.00
Laomedea flexuosa (Cn)	0.03	0.31	0.23	0.36	0.00	0.00
Elachista fucicola (Ph)	0.03	0.65	0.00	0.21	0.00	0.00
Coryne pusilla (Cn)	0.01	0.00	0.00	0.29	0.00	0.00
Sagartia troglodytes (Cn)	0.01	0.04	0.00	0.00	0.00	0.00
Porphyra umbilicalis (Rh)	0.10	0.00	0.00	0.00	0.00	0.00

Table 1 *(contd.)*

	I	II	III	IV	V	VI
Ceramium rubrum (Rh)	0.00	0.02	0.98	0.00	**2.41**	0.00
EL-*Electra pilosa* (Br)	0.00	0.00	0.39	**2.71**	0.27	0.00
Electra pilosa (Br)	0.00	0.00	0.31	**1.21**	0.18	0.00
TL-*Sargassum muticum* (Ph)	0.00	0.00	2.90	0.00	5.09	0.00
TL-*Laminaria digitata* (Ph)	0.00	0.00	0.24	0.00	3.82	0.00
EL-*Hildenbrandia rubra* (Rh)	0.00	0.67	2.71	0.00	0.41	0.00
Leucosolenia botryoides (Sp)	0.00	0.04	0.23	0.29	0.55	0.00
Flustrellidra hispida (Br)	0.00	0.00	0.06	0.00	0.18	0.00
Plumaria plumosa (Rh)	0.00	0.00	0.00	0.21	0.18	0.00
EL-*Flustrellidra hispida* (Br)	0.00	0.00	0.03	0.00	0.09	0.00
Dumontia contorta (Rh)	0.00	0.08	0.11	0.00	0.05	0.00
Nucella lapillus (Ga)	0.00	0.00	0.02	0.00	0.05	0.00
Elysia viridis (Ga)	0.00	0.04	0.01	0.00	0.05	0.00
Sagartiogeton undatus (Cn)	0.00	0.02	0.02	0.21	0.05	0.00
Codium fragile (Ch)	0.00	0.00	0.00	0.00	0.09	0.00
Pholas dactylus (Bi)	0.00	0.00	0.01	0.00	0.05	0.00
Obelia dichotoma (Cn)	0.00	0.00	0.00	0.00	0.05	0.00
EL-*Alcyonidium gelatinosum/mytili* complex (Br)	0.00	0.00	0.10	0.21	0.00	0.00
Ahnfeltia plicata (Rh)	0.00	0.00	0.01	0.29	0.00	0.00
Chaetomorpha aerea (Ch)	0.00	0.00	0.00	**1.00**	0.00	0.00
Erythrodermis traillii (Rh)	0.00	0.00	0.00	0.43	0.00	0.00
Bowerbankia imbricata (Br)	0.00	0.00	0.00	0.36	0.00	0.00
Crassostrea gigas (Bi)	0.00	0.00	0.00	0.07	0.00	0.00
Rissoa parva (Ga)	0.00	0.08	0.12	0.00	0.00	0.00
Amphipholis squamata (Ec)	0.00	0.03	0.04	0.00	0.00	0.00
EL-*Botryllus schlosseri* (Tu)	0.00	0.02	0.03	0.00	0.00	0.00
Sidnyum turbinatum (Tu)	0.00	0.01	0.12	0.00	0.00	0.00
Lanice conchilega (An)	0.00	0.13	0.02	0.00	0.00	0.00
EL-*Halichondria panicea* (Sp)	0.00	0.00	0.10	0.00	0.00	0.00
Botryllus schlosseri (Tu)	0.00	0.00	0.10	0.00	0.00	0.00
Polysiphonia fucoides (Rh)	0.00	0.00	0.08	0.00	0.00	0.00
Clavelina lepadiformis (Tu)	0.00	0.00	0.06	0.00	0.00	0.00
Alcyonidium gelatinosum/mytili complex (Br)	0.00	0.00	0.06	0.00	0.00	0.00
Didemnum maculosum (Tu)	0.00	0.00	0.03	0.00	0.00	0.00
Kirchenpaueria pinnata/similis complex (Cn)	0.00	0.00	0.02	0.00	0.00	0.00
EL-*Didemnum maculosum* (Tu)	0.00	0.00	0.02	0.00	0.00	0.00
Buccinum undatum (Ga)	0.00	0.00	0.01	0.00	0.00	0.00
Cystoclonium purpureum (Rh)	0.00	0.00	0.01	0.00	0.00	0.00
Onoba aculeus (Ga)	0.00	0.00	0.01	0.00	0.00	0.00
Molgula complanata (Tu)	0.00	0.00	0.01	0.00	0.00	0.00
Asterias rubens (Ec)	0.00	0.00	0.01	0.00	0.00	0.00
Littorina saxatilis complex (Ga)	0.00	0.02	0.00	0.00	0.00	0.00
Crepidula fornicata (Ga)	0.00	0.01	0.00	0.00	0.00	0.00
Porphyra leucosticta (Rh)	0.00	0.01	0.00	0.00	0.00	0.00
EL-bare rock/sediment	32.63	22.06	20.10	2.57	17.73	25.00
Total species richness	34	44	60	32	37	11

Communities related to environmental factors

The semi-exposed northern location was characterised by community-I, -II and -III (Fig. 3), and followed by a zonation with (1) community-I at the high intertidal, (2) community-II and -III at the mid intertidal and (3) community-III at the low intertidal (Fig. 4a). The exposed western location was characterised by community-I, -III and –V, whereas community-IV and -VI characterised the sheltered southern location (Fig. 3). In the western location community-I and -V only occurred at the low intertidal, while community-III also occurred with < 20 % at the mid intertidal (Fig. 4b).

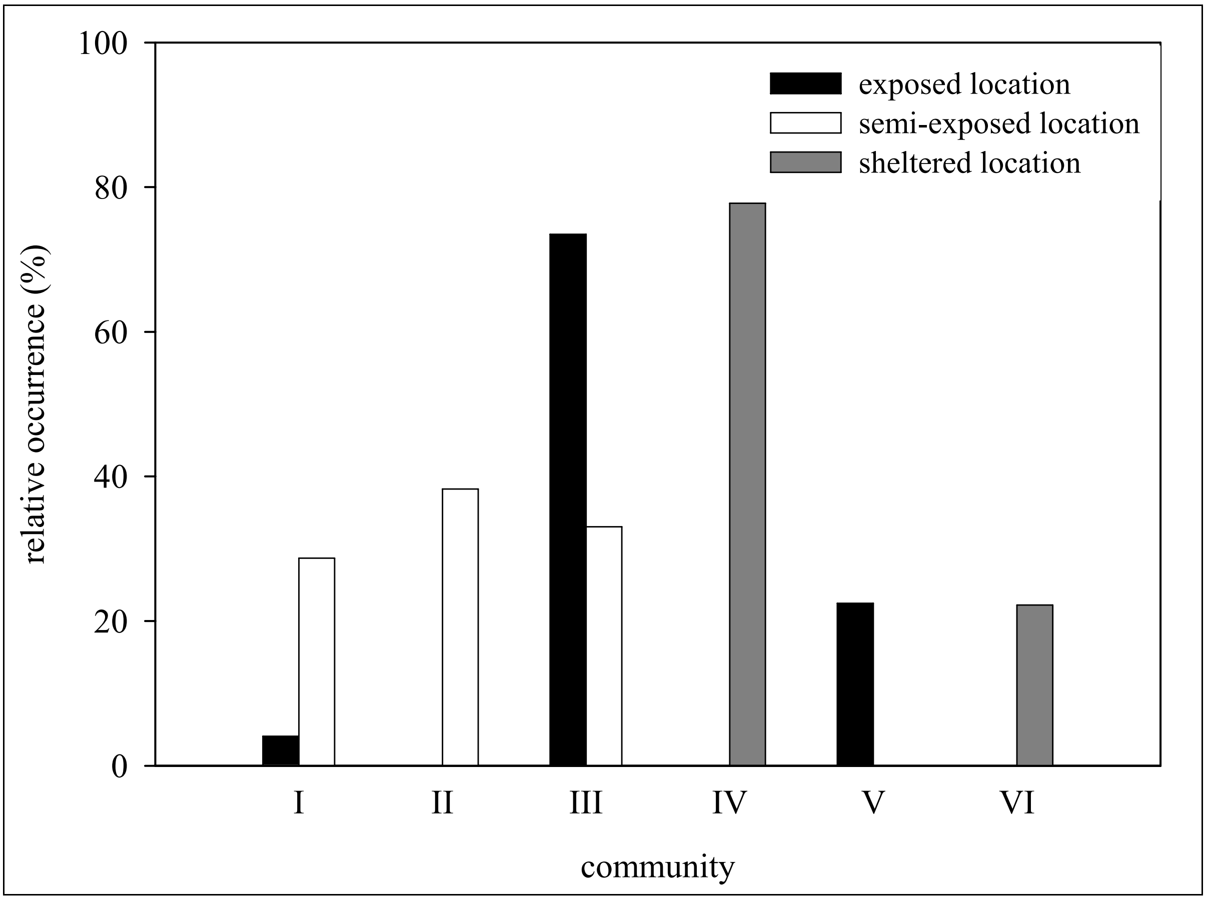

Figure 3 Relative occurrence of community-I to -VI at the exposed, semi-exposed and sheltered intertidal location.

Classification of communities

Community-I was classified as the *Ulva* spp. community which occurred mostly at the high-shore of the semi-exposed northern location (Tab. 2). Community-II was named after the main occurrence of *Mytilus edulis* - *Littorina littorea* - *Ralfsia verrucosa* at the mid-shore of the semi-exposed northern location. Community-III was classified as the *Corallina officinalis* - *Fucus serratus* community which occurred at the mid- and low-shore of the exposed western and semi-exposed northern location. Community-VI was named after the restricted occurrence of *Cryptosula pallasiana* - *Dynamena pumila* - *Ascophyllum nodosum* to horizontal sites of the harbour pier at the sheltered southern location. Community-V was classified as the *Rhodothamniella floridula* - tube-building polychaetes - *Ulva lactuca* community restricted at the low-shore of the western and northern location, and community-VI was named after the restricted occurrence of *Balanus* spp. - *Fucus spiralis* - *Porphyra* spp. to vertical sea walls at the sheltered southern location.

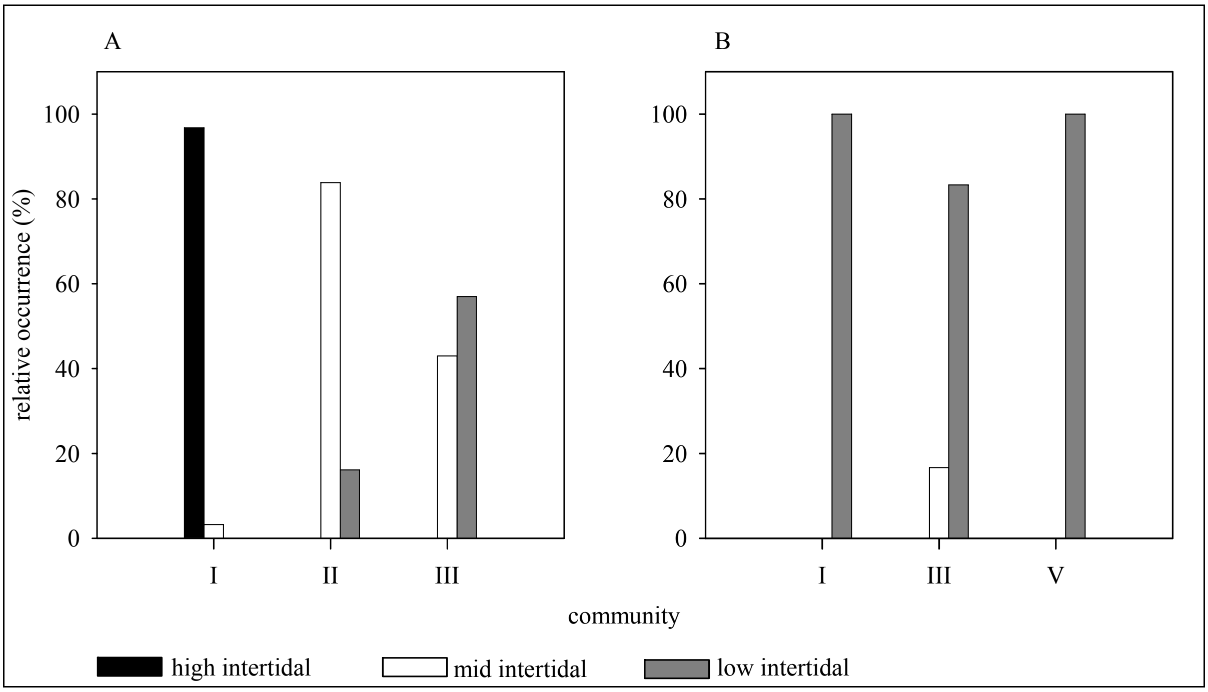

Figure 4 Relative occurrence of the communities at the high, mid and low intertidal zone of the (A) semi-exposed location and (B) exposed location.

Table 2 The communities based on the cluster analysis labelled with roman numerals, the location features (exposure of the shore; vertical zone) and the classified communities based on the inverse analysis; these communities were named after characteristic and dominant species restricted to a specific community (short names of the communities in bold). The last column showed the biotope name according to Bartsch & Tittley (2004).

Community based on cluster analysis	Location features		Community based on inverse analysis	Biotope name according to Bartsch & Tittley (2004)
	Exposure	Zone		
Community-I	Semi-exposed	High intertidal	***Ulva*** spp.	*Enteromorpha* spp. on freshwater-influenced and/or unstable upper eulittoral rock
Community-II	Semi-exposed	Mid intertidal	***Mytilus*** *edulis* - *Littorina littorea* - *Ralfsia verrucosa*	*Mytilus edulis* and *Fucus vesiculosus* on moderately exposed mid eulittoral rock
Community-III	Semi-exposed to exposed	Mid to low intertidal	*Corallina officinalis* - ***Fucus*** *serratus*	- *Corallina officinalis*, coralline crusts and brown seaweeds in shallow eulittoral rockpools - Dense *Fucus serratus* on moderately exposed to very sheltered full salinity lower eulittoral rock - *Fucus serratus* and red seaweeds on moderately exposed lower eulittoral rock - *Mastocarpus stellatus* and *Chondrus crispus* on very exposed to moderately exposed lower eulittoral rock
Community-IV	Sheltered	Mid to low intertidal (horizontal)	*Cryptosula pallasiana* - *Dynamena pumila* - ***Ascophyllum*** *nodosum*	*Ascophyllum nodosum* on very sheltered mid eulittoral rock
Community-V	Semi-exposed to exposed	Low intertidal	***Rhodothamniella*** *floridula* - tube-building polychaetes - *Ulva lactuca*	*Rhodothamniella floridula* on sand-scoured lower eulittoral rock
Community-VI	Sheltered	High intertidal (vertical)	***Balanus*** spp. - *Fucus spiralis* - *Porphyra* spp.	*Semibalanus balanoides*, *Patella vulgata* and *Littorina* spp. on exposed to moderately exposed or vertical sheltered eulittoral rock

DISCUSSION

The present study provided quantitative information on species composition and their association with environmental factors at three study locations at Helgoland. In total six intertidal communities were defined. The information obtained from the present study has clarified and set a base line with regard to (1) the distribution and abundances of the communities and (2) the effect of wave exposure and tidal height on these communities. Firstly, we take up the discussion about the community concept and explain how we used the definition of communities in the present study. Then, we discuss the distribution of the defined communities in terms of wave exposure and tidal height or possible further regulation factors, and suggestions for a future monitoring are given.

Two main lines of thought have evolved in various forms to attempt to understand the distribution patterns of marine benthic alga and invertebrate assemblages: the “level bottom” and the “zonation” approach (Erwin, 1983). An early attempt to classify the marine benthos communities according to the “level bottom” approach was carried out by Petersen (1914). He characterised the benthic communities by dominant species and related those to water depth and sediment structure. Parallel to the level bottom approach, the “zonation” approach was developed which has often been applied in the intertidal (Erwin, 1984). This school of thought has its origin in the observations of distinct bands of intertidal algae and invertebrates and relates the assemblages to a physical gradient or to a series of physical gradients which may or may not overlap (Lewis, 1978; Stephenson & Stephenson, 1949, 1972). In the “zonation” approach the bands or zones evident are not due to different species assemblages having same starting and end points in their occurrence, which are related to physical gradients. The zone is usually characterised by one or at most a few species, which in some way make themselves obvious (Erwin, 1984). Since other species occurred in the same zone led to “zone, species assemblages” as constant entities. Thus, for ecological monitoring, i.e. a survey systematically undertaken to provide an observation series in time, the definition of communities according to the “zonation” approach with relative constant entities of species is preferable. Ecological monitoring, which is under way at the Helgoland intertidal, aims at a comparison in time which is based on the similarity between entities of species. Therefore, our definition of communities used here is: a directly or indirectly interacting assemblage of algae and invertebrates which remains stable in time under a given set of abiotic factors. This classification allows to recognize different intertidal communities and to identify changes within its elements (de Kluijver, 1997). In this concept, biotic interactions are not negated, but compared to the regulation by the physical environment they are considered of minor importance. To test such assumptions, the next step may be seen in manipulative experiments aiming at clarifying if the communities defined have similar preferences for a certain set of abiotic conditions or if they are predominantly structured by biological interactions.

When we considered the different exposed intertidal locations, we concentrated on those communities which only occurred to one of the study locations, since this implies that wave exposure is a potential regulating factor for the distribution observed. The occurrence of the *Balanus*- and the *Ascophyllum*-community was restricted to the sheltered location, and both communities distinguished from all other communities by stands of the large brown alga *Ascophyllum nodosum*. The restricted occurrence of *Ascophyllum nodosum* to sheltered harbour walls was in agreement with the biotope classification by Bartsch & Tittley (2004). They identified records of *A. nodosum* in the south harbour as a biotope complex of dense fucoids on sheltered littoral fringe and littoral rock. The restricted occurrence of abundant stands of *A. nodosum* to the southern study location suggests that the settlement and recruitment success of *A. nodosum* may be enhanced by sheltered situations. Experiments by Vadas et al. (1990) showed that wave action is a major source of mortality to recently settled zygotes of *A. nodosum*, underlining the latter conclusion. Moreover, the restricted occurrence of the dense stands of *A. nodosum* can also be a direct result of substratum type. At the southern location, the harbour walls made of concrete, while at the northern and western study locations mainly red sandstone appears. However several studies showed that *A. nodosum* also occurred abundantly on granite, limestone, basalt (Dudgeon & Petraitis, 2001; Hartnoll & Hawkins, 1985; Lindegarth et al., 2001). It therefore seems unlikely that the factor substratum type was important for the restricted occurrence of the *A. nodosum*-community at the southern location.

Just as the communities showing a restricted occurrence to the sheltered location, there was the *Mytilus*-community which only occurred at the semi-exposed location. The restriction of the *Mytilus*-community to the semi-exposed northern rock-platform at Helgoland agreed with the biotope classification by Bartsch & Tittley (2004). However, on other rocky coasts the blue mussel *Mytilus edulis* are widely distributed, from sheltered to exposed areas (Dudgeon & Petraitis, 2001; Janke, 1990; Lintas & Seed, 1994). Therefore, the occurrence of the *Mytilus*-community seems not to be associated with the factor wave exposure, but may rather be a result of biotic factors, such as grazing and competition for space (Janke, 1990). The occurrence of the characteristic mussel patches seem to be related to a very high local abundance of the periwinkle *L. littorea* which additionally reaches considerable heights at

Helgoland, in contrast to specimens on other European shores (personal observation). The increased grazing of littorinids may have prevented the establishment of dense stands of macroalgae, particularly *Fucus* species, and thus in turn favoured the establishment of mussels which compete with macroalgae for space. Similar effects of biotic interactions on distribution patterns were shown in several studies on population dynamics in rocky shore communities (e.g. Lubchenco, 1983; Menge, 1976; Menge & Sutherland, 1976).

Besides the communities which were restricted to the sheltered and semi-exposed location, we also found the *Rhodothamniella*-community which only occurred at the exposed western rock-platform. However observations showed that the *Rhodothamniella*-community also occurred at the semi-exposed northern rock-platform, but was not recorded by the established line transects. This observation agreed with the biotope classification by Bartsch & Tittley (2004). They identified records of the cushion-forming *Rhodothamniella floridula* as a biotope at moderate energy eulittoral rock.

As a further step, next to the potential causes for the variation in communities among the three locations, we compared the distribution patterns of the communities at a smaller spatial scale, across the rock-platform of the northern and western location. Changes in communities at the northern location are related to variations in tidal height. A high-, mid- and low-intertidal was found consisting of distinct vertical bands of specific communities: the *Ulva*-community at high-shore, the *Mytilus*-community at mid-shore and the *Fucus*-community at low-shore. Such distinct patterns of vertical zonation with different composition of species in the high, mid and low intertidal were already reported semi-quantitatively for invertebrates (Janke, 1986; Reichert & Buchholz, 2006) and for macroalgae (Bartsch & Tittley, 2004) across the northern rock-platform at Helgoland. Accordingly, the occurrence of the different communities at different intertidal heights was to be expected. However, this structuring into spatial zonation patterns relating to tidal height, was only observed at the northern location. At the western location the tidal height does not vary much; only two categories of tidal height, the mid and low intertidal, occurred. Due to the construction of the seawall along the western part of the island, the extension of the natural rock-platform of the intertidal was reduced and results in the lack of typical high-shore assemblages at the western location. Moreover, the mid and low intertidal was not dominated by zonal communities which differed in species composition: the western intertidal was mainly distinguished by the *Fucus*-community characterised by *Coralina officinalis* and dominated by *Fucus serratus* and red algae (e.g. *Phymatolithon lenormandii*, *Chondrus crispus*). This may suggest that in the western location different alga and invertebrate assemblages are mainly distributed in patches within zones and may be termed a mosaic community (Menge et al., 1993). In recent years, it has been realized that most intertidal algae and invertebrates are distributed extremely patchy within any height on rocky shores (Aberg & Pavia, 1997; Benedetti-Cecchi, 2001; Chapman, 2002; Fraschetti et al., 2005). Dependent on the geo-morphological structures of rocky shores a variety of pools, crevices and cracks results in diverse small-scale variation in physical conditions (e.g. micro-hydrodynamic or micro-climate changes) and therefore in small-scale variation of behavioural responses. The occurrence of patchy distributed species assemblages, next to typical zonation patterns may also be assumed for the Helgoland intertidal, and thus should be tested in further studies.

For providing an improved sampling design for a monitoring at Helgoland, we suggest that this design should incorporate a variety of the communities classified here. Focusing on a single community only, at this state of knowledge would possibly lead to loss of significant information. If the communities remain stable in time or pass through different stages of succession can not be answered in the present study. The current long-time monitoring is necessary to shed light on the temporal stability of these communities. Moreover, a greater understanding of the scales-dependent distribution patterns is vital to explaining the variation in the intertidal communities at Helgoland. Experimental studies should then be designed to investigate the driving processes causing distribution patterns, their intensities and rates at relevant rather than arbitrary scales.

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REFERENCES

Aberg, P. & Pavia, H., 1997. Temporal and multiple scale spatial variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. *Marine Ecology Progress Series*, **158**, 111-119.

Bartsch, I. & Tittley, I., 2004. The rocky intertidal biotopes of Helgoland: present and past. *Helgoland Marine Research*, **58**, 289-302.

Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Marine Ecology Progress Series*, **215**, 79-92.

Boaventura, D., Ré, P., Cancela da Fonseca, L. & Hawkins, S.J., 2002. Intertidal rocky shore communities of the continental Portuguese coast: analysis of distribution patterns. *Marine Ecology*, **23**, 69-90.

Chapman, M.G., 2002. Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. *Austral Ecology*, **27**, 211-228.

De Kluijver, M.J., 1991. Sublittoral hard substrate communities off Helgoland. *Helgoländer Meeresuntersuchungen*, **45**, 317-344.

De Kluijver, M.J., 1993. Sublittoral hard-substratum communities off Orkney and St Abbs (Scotland). *Journal of the Marine Biological Association of the United Kingdom*, **73**, 733-754.

De Kluijver, M.J., 1997. *Sublittoral communities of North Sea hard-substrata*. PhD thesis, University of Amsterdam, Netherlands.

De Kluijver, M.J. & Leewis, R.J., 1994. Changes in the sublittoral hard substrate communities in the Oosterschelde Estuary (SW Netherlands), caused by changes in the environmental parameters. *Hydrobiologia*, **282-283,** 265-280.

Dudgeon, S. & Petraitis, P.S., 2001. Scale-dependent recruitment and divergence of intertidal communities. *Ecology*, **82**, 991-1006.

Erwin, D.G., 1983. The community concept. In *Sublittoral ecology. The ecology of the shallow sublittoral benthos* (ed. R. Earll & D.G. Erwin), pp. 144-164. Oxford: Clarendon Press.

Franke, H.D. & Gutow, L., 2004. Long-term changes in the macro-zoobenthos around the rocky island of Helgoland (German Bight, North Sea). *Helgoland Marine Research*, **58**, 303-310.

Fraschetti, S., Terlizzi, A. & Benedetti-Cecchi, L., 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecology Progress Series*, **296**, 13-29.

Hansen, J.R. & Ingolfsson, A., 1993. Patterns in species composition of rocky shore communities in sub-arctic fjords of eastern Iceland. *Marine Biology*, **117**, 469-481.

Harms, J., 1993. Check list of species (algae, invertebrates and vertebrates) found in the vicinity of the island of Helgoland (North Sea, German Bight) – a review of recent records. *Helgoländer Meeresuntersuchungen*, **47**, 1-34.

Hartnoll, R.G. & Hawkins, S.J., 1980. Monitoring rocky-shore communities: A critical look at spatial and temporal variation. *Helgoländer Meeresuntersuchungen*, **33**, 484-494.

Hartnoll, R.G. & Hawkins, S.J., 1985. Patchiness and fluctuations on moderately exposed shores. *Ophelia*, **24**, 53-64.

Hennig, B., 2004. Applications of hyperspectral remote sensing in coastal ecosystems: a case study from the German North Sea. Diploma thesis, University of Cologne, Germany.

Hiscock, K., Southward, A.J., Tittley, I. & Hawkins, S.J., 2004. Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation*, **14**, 333-362.

Janke, K., 1986. Die Makrofauna und ihre Verteilung im Nordost-Felswatt von Helgoland. *Helgoländer Meeresuntersuchungen*, **40**, 1-55.

Janke, K., 1990. Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). *Helgoländer Meeresuntersuchungen*, **44**, 219-263.

Kaandorp, J.A., 1986. Rocky substrate communities of the infralittoral fringe of the Boulonnais coast, NW France: A quantitative survey. *Marine Biology*, **92**, 255-265.

Kersten, T. & O'Sullivan, W., 1996. Project SWISSPHOTO - Digital orthophotos for the entire area of Switzerland. In Proceedings of the Eighteens International Society for Photogrammetry and Remote Sensing, Vienna, 12-18 July 1996. International Archives of Photogrammetry and Remote Sensing, pp. 186-191.

Lehmann, V., 2006. Empirische Genauigkeitsuntersuchungen digitaler Geländemodelle verschiedener Sensoren auf Helgoland. Diploma thesis, Department Geomatics, HafenCity University Hamburg, Germany.

Lewis, J.R., 1976. Long-term ecological surveillance: practical realities in the rocky littoral *Oceanography and Marine Biology. An Annual Review*, **14**, 371-390.

Lewis, J.R., 1978. *The ecology of rocky shores*. London: Hodder and Stoughton.

Lindegarth, M., Aberg, P., Cervin, G. & Nilsson, P., 2001. Effects of grazing on the structure of mid-shore, intertidal assemblages on moderately exposed shores of the Swedish west coast. *Marine Ecology Progress Series*, **212**, 29-38.

Lintas, C. & Seed, R., 1994. Spatial variation in the fauna associated with *Mytilus edulis* on a wave-exposed rocky shore. *Journal of Molluscan Studies,* **60**, 165-174.

Lubchenco, J., 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology*, **64**, 1116-1123.

Meijer, A.J.M. & Waardenburg, H.W., 1994. Tidal reduction and its effects on intertidal hard-substrate communities in the Oosterschelde Estuary. *Hydrobiologia*, **282-283**, 281-298.

Menge, B.A., 1976. Organization of the new England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs*, **46**, 355-393.

Menge, B.A., Farrell, T.M., Olson, A.M., van Tamelen, P. & Turner, T., 1993. Algal recruitment and the maintenance of a plant mosaic in the low intertidal region on the Oregon coast. *Journal of Experimental Marine Biology and Ecology*, **170**, 91-116.

Menge, B.A. & Sutherland, J.P., 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist*, **110**, 351-369.

Petersen, C.G.J., 1914. Valuation of the sea. II. The animal communities on the sea-bottom and their importance for marine zoogeography. *Reports of the Danish Biological Station*, **21**, 1-44.

Reichert, K. & Buchholz, F., 2006. Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002. *Helgoland Marine Research*, **60**, 213-223.

Sánchez, Í., Fernández, C. & Arrontes, J., 2005. Long-term changes in the structure of intertidal assemblages after invasion by *Sargassum muticum* (Phaeophyta). *Journal of Phycology*, **41**, 942-949.

Stephenson, T.A. & Stephenson, A., 1949. The universal features of zonation between tidemarks on rocky coasts. *Journal of Ecology*, **37**, 289-305.

Stephenson, T.A. & Stephenson, A., 1972. *Life between tidemarks on rocky shores*. San Francisco: Freeman.

Vadas, R.L., Wright, W.A. & Miller, S.T.L., 1990. Recruitment of *Ascophyllum nodosum*: Wave action as a source of mortality. *Marine Ecology Progress Series*, **61**, 263-272.

Wiltshire, K.H. & Manly, B.F.J., 2004. The warming trend at Helgoland Roads, North Sea: phytoplankton response. *Helgoland Marine Research*, **58**, 269-273.

Zhang, B. & Miller, S., 1997. Adaptive automatic terrain extraction. In *Proceedings of the Eleventh SPIE`s International Symposium on AeroSense*, Orlando, Florida, 21-23 April 1997. *Integrating Photogrammetric Techniques with Scene Analysis and Machine Vision* (ed. D.M. McKeown et al.), pp. 27-36.

Scale-dependent patterns of variability in species assemblages of the rocky intertidal at Helgoland (German Bight, North Sea)

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ABSTRACT

At two study locations at the rocky intertidal of the island of Helgoland (German Bight, North Sea) we investigated the variation in intertidal benthic assemblages at two spatial scales and evaluated the relationship between elevation and assemblages at these scales. We also evaluated the scale-dependent patterns of variation in macroalgal richness with species classified as rare, regular or common. We were also interested in using the information to develop a general method of monitoring the benthic communities on Helgoland. Data was taken from five replicates per plot, with plots located in transects (two transects per location).

At the northern location, the highest variability in species richness and total abundance occurred at the scale separated by about 50 metres (scale: transect). This was a direct result of differences between the high- and the low-shore. The species assemblage at high-shore was characterised by relatively low algal and invertebrate cover as well as invertebrate richness in contrast to high values of these variables at low-shore. The total richness and cover responded asymptotically to elevation. At the western location, the most important variation in the assemblages was at the scale of replicates (10s of centimetres apart). No relationship between elevation and species richness or total abundance occurred at this location. For macroalgae, our analysis of species-abundance classes showed that the scale-dependent patterns of variability depended on whether species were rare or common. At the northern location, the relationship between elevation and species-abundance classes depended on whether rare or common algal species were considered. Assemblages at the northern location were more consistent overtime than those at the western location. Our results suggest that the relevant processes shaping the community at the Helgoland intertidal vary between location, time of sampling and according to whether species are rare or common.

The potential causes of variation in total species richness and abundance of macroalgal and invertebrate assemblages at different spatial scales are discussed and suggestions for a future monitoring are given. Temporal inconsistency in the spatial patterns, and the fact that richness of rare and common species vary at different scales speak in favour of a multiple scale sampling design for monitoring change in the intertidal communities at Helgoland.

Keywords

Spatial scales · Variability · Algae · Invertebrates · Species-abundance classes · Elevation · Rocky intertidal · Helgoland · North Sea

INTRODUCTION

Currently, there is a considerable research effort aimed at investigating the variability in rocky shore communities, where a combination of abiotic and biotic factors operate at different spatial scales (e.g. Aberg & Pavia, 1997; Benedetti-Cecchi, 2001; Chapman, 2002; Hyder et al., 1998; Underwood, 1996). These studies have shown that patterns in species assemblages are not scale-independent, indicating that changes in the composition of assemblages are more visible at particular scales than at others. The most general conclusion is that variability at small scales, from centimetres up to 1000s of metres, is at least as high as variability at large scales of distances of several kilometres.

The approach of these studies to the analysis of spatial patterns with reference to the sources of variation investigated can be considered as a novelty in rocky shore ecology. Random sources of variation are examined at a hierarchy of spatial scales and estimates of the contribution of each scale to the total variation among samples allow comparison of variability across these scales (Morrisey et al., 1992; Underwood, 1996). These analyses include a wide range of processes that may be important in structuring rocky shore assemblages, regardless of whether specific models about relevant processes can be suggested or not (Benedetti-Cecchi, 2001). In contrast, an approach used in more traditional studies has evaluated patterns of variation in assemblages along environmental gradients (e.g. Bell et al., 1993; Stephenson & Stephenson, 1949). This approach can bias the analysis towards the most obvious source of variation that generate the specific gradient, while other potentially important, but less evident sources might remain undetected.

Most obvious on rocky coasts in many parts of the world are the spatial zonation patterns of organisms, as distinct vertical bands, in response to the major gradient of emersion (Lewis, 1978; Southward, 1958; Stephenson & Stephenson, 1972). Besides physical factors, biological interactions such as competition (e.g. Connell, 1961; Dayton, 1971), grazing (e.g. Hawkins & Hartnoll, 1983; Jenkins et al., 1999a, b) and predation (e.g. Lubchenco & Menge, 1978; Paine, 1974) are important in maintaining vertical distribution patterns of organisms on rocky shores. However, in recent years, it has been shown that most intertidal algae and invertebrates are distributed extremely patchy at small spatial scales (centimetres to metres) within any height on rocky shores (e.g. Fraschetti et al., 2005; Menconi et al., 1999; Underwood & Chapman, 1996). These complex spatial patterns may be related to small-scale changes in behavioural responses (e.g. Chapman & Underwood, 1994; Underwood & Chapman, 1989), recruitment (e.g. Chapman & Underwood, 1998), the interactive effects of abiotic and biotic factors (Benedetti-Cecchi et al., 2000a) and small-scale changes in physical factors such as slope (Benedetti-Cecchi, 2000), or elevation of the substrate at a standard height within any vertical intertidal zone. The slope of the substrate may explain spatial heterogeneity within any vertical height on the shore, whereas elevation of the substrate remains mostly unquantified. Elevation can be defined as the standard height of any intertidal location, either vertical or horizontal, calculated from a reference point. The fact that elevation remains mostly unquantified may partly be explained by the general lack of continuous measurements of the term "elevation" such as in digital elevation models constructed by e.g. airborne or terrestrial laser scanning.

Moreover, most studies examining patterns of variation of rocky shore assemblages have concentrated on geographic regions in Australia, the Mediterranean or the North Atlantic (e.g. Menconi et al., 1999; Underwood & Chapman, 1998) and have focused on a few species only (e.g. Benedetti-Cecchi et al., 2000b; Jenkins et al., 2000, 2001; Underwood & Chapman, 1996). However, studies examining spatial patterns of species assemblages in the North Sea are rare (Li et al., 1997). Species assemblages of the relatively small Helgoland rocky littoral in the German Bight (North Sea) have been studied for more than a century (Harms, 1993). However, spatial patterns of algal and invertebrate communities in rocky intertidal locations of Helgoland have only been ill defined. There are few intertidal studies which demonstrate an initial attempt to reveal possible temporal variation in the composition of algae and invertebrates over the past decades (Bartsch & Tittley, 2004; Reichert & Buchholz, 2006). However, there is no evidence so far if spatial patterns of the hard-bottom assemblages are dependent on the scale of measurement and if processes operate at one or more spatial scales.

Accordingly, the objective of this work was to investigate the variation in species richness and total abundance at defined spatial scales. Furthermore, we explored the influence of elevation on these species attributes in two rocky intertidal locations of Helgoland, the northern and western location. We examined the variation of algae and invertebrates as well as the relevance of elevation by means of a nested sampling design. Our sampling design included two spatial scales at both study locations: transects separated by 65 and 45 metres as well as plots separated between 5 - 40 and 7 - 10 metres at the northern and western location respectively. We used this sampling design to test the general hypothesis that (1) variation was important at any scale defined and (2) spatial patterns of algae and invertebrates were associated to patterns of elevation. We also used the information on the spatial patterns of algae and invertebrates as well as the patterns of elevation to provide recommendations for a monitoring programme of the rocky intertidal at Helgoland.

MATERIAL AND METHODS

Study locations

This survey was conducted at two intertidal locations at Helgoland, German Bight, North Sea (54° 11´N, 7° 55´E), from summer 2004 until spring 2006 (Fig. 1). The locations were in the northern and western part of the island, and were named after their geographic position. The northern and western intertidal location differed in wave exposure and in the geo-morphological structures of the rock-platform. The substrate was natural red sandstone and the degree of rugosity and hardness was approximately the same at both locations. The difference between mean high water spring (MHWS) and mean low water spring (MLWS) was 2.62 m (Lüning, 1985). De Kluijver (1991), using the rate of erosion of standardized gypsum blocks, showed that the intensity of water movement was higher at the west side of Helgoland (0.14-0.16 $g \cdot h^{-1}$) than at the north-eastern site (0.14 $g \cdot h^{-1}$). In shallow places at the west side the erosion rates reached 0.28 $g \cdot h^{-1}$ during westerly winds (force 4-5). The prevailing winds around Helgoland are westerly (de Kluijver, 1991). Therefore, the western intertidal was defined as the exposed and the northern intertidal as the semi-exposed location.

The geo-morphological structure of the northern location is characterized by a series of channels (mean height: ca. -1.00 m refers to the height Normal Null (NN) of the German height reference system; width: ca. 3-5 m) extending to the northwest towards the open sea, and are separated by ridges (mean height to NN: ca. -0.60 m; width: ca. 5-15 m). The ridges and channels alternated in the alongshore direction. The western location showed a more irregular order of channels (mean height to NN: ca. -1.50 m; width: ca. 2-20 m) and ridges (mean height to NN: ca. -1.00 m; width: ca. 5-25 m). The ridges form discrete patches enclosed by channels which were submerged during low tide.

The species assemblages in the northern location show distinct vertical zones, whereas in the western location such conspicuous bands do not occur (Janke, 1986; K.R. personal observation). Due to the seawall along the western part of the island high-shore assemblages are basically not existent at the rock-platform of the western location. The mid-shore assemblages of the western location are similar to those at low-shore. For the lower intertidal, both shores harbour qualitatively similar algal and invertebrate assemblages. The upper intertidal at the northern location is dominated by green algae of the genus *Ulva*. Most abundant invertebrates are tube-building polychaetes (mostly *Polydora ciliata*, *Fabricia sabella*). The mid-shore is dominated by the large brown alga *Fucus serratus*, encrusting algae (*Ralfsia verrucosa*, *Phymatolithon lenormandii*), the red alga *Chondrus crispus* and the seasonal green alga *Rhizoclonium tortuosum*. Characteristic invertebrates are the blue mussel

Mytilus edulis and the periwinkle *Littorina littorea*. At the lower intertidal, most abundant organisms are the algae *F. serratus*, *P. lenormandii*, *C. crispus* and the articulated coralline *Corallina officinalis* as well as the snails *L. littorea*, *L. mariae/obtusata* (identified as a species complex) and *Gibbula cineraria*, and the Spirorbid polychaetes (mostly *Spirorbis spirorbis*). In addition to these general patterns of distribution, there is a considerable microhabitat variation due to complex geo-morphological structures of the substrate (K.R. personal observation).

Sampling design

At the semi-exposed northern location, two transects (separated by ca. 65 metres) were selected at random from a set of possible transects, comparable in terms of type and slope of the substrate (Fig. 1). Due to the small vertical and horizontal extension of the rock-platform we had to select one transect at high-shore and the other at low-shore. Thus, the distance between transects is measured perpendicular to the island`s shoreline. The length of transects ranged between 25 and 40 metres. Along each transect, six and five plots respectively (separated by 5 - 40 metres) were chosen at random from a larger pool of plots, which were examined in a former study with reference to the community structure. Thus, for each plot the species assemblage was well-known by the results of a previous community analysis (Reichert et al., in prep.). Five replicated quadrats, separated by about one metre, were selected randomly at each plot.

At the exposed western location, two transects (separated by ca. 45 metres) were selected randomly from a set of possible transects, comparable in terms of type and slope of the substrate as well as vertical tidal height (Fig. 1). The length of the transects ranged between 7 and 10 metres. As for the northern location, along each transect plots were selected at random (three and two plots respectively, separated by 4 - 10 metres) from a larger pool of plots examined previously by means of community analysis (Reichert et al., in prep.). Five replicated quadrats (separated by about one metre) were sampled randomly at each plot. For this location we sampled the transects across the vertical axes at low-shore.

The positions of the 1st and 5th replicated quadrat at both study locations were recorded using a differential global positioning system (Geo XT, Trimble, Germany) with a mean accuracy of 1-2 m in the field. The positions of the remaining replicates were determined by recording their distance in situ, in *x* and *y* spatial coordinates, from the georeferenced replicates. The prevailing coordinates were processed with the programme ArcGIS 9.0 (ESRI).

At each study location, all plots (i.e. 55 and 25 quadrats respectively) were sampled at 3-month intervals over 2 years (summer 2004 - spring 2006). All plots at each location were sampled at each 3-month interval within a period of a few days.

The height value of each replicated quadrat was obtained from the digital elevation model, generated for both study locations (see Fig. 1). The height values refer to the height Normal Null (NN) of the German height reference system (hereafter: refer to height NN), and was taken out of the digital elevation model by means of the programme ArcGIS 9.0 (ESRI). At the northern location, the height difference (reference: height NN) was 0.75 m on average between transects, less than 0.40 m at the scale of plot and less than 0.20 m at the scale of replicate. At the western location, the difference was on average 0.10 m between transects and less than 0.30 m between plots and replicates.

Site Map and digital elevation model

Figure 1 was created on the basis of georeferenced black & white (b/w) orthophotos supplied by the Department Geomatics of the HafenCity University Hamburg, Germany. The orthophotos were generated on a digital photogrammetric workstation DPW770 from BAE Systems (using SOCET Set software) with a ground sampling distance of 10 cm per pixel using aerial images with a photo scale of 1: 7000 which were acquired on May 1999 by WESER Bildmessflug GmbH in Bremerhaven for the Landesvermessungsamt Schleswig-Holstein in Kiel. The digital aerial images were scanned with a resolution of 14 micron which corresponds to a pixel size of 10 cm on the ground, by the Landesvermessungsamt using a geometrically stable photogrammetric scanner. Subsequently, the images were transformed from central projection into orthogonal projection by differential rectification using the orientation data of each related image and a digital elevation model (DEM) which covers the both intertidal study locations. In the geometric rectification process the related height value of the orthophoto pixel will be interpolated from the DEM. For more detailed description of the generation of digital orthophotos see Kersten & O`Sullivan (1996). The DEM was generated by automatic digital image correlation on the DPW770 with grid spacing of 50 cm for the intertidal locations using b/w aerial images (photo scale 1: 7000). The used image correlation algorithm is described by Zhang & Miller (1997). Empirical accuracy investigations of the automatic generated intertidal DEM showed that the height points of the DEM have a standard deviation of ±18 cm compared to 180 check points which were measured by geodetic methods. The maximum and minimum values of the height differences were 40 cm and -79 cm compared to the reference values (Lehmann, 2006). The DEM refers to the height Normal Null (NN) of the German height reference system (DHHN).

Survey methods

In general, the communities comprised three different structural layers: top, middle and encrusting layer. The top layer (TL) usually consisted of thalli of large brown algae (e.g. *Fucus* spp., *Laminaria* spp.). The middle layer (ML) was represented by epiphytic, epizoic and endozoic species growing erect from the substrate, but not reaching the top layer (e.g. hydrozoans, mussels, tube-building polychaetes). The encrusting layer (EL) was formed by epilithic organisms adhering directly to the substrate, such as bryozoans or encrusting algae of the genus *Phymatolithon* or *Ralfsia* (see also de Kluijver, 1991, 1993). In each structural layer the percentage cover of the vertical projection of sessile, slow moving invertebrates, and algae was estimated, using a 0.25 m² quadrat. Some species were combined into a complex if the taxonomic position was tentative or if the morphological distinctions between two species were difficult to quantify or too time consuming to investigate. Examples of species combined into a complex are in Reichert & Buchholz (2006).

Data analyses

Minimal area

Minimal area tests were performed for each of in total seven plots at our study locations. In summer 2004, ten 0.25 m² quadrats were sampled at each plot which was characterised by a certain community type (Reichert et al., in prep.). Thus, the seven plots well described the community structure which occurred at the study locations. The minimal area was calculated with the Programme MINAR (Kaandorp, 1986). The algorithm used in this programme is in Weinberg (1978). Here, the similarity is calculated between each possible combination of subsets of m elements out of the ten sampled quadrats, where the same element is not used twice in one combination ($1 \leq m \leq 5$). The data were log-transformed and similarity was calculated with the Bray-Curtis coefficient. The five similarity values were used as a function of the sampled surface. The level at which the minimal area was reached has been chosen according to Weinberg (1978) who suggested a similarity level of 70 % between samples. The values for the minimal area ranged between 0.5 m² and 1.0 m². Thus, the sampled area of five quadrats (1.25 m²) seemed to be sufficient for reaching the minimal area, when the similarity level of 70 % was used.

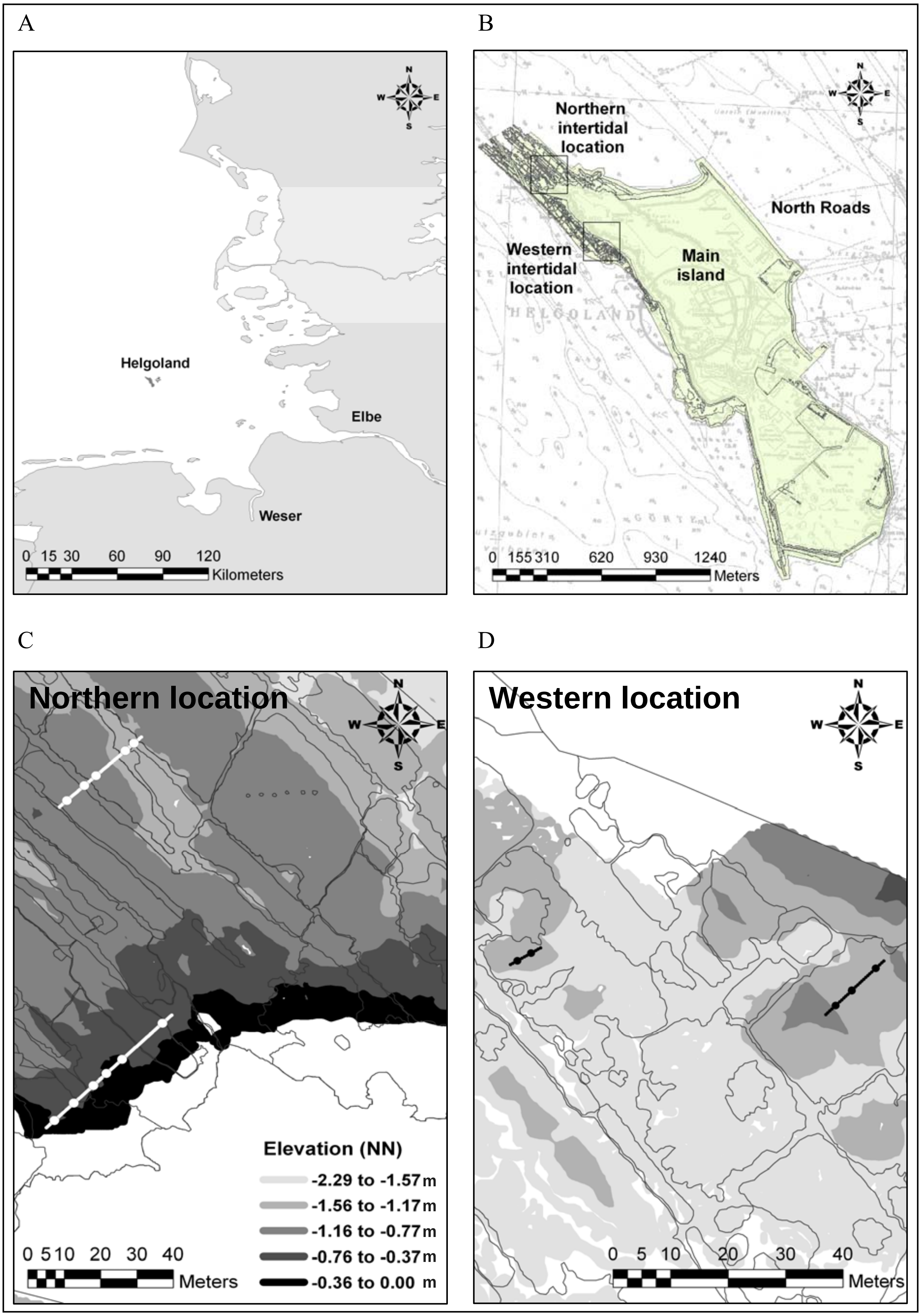

Figure 1 (A) Location of Helgoland in the German Bight, North Sea; (B) the island with the northern and western intertidal location; the scale of transects and plots at the (C) northern and (D) western study location with the drawn contours of the surface morphology and the elevation in metres refers to the height Normal Null (NN) of the German height reference system.

Species richness and total abundance

To evaluate patterns of variability in species richness or total abundance of algae and invertebrates among transects and plots at each location we used estimates of variance components. The spatial patterns of variation in these species attributes were examined for each of the eight times of sampling. Since our sampling design was not balanced due to the varying number of plots at each transect we used the restricted maximum likelihood method (REML), and also a two-way nested ANOVA with the Satterthwaite approximation (Sokal & Rohlf, 1995). Both methods used were a fully nested design with all factors random. In the design, plots were nested in transects. The REML method has been generally accepted as having good properties for unbalanced designs (Robinson, 1987; Searle, 1995). The relative variance components were estimated for each source of variation in (1) REMLs by using the Newton-Raphson iteration and (2) ANOVAs by using the observed mean squares to estimate terms identified in the expected mean squares (Searle et al., 1992; Winer et al., 1991). For the REML method the significance of random factors was tested using an asymptotic significance test, whereas for the ANOVA method F-ratio testing was produced by the STATISTICA output (StatSoft, 2001). The validity of likelihood ratio tests however has been called into question because they rely on large sample approximations (Searle, 1987; Singer, 1998). Since we had relatively small samples the significance test tended to be too conservative, and thus the power of detecting a significant variance component was reduced. Therefore, we (1) used REML to estimate the components and checked against the ANOVA method; both methods gave approximately the same results. Sometimes one or more estimates from the ANOVA method were negative; then, (2) these estimates were set to zero, removed from the model and the estimates for the remaining factor re-calculated according to Fletcher & Underwood (2002). Thereafter, (3) we used the ANOVA approach for hypothesis testing.

We used untransformed data for all analyses to provide variance components comparable across all data (Fraschetti et al., 2005). The assumption of homogeneity of variance was checked by Cochran's C test prior to analysis. When the variances were not homogeneous, we set the critical levels to a value equal to the p-value for variance heterogeneity (Underwood, 1997). Non-significant effects from analyses can still be interpreted if homogeneity is not reached (Benedetti-Cecchi, 2001; Underwood, 1997).

Relationship between elevation and species attributes

First, we used variance components, as explained for the biotic variables, to compare spatial variation across scales on the elevation within each location. Then, we used linear and nonlinear regression to explore relationships between elevation and species richness or total abundance at the scale of transect and plot at the northern and western location. The species attributes were pooled per replicate over the eight sampling times.

Species-abundance classes

Species richness refers to the total number of species collected at a certain site irrespective of the species abundance. Therefore, the species richness as a variable does not capture patterns of variability in richness related to the classes of species abundance. If for instance competition between common vs. rare species is an important structuring process in the community, the cover of both groups should be negatively (positively) correlated and in consequence both species should vary at the same spatial scales. If there is such "coupling" the patterns of richness of rare species may be predicted from the one of common species. On the other hand, if the set of factors affecting common and rare species are operating at different scales, the spatial variability in species richness of each group should be maximal at different scales (e.g. at a given scale, the richness of common species does not vary but that of rare species show a considerable variation). If there is such a "de-coupling" then further investigations will be necessary to understand how species within the same community are responding independently to different factors. For monitoring purposes a de-coupling means that it is necessary to develop particular sampling designs, targeting different scales of variation, for each species group. We explored these potential patterns of variation using species-abundance classes (SAC), where species are assigned to classes according to their abundance.

The standard method of analysis of SACs is to adjust a function (e.g. linear, log-normal), to define species-abundance distribution and to compare changes in the form of the function in space and time. This method is well established in many pollution-related studies (e.g. Gray, 1981; Gray & Pearson, 1982). For instance, Gray & Mirza (1979) showed that an undisturbed community fitted well to the log-normal distribution, while in polluted areas two lines of different slopes gave the best fit. Such a method of analysing the log-normal distribution of individuals among species has also been found useful to isolate those species which are most sensitive to pollution-induced changes (Andrews & Richard, 1980; Gulliksen et al., 1980). In such pollution-related studies, for each sample of the large number of replicated samples per time, each species was assigned to geometric abundance classes with a certain scale, e.g. x 2 scale (0-1, 2-3, 4-7, ..., 64-127, 128-255, ...). Here, differences among replicated samples reflect (1) differences in e.g. cover per species: in two different samples a given species may be assigned to a different class according to its abundance or (2) loss or appearance of species from one sample to another.

In the present study, we followed an alternative approach in order to evaluate if rare, regular and/or common species are responsible for the variation in total species richness among transects and plots at both locations. Here, the identification of the potential presence of relevant abundance classes, responsible for the patterns of variation, can be used in future reduced-scale monitoring programmes. We pooled all replicated quadrats over all seasons and calculated the mean cover for each species. Thereafter, we assigned each species to one of three geometric abundance classes (e.g. 0.01-0.08, 0.09-1.28, 1.29-81.92 %) on the basis of their mean cover. The species were classified as rare (mean cover < 0.08 %), regular (mean cover < 1.28 %) and common (mean cover > 1.29 %). Finally, we recorded, for each replicated quadrat, the number of species assigned to each class. Here, each species belonged to a fixed geometric-abundance class, irrespective of the replicated quadrat considered. Therefore, changes in the number of species per class were related exclusively to species losses and appearances. For instance, this approach is used in community phylogenetics (Swenson et al., 2006).

On the matrix of replicated quadrats x species-abundance classes, we estimated variance components as in the case of species richness and total abundance. We used linear and nonlinear regression, Pearson correlation and ANOVA F-ratio testing to explore relationship between elevation and species abundance classes at the scale of transect and plot at both locations. We applied the assignment to species-abundance classes and the following analyses to the cover of algae since they dominated both intertidal locations and were more diverse than the sessile fauna.

RESULTS

Species richness and total abundance

At the northern location, total richness was 112 species, consisting of 52 algae and 60 invertebrates. For algae, most variability in species richness occurred among plots as indicated by the large estimates of relative variance (Fig. 2a). At the scale of plot, the variability was significant for all sampling dates; at the scale of transect variability was only significant for autumn 2005. Most variability in species richness of invertebrates as well as in total cover of algae and invertebrates occurred among transects as indicated by the large estimates of relative variance (Fig. 2b-d). At the scale of transect and plot the variability was significant for all sampling dates, except of variation in invertebrate cover at the scale of transect in winter and spring 2005.

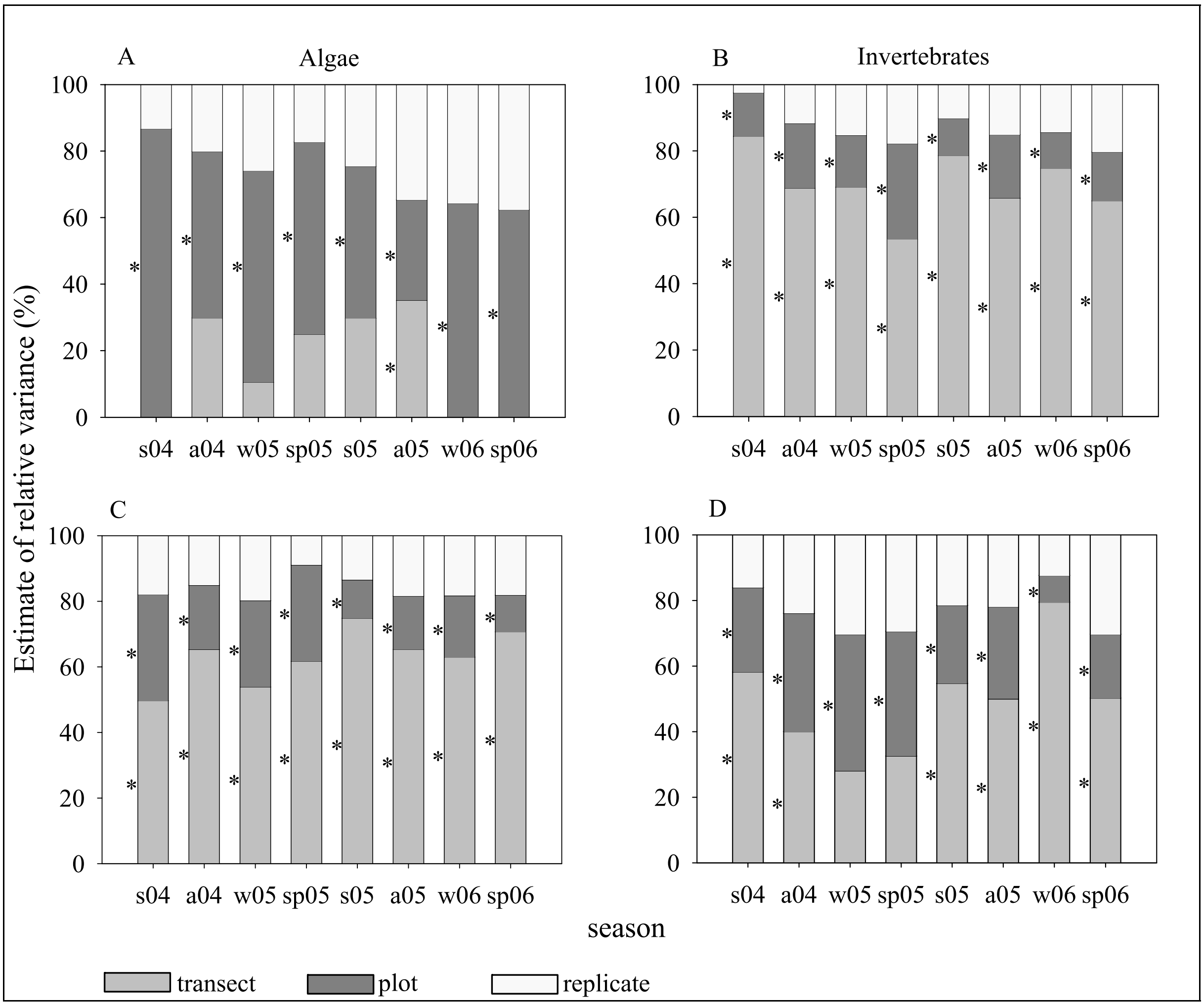

Figure 2 Estimates of variance components and ANOVA testing for spatial variability in total (A) species richness of algae, (B) species richness of invertebrates, (C) abundance of algae and (D) abundance of invertebrates in the northern intertidal location at the scale of transect, plot and replicate over the sampling seasons (* $p < 0.05$). Abbreviations of x-axis indicate season and year, e.g. s04: summer 2004.

At the western location, total richness was 104 species, consisting of 50 algae and 54 invertebrates. Most variability in species richness of macroalgae occurred at the scale of transect (significant in 50 % of the sampling dates; Fig. 3a). At the scale of plot, variability was high only in spring 2006; variability differed significantly in all sampling dates, except of autumn 2004 and winter 2005. For invertebrate richness as well as algal and invertebrate cover, the estimates of residual variance were at least in half of the sampling dates larger than the variance components among transects and plots; this indicated that the variation among replicates was important (Fig. 3b-d). At the scale of plot the variability was significant for most sampling dates, except of autumn 2004 and winter 2005 regarding invertebrate richness and autumn 2004 regarding invertebrate cover.

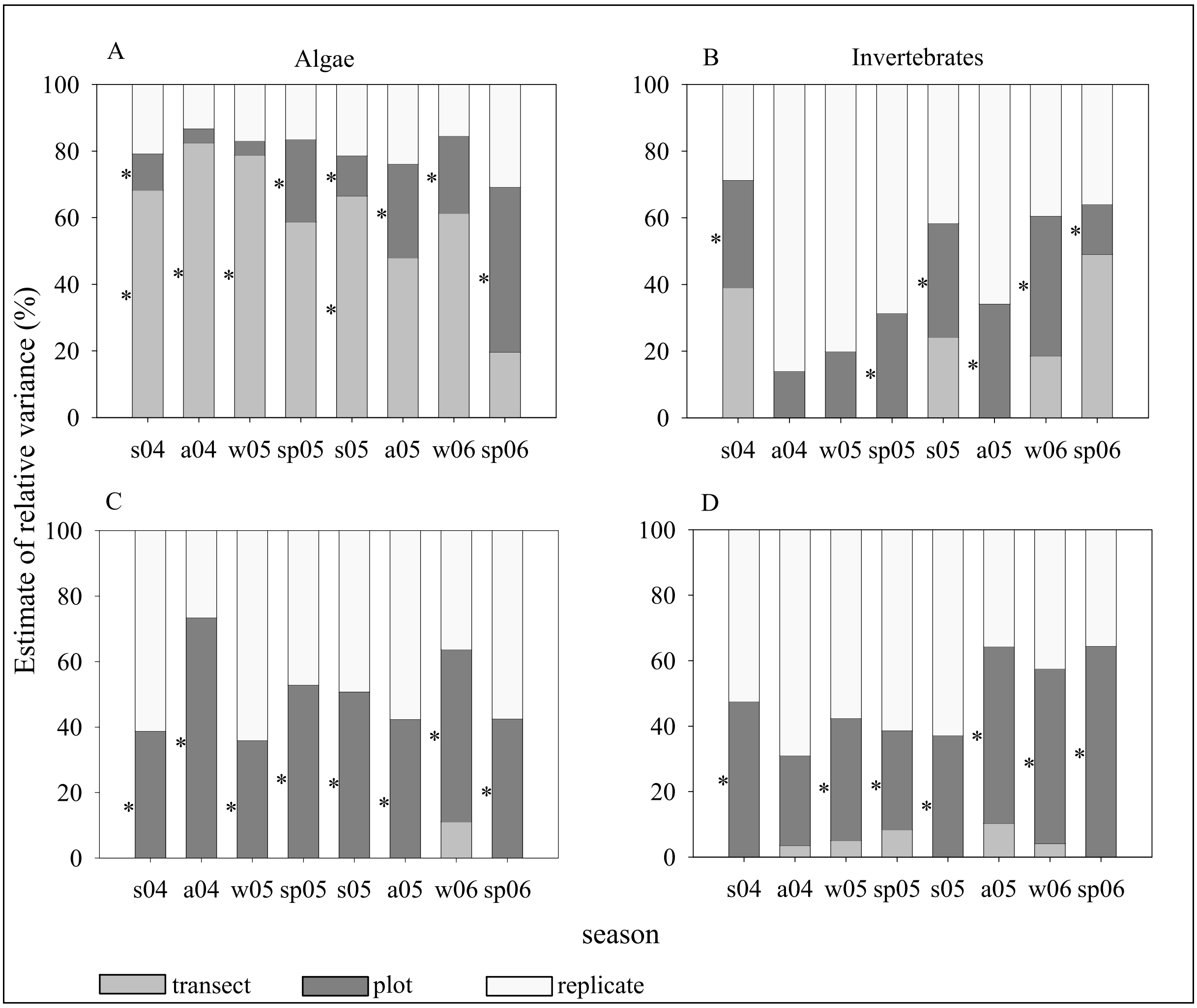

Figure 3 Estimates of variance components and ANOVA testing for spatial variability in total (A) species richness of algae, (B) species richness of invertebrates, (C) abundance of algae and (D) abundance of invertebrates in the western intertidal location at scales of transect, plot and replicate over the sampling seasons (* $p < 0.05$). Abbreviations of x-axis indicate season and year, e.g. s04: summer 2004.

Relationship between elevation and species attributes

At the northern intertidal location most variability in elevation occurred among transects, as indicated by the large estimates of relative variance (Tab. 1). At the scale of transect and plot the variability was significant. For the western intertidal location, the largest variability in elevation appeared among plots; at this scale the variability was significant (Tab. 1).

Linear and nonlinear regression were used to examine the relationship between logarithmically transformed elevation and species richness or total abundance at the scale of transect, plot and replicated quadrat. At the northern location (Fig. 4), species richness and cover of algae as well as species richness of invertebrates (all logarithmically transformed) responded asymptotically to elevation (all $p < 0.001$); these species attributes increased from high (5.8 cm) to low (7.3 cm) elevation (Fig. 4a-c). The cover of invertebrates was adjusted to a Ricker function; cover increased from high (5.8 cm) to low (6.9 cm) elevation and then tended to decrease slightly (Fig. 4d). When one replicate, characterized by an extremely high percentage cover of sediment was excluded from nonlinear regression, species richness and cover of algae as well as invertebrate richness gave better fits ($r < 0.7$ vs. $r > 0.8$). The exception of the asymptotic and the Ricker function were the replicated quadrats, belonging to two plots, and responding linearly to the elevation (Fig. 4); these plots, located between an elevation of 5.6 and 5.8 cm, showed a higher mean in (a) algal richness (> 2.2), (b) invertebrate richness (> 1.4), (c) algal cover (> 4.0 %) and (d) invertebrate cover (> 1.0 %) than several plots that were situated at an elevation > 5.8 cm. All linear regression models were significant ($p < 0.001$). At the western location there was not any significant relationship (Fig. 5).

Table 1 Estimates of variance components from REML and ANOVA method, and ANOVA testing for spatial variability in elevation carried out separately in each study location at the scale of transect and plot. The REML and ANOVA method gave approximately the same estimations.

Source	df	MS	F	p	VC ($x10^{-3}$)	VC (%)
Northern intertidal location						
Transect	1	8.18	97.60	< 0.001	294.58	94.57
Plot	9	0.08	233.97	< 0.001	16.56	5.32
Residual	38	0.00			0.36	0.11
Western intertidal location						
Transect	1	0.00	0.13	ns	0.00	0.00
Plot	3	0.07	14.60	< 0.001	10.37	67.57
Residual	17	0.01			4.98	32.43

VC, variance component; ns, not significant.

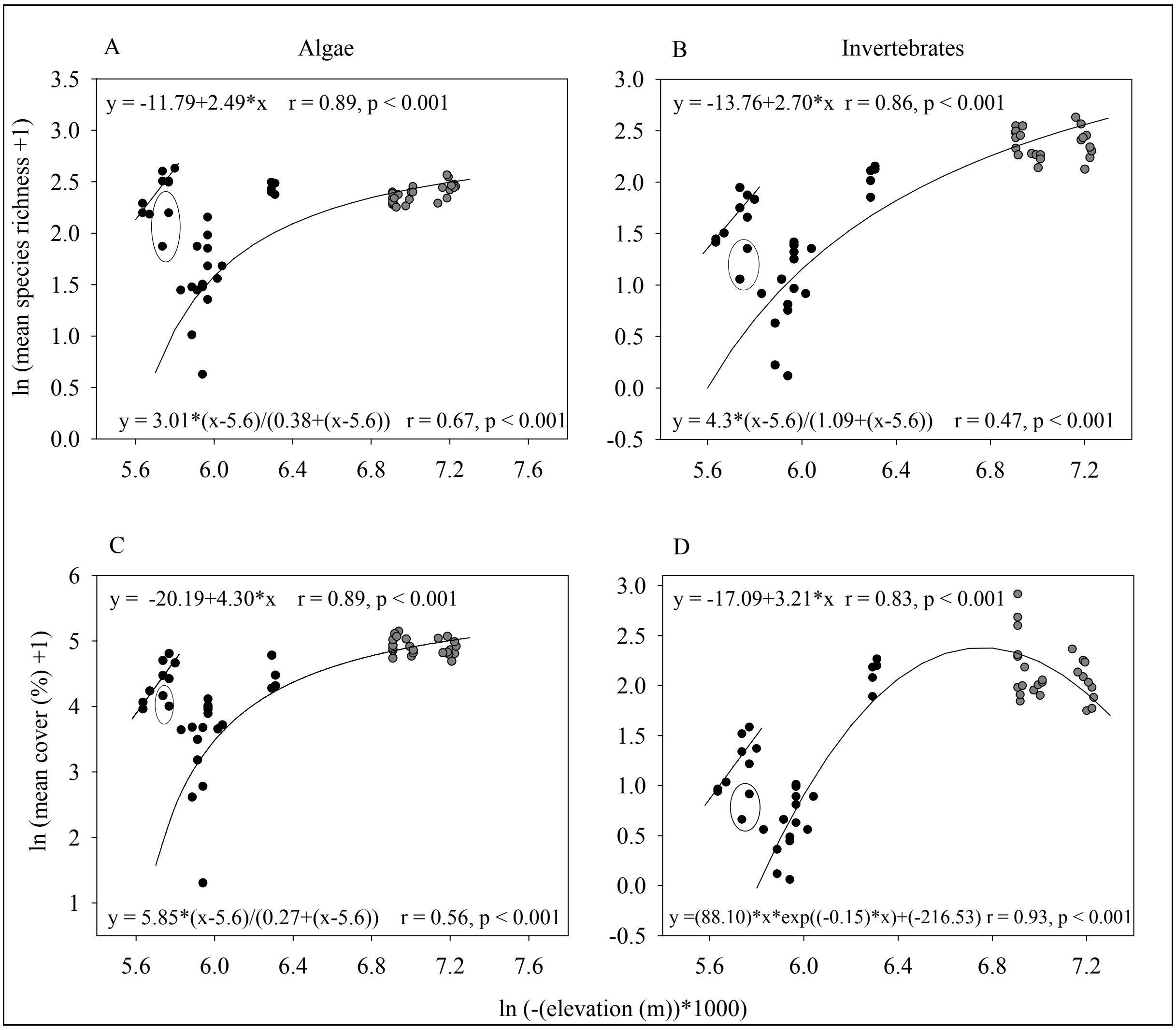

Figure 4 Linear and nonlinear regression models, Pearson correlation and ANOVA testing for relationship between elevation and (A) species richness of algae, (B) species richness of invertebrates, (C) cover of algae and (D) cover of invertebrates at the scale of transect, plot and replicate in the northern location. Different colours represent different transects. Elevation refers to the height Normal Null of the German height reference system. The circled replicates were excluded from the regression models.

Analysis of species-abundance classes

At the northern location, we obtained three abundance classes. Variance components on class I, containing the rare species, showed most variation among replicates; the variation was significant for all sampling dates among plots, except of summer 2004 and autumn 2005 (Fig. 6a). For class II, containing the regular species, estimates of variance components showed most variation at the scale of plot; among plots the variation was significant for all sampling dates, while among transects significant variation only occurred from autumn 2004 to spring 2005 (Fig. 6b). Most variation in abundance class III, containing the common species, occurred among transects. At this scale the variability was significant for all sampling dates; also, at the scale of plot, the variability was significant for all sampling dates.

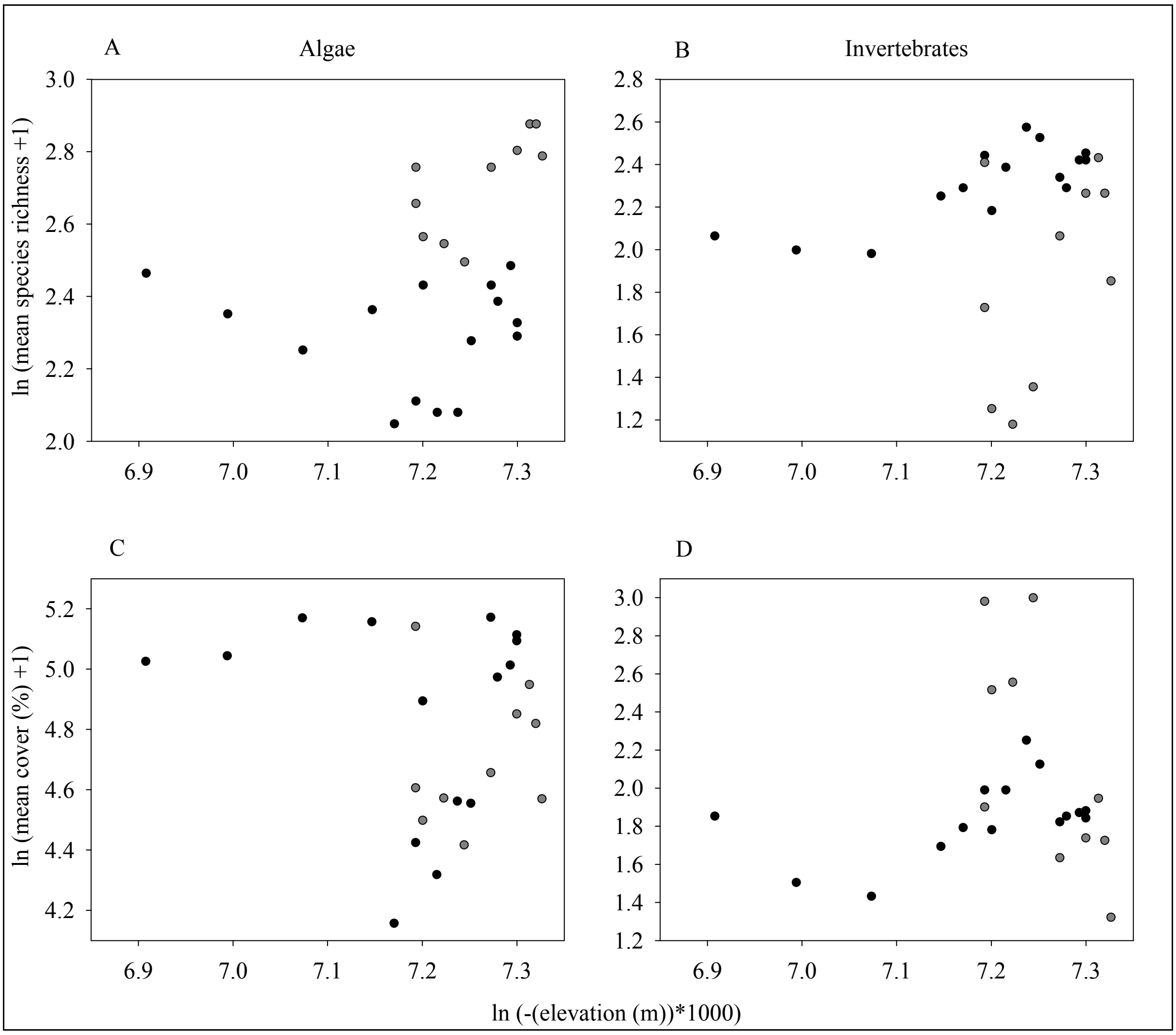

Figure 5 Scatterplot for relationship between elevation and (A) species richness of algae, (B) species richness of invertebrates, (C) cover of algae and (D) cover of invertebrates at the scale of transect, plot and replicate in the western location. Different colours represent different transects. Elevation refers to the height Normal Null of the German height reference system.

At the western location, variance components on abundance class I and II showed high variance at the scale of transect, whereas variance components on class III showed most variation at the scale of transect as well as plot (Fig. 6a-c). The variability of class I was significant for four (sp05, s05, w06, sp06) and five (s04, w05, sp05, a05, w06) sampling dates at the scale of plot and transect, respectively (Fig. 6a). For class II, variability was significant for some sampling dates among transects (a04, w05, s05, w06) and for only one sampling date among plots (s04). Significant variation in abundance class III was among plots for all sampling dates, except of winter and summer 2005; variation among transects was never significant.

At the northern location variation in richness of rare species (class I) predominated at the smallest scale (replicate), while variations in common species (class III) varied at the largest scale (transect). In contrast, in the western location variation in rare and regular species (class II) predominated among transects, whereas significant variations in common species was among plots.

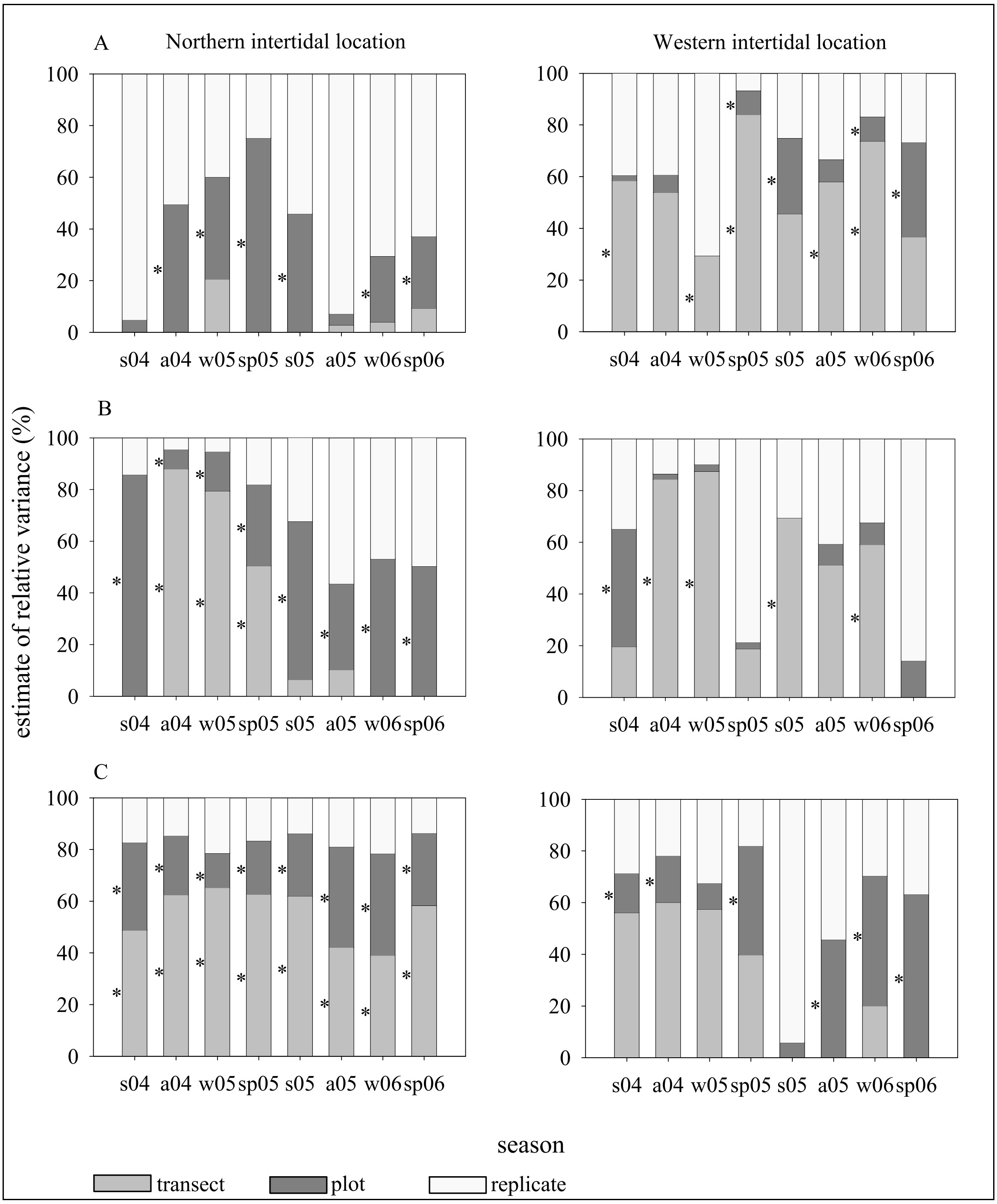

Figure 6 Estimates of variance components and ANOVA testing for spatial variability in geometric abundance class (A) I, (B) II and (C) III of macroalgae at the scale of transect, plot and replicate in the northern and western location over the sampling seasons (* $p < 0.05$). Abbreviations of x-axis indicate season and year, e.g. s04: summer 2004.

At the northern location, the richness of rare algae (class I) showed a parabola with a minimum at intermediate elevation (from 6.1 cm to 6.9 cm; Fig. 7a). For class II and III species richness responded asymptotically to elevation; species richness increased from high (5.8 cm) to low (7.3 cm) elevation (Fig. 7b, c). All nonlinear regression models were significant (all p< 0.001). When one replicate, characterized by an extremely high percentage cover of sediment was excluded from nonlinear regression, species richness of algal abundance class II and III gave better fits (r > 0.8).

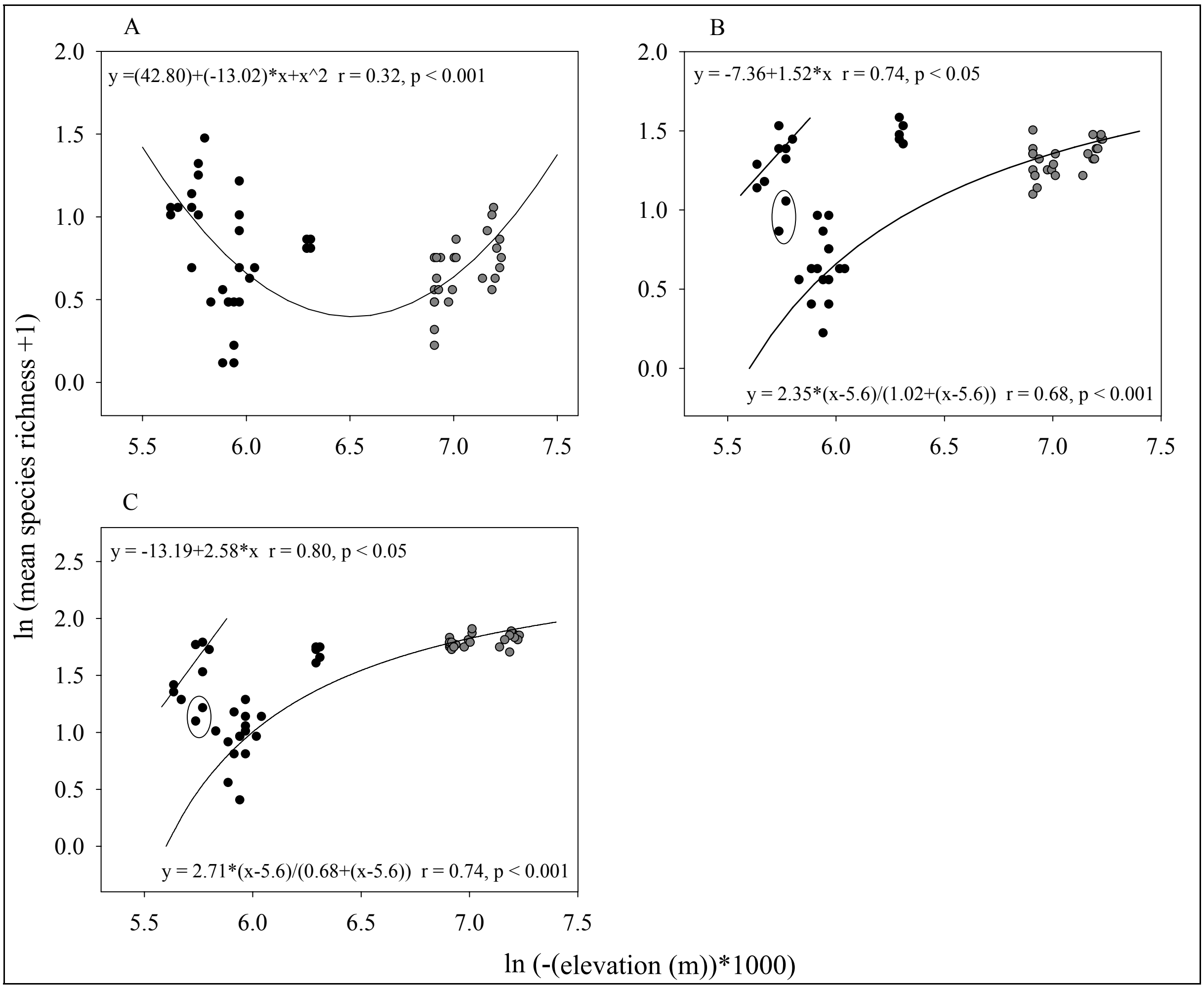

Figure 7 Linear and nonlinear regression models, Pearson correlation and ANOVA testing for relationships between elevation and richness of algal species of (A) class I, (B) class II and (C) class III at the scale of transect, plot and replicate in the northern location. Different colours represent different transects. Elevation refers to the height Normal Null of the German height reference system. The circled replicates were excluded from the regression models.

The exception of the asymptote was conformed by replicates from two plots that responded linearly; these were located between an elevation of 5.6 and 5.8 cm and showed a higher mean algal richness (> 1.1) than several plots that were lower situated (> 5.8 cm). All linear nonlinear regression models were significant (class I: $p < 0.001$; class II and III: $p< 0.05$).

In the western location, there was not any significant relationship between richness and elevation (Fig. 8).

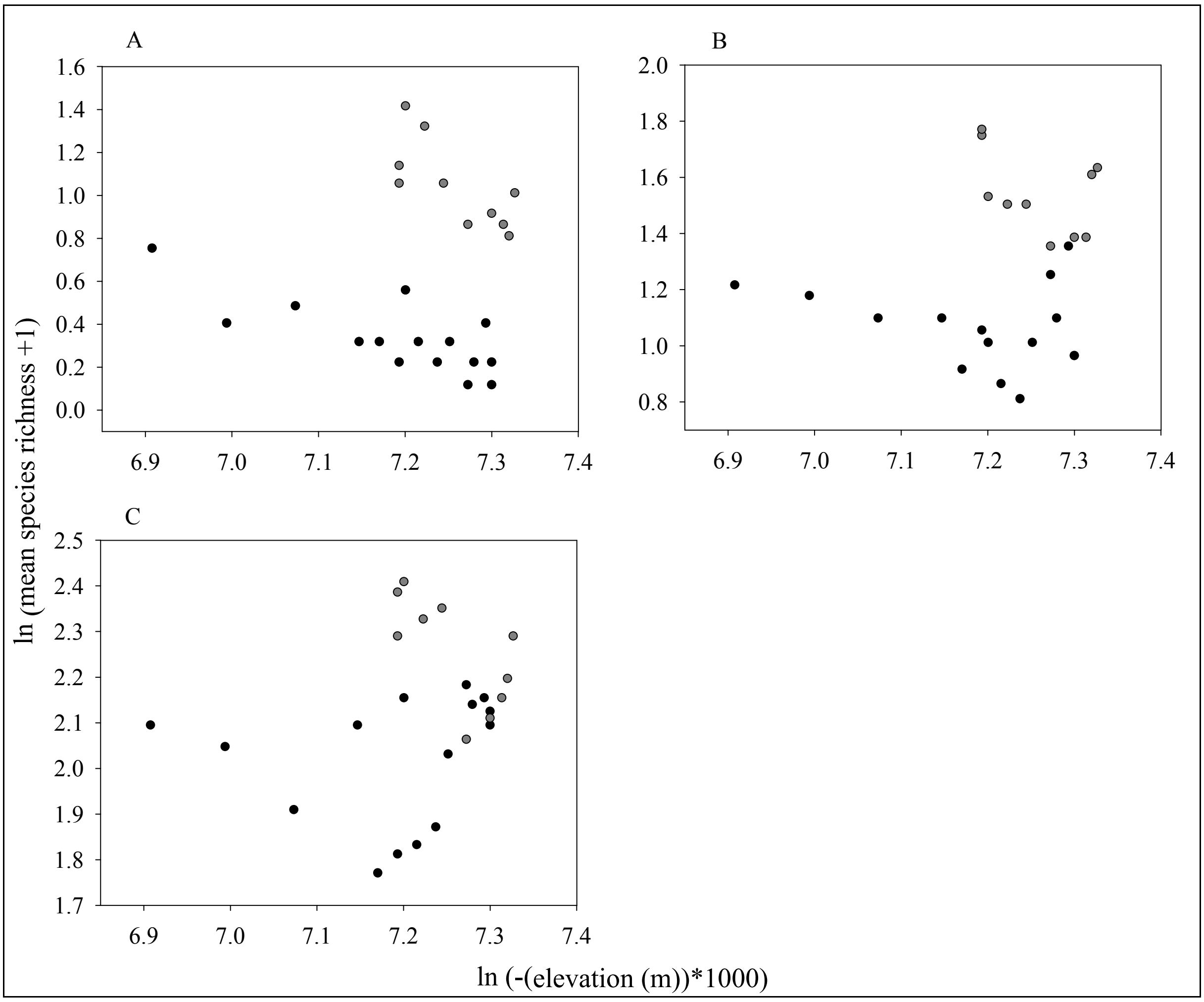

Figure 8 Scatterplot showing the relationship between elevation and richness of algal species of (A) class I, (B) class II and (C) class III at the scale of transect, plot and replicate in the western location. Different colours represent different transects. Elevation refers to the height Normal Null of the German height reference system.

DISCUSSION

For the intertidal locations at Helgoland we have shown, that variation in total species richness and abundance was mainly attributable to the factor transect at the northern location and to the factor replicate at the western location. At the northern location, the parametres of species assemblages responded asymptotically to elevation, while neither a linear nor a nonlinear relationship between elevation and species richness or total abundance occurred at the western location. For macroalgae, our analysis of species-abundance classes showed that the scale-dependent patterns of variability depended on whether species were rare or common. Our data about the intertidal community at Helgoland show that spatial patterns of species richness and total abundance were scale-dependent, but that there were a series of differences between locations. The locations varied in 1) the scale at which variations were highest (northern location: transect; western location: replicate), 2) the temporal persistence of the scale-dependent patterns (persistent only at the northern location), 3) the response to the elevation (significant only at the northern location), and 4) the degree of coupling in the scale-dependent variation in the species richness of the different abundance classes. Differences between locations, e.g. the larger variation among transects at the northern location, may be attributed to the sampling design. However, the other differences must be related with the differences in habitat structure, exposure or the presence of particular habitats occupied by characteristic species. The high variations in species richness of rare, regular and common species at the scale of transect characterizing the western location suggest that transects captured important variability in spite of covering a narrow range of elevation. The small variation in richness and abundance at low elevations of the northern location (log elevation range: 6.8-7.3) is in contrast to the high variability at the same range of elevation of the western location. In what follows we focus in patterns and processes occurring at each location separately and discuss our results in the context of a monitoring programme.

Northern location

At the northern location, variability in species richness and total abundance among transects (separated by 65 metres) was a direct result of differences between the vertical heights, the high- and low-shore; this pattern was consistent through time. The elevation (refers to height NN) also showed most variation among transects. The species assemblage at high-shore was characterised by relatively low algal and invertebrate cover as well as invertebrate richness in contrast to high values of these variables at low-shore. Several species cope with long times of emersion, whereas most others do not have abilities to avoid or endure harsher physical factors high on the shore (see reviews: Newell, 1979; Norton, 1985). The differences in the species attributes may be a result of a number of physical factors which may have changed with the vertical height on the shore such as desiccation, extremes of temperature and salinity or lack of nutrients and food. The richness and cover of algae and invertebrates responded asymptotically to elevation; this saturation may be a consequence of competitive processes. Competition were reported by many other studies on rocky shores as a prominent process maintaining differences in the structure of species assemblages among vertical tidal heights (e.g. Dayton, 1971; Hawkins & Hartnoll, 1985; Kelaher & Underwood, 2003).

Algal richness was an exception: richness showed the largest variance components among plots (separated by 4 - 40 m) and not among transects as in the case of the above mentioned variables. The algal assemblages at high-shore were characterised by relatively high richness just as those at low-shore. This pattern suggests that other factors not associated with vertical elevation on the shore are also important in affecting spatial patterns of macroalgal distribution. The algal assemblages at high-shore were characterised by relatively high richness just as those at low-shore. It is not clear why this is the case; potential factors explaining this unusual high richness may be differential substrate heterogeneity (Chapman & Underwood, 1994; Underwood & Chapman, 1989), hydrodynamic conditions (Leonard et al., 1998), intra- and interspecific interactions (Connell, 1961; Hawkins & Hartnoll, 1983) and the interplay between physical and biological processes (Benedetti-Cecchi et al., 2000a). Dependent on the geomorphology of rocky shores a variety of microhabitats with different elevation (e.g. pools, promontories) results in diverse small-scale variation in physical conditions (e.g. micro-hydrodynamic or -climate changes). In particular, the presence of promontories at the northern location of Helgoland, may contribute to the formation of particular microhabitats not found in the lower intertidal. These highly elevated patches were characterized by a multilayered algal structure: an encrusting layer, a middle layer and a top layer consisting of large brown algae (Reichert et al., in prep.). For example, exposed patches on the promontories offered an unsuitable habitat for dense stands of filamentous algae of the genus *Ulva*, whereas they supported the settlement of large brown algae such as *Fucus vesiculosus* and *Fucus spiralis*. In contrast, *Ulva* species were more abundant on the base of the promontories. A pre-emption of patches on the promontories by brown algae might have ameliorated the conditions for the establishment of other species. Thus, micro-hydrodynamic changes in the upper intertidal may have defined particular microhabitat types (Guichard & Bourget, 1998).

We found a de-coupling between the richness of regular species and rare or common species. Richness of regular species mostly varied at the scale of plot as in the case of total species richness, whereas rare and common species varied mostly at the scale of replicate and transect respectively. Since brown algae (e.g. *Fucus vesiculosus*, *Fucus spiralis*) were classified as regular species, the observed pattern of richness should be a consequence of pre-emption of high elevated rocky promontories.

Western location

At the western study location, most variability in species richness and total abundance was among replicates (separated by 10s of centimetres), and thus agreed with several investigations which revealed a considerable degree of variation in benthic assemblages at the smallest spatial scale, that is between individual replicates (Archambault & Bourget, 1996; Fraschetti et al., 2005; Menconi et al., 1999; Underwood & Chapman 1996). The variation among replicates may be explained by a haphazard scattering of suitable microhabitats across the low-shore of the western study location. However, most differences in elevation (refers to height NN) as one topographic feature was among plots and not among replicates, and the relationship between elevation and species richness or total abundance was not significant. Other geo-morphological structures (e.g. crevices, holes, cracks) within each plot may govern patterns at scales smaller than a few metres (Underwood & Chapman, 1996). Differences in abundance of dominant periwinkles (e.g. *Littorina littorea*, *Littorina mariae*/*obtusata*) among replicated quadrats may be affected by their behaviour dispersing among patches of microhabitats during a period of activity. Foraging movements of these grazing periwinkles may subsequently influence the patterns of distribution of the preferred sessile algae, such as *Fucus* species. Manipulative experiments to test such a hypothesis may be important and should be planned in future.

Algal richness was also an exception as in the case of the northern study location. Species richness of algae showed the largest variance components among transects (separated by ca. 45 m). The differences in algal richness among transects may be a result of substrate heterogeneity in combination with interspecific interactions. Personal observations showed a considerable variability in the abundance of burrowing and/or tube-building polychaetes (e.g. *Polydora ciliata*, *Fabricia sabella*) found in patches of relatively soft red sandstone scattered at low intertidal. Patchiness in local abundance of polychaetes appears to be also related with the occurrence of seagulls feeding on them (K.R. personal observation). The faeces of the polychaetes and seagulls can cause a local increase of ammonium, which in turn serves as nutrient for algae, and may increase algal richness. The close relationship between the occurrence of green and red macroalgae and eutrophication has been documented elsewhere (e.g. Chryssovergis & Panayotidis, 1995) and should be studied in detail at Helgoland.

The results of species-abundance distribution of macroalgae supported our assumption that interspecific interactions between animals and green and red macroalgae may be responsible for spatial variation among transects. We found that rare species, such as *Rhizoclonium tortuosum*, *Spongomorpha aeruginosa* or *Porphyra species*, mostly showed significant variation at the scale of transect as for total species richness of algae. Thus, it appears that the distribution of rare occurring algae at the western location were mainly responsible for the general pattern of total richness, which may be caused by an interplay of physical and biological processes.

The richness of species-abundance classes of macroalgae did not show a de-coupling as in the northern location: richness of rare, regular and common species varied mostly at the scale of transect. The consistent variation in the variability among classes at the scale of transect (i.e. higher richness along the transect at the lower intertidal level) may be the consequence of favourable physical conditions, animal-macroalgal interactions or facilitation effects among macroalgae.

Perspectives for monitoring

Our data show that monitoring may not be a simple task in marine benthic communities. Monitoring may take into account that 1) community structure varies at several scales, 2) scale-dependent variations depend on the location, 3) scale-dependent variation may be inconsistent through time and 4) de-coupling may occur among species richness per abundance class.

Monitoring of the community may try to control variation at particular spatial scales. The identification of a characteristic scale of variation at each location helps to design a monitoring program targeting the appropriate scale at each location separately. However, temporal inconsistencies of the scale-dependent variation show that monitoring should involve a multiple-scale sampling design. In particular, the monitoring should focus on smaller spatial scales (centimetres to 10s of metres apart) since temporal changes in the variation of assemblages at these scales may be a diagnostic feature for stressed benthic communities (e.g. Chapman et al., 1995; Terlizzi et al., 2005). In our case, inconsistencies through time appeared in the western location and warn against using a one-scale sampling approach. The de-coupling among species richness per abundance class also argue for a multiple-scale approach in order to capture the relevant variation. Alternatively, monitoring may concentrate on the species groups displaying least variation (Hartnoll & Hawkins, 1980). In our case, richness of the common species showed a consistent pattern of variation at the northern location and should be targeted in the monitoring programme.

In conclusion, although processes causing spatial patterns cannot be determined from observational studies, the identification of relevant scales of variation helps to formulate hypotheses, and to design manipulative experiments or monitoring programmes at the appropriate scale. At the northern location, processes structuring communities appear to be associated with intertidal elevation. These processes may be affecting rare, regular and common species in a different way. In contrast, at the western location, other processes (e.g. geo-morphological structures, behavioural responses, interactive effects of abiotic and biotic factors) appear to structure the intertidal communities and affect rare, regular as well as common species in a similar way. Experiments are vital to explain particularly the processes causing the high small-scale variability of assemblages and their temporal changes at the western location. To date, for both locations at Helgoland the monitoring should consider variation at several spatial scales and should follow a multiple-scale sampling approach.

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REFERENCES

Aberg, P. & Pavia, H., 1997. Temporal and multiple scale spatial variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. *Marine Ecology Progress Series*, **158**, 111-119.

Andrews, M.J. & Richard, D., 1980. Rehabilitation of the Inner Thames Estuary. *Marine Pollution Bulletin*, **11**, 327-331.

Archambault, P. & Bourget, E., 1996. Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. *Marine Ecology Progress Series*, **136**, 111-121.

Bartsch, I. & Tittley, I., 2004. The rocky intertidal biotopes of Helgoland: present and past. *Helgoland Marine Research*, **58**, 289-302.

Bell, G., Lechowicz, M.J., Appenzeller, A., Chandler, M., DeBlois, E., Jackson, L., Mackenzie, B., Preziosi, R., Schallenberg, M. & Tinker, N., 1993. The spatial structure of the physical environment. *Oecologia*, **96**, 114-121.

Benedetti-Cecchi, L., 2000. Predicting direct and indirect interactions during succession in a midlittoral rocky shore assemblage. *Ecological Monographs*, **70**, 45-72.

Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Marine Ecology Progress Series*, **215**, 79-92.

Benedetti-Cecchi, L., Bulleri, F. & Cinelli, F., 2000a. The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the north-west Mediterranean. *Oecologia*, **123**, 406-417.

Benedetti-Cecchi, L., Acunto, S., Bulleri, F. & Cinelli, F., 2000b. Population ecology of the barnacle *Chthamalus stellatus* in the northwest Mediterranean. *Marine Ecology Progress Series*, **198**, 157-170.

Chapman, M.G., 2002. Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. *Austral Ecology*, **27**, 211-228.

Chapman, M.G. & Underwood, A.J., 1994. Dispersal of the intertidal snail, *Nodilittorina pyramidalis*, in response to the topographic complexity of the substratum. *Journal of Experimental Marine Biology and Ecology*, **179**, 145-169.

Chapman, M.G., Underwood, A.J. & Skilleter, 1995. Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage and two control assemblages. *Journal of Experimental Marine Biology and Ecology*, **189**, 103-122.

Chapman, M.G. & Underwood, A.J., 1998. Inconsistency and variation in the development of rocky intertidal algal assemblages. *Journal of Experimental Marine Biology and Ecology*, **224**, 265-289.

Connell, J.H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthalamus stellatus*. *Ecology*, **42**, 710-723.

Chryssovergis, F. & Panayotidis, P., 1995. Communities of macrophytobenthos along an eutrophication gradient (Maliakos Gulf, Aegean Sea, Greece). *Oceanologica Acta*, **18**, 649-658.

Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, **41**, 351-389

De Kluijver, M.J., 1991. Sublittoral hard substrate communities off Helgoland. *Helgoländer Meeresuntersuchungen*, **45**, 317-344.

De Kluijver, M.J., 1993. Sublittoral hard-substratum communities off Orkney and St Abbs (Scotland). *Journal of the Marine Biological Association of the United Kingdom*, **73**, 733-754.

Fletcher, D.J. & Underwood, A.J., 2002. How to cope with negative estimates of components of variance in ecological field studies. *Journal of Experimental Marine Biology and Ecology*, **273**, 89-95.

Fraschetti, S., Terlizzi, A. & Benedetti-Cecchi, L., 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecology Progress Series*, **296**, 13-29.

Gray, J.S., 1981. *The ecology of marine sediments*, Cambridge: Cambridge University Press.

Gray, J.S. & Mirza, F.B., 1979. A possible method for detecting pollution indicated disturbance on marine benthic communities. *Marine Pollution Bulletin*, **10**, 142-146.

Gray, J.S. & Pearson, T.H., 1982. Objective selection of sensitive species indicative of pollution-induced change in benthic communities. I. Comparative Methodology. *Marine Ecology Progress Series*, **9**, 111-119.

Guichard, F. & Bourget, E., 1998. Topographic heterogeneity, hydrodynamics, and benthic community structure: A scale-dependent cascade. *Marine Ecology Progress Series*, **171**, 59-70.

Gulliksen, B., Haug, T. & Sandnes, O.K., 1980. Benthic macrofauna on new and old grounds at Jan Mayen. *Sarsia*, **65**, 137-148.

Harms, J., 1993. Check list of species (algae, invertebrates and vertebrates) found in the vicinity of the island of Helgoland (North Sea, German Bight) – a review of recent records. *Helgoländer Meeresuntersuchungen*, **47**, 1-34.

Hartnoll, R.G. & Hawkins, S.J., 1980. Monitoring rocky-shore communities: A critical look at spatial and temporal variation. *Helgoländer Meeresuntersuchungen*, **33**, 484-494.

Hawkins, S.J. & Hartnoll, R.G., 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology*, **21**, 195-282.

Hawkins, S.J. & Hartnoll, R.G., 1985. Factors determining the upper limits of intertidal canopy-forming algae. *Marine Ecology Progress Series*, **20**, 265-271.

Hyder, K., Johnson, M.P., Hawkins, S.J. & Gurney, W.S.C., 1998. Barnacle demography: Evidence for an existing model and spatial scales of variation. *Marine Ecology Progress Series*, **174**, 89-99.

Janke, K., 1986. Die Makrofauna und ihre Verteilung im Nordost-Felswatt von Helgoland. *Helgoländer Meeresuntersuchungen*, **40**, 1-55.

Jenkins, S.R., Hawkins, S.J. & Norton, T.A., 1999a. Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community. *Journal of Experimental Marine Biology and Ecology*, **233**, 41-63.

Jenkins, S.R., Hawkins, S.J. & Norton, T.A., 1999b. Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Marine Ecology Progress Series*, **188**, 81-92.

Jenkins, S.R., Aeberg, P., Cervin, G., Coleman, R.A., Delany, J., Della Santina, P., Hawkins, S.J., LaCroix, E., Myers, A.A., Lindegarth, M., Power, A.M., Roberts, M.F. & Hartnoll, R.G., 2000. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology*, **243**, 209-225.

Jenkins, S.R., Arenas, F., Arrontes, J., Bussell, J., Castro, J., Coleman, R.A., Hawkins, S.J., Kay, S., Martinez, B., Oliveros, J., Roberts, M.F., Sousa, S., Thompson, R.C. & Hartnoll, R.G., 2001. European-scale analysis of seasonal variability in limpet grazing activity and microalgal abundance. *Marine Ecology Progress Series*, **211**, 193-203.

Kaandorp, J.A., 1986. Rocky substrate communities of the infralittoral fringe of the Boulonnais coast, NW France: A quantitative survey. *Marine Biology*, **92**, 255-265.

Kelaher, B.P., Underwood, A.J. & Chapman, M.G., 2003. Experimental transplantations of coralline algal turf to demonstrate causes of differences in macrofauna at different tidal heights. *Journal of Experimental Marine Biology and Ecology*, **282**, 23-41.

Kersten, T. & O'Sullivan, W., 1996. Project SWISSPHOTO - Digital orthophotos for the entire area of Switzerland. In Proceedings of the Eighteens International Society for Photogrammetry and Remote Sensing, Vienna, 12-18 July 1996. International Archives of Photogrammetry and Remote Sensing, pp. 186-191.

Lehmann, V., 2006. Empirische Genauigkeitsuntersuchungen digitaler Geländemodelle verschiedener Sensoren auf Helgoland. Diploma thesis, Department Geomatics, HafenCity University Hamburg, Germany.

Leonard, G.H., Levine, J.M., Schmidt, P.R. & Bertness, M.D., 1998. Flow driven variation in intertidal community structure in a Maine estuary. *Ecology*, **79**, 1395-1411.

Lewis, J.R., 1978. *The ecology of rocky shores*. London: Hodder and Stoughton.

Li, J., Vincx, M., Herman, P.M.J. & Heip, C., 1997. Monitoring meiobenthos using cm-, m- and km-scales in the Southern Bight of the North Sea. *Marine Environmetal Research*, **43**, 265-278.

Lubchenco, J., 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology*, **64**, 1116-1123.

Lubchenco, J. & Menge, B.A., 1978. Community development and persistance in a low rocky intertidal zone. *Ecological Monographs*, **48**, 67-94.

Lüning, K., 1985. *Meeresbotanik*. Stuttgart: Georg Thieme Verlag.

Menconi, M., Benedetti-Cecchi, L. & Cinelli, F., 1999. Spatial and temporal variability in the distribution of algae and invertebrates on rocky shores in the Northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, **233**, 1-23.

Morrisey, D.J., Howitt, L., Underwood, A.J. & Stark, J.S., 1992. Spatial variation in soft-sediment benthos. *Marine ecology progress series*, **81**, 197-204.

Newell, R.C., 1979. *Biology of intertidal animals*. Faversham: Marine Ecological Survey Ltd.

Norton, T.A., 1985. The zonation of seaweeds on rocky shores. In *The ecology of rocky coasts*. (eds. P.G. Moore & R. Seed), pp. 7-21. London: Hodder & Stoughton.

Paine, R.T., 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, **15**, 93-120.

Reichert, K. & Buchholz, F., 2006. Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002. *Helgoland Marine Research*, **60**, 213-223.

Robinson, D.L., 1987. Estimation and use of variance components. *The Statistician*, 36, 3-14.

Searle, S.R., 1987. *Linear models for unbalanced data*. New York: Wiley.

Searle, S.R., Casella, G. & McCulloch, C.E., 1992. *Variance components*. New York: Wiley.

Searle, S.R., 1995. An overview of variance component estimation. *Metrika*, **42**, 215-230.

Singer, J.D., 1998. Using SAS PROC MIXED to fit multilevel models, hierarchical models, and individual growth models. *Journal of Educational and Behavioral Statistics*, **24**, 323-355.

Sokal, R.R. & Rohlf, F.J., 1995. *Biometry: the principles and practise of statistics in biological research*, 3rd edn. New York: Freeman.

Southward, A.J., 1958. The zonation of plants and animals on rocky sea shores. *Biological Reviews*, **33**, 137-177.

Stephenson, T.A. & Stephenson, A., 1949. The universal features of zonation between tidemarks on rocky coasts. *Journal of Ecology*, **37**, 289-305.

Stephenson, T.A. & Stephenson, A., 1972. *Life between tidemarks on rocky shores*. San Francisco: Freeman.

Swenson, N.G., Enquist, B.J., Jason, P., Thompson, J. & Zimmermann, J.K., 2006. The problem and promise of scale dependency in community phylogenetics. *Ecology*, **87**, 2418-2424.

Terlizzi, A., Benedetti-Cecchi, L., Bevilacqua, S., Fraschetti, S., Guidetti, P. & Anderson, M.J., 2005. Multivariate and univariate asymmetrical analyses in environmental impact assessment: a case study of Mediterranean subtidal sessile assemblages. *Marine ecology progress series*, **289**, 27-42.

Underwood, A.J., 1996. Spatial patterns of variance in density of intertidal populations. In *Frontiers of population ecology* (eds. Floyd, R.B., Sheppard, A.W. & De Barro, P.J.), pp. 369-389. Melbourne: CSIRO Publishing.

Underwood, A.J., 1997. *Experiments in ecology: their logical design and interpretation using analysis of variances*, Cambridge: Cambridge University Press.

Underwood, A.J. & Chapman, M.G., 1989. Experimental analyses of the influences of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata*. *Journal of Experimental Marine Biology and Ecology*, **134**, 175-196.

Underwood, A.J. & Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia*, **107**, 212-224.

Underwood, A.J. & Chapman, M.G., 1998. Spatial analyses of intertidal assemblages on sheltered rocky shores. *Austral Ecology*, **23**, 138-157.

Weinberg, S., 1978. The minimal area problem in invertebrate communities of Mediterranean rocky substrata. *Marine Biology*, **49**, 33-40.

Winer, B.J., Brown, D.R. & Michels, K.M., 1991. *Statistical principles in experimental designs*, 3rd edn. New York: McGraw-Hill.

Zhang, B. & Miller, S., 1997. Adaptive automatic terrain extraction. In *Proceedings of the Eleventh SPIE`s International Symposium on AeroSense*, Orlando, Florida, 21-23 April 1997. *Integrating Photogrammetric Techniques with Scene Analysis and Machine Vision* (ed. D.M. McKeown et al.), pp. 27-36.

Scale-dependent patterns of variability in the abundance of macroalgae and invertebrates of the rocky intertidal at Helgoland (German Bight, North Sea)

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ABSTRACT

A growing body of literature shows that benthic communities are hierarchically structured on spatial and temporal scales. In two study locations at Helgoland (North Sea), the northern and the western location, we (1) investigated the variation in abundance of specific algae and invertebrates at two spatial scales and (2) evaluated the relationship between elevation and specific species at these scales. We were also interested in using this information about the spatial pattern of individual algae and invertebrates as well as the patterns of elevation to help developing a monitoring programme of the rocky intertidal. We examined the variation of individual algae and invertebrates by means of a hierarchical nested design. Data were taken from five replicates per plot, with plots located in transects (two transects per location).

At the northern location, the highest variability in cover of most algae and invertebrates occurred at the scale separated by about 50 metres (scale: transect). This was a direct result of differences between the high- and the low-shore. Most species at high-shore showed a relatively low frequency of occurrence in contrast to a highest frequency of occurrence (ca. 100 %) and maximal values of cover at low-shore. However, neither a linear nor a nonlinear relationship between elevation and the specific species occurred. At the western location, the highest variability in most macroalgae and invertebrates investigated was among replicates (10s of centimetres apart). No relationship between elevation and individual species occurred at this location. Macroalgae at both locations were more consistent overtime than invertebrate species. Our results suggest that the relevant processes shaping the individual macroalgae and invertebrates at the Helgoland rocky intertidal vary between locations and the specific species.

The potential causes of variation in macroalgal and invertebrate species at different spatial scales are discussed and suggestions for a future monitoring programme are given. Temporal inconsistency in the spatial patterns, and the fact that some individual algae and invertebrates comprising the benthic assemblages vary at different scales, speak in favour of a multiple-scale sampling approach for monitoring change in the intertidal communities at Helgoland.

Keywords

Spatial scales · Variability · Algae · Invertebrates · Elevation · Rocky intertidal · Helgoland · North Sea

INTRODUCTION

The objective of much current ecological research is the understanding of variation of plant and animal individuals, populations and communities in space and time. To identify spatial and temporal ecological processes, an appropriate description of patterns on one or several spatial and/or temporal scales is often a suited starting point from which questions and hypotheses arise. As a next step, manipulative experiments are necessary to identify the processes and causal relationships underlying the observed patterns. Patterns in assemblages (from terrestrial to aquatic systems) are caused by abiotic and biotic factors operating at different spatial and temporal scales (e.g. grassland vegetation: Perelman et al., 2001; terrestrial tardigrades: Meyer, 2006; freshwater assemblages: Boyero, 2003; Heino et al., 2004 and estuarine assemblages: Azovsky et al., 2004; Dethier & Schoch, 2005). Particularly for rocky shores small-scale spatial variation (cm up to 1000s of m) appears to be a general pattern of algal and invertebrate assemblages around the world (e.g. Aberg & Pavia, 1997; Chapman, 2002; Hyder et al., 1998; Underwood, 1996). The ecological mechanisms accounting for these small-scale patchiness may be related to changes in behavioural responses (e.g. Chapman & Underwood, 1994; Underwood & Chapman, 1989), recruitment (e.g. Chapman & Underwood, 1998), biological interactions (Benedetti-Cecchi, 2001), the interactive effects of abiotic and biotic factors (Benedetti-Cecchi et al., 2000) and small-scale changes in physical conditions such as slope of the substratum (Benedetti-Cecchi, 2000) or elevation of the substratum (refers to a standard height) within any vertical zone on rock-platforms. The slope of the substratum has been invoked to explain small-scale spatial heterogeneity, whereas elevation of the substratum remains mostly unquantified. Elevation can be defined as the standard height of any intertidal location, either vertical or horizontal, calculated from a reference point. That elevation remains mostly unquantified may partly be explained by the general lack of continuous measurements of the term "elevation" such as digital elevation models constructed by e.g. airborne or terrestrial laser scanning.

Most investigations of rocky shore assemblages have concentrated on geographic regions in Australia, the Mediterranean or the North Atlantic (e.g. Menconi et al., 1999; Underwood & Chapman, 1998). In contrast, studies examining spatial patterns of species assemblages in the North Sea are rare (Li et al., 1997). Although, algal and invertebrate assemblages of the relatively small Helgoland rocky littoral in the German Bight (North Sea) have been studied for more than a century (Harms, 1993) spatial patterns of algal and invertebrate assemblages in the rocky intertidal of Helgoland have only been ill defined. To date, there are only few intertidal studies as initial attempts to describe distribution patterns and to reveal possible temporal variations in macroalgae or invertebrates over the past decades (Bartsch & Tittley, 2004; Reichert & Buchholz, 2006). A previous study at Helgoland had concentrated on variation in species richness and total abundance of intertidal assemblages at different spatial scales by means of a nested sampling design (Reichert et al., submitted). It was shown that spatial patterns of the assemblages were particularly dependent on scales separated by ca. 50 metres as well as 10s of centimetres. However, the scale-dependent patterns of variability in individual macroalgae and invertebrates comprising these intertidal assemblages are not studied yet.

Accordingly, the overall aim of the present study was to investigate the variation in the abundance of several macroalgae and invertebrates at defined spatial scales. Furthermore, we explored the influence of elevation on specific macroalgae and invertebrates at two rocky intertidal locations at Helgoland, the northern and western location. We examined the variation of algae and invertebrates as well as the relevance of elevation by means of a nested sampling design. Our sampling design included two spatial scales at both study locations: transect separated by 45 and 65 metres as well as plots separated between 5 - 40 and 7 - 10 metres at the northern and western location, respectively. We used this sampling design to test the general hypothesis that (1) variation was important among transects and replicates at the northern and western location respectively, as in the case of total abundance of the entire algal and invertebrate assemblage and (2) spatial patterns of specific species were associated to patterns of elevation. We also aim at using the identification of relevant scales of variation to formulate hypotheses, design manipulative experiments or provide recommendations for a monitoring programme of the rocky intertidal at Helgoland.

MATERIAL AND METHODS

Study locations

This survey was conducted at two intertidal locations at Helgoland, German Bight, North Sea (54° 11′N, 7° 55′E), from summer 2004 until spring 2006 (Fig. 1). The locations were in the northern and western part of the island, and were named after their geographic position. The northern and western intertidal location differed in wave exposure and in the geo-morphological structures of the rock-platform. The northern location was semi-exposed, while the western location was exposed to wave action (see de Kluijver, 1991). The geo-morphological structure of the northern location is characterized by a series of channels extending to the northwest towards the open sea, and are separated by ridges. The ridges and channels showed an alternating pattern along the shore. The western location shows similar heights and widths of channels and ridges as the northern location, but the geo-morphological features are more irregular. The ridges form rather discrete patches enclosed by channels which also submerged during low tide (for more details see Reichert et al., submitted). At both locations, the substratum was mostly relative soft natural red sandstone, and the difference between mean high water spring (MHWS) and mean low water spring (MLWS) is 2.62 m (Lüning, 1985).

The species assemblages in the northern location showed distinct vertical zones, whereas in the western location such conspicuous bands did not occur. Due to the seawall along the western part of the island high-shore assemblages were basically non-existent at the rock-platform of the western location. The mid-shore assemblages of the western location were similar to those at low-shore. For the lower intertidal, both shores harboured qualitatively similar algal and invertebrate assemblages. The upper intertidal at the northern location was dominated by green algae of the genus *Ulva*. Most abundant invertebrates were tube-building polychaetes (mostly *Polydora ciliata*, *Fabricia sabella*). The mid-shore was dominated by the large brown alga *Fucus serratus*, encrusting algae (*Ralfsia verrucosa*, *Phymatolithon lenormandii*), the red alga *Chondrus crispus* and the seasonal green alga *Rhizoclonium tortuosum*. Characteristic invertebrates were the blue mussel *Mytilus edulis* and the periwinkle *Littorina littorea*. At the lower intertidal, most abundant organisms were the algae *F. serratus*, *P. lenormandii*, *C. crispus* and the articulated coralline *Corallina officinalis* as well as the snails *L. littorea*, *L. mariae*/*obtusata* (identified as a species complex) and *Gibbula cineraria* and the Spirorbid polychaetes (mostly *Spirorbis spirorbis*). Moreover, there were discrete patches in the lower intertidal harboured a special assemblages mostly characterised by green algae (*Ulva lactuca*, *Spongomorpha arcta*), red algae (*Rhodothamniella floridula*, *Ceramium rubrum*) and tube-building polychaetes. In addition to these general patterns of distribution, there is a considerable microhabitat variation due to complex geo-morphological structure of the substratum (personal observation).

Sampling design

At the semi-exposed northern location, two transects (separated by ca. 65 metres) were selected at random from a set of possible transects, comparable in terms of type and slope of the substratum (Fig. 1). Due to the small vertical and horizontal extension of the rocky-platform we had to select one transect at high- and the other at low-shore. Thus, the distance between transects is measured perpendicular to the island. The length of the transects ranged between 25 and 40 metres. Along each transect, six and five plots respectively (separated by 5 - 40 metres) were chosen at random from a larger pool of plots, which were examined in a former study with reference to the community structure. Thus, for each plot the species assemblage was well-known by the results of a previous community analysis (Reichert et al., in prep.). The distance between plots was measured alongshore, and thus horizontal variation was sampled. Five replicated quadrats, separated by about one metre, were selected randomly at each plot.

At the exposed western location, two transects (separated by ca. 45 metres) were selected randomly from a set of possible transects, comparable in terms of type and slope of the substratum as well as vertical tidal height (Fig. 1). The length of the transects ranged between 7 and 10 metres. As for the northern location, along each transect plots were selected at random (three and two plots respectively, separated by 4 - 10 metres) from a larger pool of plots examined previously by means of a community analysis (Reichert et al., in prep.). Five replicated quadrats (separated by about one metre) were sampled randomly at each plot. For this location we sampled the transects across the vertical axes at low-shore.

The positions of the 1st and 5th replicated quadrat in both study locations were recorded using a differential global positioning system (Geo XT, Trimble, Germany) with a mean accuracy of 1-2 m in the field. The positions of the remaining replicates were determined by recording their distance in situ, in *x* and *y* spatial coordinates, from the georeferenced replicates. The prevailing coordinates were processed with the programme ArcGIS 9.0 (ESRI).

At each study locations, all plots (i.e. 55 and 25 quadrats respectively) were sampled at 3-month intervals over 2 years (summer 2004 - spring 2006). All plots at each location were sampled at each 3-month interval within a period of a few days.

The height value of each replicated quadrat was received from the digital elevation model, generated for both study locations. The height values refer to the height Normal Null (NN) of the German height reference system (hereafter: refer to height NN), and was taken out of the digital elevation model by means of the programme ArcGIS 9.0 (ESRI). At the northern location, the height difference (reference: height NN) was on average 0.75 m between transects, less than 0.40 m at the scale of plots and less than 0.20 m at the scale of replicates. At the western location, the difference was on average 0.10 m between transects as well as less than 0.30 m between plots and replicates.

Site Map and digital elevation model

Figure 1 was created on the basis of georeferenced black & white (b/w) orthophotos supplied by the Department Geomatics of the HafenCity University Hamburg, Germany. A digital elevation model (DEM) was generated by automatic digital image correlation for the northern and western study location. The DEM refers to the height Normal Null (NN) of the German height reference system (DHHN). A detailed description of the generation of the orthophotos and the DEM is given in Reichert et al. (submitted).

Survey methods

In general, the communities comprised three different structural layers: top, middle and encrusting layer. The top layer (TL) usually consisted of thalli of large brown algae. The middle layer (ML) was represented by epiphytic, epizoic and endozoic species growing erect from the substrate, but not reaching the top layer. The encrusting layer (EL) was formed by epilithic organisms adhering directly to the substratum (see also de Kluijver, 1991, 1993; Reichert et al., in prep.). In each structural layer the percentage cover of the vertical projection of sessile, slow moving invertebrates, and algae was estimated, using a 0.25 m² quadrat. Some species were combined into a complex if the taxonomic position was tentative or if the morphological distinctions between two species were difficult to quantify or too time consuming to investigate. Examples of species combined into a complex are in Reichert and Buchholz (2006).

Data analyses

Minimal area

Minimal area tests were performed for each of in total seven plots at our study locations. In summer 2004, ten 0.25 m² quadrats were sampled at each plot which was characterised by a certain community type (Reichert et al., in prep.). Thus, the seven plots well-described the community structure which occurred at the study locations. The minimal area was calculated with the Programme MINAR (Kaandorp, 1986). The algorithm used in this programme has been described by Weinberg (1978). In this, the similarity is calculated between each possible combination of subsets of m elements out of the ten sampled quadrats, where the same element is not use twice in one combination ($1 \leq m \leq 5$). The data were log-transformed and similarity was calculated with the Bray-Curtis coefficient. The five similarity values calculated were used as a function of the sampled surface. The level of which the minimal area is reached has been artificially chosen. We followed Weinberg (1978) who suggested a similarity level of 70 % between samples. The values for the minimal area ranged beween 0.5 m² and 1.0 m². Thus, the sampled area of five quadrats (1.25 m²) seemed to be sufficient for reaching the minimal area, when the similarity level of 70 % is used.

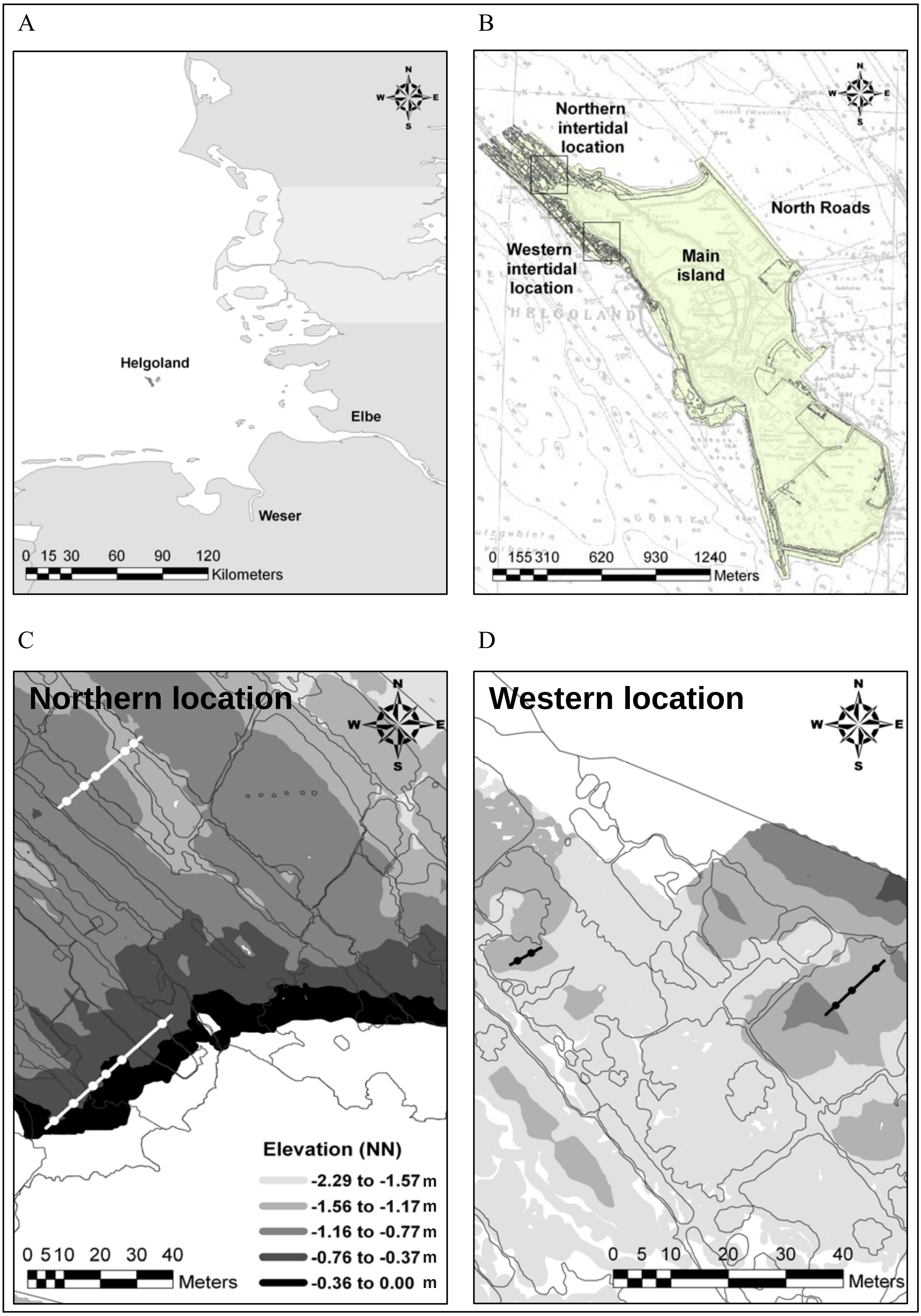

Figure 1 (A) Location of Helgoland in the German Bight, North Sea; (B) the island with the northern and western intertidal location; the scale of transects and plots at the (C) northern and (D) western study location with the drawn contours of the surface morphology and the elevation in metres refers to the height Normal Null (NN) of the German height reference system.

Spatial patterns of abundance of specific algae and invertebrates

Before we used estimates of variance components to evaluate the spatial variation in the abundance of algae and invertebrates, we selected most variable species from the whole pool of algae and invertebrates found. Therefore, we ran a principal coordinate analysis (PCoA; Anderson, 2003) with fourth-root transformed data for algae and log-transformed data for invertebrates, using the Bray-Curtis index thereafter. For the PCoA, we excluded all algal and invertebrate species with a total abundance < 8 % to prevent too much zeros in the data matrix. Due to in total 8 times of sampling, the excluded algae and invertebrates were such species which occurred < 1% per season at the northern and western study location, respectively. For the northern location, we did the PCoA with 36 algae and 27 invertebrates, while for the western location the analysis was run with in total 27 algae and 21 invertebrates.

For the species that correlated most to the formation of the principal coordinates, we estimated variance components to evaluate the variation in the abundance of these species among transects and plots at the northern and western location, respectively. Since our sampling design was not balanced due to the varying number of plots at each transect we used the restricted maximum likelihood method (REML), and also a two-way nested ANOVA with the Satterthwaite approximation (Sokal & Rohlf, 1995). Both methods used were a fully nested design with all factors random. In the design, plots were nested in transects. The REML method has been generally accepted as having good properties for unbalanced designs (Robinson, 1987; Searle, 1995). The relative variance components were estimated for each source of variation in (1) REMLs by using the Newton-Raphson iteration and (2) ANOVAs by using the observed mean squares to estimate terms identified in the expected mean squares (Searle et al., 1992; Winer et al., 1991). For the REML method the significance of random factors was tested using an asymptotic significance test, whereas for the ANOVA method F-ratio testing was produced by the STATISTICA output (StatSoft, 2001). The validity of likelihood ratio tests however has been called into question because they rely on large sample approximations (Searle, 1987; Singer, 1998). Since we have relatively small samples the significance test tended to be too conservative, and thus the power of detecting a significant variance component will be reduced. Therefore, we (1) used REML to estimate the components and checked against the ANOVA method: both methods gave approximately the same results. Sometimes one or more estimates from the ANOVA method were negative; then, (2) these estimates were set to zero, removed from the model and the estimates for the remaining factor re-calculated (Fletcher & Underwood, 2002). Thereafter, (3) we used the

ANOVA approach for hypothesis testing. we used the ANOVA approach for hypothesis testing.

We used untransformed data for all analyses to provide variance components comparable across all data (Fraschetti et al., 2005). The assumption of homogeneity of variance was checked by Cochran's C test prior to analysis. When the variances were not homogeneous, we set the critical levels to a value equal to the p-value for variance heterogeneity (Underwood, 1997). Non-significant effects from analyses can still be interpreted if homogeneity is not reached (Benedetti-Cecchi, 2001; Underwood, 1997). For all analyses the STATISTICA software package (StatSoft, 2001) was used.

Relationship between elevation and specific algae and invertebrates

First, we used variance components, as explained for the biotic variables, to compare spatial variation across scales on the elevation within each location. Then, we explored the relationships between elevation and the most variable algae as well as invertebrates among the spatial scales at the northern and western location. This was done in using (1) frequency of occurrence and (2) maximal cover by means of the 90 % upper percentile of algae and invertebrates. This approach examines the possibility that environmental factors, such as elevation, constrain the frequency of occurrence and the maximal cover of macroalgae and invertebrates (Trush et al., 2005; Giménez et al., 2006). For this approach, we defined four and three categories for elevation at the northern and western location respectively (northern location: 5.5-5.99, 6-6.49, 6.5-6.99, 7-7.49 m; western location: <7.15, 7.15-7.249, 7.25-7.349 m). Then, for each algae and invertebrate, data of cover were binned into these categories, according to the elevation present in each replicated quadrat, and the frequency of occurrence as well as the maximal cover was calculated for each category.

RESULTS

Spatial patterns of abundance of algal and invertebrate assemblages

At the northern intertidal location a total of 36 macroalgae and 440 samples were analysed. The two principal axes obtained by PCoA on macroalgal abundance explained 61 % of the total variance (Fig. 2). Species of the green alga *Ulva*, the encrusting red alga *Phymatolithon lenormandii* and the large brown alga *Fucus serratus* correlated best with the first axis. The encrusting brown alga *Ralfsia verrucosa* showed a high correlation with the second axis.

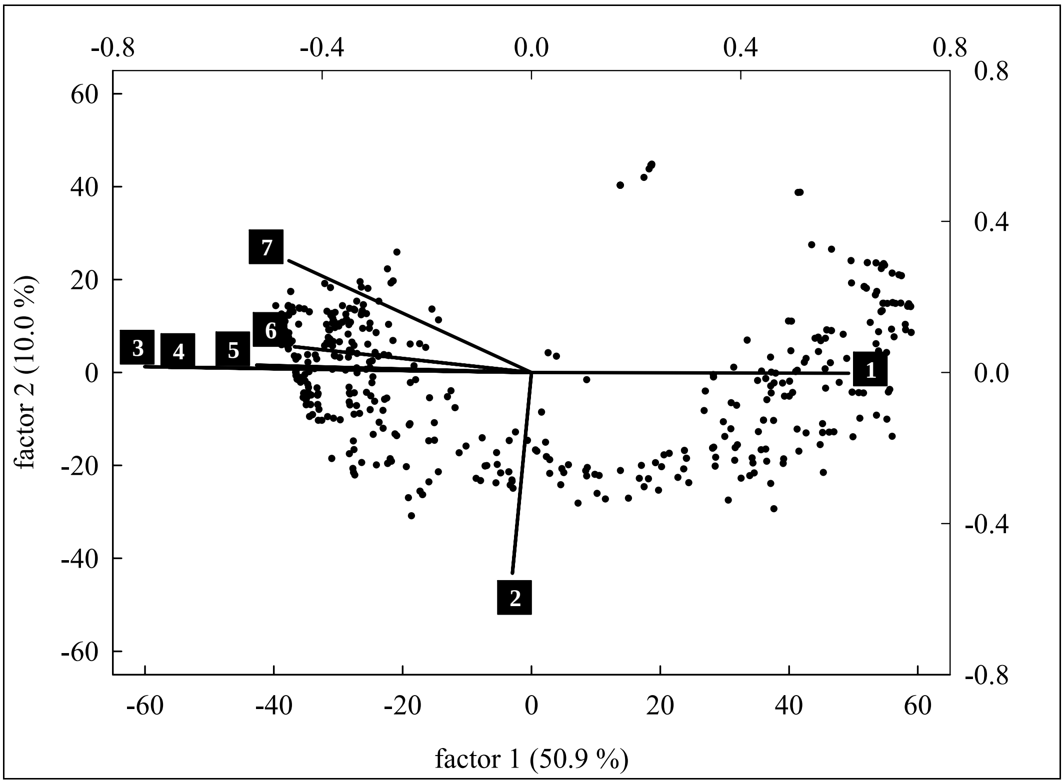

Figure 2 Biplot of principal coordinate analysis on macroalgae at the northern location. Points are replicates per time of sampling. Lines show correlation among macroalgal species and the first two coordinate axes. The numbers in the plot indicates species as follows: 1: *Ulva* spp., 2: *Ralfsia verrucosa*, 3: *Phymatolithon lenormandii*, 4: *Fucus serratus*, 5: *Chondrus crispus*, 6: *Cladophora rupestris* and 7: *Corallina officinalis*.

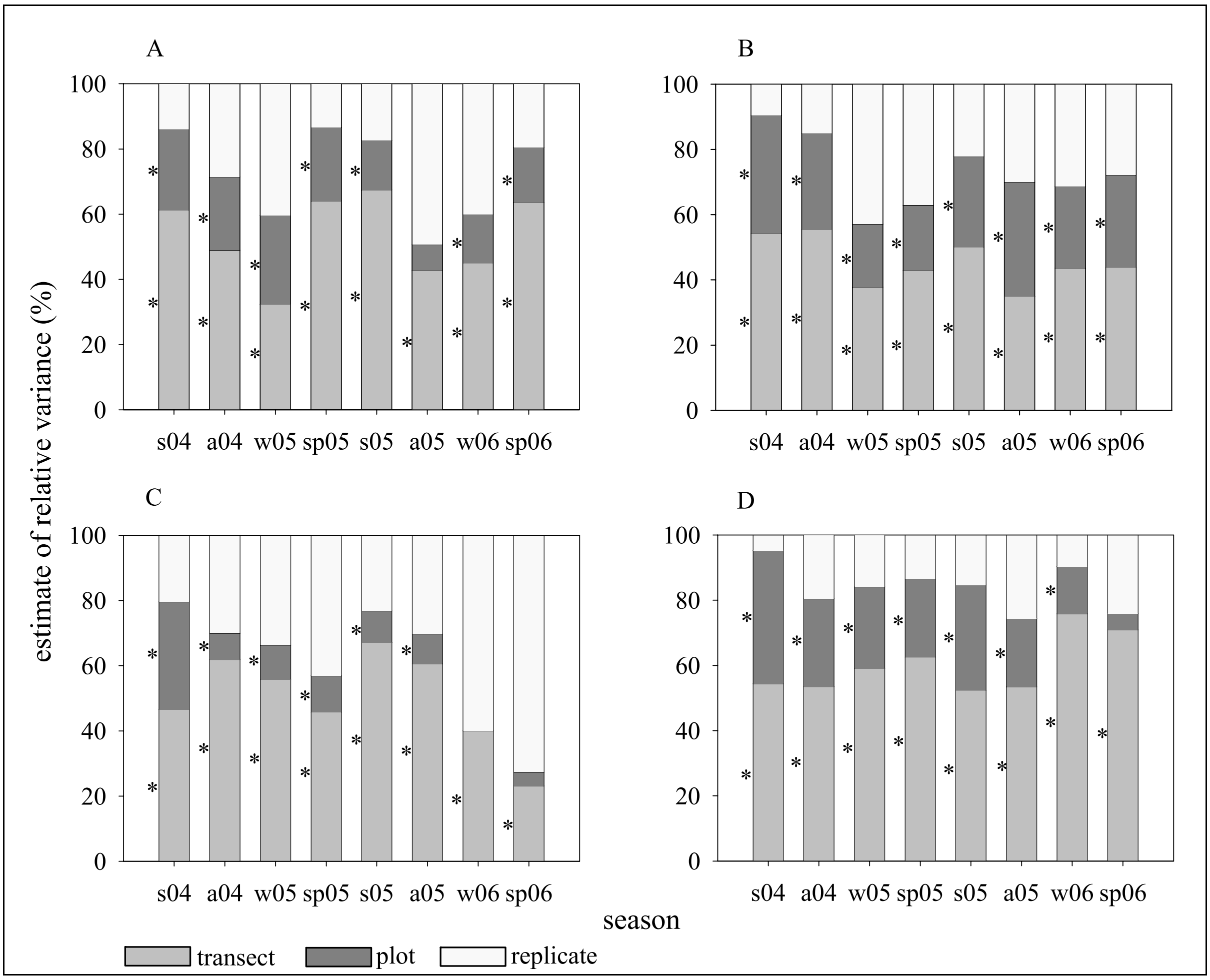

Figure 3 Estimates of variance components and ANOVA testing for spatial variability in cover of (A) *Fucus serratus*, (B) *Chondrus crispus*, (C) *Corallina officinalis* and (D) *Phymatolithon lenormandii* among transects, plots and replicates at the northern location over the sampling seasons (* $p < 0.05$).

The estimates of variance components of all four macroalgal species were highest at the scale of transect (Fig. 3). For these algae, the variability among transects was significant for all sampling dates. Also the variability among plots was significant for all times of sampling, except of a few dates of the second sampling year (*Fucus serratus*: a05; *Corallina officinalis*: w06, sp06; *Phymatolithon lenormandii*: sp06). At the scale of transect the estimates of variance components of the encrusting alga *P. lenormandii* were consistent overtime.

Besides the macroalgae, a total of 27 species of invertebrates were analysed at the northern intertidal location. The two principal axes obtained by PCoA on the abundance of invertebrates explained 53 % of the total variance (Fig. 4). The snail *Gibbula cineraria* and species of Thoracica (e.g. *Elminius modestus*, *Verruca stroemia*) correlated best with the first axis, whereas burrowing polychaetes (e.g. *Polydora ciliata*) showed a high correlation with the second axis.

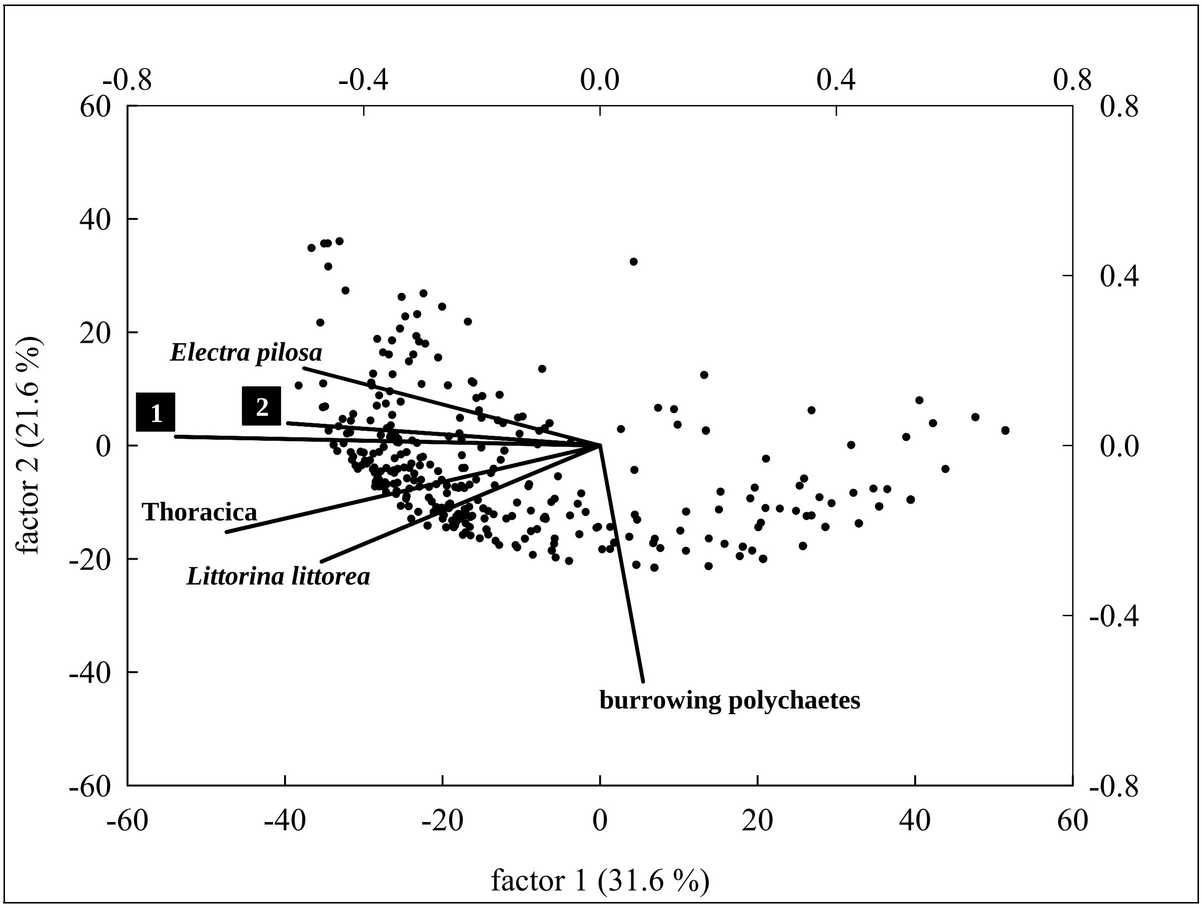

Figure 4 Biplot of principal coordinate analysis on invertebrates at the northern location. Points are replicates per time of sampling. Lines show correlation among invertebrate species and the first two coordinate axes. The numbers in the plot indicates species as follows: 1: *Gibbula cineraria* and 2: Spirorbidae.

Species of the Spirorbidae and the bryozoan *Electra pilosa* showed highest estimates of variance components at the scale of transect (Fig. 5a, d). The variability at the scale of transect was significant for all sampling dates, except of the variation in the cover of *E. pilosa* in spring 2005 and 2006 (Fig. 5d). The periwinkle *Littorina littorea* was the only invertebrate which showed high variance among plots; here, the variability was significant in all sampling dates (Fig. 5c). The burrowing polychaetes showed highest variance among replicates (Fig. 5b). Over the time of sampling the variance among the spatial scales was inconsistent for all invertebrates.

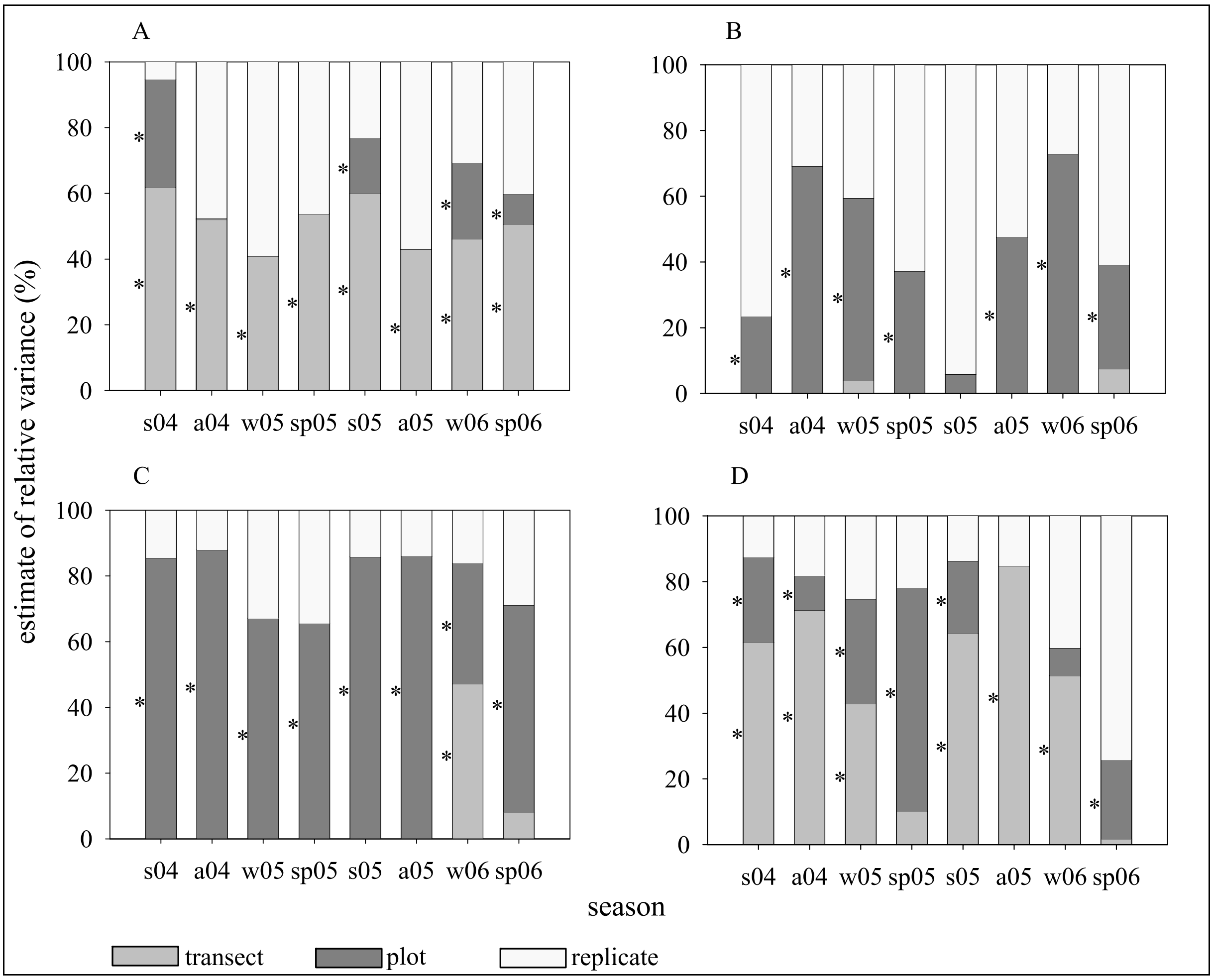

Figure 5 Estimates of variance components and ANOVA testing for spatial variability in abundance of (A) Spirorbidae, (B) burrowing polychaetes, (C) *Littorina littorea*, (D) *Electra pilosa* among transects, plots and replicates at the northern location over the sampling seasons (* $p < 0.05$).

At the western intertidal location a total of 36 macroalgae and 200 samples were analysed. The two principal axes obtained by PCoA on the macroalgal cover explained 59 % of the total variance (Fig. 6). The green alga *Ulva lactuca* and the red alga *Mastocarpus stellatus* correlated best with the first axis. A high correlation with the second axis showed also *M. stellatus* as well as the brown alga *Fucus serratus*. The red alga *Chondrus crispus* showed low correlation with the principal axes.

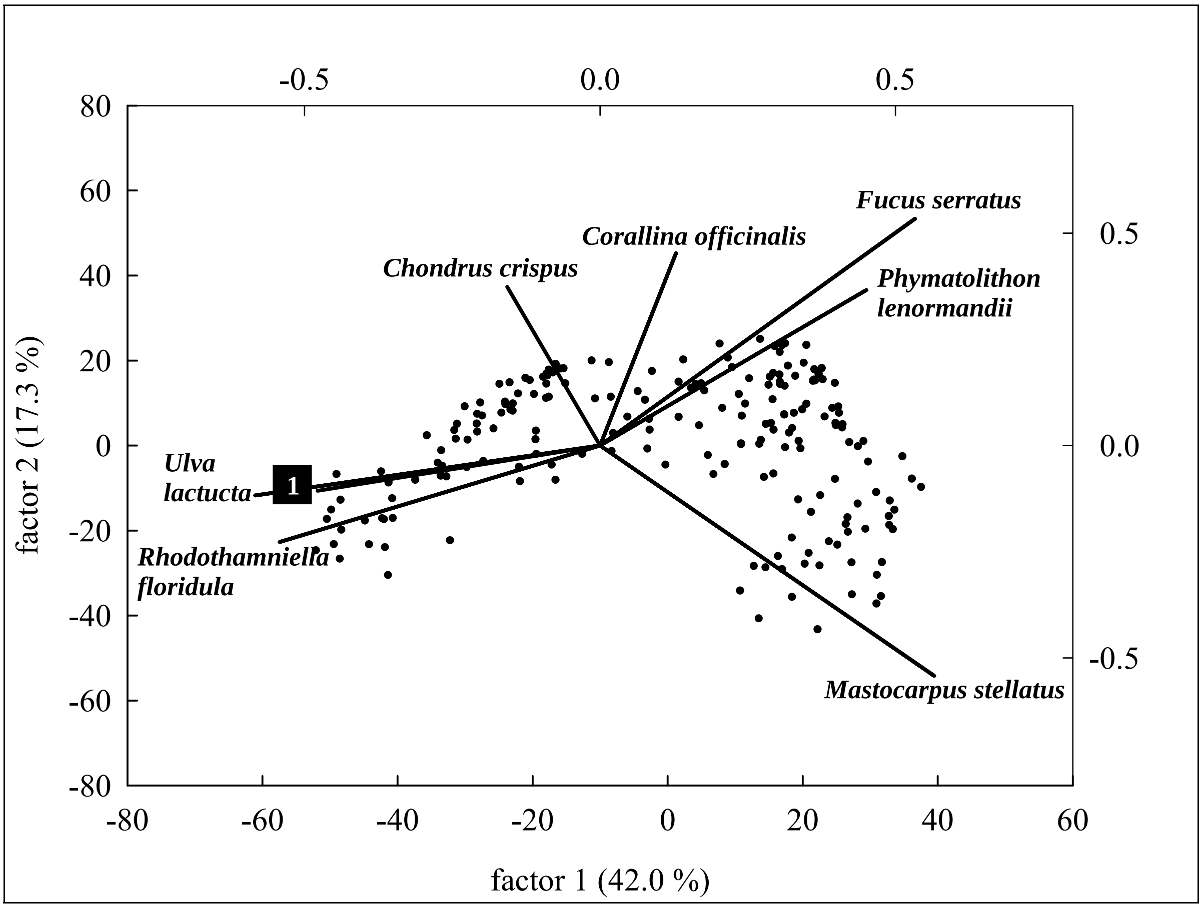

Figure 6 Biplot of principal coordinate analysis on macroalgae at the western location. Points are replicates per time of sampling. Lines show correlation among algal species and the first two coordinate axes; the number 1 in the plot indicates the red alga *Ceramium deslongchampsii*.

The estimates of residual variance of the cover of the brown alga *Fucus serratus* and the red alga *Chondrus crispus* were larger than the variance associated with plots or transects, indicating that the variation among replicates was important (Fig. 7a, b). At the scale of replicate the estimates of variance components of the red alga *C. crispus* were consistent overtime. The encrusting alga *Phymatolithon lenormandii* showed high variance among plots; here, the variability at the scale of plot was significant for all sampling dates, except of the variation in the cover of *P. lenormandii* in spring 2006 (Fig. 7d). The coralline alga *Corallina officinalis* showed an inter-annual variation (Fig. 7c). In the first period of sampling (s04-sp05) the highest variance occurred among replicates, while in the second sampling period (s05-sp06) the cover showed most variance among plots.

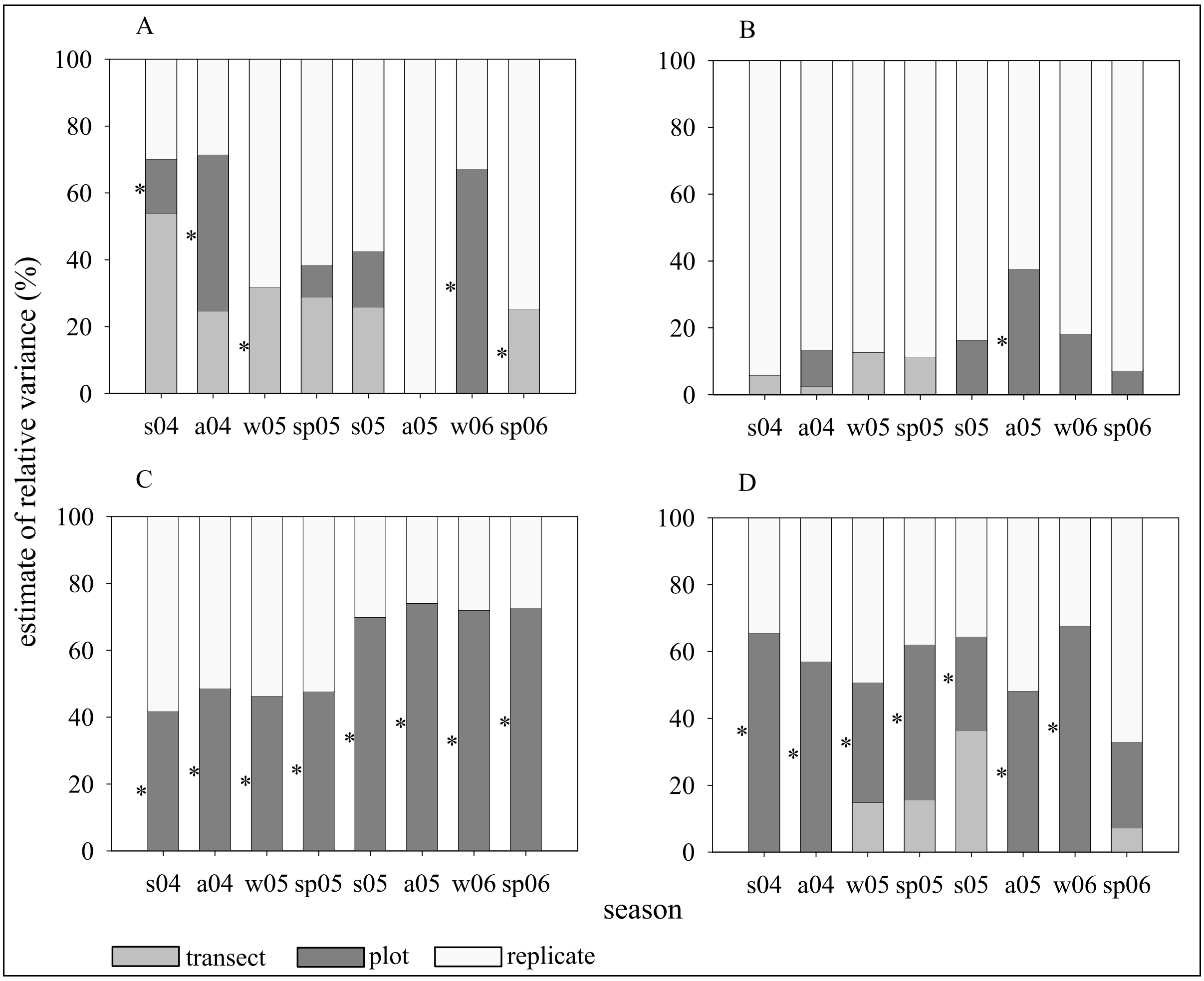

Figure 7 Estimates of variance components and ANOVA testing for spatial variability in cover of (A) *Fucus serratus*, (B) *Chondrus crispus*, (C) *Corallina officinalis* and (D) *Phymatolithon lenormandii* among transects, plots and replicates at the western location over the sampling seasons (* $p < 0.05$).

Besides the macroalgae, a total of 21 species of invertebrates were analysed at the western intertidal location. The two principal axes obtained by PCoA on the abundance of invertebrates explained 56 % of the total variance (Fig. 8). Burrowing polychaetes (e.g. *Polydora ciliata*) correlated best with the first axis, while species of the Actiniaria (e.g. *Sagartiogeton undatus*, *Sagartia troglodytes*) showed a high correlation with the second axis. Lowest correlation with the principal axes showed the periwinkle *Littorina littorea*.

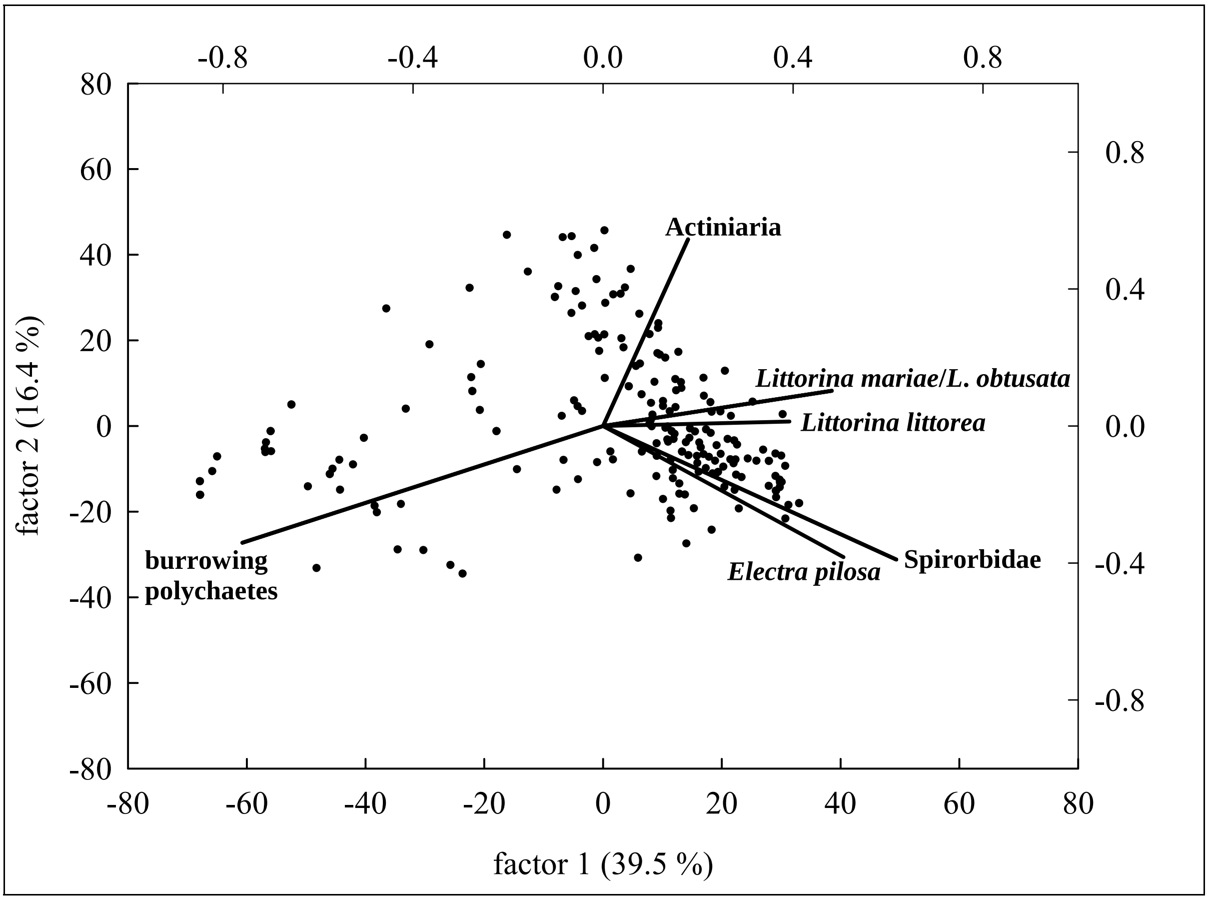

Figure 8 Biplot of principal coordinate analysis on invertebrates at the western location. Points are replicates per time of sampling. Lines show correlation among invertebrate species and the first two coordinate axes.

The abundance of species of the Spirorbidae and the bryozoan *Electra pilosa* showed largest variance at the smallest spatial scale, i.e. the replicates (Fig. 9a, d). High variance among plots occurred in the abundance of burrowing polychaetes, such as *Polydora ciliata*; here, the variability was significant for all sampling dates (Fig. 9b). The periwinkle *Littorina littorea* showed most variability among transects (s04, w05, sp06) and replicates (a04, sp05, w06; Fig. 9c); for only a few sampling dates the variability was significant among plots (s04, s05-w06) and transects (w05, sp06). At the spatial scales a temporal consistency did not occur in the estimates of variance components of the invertebrates (Fig. 9).

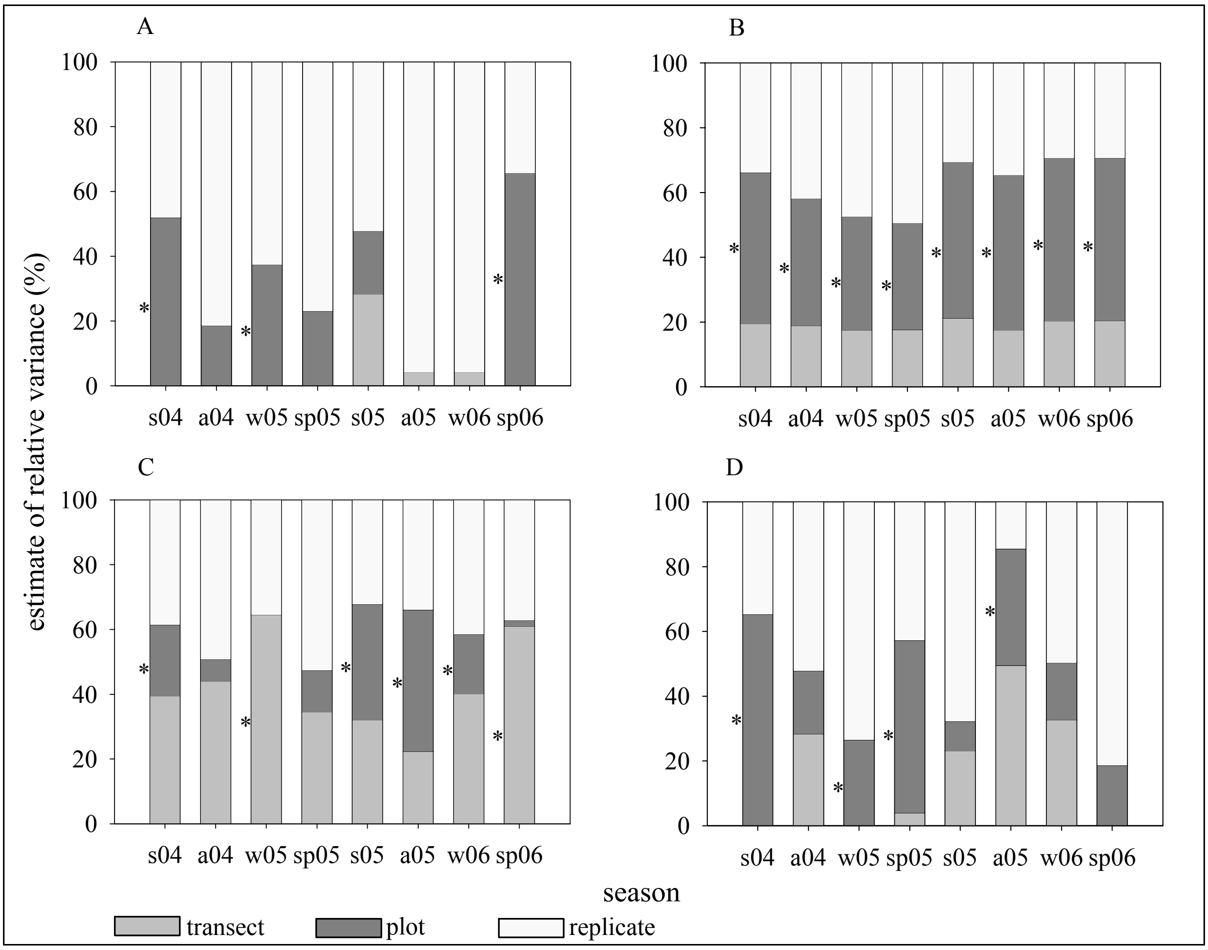

Figure 9 Estimates of variance components and ANOVA testing for spatial variability in abundance of (A) Spirorbidae, (B) burrowing polychaetes, (C) *Littorina littorea* and (D) *Electra pilosa* among transects, plots and replicates at the western location over the sampling seasons (* p < 0.05).

Relationship between elevation and algae or invertebrates

At the northern intertidal location most variability in elevation occurred among transects, as indicated by the large estimates of relative variance (Tab. 1). At the scale of transect and plot the variability was significant. For the western intertidal location, the largest variability in elevation appeared among plots; at this scale the variability was significant (Tab. 1). At the northern and the western location neither a linear nor a nonlinear relationship between elevation and the specific maroalgae and invertebrates occurred (Fig. 10-13).

At the northern location, however, we have shown that the elevation determined the frequency of occurrence and the maximal cover of most macroalgae and invertebrates (Fig. 10, 11). The large brown alga *Fucus serratus* showed highest cover at low elevations (> 6.5 m) and the frequency of occurrence as well as the upper percentile increased slightly with the decreasing elevation (Fig. 10a). The red algae *Chondrus crispus* and *Phymatolithon lenormandii* increased from high to low elevation and then tended to decrease slightly; Also the frequency of occurrence and the upper percentile increased with the decreasing elevation and then decreased slightly at the lowest elevation scale (7.0-7.5 m; Fig. 10b, d). The coralline alga *Corallina officinalis* did not occur at high elevations (< 6.0 m) and the frequency of occurrence as well as the 90 % upper percentile showed a conspicuous increase from the elevation scale of 6-6.49 m to the scale of 6.5-6.99 m and 7-7.49 m (Fig. 10c).

Species of the Spirorbidae increased from high to low elevation; also the frequency of occurrence and the upper percentile (90 %) increased with the decreasing elevation (Fig.11a). The cover of burrowing polychaetes showed no relationship with elevation. The polychaetes occurred with a probability of about 100 % and the upper percentile ranged between 0.4 and 0.5 % cover of the polychaetes irrespective of the scale of elevation (Fig. 11b). The periwinkle *Littorina littorea* increased from high (< 6.0 m) to intermediate elevation (6.0 - 7.0 m) and decreased at low elevation (> 7.0 m); the upper percentile also showed maximal abundance of the periwinkle at the intermediate scales of elevation (6-6.49 m and 6.5-6.99 m), while the frequency of occurrence ranged between 80 and 100 % at all elevation scales (Fig. 11c). The bryozoan *Electra pilosa* showed maximal cover at lowest elevation; the frequency of occurrence was 100 % at the elevation scales of 6.5-6.99 m and 7.0-7.49 m, while at the highest elevated scales *E. pilosa* only occurred with a probability of about 10 % (Fig. 11d).

At the western location, the elevation did mostly not constrain the frequency of occurrence and the maximal cover of the macroalgae and invertebrates (Fig. 12, 13). All four macroalgae occurred with a probability of 100 % irrespective of the scale of elevation (Fig. 12). Maximal cover of *Fucus serratus* as well as of *Phymatolithon lenormandii* was about 4 % irrespective of the scale of elevation (Fig. 12a). The red alga *Chondrus crispus* showed slight decreasing values of the upper percentile with decreasing elevation, whereas the upper percentile of the cover of *Corallina officinalis* increased with the decreasing elevation (Fig. 12b, c).

Species of the Spirorbidae were not constrain in their frequency of occurrence and the maximal cover due to the elevation; they occurred with a probability of 100 % and the upper percentile was about 0.4 % cover of Spirorbidae irrespective of the scale of elevation (Fig. 13a). The burrowing polychaetes showed a maximum cover at the lowest scale of elevation (7.25-7.35 m), while the frequency of the polychaetes occurrence was 100 % irrespective of the scale of elevation (Fig. 13b). The periwinkle *Littorina littorea* occurred with maximal abundance at the intermediate scale of elevation, while the probability to come across the periwinkle decreased with decreasing elevation (Fig. 13c). The bryozoan *Electra* *pilosa* showed maximal cover as well as the highest frequency of occurrence at the intermediate elevation scale (7.15 m-7.25 m; Fig. 13d).

Table 1 Estimates of variance components from REML and ANOVA method, and ANOVA testing for spatial variability in elevation carried out separately in each study location at the scale of transect and plot. The REML and ANOVA method gave approximately the same estimations.

Source	df	MS	F	p	VC ($x10^{-3}$)	VC (%)
Northern intertidal location						
Transect	1	8.18	97.60	< 0.001	294.58	94.57
Plot	9	0.08	233.97	< 0.001	16.56	5.32
Residual	38	0.00			0.36	0.11
Western intertidal location						
Transect	1	0.00	0.13	ns	0.00	0.00
Plot	3	0.07	14.60	< 0.001	10.37	67.57
Residual	17	0.01			4.98	32.43

VC, variance component; ns, not significant.

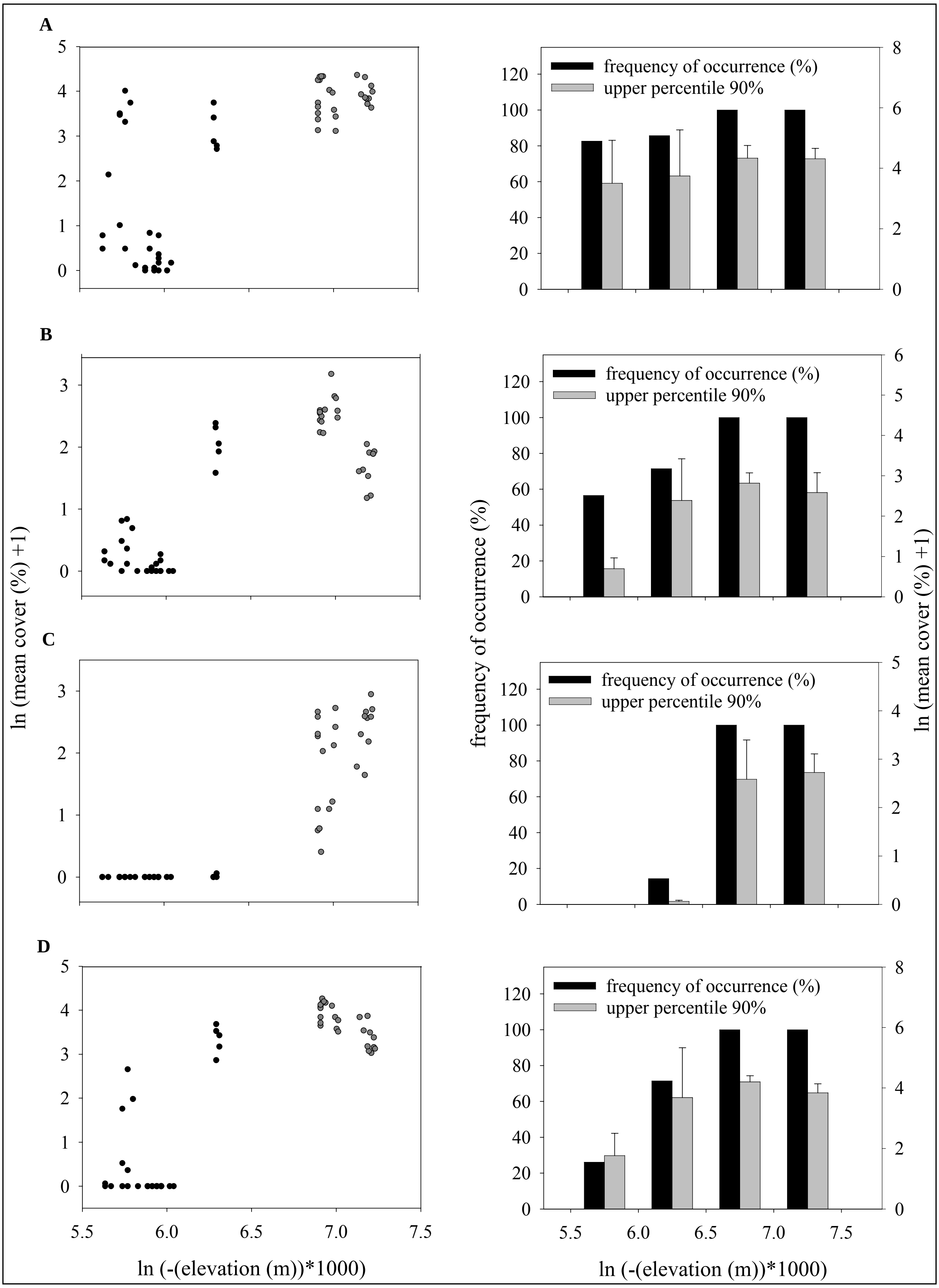

Figure 10 Left-hand side: Scatterplot showing the relationship between elevation and cover of (A) *Fucus serratus*, (B) *Chondrus crispus*, (C) *Corallina officinalis* and (D) *Phymatolithon lenormandii* at the northern location; different colours represent different transects; elevation refers to the height Normal Null of the German height reference system. Right-hand side: The frequency of occurrence and the upper percentile (90 %) of these four macroalgae at the elevation scales (5.5-5.99 m, 6-6.49 m, 6.5-6.99 m, 7-7.49 m). Error bars are standard deviations. All variables are logarithmically transformed.

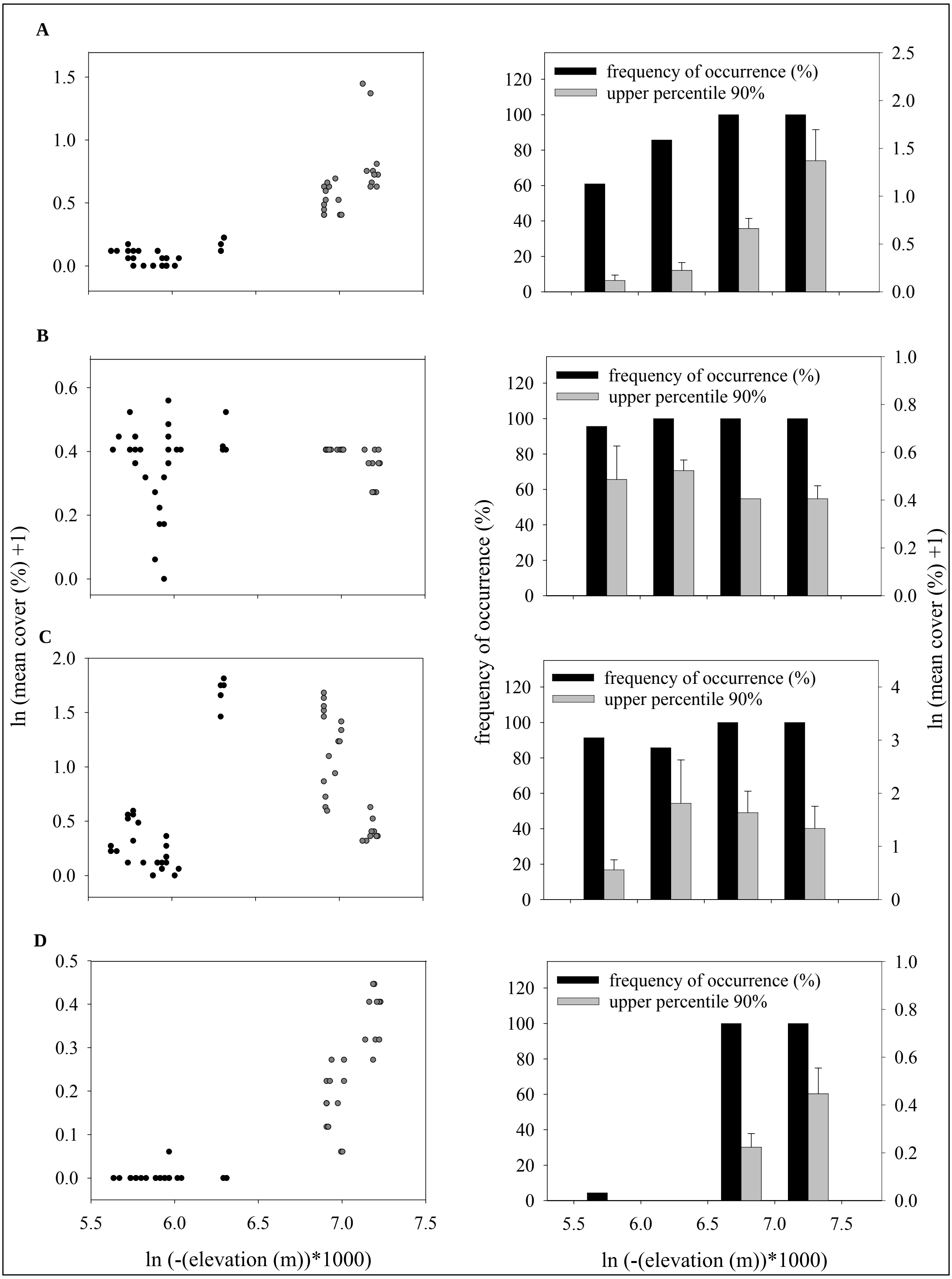

Figure 11 Left-hand side: Scatterplot showing the relationship between elevation and cover of (A) Spirorbidae, (B) burrowing polychaetes, (C) *Littorina littorea* and (C) *Electra pilosa* at the northern location; different colours represent different transects; elevation refers to the height Normal Null of the German height reference system. Right-hand side: The frequency of occurrence and the upper percentile (90 %) of these four invertebrates at the elevation scales (5.5-5.99 m, 6-6.49 m, 6.5-6.99 m, 7-7.49 m). Error bars are standard deviations. All variables are logarithmically transformed.

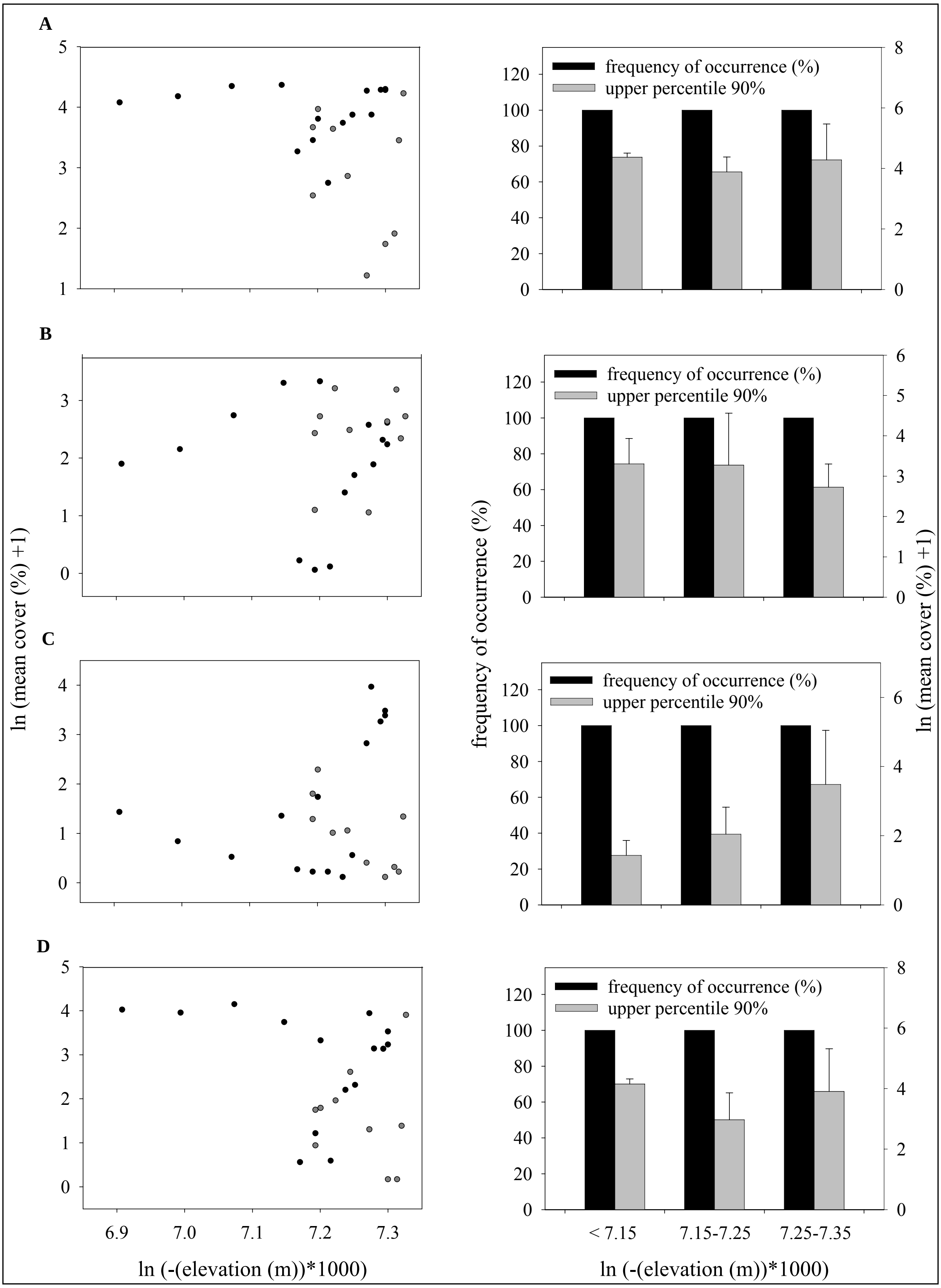

Figure 12 Left-hand side: Scatterplot showing the relationship between elevation and cover of (A) *Fucus serratus*, (B) *Chondrus crispus*, (C) *Corallina officinalis* and (D) *Phymatolithon lenormandii* at the western location; different colours represent different transects; elevation refers to the height Normal Null of the German height reference system. Right-hand side: The frequency of occurrence and the upper percentile (90 %) of these four macroalgae at the elevation scales (< 7.15 m, 7.15-7.25 m, 7.25-7.35 m). Error bars are standard deviations. All variables are logarithmically transformed.

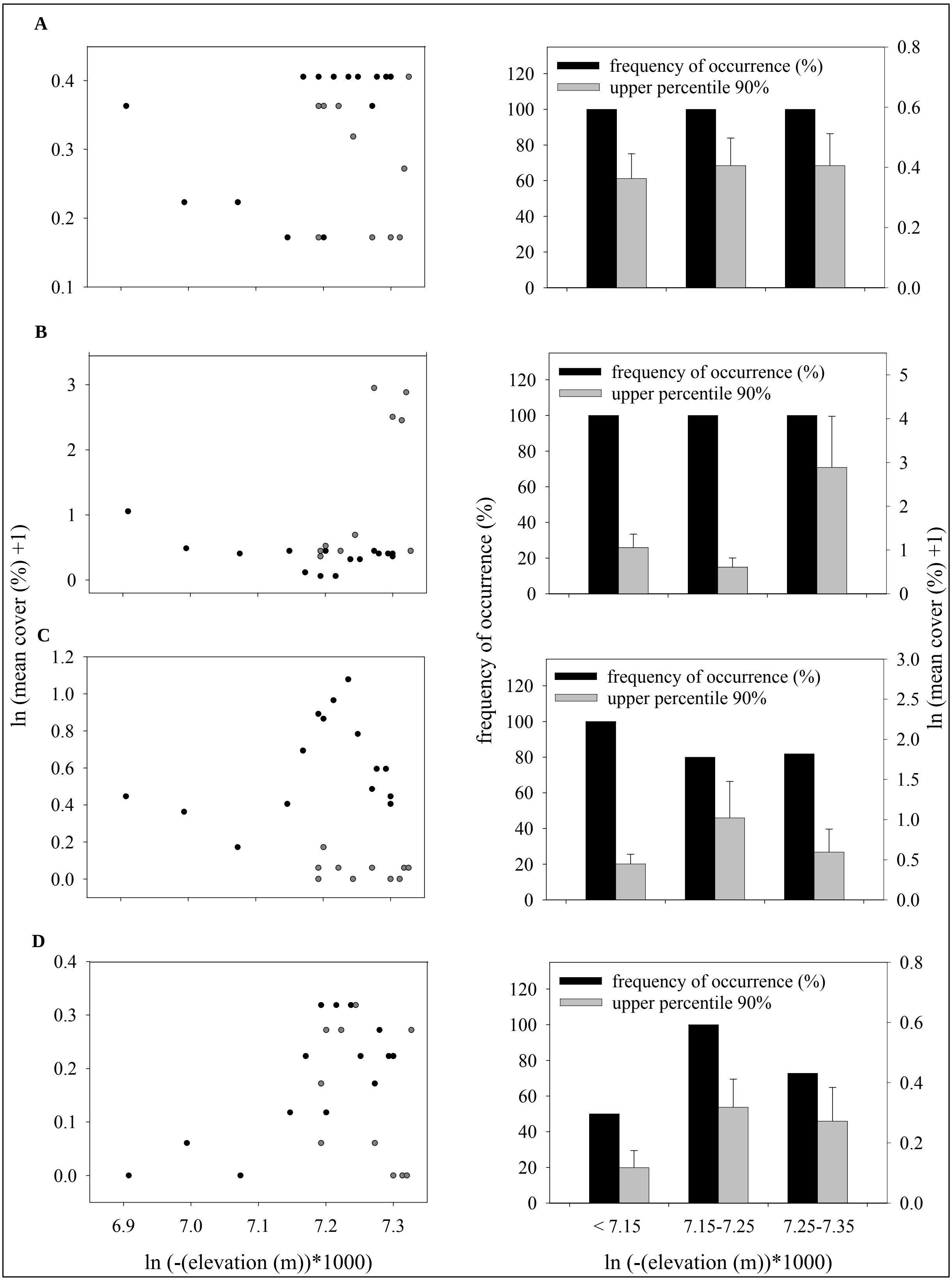

Figure 13 Left-hand side: Scatterplot showing the relationship between elevation and cover of (A) Spirorbidae, (B) burrowing polychaetes, (C) *Littorina littorea* and (C) *Electra pilosa* at the northern location; different colours represent different transects; elevation refers to the height Normal Null of the German height reference system. Right-hand side: The frequency of occurrence and the upper percentile (90 %) of these four invertebrates at the elevation scales (< 7.15 m, 7.15-7.25 m, 7.25-7.35 m). Error bars are standard deviations. All variables are logarithmically transformed.

DISCUSSION

For the intertidal locations at Helgoland we have shown, that variation in the abundance of individual macroalgae and invertebrates was mainly attributable to the factor transect at the northern location and to the factor replicate at the western location. At the northern as well as at the western location neither a linear nor a nonlinear relationship between elevation and the specific species occurred. However, we have shown that the elevation determined the frequency of occurrence and the maximal cover of most macroalgae and invertebrates at the northern location, but not at the western location.

Our data about the intertidal community at Helgoland show that the spatial patterns of the individual algal and invertebrate species were scale-dependent, but that there were differences between locations. The locations varied in 1) the scale at which variations of the algae and invertebrates were mainly highest (northern location: transect; western location: replicate) and 2) the response to the elevation (only at the northern location). Differences of the macroalgae and invertebrates between locations, e.g. the larger variation among transects at the northern location, may be attributed to the sampling design. However, the response to the elevation may be related with the differences in habitat structure, exposure or the presence of particular habitats occupied by characteristic species. For instance, the small variation in the abundance of macroalgae, such as *Fucus serratus* and *Phymatolithon lenormandii*, at low elevations of the northern location (log elevation range: 6.8-7.4 m) is in contrast to the high variability at the same range of elevation of the western location. Although the present study did not study causal processes explicitly, the patterns discussed here may provide some clues on the causes of spatial variation at the Helgoland rocky intertidal. In what follows we focus in patterns and processes occurring at each location separately.

Northern location

At the northern location, variability in the abundance of macroalgae and invertebrates among transects (separated by 65 metres) was a direct result of differences between the vertical heights, the high- and low-shore; this pattern was only consistent through time for the encrusting alga *Phymatolithon lenormandii*, but not for any invertebrate investigated. The elevation (refers to height NN) also showed most variation among transects. At high-shore most algae and invertebrates (e.g. *Chondrus crispus*, species of the Spirorbidae) were characterised by relatively low mean cover in contrast to higher values at low-shore; at high elevation the frequency of occurrence and the maximal cover of most macroalgae and invertebrates investigated were constrained. These distribution patterns indicate an association between elevation and the occurrence of these species. However, neither a linear nor a nonlinear relationship between elevation and the individual species occurred, such as it was the case in regression models between elevation and total abundance of the hard-bottom assemblages at the Helgoland rocky intertidal (Reichert et al., submitted).

The differences in the cover of algae and invertebrates may be a result of a number of physical factors which may have changed with the vertical height on the shore such as desiccation, extremes of temperature and salinity or lack of nutrients and food. Several species cope with long times of emersion, whereas most others do not have abilities to avoid or endure harsher physical factors high on the shore (see reviews: Newell, 1979; Norton, 1985). However, variation in the abundance of intertidal species according to the vertical height on the shore is not only attributable to physiological stresses, but also to biological interactions, such as competition (e.g. Connell, 1961; Hawkins & Hartnoll, 1985), grazing (e.g. Lubchenco, 1982; Jenkins et al., 1999a, b) and predation (e.g. Paine, 1974; Lubchenco & Menge, 1978). Also habitat provision by macroalgae which show a distinctive zonation pattern may be a prominent process maintaining differences in epiphytic invertebrates, such as polychaetes and bryozoans, among vertical tidal heights. Personal observations showed a prevalent occurrence of Spirorbid polychaetes (mainly *Spirorbis spirorbis*) and *Electra pilosa* particularly on thalli of the large brown alga *Fucus serratus*. This biological interaction corroborated the findings of many other studies on rocky shores, reporting a close relationship between the occurrence of *Fucus* species and these epiphytic invertebrates (e.g. Stebbing, 1973; Knight-Jones & Knight-Jones, 1977; Gillandt, 1979; Hartmann-Schröder, 1996).

Polychaetes, such as *Polydora ciliata* and *Fabricia sabella*, and the periwinkle *Littorina littorea* were an exception: mean cover showed the largest variance components among replicates (separated by < 1 m) and plots (separated by 4 - 40 m) respectively, and not among transects as in the case of the above mentioned invertebrates and algae. The polychaetes and the periwinkle showed no relationship to the vertical height on the shore. These patterns suggest that other factors not associated with vertical elevation on the shore are also important in affecting spatial patterns of invertebrate distribution. Why the polychaetes and periwinkle mostly varied among replicates and plots respectively is not possible to explain. The sessile polychaetes may be affected by small-scale substrate heterogeneity directly constraining abundance, such as the hardness of the substrate in which they burrow (Gillandt, 1979), or by localized behaviour of mobile predators, such as seagulls. Prominent process maintaining differences in *L. littorea* as a species in which adults can disperse and respond to their habitat may be differential substrate heterogeneity (Chapman & Underwood, 1994; Underwood &

Chapman, 1989) and behavioural intra- or interspecific interactions (Dayton, 1971; Hawkins & Hartnoll, 1985; Kelaher & Underwood, 2003). The geo-morphological structures along each transect may govern patterns at scales smaller than a few metres (Underwood & Chapman, 1996), such as the alternating pattern of ridges and channels along the transect. Personal observations showed that other snails (e.g. *Gibbula cineraria*, *Littorina mariae*/*obtusata* complex) dominated in the deeply elevated channels which are submerged during low tide. It appears that these snails pre-empt the channels, while *L. littorea* was forced back to the exposed elevated ridges with harsher physical conditions.

Western location

At the western location, high variability in the abundance of most macroalgae (e.g. *Fucus serratus*, *Chondrus crispus*) and invertebrates (e.g. species of the Spirorbidae, *Electra pilosa*) was among replicates (separated by 10s of centimetres). Small-scale spatial variation appears to be a general pattern of algal and invertebrate assemblages on rocky shores around the world (Aberg & Pavia, 1997; Chapman, 2002; Coleman, 2002; Underwood & Chapman, 1996). The variation among replicates may be explained by a topographic complexity across the low-shore of the western study location. The elevation (refers to height NN), as one topographic feature, however showed significant differences among plots and not among replicates, and neither a linear nor a nonlinear relationship between elevation and algal and invertebrate species occurred. In addition, the elevation did not constrain the frequency of occurrence and the maximal cover of the species. This indicates that at the western location other physical or biological processes, next to elevation, have an effect on the abundances of the individual macroalgae and invertebrates. Small-scale patchiness in sedimentation, in microhabitats as well as in the dispersal of propagules and post-settlement processes, such as competition, grazing and desiccation, are known to account for some of the variation in macroalgae among small spatial scale. For instance, propagules of *Sargassum muticum* settle within metres from their source (Kendrick & Walker, 1995) or survival of embryos of *Pelvetia fastigiata* varied among microhabitats (canopy present, red algal turf, exposed; Brawley & Johnson, 1991). To determine mechanisms causing the small-scale patterns in macroalgae in the present study, the local ecology of recruitment, survival, growth and dynamics of these algae have to be studied in manipulative experiments incorporating small spatial scales. Patchiness in macroalgae may be in turn a prominent process maintaining differences in epiphytic invertebrates, such as species of the Spirorbidae and the bryozoan *Electra pilosa*. As at the northern location, personal observations showed a close relationship between the small-scale variation in the abundance of *Fucus serratus* and these epiphytic invertebrates.

A temporal consistency in small-scale spatial variation, i.e. among replicates, was only shown for the red alga *Chondrus crispus*. A distinctive inter-annual variation pattern showed *Corallina officinalis* at the scale of plot and replicate (1st time period: most variance among replicates; 2nd time period: most variance among plots). This pattern indicates that the coralline alga became more abundant in the second sampling year, and thus defined patches at the western location that were too large to be detected at the scale of replicate. Although a period of two years appears too short to draw general conclusions about such temporal variation patterns, it appears that individual algae and particularly invertebrates tended to be inconsistent over time, as it was the case for the northern location.

In summary, although processes causing spatial patterns in individual algae and invertebrates cannot be determined from observational studies, the identification of relevant scales of variation helps to formulate hypotheses, and to design manipulative experiments or monitoring programmes at the appropriate scale. Our results verified that variation in most individual macroalgae and invertebrates was attributable to the factor transect at the northern location and to the factor replicate at the western location. At the northern location, processes structuring the algae and invertebrates appear to be associated with intertidal elevation, whereas other processes next to elevation, such as substrate heterogeneity, biological interaction, may structure the assemblages. To understand this small-scale variation it appears necessary to take a species specific approach which examines each individual species comprising the benthic assemblages separately. This appears logical considering the vastly different modes of life histories of macroalgae and invertebrates and the way this is manifested in patterns of their distribution and abundance. Furthermore, a monitoring may take into account that 1) individual algae and invertebrates varies at several scales, 2) scale-dependent variations depend on the location and 3) scale-dependent variation may be inconsistent through time. The identification of the characteristic scales of variation at each location helps to design a monitoring programme targeting the appropriate scale at each location separately. However, temporal inconsistencies of the scale-dependent variation show that monitoring should involve a multiple-scale sampling design. In the present study, particularly the invertebrate species showed inconsistency through time, independent of the location considered, and warn against using a one-scale sampling approach. Alternatively, monitoring may concentrate on species comprising algal and invertebrate assemblages which display least variation (Hartnoll & Hawkins, 1980). To date, for both locations at Helgoland the monitoring should consider variation at several spatial scales, and thus should follow a multiple-scale sampling approach.

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REFERENCES

Aberg, P. & Pavia, H., 1997. Temporal and multiple scale spatial variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. *Marine Ecology Progress Series*, **158**, 111-119.

Anderson, M., 2003. PCO: A FORTRAN computer program for principal coordinate analysis. Department of Statistics, University of Auckland, New Zealand.

Azovsky,A.I., Chertoprooda, E.S., Saburovab, M.A. & Polikarpovb, I.G., 2004. Spatio-temporal variability of micro- and meiobenthic communities in a White Sea intertidal sandflat. *Estuarine, Coastal and Shelf Science*, **60**, 663-671.

Bartsch, I. & Tittley, I., 2004. The rocky intertidal biotopes of Helgoland: present and past. *Helgoland Marine Research*, **58**, 289-302.

Benedetti-Cecchi, L., 2000. Predicting direct and indirect interactions during succession in a midlittoral rocky shore assemblage. *Ecological Monographs*, **70**, 45-72.

Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Marine Ecology Progress Series*, **215**, 79-92.

Benedetti-Cecchi, L., Bulleri, F. & Cinelli, F., 2000. The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the north-west Mediterranean. *Oecologia*, **123**, 406-417.

Boyero, L., 2003. Multiscale patterns of spatial variation in stream macroinvertebrate communities. *Ecological Research*, **18**, 365–379.

Brawley, S.H. & Johnson, L.E., 1991. Survival of fucoid embryos in the intertidal zone depends on developmental stage and microhabitat. *Journal of Phycology*, **27**, 179-186.

Chapman, M.G., 2002. Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. *Austral Ecology*, **27**, 211-228.

Chapman, M.G. & Underwood, A.J., 1994. Dispersal of the intertidal snail, *Nodilittorina pyramidalis*, in response to the topographic complexity of the substratum. *Journal of Experimental Marine Biology and Ecology*, **179**, 145-169.

Chapman, M.G. & Underwood, A.J., 1998. Inconsistency and variation in the development of rocky intertidal algal assemblages. *Journal of Experimental Marine Biology and Ecology*, **224**, 265-289.

Coleman, M.A., 2002. Small-scale spatial variability in intertidal and subtidal turfing algal assemblages and the temporal generality of these patterns. *Journal of Experimental Marine Biology and Ecology*, **267**, 53-74.

Connell, J.H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthalamus stellatus*. *Ecology*, **42**, 710-723.

Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, **41**, 351–389.

De Kluijver, M.J., 1991. Sublittoral hard substrate communities off Helgoland. *Helgoländer Meeresuntersuchungen*, **45**, 317-344.

De Kluijver, M.J., 1993. Sublittoral hard-substratum communities off Orkney and St Abbs (Scotland). *Journal of the Marine Biological Association of the United Kingdom*, **73**, 733-754.

Dethier, M.N. & Schoch, G.C., 2005. The consequences of scale: assessing the distribution of benthic populations in a complex estuarine fjord. *Estuarine, Coastal and Shelf Science*, **62**, 253–270.

Fletcher, D.J. & Underwood, A.J., 2002. How to cope with negative estimates of components of variance in ecological field studies. *Journal of Experimental Marine Biology and Ecology*, **273**, 89-95.

Fraschetti, S., Terlizzi, A. & Benedetti-Cecchi, L., 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecology Progress Series*, **296**, 13-29.

Gillandt, L., 1979. Zur Systematik, Autökologie und Biologie der Polychaeten des Helgoländer Felslitorals. *Mitteilung aus dem Hamburgischen Zoologischen Museum und Institut*, **76**, 19-73.

Giménez, L., Dimitriadis, C., Carranza, A., Borthagaray, A.I. & Rodríguez, M., 2006. Unravelling the complex structure of a benthic community: A multiscale-multianalytical approach to an estuarine sandflat. *Estuarine, Coastal and Shelf Science*, **68**, 462-472.

Harms, J., 1993. Check list of species (algae, invertebrates and vertebrates) found in the vicinity of the island of Helgoland (North Sea, German Bight) – a review of recent records. *Helgoländer Meeresuntersuchungen*, **47**, 1-34.

Hartmann-Schröder, G., 1996. Polychaeta. In *Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise* (ed. F. Dahl), pp. 1-648. Jena: Gustav Fischer Verlag.

Hartnoll, R.G. & Hawkins, S.J., 1980. Monitoring rocky-shore communities: A critical look at spatial and temporal variation. *Helgoländer Meeresuntersuchungen*, **33**, 484-494.

Hawkins, S.J. & Hartnoll, R.G., 1985. Factors determining the upper limits of intertidal canopy-forming algae. *Marine Ecology Progress Series*, **20**, 265-271.

Heino, J., Louhi, P. & Muotka, T., 2004. Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure. *Freshwater biology*, **49**, 1230-1239.

Hyder, K., Johnson, M.P., Hawkins, S.J. & Gurney, W.S.C., 1998. Barnacle demography: Evidence for an existing model and spatial scales of variation. *Marine Ecology Progress Series*, **174**, 89-99.

Jenkins, S.R., Hawkins, S.J. & Norton, T.A., 1999a. Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Marine Ecology Progress Series*, **188**, 81-92.

Jenkins, S.R., Hawkins, S.J. & Norton, T.A., 1999b. Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community. *Journal of Experimental Marine Biology and Ecology*, **233**, 41-63.

Kaandorp, J.A., 1986. Rocky substrate communities of the infralittoral fringe of the Boulonnais coast, NW France: A quantitative survey. *Marine Biology*, **92**, 255-265.

Kelaher, B.P., Underwood, A.J. & Chapman, M.G., 2003. Experimental transplantations of coralline algal turf to demonstrate causes of differences in macrofauna at different tidal heights. *Journal of Experimental Marine Biology and Ecology*, **282**, 23-41.

Kendrick, G.A. & Walker, D.I., 1995. Dispersal of propagules of *Sargassum* spp. (Sargassaceae: Phaeophyta): observations of local patterns of dispersal and consequences for recruitment and population structure. *Journal of Experimental Marine Biology and Ecology*, **192**, 273-288.

Knight-Jones, P. & Knight-Jones, E.W., 1977. Taxonomy and ecology of British Spirorbidae (Polychaeta). *Journal of the Marine Biological Association of the United Kingdom*, **57**, 453-499.

Li, J., Vincx, M., Herman, P.M.J. & Heip, C., 1997. Monitoring meiobenthos using cm-, m- and km-scales in the Southern Bight of the North Sea. *Marine Environmetal Research*, **43**, 265-278.

Lubchenco, J., 1982. Effects of grazers and algal competitors on fucoid colonization in tide pools. *Journal of Phycology*, **18**, 544-580.

Lubchenco, J. & Menge, B.A., 1978. Community development and persistence in a low rocky intertidal zone. *Ecological Monographs*, **59**, 67-94.

Lüning, K., 1985. *Meeresbotanik*. Stuttgart: Georg Thieme Verlag.

Menconi, M., Benedetti-Cecchi, L. & Cinelli, F., 1999. Spatial and temporal variability in the distribution of algae and invertebrates on rocky shores in the Northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, **233**, 1-23.

Meyer, H.A., 2006. Small-scale spatial distribution variability in terrestrial tardigrade populations. *Hydrobiologia*, **558**, 133–139.

Newell, R.C., 1979. *Biology of intertidal animals*. Faversham: Marine Ecological Survey Ltd.

Norton, T.A., 1985. The zonation of seaweeds on rocky shores. In *The ecology of rocky coasts*. (eds. P.G. Moore & R. Seed), pp. 7-21. London: Hodder & Stoughton.

Paine, R.T., 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, **15**, 93-120.

Perelman, S.B., León, R.J.C. & Oesterheld, M., 2001. Cross-scale vegetation patterns of Flooding Pampa grasslands. *Journal of Ecology*, **89**, 562–577.

Reichert, K. & Buchholz, F., 2006. Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002. *Helgoland Marine Research*, **60**, 213-223.

Reichert, K., Buchholz, F., Bartsch, I., Kersten, T. & Giménez, L., submitted. Scale-dependent patterns of variability in species assemblages of the rocky intertidal of Helgoland (German Bight, North Sea). *Journal of the Marine Biological Association of the United Kingdom*.

Reichert, K., Buchholz, F. & Giménez, L., submitted. Community composition of the rocky intertidal of Helgoland (German Bight, North Sea). *Aquatic Biology*.

Robinson, D.L., 1987. Estimation and use of variance components. *The Statistician*, 36, 3-14.

Searle, S.R., 1987. *Linear models for unbalanced data*. New York: Wiley.

Searle, S.R., Casella, G. & McCulloch, C.E., 1992. *Variance components*. New York: Wiley.

Searle, S.R., 1995. An overview of variance component estimation. *Metrika*, **42**, 215-230.

Singer, J.D., 1998. Using SAS PROC MIXED to fit multilevel models, hierarchical models, and individual growth models. *Journal of Educational and Behavioral Statistics*, **24**, 323-355.

Sokal, R.R. & Rohlf, F.J., 1995. *Biometry: the principles and practise of statistics in biological research*, 3rd edn. New York: Freeman.

Stebbing, A.R.D., 1973. Competition for space between the epiphytes of *Fucus serratus* L.. *Journal of the Marine Biological Association of the United Kingdom*, **53**, 247-261.

Trush, S., Hewitt, J., Herman, P. & Ysebaert, T., 2005. Multi-scale analysis of species-environment relationships. *Marine Ecology Progress Series*, **302**, 13-26.

Underwood, A.J., 1996. Spatial patterns of variance in density of intertidal populations. In *Frontiers of population ecology* (eds. Floyd, R.B., Sheppard, A.W. & De Barro, P.J.), pp. 369-389. Melbourne: CSIRO Publishing.

Underwood, A.J., 1997. *Experiments in ecology: their logical design and interpretation using analysis of variances*, Cambridge: Cambridge University Press.

Underwood, A.J. & Chapman, M.G., 1989. Experimental analyses of the influences of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata*. *Journal of Experimental Marine Biology and Ecology*, **134**, 175-196.

Underwood, A.J. & Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia*, **107**, 212-224.

Underwood, A.J. & Chapman, M.G., 1998. Spatial analyses of intertidal assemblages on sheltered rocky shores. *Austral Ecology*, **23**, 138-157.

Weinberg, S., 1978. The minimal area problem in invertebrate communities of Mediterranean rocky substrata. *Marine Biology*, **49**, 33-40.

Winer, B.J., Brown, D.R. & Michels, K.M., 1991. *Statistical principles in experimental designs*, 3rd edn. New York: McGraw-Hill.

GENERAL DISCUSSION AND CONCLUSIONS

The present study has examined the composition, abundance and distribution patterns of intertidal assemblages at Helgoland. Scale-dependent patterns of variation in macroalgae and invertebrates were tested at defined spatial scales and in relation to environmental conditions. The macrobenthic assemblages varied in space and time in relation to wave exposure and elevation. The snapshots at two points in time (1984 vs. 2002) as well as the short time scale (2004-2006) of the study does not make it possible to evaluate if the observed variation is, at least in part, the result of any human activity. Thus, most of the variations are to be regarded as examples of natural community variation, i.e. the background "noise" against which any human-induced changes may be detected. In the following discussion, several points are considered critically in order to evaluate the nature of this "noise" and its implications for the design and practicability of further studies, including those concerned with environmental monitoring programmes.

Variation between snapshots at two points in time

Considerable variation in the invertebrate assemblages occurred at the northern intertidal rock-platform at Helgoland between Janke`s study in 1984 and the present one in 2002 (Manuscript I). Most of these changes were localized to the lower intertidal. However, the processes causing or maintaining the changes in the invertebrate assemblages between both sampling years were speculative to a great extent. Due to the snapshots at two points in time, it is not possible to ascertain whether the observed differences reflect trends at the scales of decades or longer, or among-year variation. To define variation in seasonal cycles from year to year as well as in a-seasonal cycles, such as fluctuation with a periodicity of decades, a sampling over several years is a prerequisite (Hawkins & Hartnoll, 1983; Southward, 1995).

Besides the variation in the invertebrate assemblages caused by natural or anthropogenic processes, there is also a risk that the changes occurred to a certain degree due to sampling error. The method of abundance estimation of the invertebrates in categories taken from Janke (1986) has the advantage of counteracting small-scale heterogeneity, but is highly affected by the investigator (Hartnoll & Hawkins, 1980). Particularly for long-term observations where often several observers are involved, this subjectivity is a severe restriction. It is indispensable to turn to defined quantitative sampling techniques, where the observer bias is minimised, even though this change to a new approach introduces its own problems. A change from a semi-quantitative to a quantitative sampling approach presents problems with subsequent statistical analysis, when semi-quantitative data gathered formerly should be compared with quantitative data that are gathered later in long-term data series; there is no opportunity to treat semi-quantitative and quantitative data in one analysis without transforming the quantitative data to the semi-quantitative one. Since often a loss of data quality is not desired, the only opportunity is to handle the semi-quantitative as well as the quantitative data on their own merits, and thus one long-term observation would be separated into two medium-term series.

A further sampling error, the precision of data gathering and the identification of species, may have caused variation particularly within the mobile invertebrates between both studies. The results indicated a possible sampling error by the different investigators: most pronounced changes occurred within the molluscs, the annelids and the crustaceans containing mainly mobile species (Manuscript I). To maximize the accuracy, it is possible to focus on sessile species exclusively. Moreover, for a long-term programme, limiting the study to the sessile species would have the advantage that the sampling process would speed up (Jones et al., 1980; Lewis, 1980). In addition, sessile species are more sensitive to short-term factors since the sessile way of life prevents the organisms from avoiding short-term disturbances in the marine environment, such as extreme weather conditions and toxic algal blooms (de Kluijver, 1997; Franke & Gutow, 2004). Consequently, long-term trends in assemblages may be revealed more rapidly and reliably in species which are sessile for most time in their life.

Implications for further sampling (Manuscript I)

- Continued sampling is necessary to assess inter-annual variation and to separate this short-term variation from longer term trends.
- A quantitative survey method (e.g. percentage cover) should be used to minimise the sampling error.
- Further sampling should focus on sessile species to (1) minimise the sampling error, (2) speed up the sampling process and (3) reveal long-term trends in assemblages more rapidly and reliably.

Species-environmental relationships

The communities, including macroalgae and invertebrates, mostly varied between the southern location and the other two locations, the northern and the western rock-platform (Manuscript II). A direct relationship between wave exposure and the occurrence of specific communities was shown for the sheltered southern location. In contrast, the species spectra and the distribution of the communities at the semi-exposed northern and exposed western location appeared to have little association to wave exposure directly. It rather appears that other processes, such as grazing and/or competitive interactions, may have caused the differences in the occurrence of the communities. However, Menge (1976) showed that such biological processes are dependent on the degree of wave exposure in turn. Thus, the differences in communities between the northern and western location may be caused by exposure to waves indirectly. For a better understanding of the influence of wave exposure on the degree of biological interactions, manipulative experiments should be designed. Further, it is suggested that the design of these experiments be focused on wave exposure itself. Due to the categorical definition it is possible that the locations, which were classified differently in the present study, are in fact similar in their physical mechanisms of exposure. This uncertainty can be alleviated if quantitative measures are used in combination with appropriate methods of analysis (e.g. Harley & Helmuth, 2003; Lindegarth & Gamfeldt, 2005; Palumbi, 1984).

Besides the community-wave exposure relationship, the distribution of the communities was clearly related to variations in tidal height at the northern location; a structuring into spatial zonation patterns was observed (Manuscript II). The relationship between categories of tidal height and communities was supported by regression-based models where continuous height data were taken into account. However, the models developed for the assemblages at the northern location were not significant for the western location (Manuscript III, IV).

The regression-based models refine our understanding of distribution patterns and help develop hypotheses and design experiments to investigate the mechanistic processes that underpin these models. Statistical models play an increasingly important role in risk assessment, as the threat of changes in marine habitats due to alterations in sea level and climate are recognised by resource managers (Warwick et al., 1991; Ysebaert et al., 2002). To apply models for forecasting changes in the occurrence of assemblages associated with changes in environmental factors, they should be verified at different space and time scales (Ysebaert & Herman, 2002).

The results of the present study suggest that the shape of the relationship between environmental conditions and community attributes depend on the particular attribute under evaluation. Total species richness and total abundance of the assemblages at the northern location responded asymptotically to elevation, whereas the abundance of individual species showed neither a linear nor a non-linear response to elevation (Manuscript III, IV). However, at the northern location the elevation determined the frequency of occurrence and the maximal cover of most individual algae and invertebrates. If regression-based models cannot be developed, the approach of frequency of occurrence and maximal cover can be used to interpret changes in the distribution and abundances of species (Giménez et al., 2006; Trush et al., 2005).

Implications for further sampling (Manuscript II, III, IV)

- Physical mechanisms of wave exposure should be examined quantitatively.
- Further sampling should verify the direct community-wave exposure relationship at the southern location and the more indirect relation at the northern and western rock-platform.
- The validity of the regression-based models should be tested at broader spatial and temporal scales.

Scale-dependent patterns of variation

The present study shows that (1) total species richness, (2) total abundance of the assemblages and (3) abundance of individual algae and invertebrates varied mostly at spatial scales of about 50 m (transect) and 10s of centimetres (replicate) at the northern and western location respectively (Manuscript III, IV). Patterns of variation in studies, such as the present one, may provide indicators of the mechanisms causing the variation observed. Although processes causing spatial patterns cannot be determined from observational studies, the identification of relevant scales of variation helps to formulate hypotheses and design manipulative experiments at the appropriate scale. For instance, at the western location (low-shore) differences in abundance of dominant periwinkles, such as *Littorina littorea* or *L. mariae*/*L. obtusata*, among replicated quadrats may be affected by geo-morphological structures (e.g. crevices, holes, cracks) within each plot. There are several studies reporting influences of topography on the small-scale variability in high-shore littorinid snails (Chapman, 1994; Chapman & Underwood, 1994; Underwood & Chapman, 1989). A further study at the western location of Helgoland could be undertaken to determine the influences of topography on the distribution of periwinkles. Several topographic features, such as narrow cracks and small pits, could be established experimentally at low-shore in randomly-chosen sites on the western rock-platform. Then, the total number of littorinid snails in those experimental arrays could be counted to test the hypothesis that topographic features will enhance the occurrence of these snails.

Moreover, the present findings have important consequences for the design of environmental monitoring studies. Patchiness at the western location will not cause errors in identification of differences among the largest spatial scale (transects). Any spatial variation at scales between that of the spacing of replicates and the spacing of transects will be incorporated into the variation among transects in the statistical comparison of transects. Also, scales of variation smaller than the spacing of replicate quadrats will be included in estimates of variation among transects and among replicates within each transect. However, such small-scale variation may reduce the power of statistical tests, and therefore calls for careful optimization of designs of environmental monitoring programmes (Fraschetti et al., 2005; Morrisey et al., 1992; Underwood & Chapman, 2003). A crucial point to increase power is by increasing sizes of samples (Mapstone, 1995). For disturbed assemblages, where changes in small-scale variation have been repeatedly proposed as a diagnostic feature, the power can be increased by sampling adequate reference locations (Chapman et al., 1995; Terlizzi et al., 2005); since the greater the differences between disturbed and control places, the more likely it is that a test will detect it. However, these optimizations of the sampling design lead to more time-consuming sampling and do not add to the feasibility of a monitoring programme. Thus, an optimization could also lie in the exclusion of locations with particularly patchy distribution patterns of assemblages, such as the western location. Moreover, the northern location may be preferred to the western rock-platform due to its accessibility and facility for sampling, especially during bad weather phases.

A further important consideration for long-term observation, i.e. for the comparison of the same location over time, is that the variables being measured should generate data which conform to the assumptions of the subsequent statistical analyses (for discussion see e.g. Hurlbert, 1984; Underwood, 1997). Regarding the sampling design, a fixed-site approach, often used in many long-term studies (e.g. Jones et al., 1980; Sagarin et al., 1999) and also in the present study, created a situation in which the repeated measures are not independent of each other, and thus violate the most important assumption of the familiar parametric statistics, such as analyses of variance. In contrast, the use of randomly relocated replicates for each time a new sampling is conducted may cause confounding of temporal variation with small-scale spatial variation. To avoid dependent samples in a fixed-site approach, a certain number of randomly chosen quadrats from the whole set of sampling units at each location and time should be analysed.

Finally, it is important to note that the spatial patterns identified in the present study are likely to change with time, and interactive effects of space and time are probable. In the present study, species assemblages at the northern location (particularly macroalgae) were more consistent overtime than those at the western location (Manuscript III, IV). As in the small-scale spatial variation considered above, also short-term temporal variation will have similar effects of confounding or reduction of power on long-term comparisons. To reduce smaller temporal changes and to simultaneously minimise the sampling approach, perhaps an answer could lie in monitoring communities which are less subject to natural variation (see e.g. Hawkins & Hartnoll, 1983; Lewis, 1977). Therefore, for a long-term observation it appears useful to focus on the more sheltered communities at the northern location.

Implications for further sampling (Manuscript III, IV)

- Mechanisms causing observed spatial variation should be investigated by means of manipulative experiments at appropriate scales.
- Further sampling should concentrate on locations with few patchy distribution patterns of assemblages.
- Further sampling should concentrate on assemblages which display the least temporal variation.

In conclusion, the present study shows that monitoring may not be a simple task in marine benthic communities. Monitoring may take into account that (1) the power to detect long-term trends depends on the sampling method and the response variables (Manuscript I), (2) species-environmental relationships depend on the location (Manuscript II, III, IV), (3) scale-dependent variations depend on the location (Manuscript III, IV), and (4) scale-dependent variation may be inconsistent through time (Manuscript III, IV).

Perspectives for monitoring

For a precise and accurate sampling design, clearly defined aims of the monitoring programme are indispensable: what kind of variation, what response variables (i.e. indicator species or assemblages) and what rates of change may be anticipated in the assemblages at Helgoland? In addition, detailed considerations are needed in order to make quantitative and realistic predictions of effects and to suggest criteria for testing such predictions. In the following section, several changes which can be assumed for the Helgoland intertidal in the future are considered critically in order to suggest possible aims of the monitoring programme.

The relevant spatial scales of former ecological studies at the Helgoland intertidal were all small-scale, and thus a clear understanding of the role of local versus regional or global environmental processes in dynamics of benthic assemblages is lacking. Since the Helgoland intertidal is small and surrounded by soft bottom, only local variations in assemblages can be detected easily. However, the variation of the biota of rocky shores is mostly set by the interplay of broad-scale factors (e.g. climate, oceanic circulation pattern) and local-scale processes (e.g. biological interactions, variables relating to local topography and hydrography). To ensure that monitoring at Helgoland detects also possible large-scale trends, such as the effects of climate change on the abundance of species, it will be necessary to extract broad-scale signals from the noise caused by local-scale factors. Therefore, comparisons of variation in species assemblages over a latitudinal/longitudinal gradient are recommended in the future. A first important step for European ecological comparisons was the BIOMARE project (Implementation and Networking of large-scale long-term Marine Biodiversity research in Europe) which declared the rocky littoral of Helgoland as reference site (Warwick et al., 2003).

Moreover, the role of short-term versus long-term environmental processes in the assemblages at Helgoland is unclear since former studies at the Helgoland intertidal were all short-term. Thus, a future aim is to establish a long-term monitoring programme which allows the detection of changes on large temporal scales which may partly be due to human activities, against changes on smaller temporal scales which mostly reflect natural variation. Variation in species assemblages at time scales spanning decades are often related to human impacts such as pollution (e.g. eutrophication; Baeck et al., 2002; Worm & Lotze, 2006), exploitation of natural resources (e.g. fishery; Fraschetti et al., 2001) and finally global climate change (e.g. warming, sea-level rise, extreme weathers; Hiscock et al., 2004; Sagarin et al., 1999). In contrast to more coastal macrobenthic communities, the assemblages at Helgoland seem to be less affected by an input and accumulation of harmful substances and nutrients. As the rocky littoral of Helgoland is a marine protected area (since 1981) it can be presumed that the assemblages are also relatively little affected by exploitation of natural resources. However, the shift in North Sea climate may be an important factor driving changes in species composition. Many species which newly appeared at the island of Helgoland during the past decade are oceanic-southern species which may be considered as indicators of a warming trend. Shifts in the range of distribution and abundance of species along environmental gradients are anticipated at large spatial scales, separated by 10s to 100s of kilometres. However, the decline in the abundance of northern species or the increase in the abundance of southern species can also investigated at smaller spatial scales (10s to 100s of metres). In addition to the long-term monitoring of the abundance and distribution of northern and/or southern species, experiments should evaluate the effects of warming on species reproduction and recruitment of cold water and/or Lusitanian species. This will strengthen the knowledge of the mechanisms that influence the decrease or increase in abundance of these species. For instance, the decrease of the blue mussel *Mytilus edulis* is likely be driven by a reduction in reproductive output during milder winters. Moreover, manipulative experiments may help to elucidate interactions between northern species and new southern species (e.g. focusing on the blue mussel: *Mytilus edulis* vs. the Pacific oyster *Crassostrea gigas*). Based on a data series over several years, individually-based models can also be constructed to assess the future distribution of intertidal species or assemblages.

Besides the warming of the North Sea, a predicted consequence of global change is a greater frequency of extreme events such as storms. An increase in wave action associated with storms is likely to be related to a reduction in the abundance of macroalgae and grazers, while the abundance of species which do well in stormy conditions (e.g. filter feeders) will increase (Thompson et al., 2002). The decrease in abundance of the brown alga *Fucus serratus* and an associated increase in free space has already been observed at the Helgoland intertidal (K.R. personal observations). The investigation of changes in the *F. serratus* community combined with measurements of wave action can be a further aim of the long-term monitoring. Additional experiments should examine recovery from disturbance events such as storms to the canopy of the alga *Fucus serratus*. Furthermore, at smaller spatial scales (10s to 100s of metres), variation in the vertical distribution pattern of assemblages is anticipated due to sea-level rise. Direct consequences of sea-level rise for rocky shore organisms are likely to be minimal compared to those of temperature changes or storminess on most rocky shores (Thompson et al., 2002). Here, the strong slope of the seashore continues well above the level of high water, and thus there is free space available at the top of the shore; the physical zones occupied by each species will move up-shore without the displacement of species. However, at Helgoland where there is a wave-cut platform beneath the main island, as well as a wave-cut platform which has been topped by an artificial sea wall, increasing sea-level will compress existing patterns of zonation. Therefore, the investigation of variation in the vertical distribution pattern of assemblages should be a further aim of the long-term monitoring at Helgoland.

Predictions on the responses of the intertidal assemblages to variations in climate change should be tested:

- Northern species will decline in their abundance; such variation is likely be driven by a reduction in reproductive output and/or decreased juvenile or adult survival during warmer summer periods.
- Southern species will increase in their abundance; such variation is likely be driven by an increase in reproductive output and/or decreased juvenile survival during warmer summer periods and milder winters.
- Biological interactions such as predation and competition will modulate the response of the increase of southern species and the decrease of northern species with consequences for the structure of assemblages and ecosystem functioning.
- Macroalgae and grazers will decline in their abundance, while filter feeders such as mussels or barnacles will increase in their abundance; such variations are likely be driven by greater frequency of extreme events such as storms.
- Lower shore assemblages will expand in the direction of the upper shore; such variation is also likely be driven by an increase of wave action and/or a rise in sea level.

REFERENCES

Aberg, P. & Pavia, H., 1997. Temporal and multiple scale spatial variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. *Marine Ecology Progress Series*, **158**, 111-119.

Airoldi, L. & Cinelli, F., 1997. Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a Mediterranean rocky shore. *Journal of Experimental Marine Biology and Ecology*, **215**, 269-288.

Anderson, M., 2003. PCO: A FORTRAN computer program for principal coordinate analysis. Department of Statistics, University of Auckland, New Zealand.

Andrew, N.L. & Mapstone, B.D., 1987. Sampling and the description of spatial pattern in marine ecology. *Oceanography and Marine Biology*: *an Annual Review*, **25**, 39-90.

Ankel, W.E., 1936. Prosobranchia. In *Tierwelt der Nord- und Ostsee* (eds. G. Grimpe & E. Wagler), pp. 1-240. Leipzig: Geest & Portig.

Baeck, S., Ekebom, J. & Kangas, P., 2002. A proposal for a long-term baseline phytobenthos monitoring programme for the Finnish Baltic coastal waters: Monitoring submerged rocky shore vegetation. *Environmental Monitoring and Assessment*, **79**, 13-27.

Bartsch, I. & Tittley, I., 2004. The rocky intertidal biotopes of Helgoland: present and past. *Helgoland Marine Research*, **58**, 289-302.

Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Marine Ecology Progress Series*, **215**, 79-92.

Benedetti-Cecchi, L., Bulleri, F. & Cinelli, F., 2000a. The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the north-west Mediterranean. *Oecologia*, **123**, 406-417.

Benedetti-Cecchi, L., Acunto, S., Bulleri, F. & Cinelli, F., 2000b. Population ecology of the barnacle *Chthamalus stellatus* in the northwest Mediterranean. *Marine Ecology Progress Series*, **198**, 157-170.

Benedetti-Cecchi, L., Bertocci, I., Micheli, F., Maggi, E., Fosella, T. & Vaselli, S., 2003. Implications of spatial heterogeneity for management of marine protected areas (MPAs): examples from assemblages of rocky coasts in the northwest Mediterranean. *Marine Environmental Research*, **55,** 429-458.

Bertness, M.D., Gaines, S.D., Stephens, E.G. & Yund, P.O., 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, **156**, 199-215.

Beukema, J.J., Dekker, R., Essink, K. & Michaelis, H., 2001. Synchronized reproductive success of the main bivalve species in the Wadden Sea: Causes and consequences. *Marine Ecology Progress Series*, **211**, 143-155.

Bray, J.R. & Curtis, J.T., 1957. An ordination of the upland forest of Southern Wisconsin. *Ecological Monographs*, **27**, 225-349.

Brinkhurst, R.O., 1982. British and other marine and estuarine Oligochaetes. In *Synopses of the British Fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-127. Cambridge: Cambridge University Press. [New Series, no. 21].

Burrows, E.M., 1991. Chlorophyta. In *Seaweeds of the British Isles*, vol. 2, pp. 1-238. Dorchester: The Dorset Press.

Chapman, M.G., 1994. Small- and broad-scale patterns of distribution of the upper-shore littorinid, *Nodilittorina pyramidalis,* in New South Wales. *Australian Journal of Ecology,* **19**, 83-95.

Chapman, M.G., 2002. Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. *Austral Ecology*, **27**, 211-228.

Chapman, M.G. & Underwood, A.J., 1994. Dispersal of the intertidal snail, *Nodilittorina pyramidalis*, in response to the topographic complexity of the substratum. *Journal of Experimental Marine Biology and Ecology*, **179**, 145-169.

Chapman, M.G., Underwood, A.J. & Skilleter, G.A., 1995. Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage and two control assemblages. *Journal of Experimental Marine Biology and Ecology*, **189**, 103-122.

Chapman, M.G. & Underwood, A.J., 1998. Inconsistency and variation in the development of rocky intertidal algal assemblages. *Journal of Experimental Marine Biology and Ecology*, **224**, 265-289.

Cheng, L., 1976. *Marine insects*. Amsterdam: North-Holland Publishing Company.

Clarke, K.R. & Warwick, R.M., 2001. *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth: PRIMER-E.

Clifford, H.T. & Stephenson, W., 1975. *An introduction to numerical classification*. New York: Academic Press.

Connell, J.H., 1961. The influence of interspecific competition and other factors on the barnacle *Chthamalus stellatus*. Ecology, **42**, 710-723.

Cornelius, P.F.S., 1995a. North-West European thecate hydroids and their medusae. Part 1. In *Synopses of the British Fauna*. (eds. R.S.K. Barnes & J.H. Crothers), pp. 1-347. Shrewsbury: FSC Publications. [New Series, no. 50].

Cornelius, P.F.S., 1995b. North-West European thecate hydroids and their medusae. Part 2. In *Synopses of the British Fauna* (eds. R.S.K. Barnes & J.H. Crothers), pp. 1-386. Shrewsbury: FSC Publications. [New Series, no. 50].

Crisp, D.J., 1964. The effects of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*, **33**, 165-211.

Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, **41**, 351–389.

De Kluijver, M.J., 1991. Sublittoral hard substrate communities off Helgoland. *Helgoländer Meeresuntersuchungen*, **45**, 317-344.

De Kluijver, M.J., 1993. Sublittoral hard-substratum communities off Orkney and St Abbs (Scotland). *Journal of the Marine Biological Association of the United Kingdom*, **73**, 733-754.

De Kluijver, M.J., 1997. *Sublittoral communities of North Sea hard-substrata*. PhD thesis, University of Amsterdam, Netherlands.

De Kluijver, M.J. & Leewis, R.J., 1994. Changes in the sublittoral hard substrate communities in the Oosterschelde Estuary (SW Netherlands), caused by changes in the environmental parameters. *Hydrobiologia*, **282-283,** 265-280.

Digby, P.G.N. & Kempton, R.A., 1987. *Multivariate analysis of ecological communities*. London: Chapman and Hall.

Dixon, P.S. & Irvine, L.M., 1983. Introduction, Nemaliales, Gigartinales. In *Seaweeds of the British Isles*, vol. 1, part 1, pp. 1-252. Kettering: The George Press.

ESRI Geoinformatik, 2004. *ArcGIS integrated collection of GIS software products*. California, USA.

Fauchald, K., 1977. The polychaete worms. Definitions and keys to the order, families and genera. *Science Series, Natural History Museum of Los Angeles County*, 28, 1-188.

Field, J.G., Clarke, K.R. & Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*, **8**, 37-52.

Fletcher, R.L., 1987. Fucophyceae (Phaeophyceae). In *Seaweeds of the British Isles*, vol. 3, part 1, pp. 1-359. Dorchester: The Dorset Press.

Fletcher, D.J. & Underwood, A.J., 2002. How to cope with negative estimates of components of variance in ecological field studies. *Journal of Experimental Marine Biology and Ecology*, **273**, 89-95.

Foster, M.S., Nigg, E.W., Kiguchi, L.M., Hardin, D.D. & Pearse, J.S., 2003. Temporal variation and succession in an algal-dominated high intertidal assemblage. *Journal of Experimental Marine Biology and Ecology*, **289**, 15-39.

Franke, H.D. & Gutow, L., 2004. Long-term changes in the macro-zoobenthos around the rocky island of Helgoland (German Bight, North Sea). *Helgoland Marine Research*, **58**, 303-310.

Fraschetti, S., Bianchi, C.N., Terlizzi, A., Fanelli, G., Morri, C. & Boero, F., 2001. Spatial variability and human disturbance in shallow subtidal hard substrate assemblages: A regional approach. *Marine Ecology Progress Series*, **212**, 1-12.

Fraschetti, S., Terlizzi, A. & Benedetti-Cecchi, L., 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecology Progress Series*, **296**, 13-29.

Gibbs, P.E., 1977. British sipunculans. In *Synopses of the British Fauna* (ed. D.M. Kermack), pp. 1-34. London: Academic Press. [New Series, no. 12].

Gibson, R., 1982. British nemerteans. In *Synopses of the British Fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-212. Cambridge: Cambridge University Press. [New Series, no. 24].

Gillandt, L., 1979. Zur Systematik, Autökologie und Biologie der Polychaeten des Helgoländer Felslitorals. *Mitteilung aus dem Hamburgischen Zoologischen Museum und Institut*, **76**, 19-73.

Giménez, L., Dimitriadis, C., Carranza, A., Borthagaray, A.I. & Rodríguez, M., 2006. Unravelling the complex structure of a benthic community: A multiscale-multianalytical approach to an estuarine sandflat. *Estuarine, Coastal and Shelf Science*, **68**, 462-472.

Graham, A., 1988. Molluscs: prosobranch and pyramidellid gastropods. In *Synopses of the British Fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-662. Leiden: E.J. Brill & Dr W. Backhuys. [New Series, no. 2].

Hagmeier, A., 1930. Die Besiedlung des Felsstrandes und der Klippen von Helgoland. I. Der Lebensraum. *Wissenschaftliche Meeresuntersuchungen*, **15**,1-35.

Harley, C.D.G. & Helmuth, B.S.T., 2003. Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnology and Oceanography*, **48**, 1498-1508.

Harms, J., 1993. Check list of species (algae, invertebrates and vertebrates) found in the vicinity of the island of Helgoland (North Sea, German Bight) – a review of recent records. *Helgoländer Meeresuntersuchungen*, **47**, 1-34.

Hartmann-Schröder, G., 1996. Polychaeta. In *Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise* (ed. F. Dahl), pp. 1-648. Jena: Gustav Fischer Verlag.

Hartnoll, R.G. & Hawkins, S.J., 1980. Monitoring rocky-shore communities: A critical look at spatial and temporal variation. *Helgoländer Meeresuntersuchungen*, **33**, 484-494.

Hawkins, S.J. & Hartnoll, R.G., 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology. An Annual Review*, **21**, 195-282.

Hawkins, S.J. & Hartnoll, R.G., 1985. Factors determining the upper limits of intertidal canopy-forming algae. *Marine Ecology Progress Series*, **20**, 265-271.

Hayward, P.J., 1985. Ctenostome bryozoans. In *Synopses of the British Fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-169. London: E.J. Brill & Dr W. Backhuys. [New Series, no. 33].

Hayward, P.J. & Ryland, P.J., 1979. British ascophoran bryozoans. In *Synopses of the British Fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-312. London: Academic Press. [New Series, no. 14].

Hayward, P.J. & Ryland, P.J., 1995. *Handbook of the marine fauna of North-West Europe*. Oxford: Oxford University Press.

Hiscock, K., Southward, A.J., Tittley, I. & Hawkins, S.J., 2004. Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation*, **14**, 333-362.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187-211.

Ingle, R.W., 1983. Shallow-water crabs. In *Synopses of the British Fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-206. Cambridge: Cambridge University Press. [New Series, no. 25].

Irvine, L.M., 1983. Cryptonemiales (sensu stricto), Palmariales, Rhodymeniales. In *Seaweeds of the British Isles*, vol. 1, part 2A, pp. 1-115. British Museum (Natural History).

Irvine, L.M. & Chamberlain, Y.M., 1994. Corallinales, Hildenbrandiales. In *Seaweeds of the British Isles*, vol. 1, part 2B, pp. 1-276. Bury St Edmunds: St Edmundsbury Press.

Janke, K., 1986. Die Makrofauna und ihre Verteilung im Nordost-Felswatt von Helgoland. *Helgoländer Meeresuntersuchungen*, **40**, 1-55.

Janke, K., 1990. Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). *Helgoländer Meeresuntersuchungen*, **44**, 219-263.

Jenkins, S.R., Hawkins, S.J. & Norton, T.A., 1999a. Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Marine Ecology Progress Series*, **188**, 81-92.

Jenkins, S.R., Hawkins, S.J. & Norton, T.A., 1999b. Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community. *Journal of Experimental Marine Biology and Ecology*, **233**, 41-63.

Jenkins, S.R., Aeberg, P., Cervin, G., Coleman, R.A., Delany, J., Della Santina, P., Hawkins, S.J., LaCroix, E., Myers, A.A., Lindegarth, M., Power, A.M., Roberts, M.F. & Hartnoll, R.G., 2000. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology*, **243**, 209-225.

Jenkins, S.R., Arenas, F., Arrontes, J., Bussell, J., Castro, J., Coleman, R.A., Hawkins, S.J., Kay, S., Martinez, B., Oliveros, J., Roberts, M.F., Sousa, S., Thompson, R.C. & Hartnoll, R.G., 2001. European-scale analysis of seasonal variability in limpet grazing activity and microalgal abundance. *Marine Ecology Progress Series*, **211**, 193-203.

Jones, N.S., 1976. British cumaceans. In *Synopses of the British Fauna* (ed. D.M. Kermack), pp. 1-62. London: Academic Press. [New Series, no. 7].

Jones, W.E., Bennell, S., Beveridge, C., McConnell, B., Mack-Smith, S. & Mitchell, J., 1980. Methods of data collection and processing in rocky intertidal monitoring. In *The shore environment, Vol. 1: Methods*. (eds. J.H. Price, D.E.G. Irvine & W.F. Farnham), pp. 137-170. London: Academic Press. [Systematics Association Special Volume No.17A]

Kaandorp, J.A., 1986. Rocky substrate communities of the infralittoral fringe of the Boulonnais coast, NW France: A quantitative survey. *Marine Biology*, **92**, 255-265.

King, P.E., 1974. British sea spiders. In *Synopses of the British Fauna* (ed. D.M. Kermack), pp. 1-68. London: Academic Press. [New Series, no. 5].

Kornmann, P. & Sahling, P.-H., 1977. Meeresalgen von Helgoland. Benthische Grün-, Braun- und Rotalgen. *Helgoländer wissenschaftliche Meeresuntersuchungen*, **29**, 1-289.

Kruskal, J.B., 1964. Multidimensional scaling by optimising goodness of fit to a non-metric hypothesis. *Psychometrika*, **29**, 1-27.

Legendre, L. & Legendre, P., 1998. *Numerical ecology*. Amsterdam: Elsevier.

Lewis, J.R., 1964. *The ecology of rocky shores*. London: English Universities Press.

Lewis, J.R., 1977. The role of physical and biological factors in the distribution and stability of rocky shore communities. In *Biology of benthic organisms* (eds. B.F. Keegan, P. O´Ceidigh & P.J.S. Boaden), pp. 417-424. Oxford: Pergamon Press.

Lewis, J.R., 1980. Objectives in littoral ecology - a personal viewpoint. In *The shore environment, Vol. 1: Methods*. (eds. J.H. Price, D.E.G. Irvine & W.F. Farnham), pp. 1-18. London: Academic Press. [Systematics Association Special Volume No.17A]

Lincoln, R.J., 1979. *British marine amphipoda: Gammaridea*. Bungay: Richard Clay (The Chaucer Press).

Lindegarth, M. & Gamfeldt, L., 2005. Comparing categorical and continuous ecological analyses: Effects of "wave exposure" on rocky shores. *Ecology*, **86**, 1346-1357.

Lubchenco, J., 1982. Effects of grazers and algal competitors on fucoid colonization in tide pools. *Journal of Phycology*, 18, 544-580.

Lubchenco, J. & Menge, B.A., 1978. Community development and persistence in a low rocky intertidal zone. *Ecological Monographs*, **59**, 67-94.

Luther, G., 1987. Seepocken der deutschen Küstengewässer. *Helgoländer Meeresuntersuchungen*, **41**, 1-43.

Maggs, C.A. & Hommersand, M.H., 1993. Ceramiales. In *Seaweeds of the British Isles*, vol. 1, part 3A, pp. 1-444. Bury St Edmunds: St Edmundsbury Press.

Manuel, R.L., 1988. British anthozoa. In *Synopses of the British Fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-241. Leiden: E.J. Brill & Dr W. Backhuys. [New Series, no. 18].

Mapstone, B.D., 1995. Scalable decision rules for environmental impact studies: effect size, Type I, and Type II errors. *Ecological Applications*, **5**, 401-410.

McCook, L.J. & Chapman, A.R.O., 1997. Patterns and variations in natural succession following massive ice-scour of a rocky intertidal seashore. *Journal of Experimental Marine Biology and Ecology*, **214**, 121-147.

Menge, B.A., 1976. Organization of the new England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs*, **46**, 355-393.

Morrisey, D.J., Howitt, L., Underwood, A.J. & Stark, J.S., 1992. Spatial variation in soft-sediment benthos. *Marine Ecology Progress Series*, **81**, 197–204.

Naylor, E., 1972. British marine isopods. In *Synopses of the British Fauna* (ed. D.M. Kermack), pp. 1-86. London: Academic Press. [New series, no. 3].

Nordsieck, F., 1982. *Die europäischen Meeres-Gehäuseschnecken (Prosobranchia)*. Stuttgart: Gustav Fischer Verlag.

Paine, R.T., 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, **15**, 93-120.

Palumbi, S.R., 1984. Measuring intertidal wave forces. *Journal of Experimental Marine Biology and Ecology*, **81**, 171-179.

Primer-E, 2000. PRIMER 5 for Windows: *Plymouth routines in multivariate ecological research*. Plymouth, UK.

Quinn, G.P. & Keough, M.J., 2002. *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

Raffaelli, D. & Hawkins, S., 1996. *Intertidal Ecology*, 1st edn. London: Chapman and Hall.

Reichert, K. & Buchholz, F., 2006. Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002. *Helgoland Marine Research*, **60**, 213-223.

Rietdorf, D., 2001. Studien zur Taxonomie und Physiologie der Ascidien vor Helgoland (Nordsee). Diploma thesis, University of Veterinary Medicine Hannover, Germany.

Robinson, D.L., 1987. Estimation and use of variance components. *The Statistician*, 36, 3-14.

Rumohr, H., Karakassis, I. & Nørrevang Jensen, J., 2001. Estimating species richness, abundance and diversity with 70 macrobenthic replicates in the Western Baltic Sea. *Marine Ecology Progress Series*, **214**, 103-110.

Ryland, J.S. & Hayward, P.J., 1977. British anascan bryozoans. In *Synopses of the British Fauna* (ed. D.M. Kermack), pp. 1-188. London: Academic Press. [New Series, no. 10].

Sagarin, R.D., Barry, J.P., Gilman, S.E. & Baxter, C.H., 1999. Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs*, **69**, 465-490.

Schellenberg, A., 1942. Krebstiere oder Crustacea. IV. Flohkrebs oder Amphipoda. In *Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise* (ed. F. Dahl), pp. 1-252. Jena: Gustav Fischer Verlag.

Searle, S.R., 1987. *Linear models for unbalanced data*. New York: Wiley.

Searle, S.R., Casella, G. & McCulloch, C.E., 1992. *Variance components*. New York: Wiley.

Searle, S.R., 1995. An overview of variance component estimation. *Metrika*, **42**, 215-230.

Singer, J.D., 1998. Using SAS PROC MIXED to fit multilevel models, hierarchical models, and individual growth models. *Journal of Educational and Behavioral Statistics*, **24**, 323-355.

Shephard, R.N., 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. *Psychometrika*, **27**, 125-140.

Smaldon, G., 1979. British coastal shrimps and prawns. In *Synopses of the British Fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-126. London: Academic Press. [New Series, no. 15].

Southward, A.J., 1958. The zonation of plants and animals on rocky sea shores. *Biological Reviews*, **33**, 137-177.

Southward, A.J., 1995. The importance of long time-series in understanding the variability of natural systems. *Helgoländer Meeresuntersuchungen*, **49**, 329-333.

StatSoft, 2001. *STATISTICA software package*. Oklahoma, USA.

Stephenson, T.A. & Stephenson, A., 1972. *Life between tidemarks on rocky shores*. San Francisco: W.H. Freeman.

Tebble, N., 1966. *British bivalve seashells*. Oxford: The Alden Press Osney Mead.

Thompson, T.E., 1988. Molluscs: benthic opisthobranchs. In *Synopses of the British Fauna* (eds. D.M. Kermack & R.S.K. Barnes), pp. 1-356. Leiden: E.J. Brill & Dr W. Backhuys. [New Series, no. 8].

Thompson, R.C., Crowe, T.P. & Hawkins, S.J., 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environmental Conservation*, **29**, 168-191.

Terlizzi, A., Benedetti-Cecchi, L., Bevilacqua, S., Fraschetti, S., Guidetti, P. & Anderson, M.J., 2005. Multivariate and univariate asymmetrical analyses in environmental impact assessment: a case study of Mediterranean subtidal sessile assemblages. *Marine Ecology Progress Series*, **289**, 27-42.

Trush, S., Hewitt, J., Herman, P. & Ysebaert, T., 2005. Multi-scale analysis of species-environment relationships. *Marine Ecology Progress Series*, **302**, 13-26.

Underwood, A.J., 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge: Cambridge University Press.

Underwood, A.J., 2000. Experimental ecology of rocky intertidal habitats: what are we learning? *Journal of Experimental Marine Biology and Ecology*, **250**, 51-76.

Underwood, A.J. & Chapman, M.G., 1989. Experimental analyses of the influences of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata*. *Journal of Experimental Marine Biology and Ecology*, **134**, 175-196.

Underwood, A.J. & Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia*, **107**, 212-224.

Underwood, A.J. & Chapman, M.G., 2003. Power, precaution, Type II error and sampling design in assessment of environmental impacts. *Journal of Experimental Marine Biology and Ecology*, **296**, 49-70.

Vadas, R.L., Wright, W.A. & Mille, S.L., 1990. Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Marine Ecology Progress Series*, **61**, 263-272.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F., 2002. Ecological responses to recent climate change. *Nature*, **416**, 389-395.

Warwick, R.M., Goss-Custard, J.D., Kirby, R., George, C.L., Pope, N.D. & Rowden, A.A., 1991. Static and dynamic environmental factors determining the community structure of estuarine macrobenthos in SW Britain: why is the Severn estuary different? *Journal of Applied Ecology*, **28**, 1004–1026.

Warwick, R.M., Emblow, C., Féral, J.-P., Hummel, H., van Avesaath, P. & Heip, C., 2003. European Marine Biodiversity Research Sites. *Report of the European Concerted Action: BIOMARE*. Yerseke: NIOO-CEME, 135 pp.

Weinberg, S., 1978. The minimal area problem in invertebrate communities of Mediterranean rocky substrata. *Marine Biology*, **49**, 33-40.

Wiltshire, K.H. & Manly, B.F.J., 2004. The warming trend at Helgoland Roads, North Sea: phytoplankton response. *Helgoland Marine Research*, **58**, 269-273.

Winer, B.J., Brown, D.R. & Michels, K.M., 1991. *Statistical principles in experimental design*. New York: McGraw-Hill.

Worm, B. & Lotze, H.K., 2006. Effects of eutrophication, grazing, and algal blooms on rocky shores. *Limnology and Oceanography*, **51**, 569-579.

Ysebaert, T. & Herman, P.M.J., 2002. Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. *Marine Ecology Progress Series*, **244**, 105–124.

Ysebaert, T., Meire, P., Herman, P.M.J. & Verbeek, H., 2002. Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. *Marine Ecology Progress Series*, **225**, 79–95.

Ziegelmeier, E., 1957. Die Muscheln (Bivalvia) der deutschen Meeresgebiete. *Helgoländer wissenschaftliche Meeresuntersuchungen*, **6**, 1-64.

Ziegelmeier, E., 1966. Die Schnecken (Gastropoda, Prosobranchia) der deutschen Meeresgebiete und brackigen Küstengewässer. *Helgoländer wissenschaftliche Meeresuntersuchungen*, **13**, 1-61.

Zuur, A.F., Ieno, E.N. & Smith, G.M., 2007. *Analyzing ecological data*. Berlin: Springer.

SUMMARY

The composition, abundance and distribution patterns of benthic assemblages were examined at the Helgoland intertidal at two points in time (1984 vs. 2002), and subsequently and repeatedly at a short-time scale from 2004 to 2006. Despite the comparatively large amount of literature on the ecology of benthic assemblages at Helgoland to date, there are only few intertidal studies which describe distribution patterns and reveal possible temporal variation in the composition of algae or invertebrates at specific locations; a comprehensive review of the intertidal communities at Helgoland had not yet been carried out. To date, all intertidal studies deal with only one particular taxonomic group or are semi-quantitative; altogether, there is no thorough quantitative description of communities, including both algal and invertebrate species. Moreover, there is no evidence to date whether spatial patterns of these hard-bottom assemblages are dependent on the scale of measurement, and if processes operate at one or more spatial scales.

Thus the specific objectives of the present study were (1) to assess the variation in assemblages at two points in time and at a short-time scale from 2004 to 2006, (2) to determine characteristic communities, their abundance and distribution patterns, (3) to evaluate the patterns of variations in assemblages at defined spatial scales, and (4) to explore species-environmental relationships.

The macrobenthic assemblages varied in time as well as in space in relation to wave exposure and elevation.

The comparison of invertebrate assemblages in 1984 and 2002 showed considerable temporal variation at the northern rock-platform at Helgoland. For instance, the increase in abundance or the new occurrence of southern species in 2002 implied that recent climate changes have already affected the composition of benthic communities at Helgoland. However, the processes maintaining a large part of the changes in the invertebrate assemblages between both sampling years were, to a great extent, speculative. Due to the snapshots at two points in time, clear evidence that changes are dependent on man-induced factors, and do not reflect natural cycles, could not be obtained. During the short-time scale from 2004 to 2006, it was shown that the identified spatial patterns at the northern rock-platform were consistent through time for total species richness and total abundance of the assemblages. Regarding individual species, it could be shown that the spatial pattern was only consistent through time for some macroalgal species, but not for any invertebrate species investigated. In contrast, at the western rock-platform spatial patterns changed with time (seasonal or inter-annual) for parameters of species assemblages, as well as specific species.

Besides temporal variation of the species assemblages, spatial distribution patterns were evaluated in the present study. As a first step, communities were defined at three locations at the Helgoland intertidal and were compared among these locations. In total, six communities were evaluated, with most of the variation occcurring between the southern location and the other two locations, the northern and the western rock-platform. A direct relationship between wave exposure and the occurrence of specific communities was shown for the sheltered southern location. In contrast, the species spectra and the distribution of the communities at the semi-exposed northern and exposed western location appeared to have little association to wave exposure directly. Other processes, such as grazing and/or competitive interactions, may have caused the differences in the occurrence of the communities. Besides the community-wave exposure relationship, the distribution of the communities was clearly related to variations in tidal height at the northern location; a structuring into spatial zonation patterns was observed. At the western location, changes in the communities were not related to variations in tidal height.

Distribution patterns at different spatial scales which were evaluated at the northern and western location separately showed that (1) total species richness, (2) total abundance of the assemblages, and (3) abundance of individual algae and invertebrates varied mostly at scales of about 50 metres (scale: transect) and 10s of centimetres (scale: replicate) at the northern and western location respectively. At the northern location, variability in all studied parameters of assemblages among transects was a direct result of differences between the vertical heights, the high- and low-shore. The species assemblage at high-shore was characterised by relatively low algal and invertebrate cover as well as invertebrate richness. This was in contrast with high values of these variables at low-shore. The total richness and cover responded asymptotically to elevation, whereas specific species showed neither a linear nor a nonlinear relationship to elevation. However, the elevation determined the frequency of occurrence and the maximal cover of most macroalgae and invertebrates. At the western location no relationship between elevation and all parametres (total richness, total abundance, abundance of specific species) occurred. In addition, the elevation did not determine the frequency of occurrence or the maximal cover of species. The spatial variation at the western study location may rather be explained by a haphazard scattering of suitable microhabitats.

In conclusion, although processes causing any spatial and/or temporal variation cannot be determined from observational studies, such as the present one, the identification of relevant scales of variation helps to formulate hypotheses, and to design manipulative experiments or monitoring programmes at appropriate scales. The identification of a characteristic scale of variation at each location at Helgoland aims at a monitoring program targeting the appropriate scale at each location separately. However, temporal inconsistencies of the scale-dependent variation, particularly at the western location, showed that monitoring should involve a multiple-scale sampling design. Moreover, particularly at the western location, experiments are vital to explain the processes causing the high small-scale variability of assemblages and their temporal changes.

ZUSAMMENFASSUNG

In der vorliegenden Arbeit wurden die Makrobenthos-Gemeinschaften, ihre Verteilung sowie ihre Dynamik im Helgoländer Felswatt untersucht. Eine Aufnahme des Makrobenthos im Jahr 1984 wurde im Jahr 2002 wiederholt. Daran schlossen sich saisonale Beprobungen in den Jahren 2004 bis 2006 an.

Trotz der vergleichsweise großen Anzahl an bestehender Literatur über die Ökologie des Helgoländer Makrobenthos gibt es bisher nur wenige Studien, die über räumliche Unterschiede oder zeitliche Veränderungen in der Artzusammensetzung der Makroalgen und Invertebraten des Helgoländer Eulitorals berichten; bis heute besteht kein umfassender Überblick über die Makrobenthos-Gemeinschaften des Helgoländer Eulitorals. Die bisher durchgeführten Arbeiten im Eulitoral beschäftigten sich entweder mit nur einer bestimmten taxonomischen Gruppe und/oder benutzen nur semi-quantitative Beprobungsverfahren; letztendlich existiert keine eingehende quantitative Beschreibung der Makrobenthos-Gemeinschaften, die sowohl durch Makroalgen als auch durch Invertebraten definiert sind. Darüber hinaus gibt es ebenso wenig Anhaltspunkte darüber, ob räumliche Unterschiede der Gemeinschaften von der Beprobungsskala abhängen und ob Prozesse, welche räumliche Variationen bedingen, auf nur einer oder aber mehreren Skalen ablaufen.

Somit war die spezielle Zielsetzung der vorliegenden Arbeit (1) Unterschiede in den Artgemeinschaften zwischen den beiden Jahren 1984 und 2002 sowie saisonale und jährliche Veränderungen von 2004 bis 2006 zu bewerten, (2) charakteristische Gemeinschaften, ihre Abundanzen und räumliche Verteilungsmuster zu erfassen, (3) Unterschiede der Gemeinschaften auf definierten räumlichen Skalen zu beurteilen und (4) Beziehungen zwischen Arten oder Gemeinschaften und abiotischen Faktoren zu untersuchen.

Die Makrobenthos-Gemeinschaften unterschieden sich zeitlich sowie räumlich in Bezug auf die Wellenexposition und die Höhe im Gezeitenbereich.

Die Makrofauna des Helgoländer Nordwatts unterschied sich beträchtlich zwischen der Untersuchung im Jahr 1984 und jener im Jahr 2002. Es traten beispielsweise südliche Arten im Jahr 2002 auf, welche im Artenspektrum von 1984 nicht festgestellt wurden. Des Weiteren wurde im Jahr 2002, verglichen zu 1984, ein Anstieg der Abundanz wärmeliebender Arten verzeichnet. Diese Ergebnisse deuten darauf hin, dass der Klimawandel bereits einen Einfluss auf die Artzusammensetzung der Makrofauna des Helgoländer Watts hat. Andererseits jedoch sind weitere Prozesse (natürliche und/oder menschgemachte), welche einen großen Teil der Veränderungen der Makrofauna zwischen den beiden Untersuchungen verursachen, zu einem großen Maße spekulativ. Aufgrund der beiden zeitlichen Momentaufnahmen (1984 vs. 2002)

allein ist es nicht möglich zu belegen, ob die Veränderungen von Faktoren abhängen, welche vom Menschen verursacht wurden oder ob diese eher natürliche Zyklen reflektieren. Während der Untersuchung zwischen den Jahren 2004 und 2006 konnte gezeigt werden, dass die räumlichen Verteilungsmuster der Makroalgen- und Invertebraten-Gemeinschaften im Helgoländer Nordwatt über die Zeit konstant blieben; ebenso waren die Verteilungsmuster einzelner Makroalgenarten zeitlich konstant, wohingegen die räumliche Verteilungsmuster der Makrofaunenarten offenbar zeitlichen Veränderungen unterlegen waren. Beispielsweise zeigten Makrofaunenarten in einigen wenigen Beprobungsmonaten die größten Abundanzunterschiede im Zentimeterbereich, wohingegen sie sich in den meisten anderen Monaten am deutlichsten im Bereich von ca. 50 Metern unterschieden. Im Helgoländer Westwatt änderte sich die räumliche Variation auf definierten Skalen während der Untersuchungsjahren (saisonal und inter-annuell) sowohl für den Gesamtartenreichtum und die -abundanz der Gemeinschaften als auch für die Abundanz einzelner Arten.

Neben der zeitlichen Veränderung der Artgemeinschaften wurden in der vorliegenden Arbeit räumliche Verteilungsmuster untersucht. Als erster Schritt wurden unterschiedliche Artgemeinschaften an drei verschiedenen Standorten des Helgoländer Felswatts beschrieben und zwischen den Standorten verglichen. Insgesamt konnten sechs verschiedene Artgemeinschaften definiert werden, wovon sich die Gemeinschaften des südlichen Standortes von jenen des Nord- als auch Westwatts am deutlichsten in der Artzusammensetzung und den Abundanzen charakteristischer Arten unterschieden. Eine direkte Beziehung zwischen der Wellenexposition und dem Auftreten der Gemeinschaften des wellengeschützten südlichen Standortes konnte festgestellt werden. Im Gegensatz dazu scheint es, dass das Artenspektrum und die Abundanzen der Artgemeinschaften des semi-exponierten Nordwatts und des exponierten Westwatts weniger direkt durch die Wellenexposition beeinflusst sind. Prozesse wie beispielsweise das Weiden von Schnecken und/oder konkurrierende Interaktionen zwischen Arten scheinen vielmehr die Unterschiede im Auftreten der Gemeinschaften zwischen dem Nord- und Westwatt zu verursachen. Neben der Beziehung zwischen der Wellenexposition und den Gemeinschaften, konnte gezeigt werden, dass kleinräumigere Gemeinschaftsunterschiede innerhalb des Nordwatts deutlich mit Höhenunterschieden im Gezeitenbereich in Verbindung stehen; eine räumliche Zonierung der Gemeinschaften wurde beobachtet. Kleinräumigere Gemeinschaftsunterschiede innerhalb des Westwatts konnten wiederum nicht mit Höhenunterschieden im Gezeitenbereich in Verbindung gebracht werden.

Verteilungsmuster auf unterschiedlichen räumlichen Skalen, welche im Nord- und Westwatt untersucht wurden, zeigten, dass (1) der Gesamtartenreichtum, (2) die Gesamtabundanz der Gemeinschaften und (3) die Abundanz einzelner Algen- und Invertebratenarten sich am stärksten auf Skalen unterschieden, welche ungefähr 50 Meter (Skala: Transekte) im Nordwatt beziehungsweise mehrere Zentimeter (Skala: Replikate) im Westwatt voneinander entfernt waren. Im Nordwatt waren die Unterschiede aller oben genannten Gemeinschaftsparameter ein direktes Ergebnis der Höhenunterschiede zwischen dem oberen und dem unteren Eulitoral. Die Artgemeinschaften des oberen Eulitorals waren durch relativ niedrige prozentuale Bedeckung an Algen und Invertebraten als auch durch einen geringeren Artenreichtum der Invertebraten charakterisiert, während hohe Werte dieser Parameter im unteren Eulitoral auftraten. Der Gesamtartenreichtum und die Gesamtabundanz verliefen asymptotisch zu der Höhe im Gezeitenbereich, wohingegen auf Artniveau weder eine lineare noch eine nicht-lineare Beziehung zur Höhe gezeigt werden konnte. Jedoch beeinflusste die Höhe im Gezeitenbereich die Häufigkeit des Auftretens sowie die maximale Bedeckung der meisten Algen und Invertebraten. Im Westwatt trat keine Beziehung zwischen der Höhe im Gezeitenbereich und den Parametern (Gesamtartenreichtum, -abundanz und Abundanz einzelner Arten) auf. Darüber hinaus bestimmte die Höhe weder die Häufigkeit des Auftretens noch die maximale Bedeckung einzelner Algen und Invertebraten. Die räumlichen Variationsmuster der Gemeinschaften im Westwatt können vielmehr durch eine zufällige Verteilung geeigneter Mikrohabitate erklärt werden.

Zusammenfassend lässt sich sagen, dass Prozesse, welche räumliche und/oder zeitliche Variationen hervorrufen, nicht durch beobachtende Studien allein bestimmt werden können. Beobachtende Studien, zu welchen die vorliegende Arbeit zählt, können jedoch durch Identifizierung relevanter Skalen dazu beitragen, Hypothesen zu formulieren und manipulative Experimente oder Monitoringprogramme auf angemessenen räumlichen und zeitlichen Skalen zu entwerfen. Die Identifizierung einer charakteristischen räumlichen Skala im Nord- als auch im Westwatt Helgolands zielt darauf ab, solche Skalen in ein Monitoringprogramm aufzunehmen. Jedoch wird aufgrund der zeitlichen Variation der räumlichen Verteilungsmuster, welche insbesondere im Westwatt auftrat, von einem Beprobungsdesign mit nur einer räumlichen Skala abgesehen; dagegen sollte ein Beprobungsdesign mit mehreren räumlichen Skalen etabliert werden. Darüber hinaus sollten besonders im Westwatt Experimente geplant werden, die die Prozesse untersuchen, welche die beträchtlichen kleinräumigen Unterschiede der Gemeinschaften und ihre zeitlichen Veränderungen verursachen.

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