

Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea)

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ABSTRACT: Over 3 successive seasonal cycles (April 1986 to October 1988), field experiments were established within 3 intertidal levels in the sheltered rocky intertidal of Helgoland (North Sea, German Bight). Competitors for space (*Mytilus edulis*, macroalgae), herbivores (*Littorina* spp.) and predators (*Carcinus maenas*) were either excluded from areas (0.25 m²) covered by undisturbed communities or enclosed at natural densities on areas that were cleared before of animals and plants. All the experimental fields (each 0.25 m²) were covered by cages with 4 mm gauze at the sides and a plexiglas top. The results of the experiments in the upper intertidal (occupied by *Littorina* spp. and *Enteromorpha*) showed that a natural density of herbivores could not prevent algal settlement and had only little influence on algal growth. Instead, abiotic factors (storms, algae washed ashore) decreased the stock of the green algae. Experiments in the mid intertidal, dominated by *Mytilus* (50 % cover), *Fucus* spp. (20 %) and grazing *L. littorea* (100 ind. m⁻²) showed that community structure was directly changed both by grazing periwinkles and by competition for space between mussels and macroalgae. Whenever *Littorina* was excluded, the canopy of *Fucus* spp. increased continuously and reached total cover within two years. In addition to the increase of *Fucus* spp., the rock surface and the mussel shells were overgrown by *Ulva pseudocurvata*, which covered the experimental fields during parts of the summer in the absence of herbivores. As soon as perennial species (fucooids) covered most of the experimental areas, the seasonal growth of *Ulva* decreased drastically. Presence and growth of macroalgae were also controlled by serious competition for space with mussels. Established *Mytilus* prevented the growth of all perennial and ephemeral algae on the rocks. However, the shells of the mussels provided free space for a new settlement of *Fucus* and *Ulva*. In the lower intertidal (dominated by total algal cover of *F. serratus*, herbivores such as *L. littorea* and *L. mariae*, and increasing number of predators such as *Carcinus*), the feeding activity of herbivores can neither prevent the settlement of the fucooid sporelings nor reduce the growth of macroalgae. *F. serratus* achieved a total canopy on the rock within one year. Doubled density of herbivores prevented the settlement of *Fucus* and most of the undercover algae. Predation by *Carcinus* on *Littorina* spp. had little influence on the herbivore community patterns. However, the crabs supported the establishment of macroalgae by excluding the mussels from the lower intertidal. In summary, the community organization and maintenance in the mid and lower intertidal is influenced to a high degree by biological interactions. Whereas both the relatively important herbivory by *L. littorea* and competition for space between mussels and macroalgae dominate in the mid intertidal, predation reaches its highest relative degree of importance for community structure in the lower intertidal.

INTRODUCTION

Intertidal rocky shore communities, their organisms, distribution and abundance have been studied worldwide during the recent decades (e.g. Stephenson & Stephenson, 1949, 1972; Southward, 1958; Lewis, 1964). The results of nearly all investigations have demonstrated that "amphibian" communities are structured in correlation with gradients of different abiotic factors, such as vertical tide level and exposure to wave action, even under different climatic conditions (Ballantine, 1961; Stephenson & Stephenson, 1972; Dalby et al., 1978). For instance, for cold temperate regions Lewis (1964) described three different types of community pattern: (1) Shores dominated by barnacles (wave exposure high), (2) shores dominated by mussels (wave exposure intermediate) and (3) shores dominated by furoid algae (wave exposure low). According to these descriptive investigations, it seemed obvious that intertidal hard bottom communities are mainly (or exclusively) structured and controlled by abiotic factors (cf. Doty, 1946; Lewis, 1961, 1977).

Our scientific knowledge in this field has drastically increased within the last three decades. Experimental studies on the distribution and abundance of species and their activity have provided many arguments for a significant role of biological interactions in the community structure (starting with Connell, 1961; Southward, 1964; Paine, 1966; Dayton, 1971). Investigations on recruiting communities destroyed by disastrous oil spills after nearshore tanker accidents (cf. Mann & Clark, 1978; Southward & Southward, 1978; Anonymus, 1981) have also focussed scientific interest on the development and maintenance of intertidal rocky shore communities. Considering the dominant species, their feeding habits and mechanisms of adaptations to environmental factors, four types of biological interactions may influence the community patterns: (1) **Predation** (see Connell, 1970, 1975; Dayton, 1971, 1975; Paine, 1974, 1976; Menge, 1976, 1978a, 1978b, 1983; Menge & Sutherland, 1976, 1987; Connell & Slatyer, 1977; Lubchenco & Menge, 1978; Hughes, 1985; Marsh, 1986; Petraitis, 1987). (2) **Herbivory** (sometimes also called "grazing", though this means something different to a lot of scientists: see Paine & Vadas, 1969; Dayton, 1971, 1975; Connell & Slatyer, 1977; Lubchenco, 1978, 1980, 1982, 1983; Lubchenco & Menge, 1978; Kitting, 1980; Lein, 1980; Lubchenco & Cubitt, 1980; Underwood, 1980, 1984a, 1984b; Lubchenco & Gaines, 1981; Robles & Cubitt, 1981; Underwood & Jernakoff, 1981; Gaines & Lubchenco, 1982; Steneck, 1982; Bertness et al., 1983; Hawkins & Hartnoll, 1983; Cubitt, 1984; Hartnoll & Hawkins, 1985; Jernakoff, 1985a, 1985b; Petraitis, 1987). (3) **Competition for space** (see Connell 1964, 1985; Dayton, 1971; Levin & Paine, 1974; Scheltema, 1974; Jackson, 1977a, 1977b; Lubchenco & Menge, 1978; Menge & Lubchenco, 1981; Paine, 1984; Hartnoll & Hawkins, 1985; Suchanek, 1985). (4) **Competition for food** (see Menge, 1972; Creese & Underwood, 1982; Fletcher & Creese, 1985; Ortega, 1985; Petraitis, 1989; Quinn & Ryan, 1989).

Results of all these publications have documented that biological interactions (= biotic factors) may play an important role in the development and maintenance of intertidal communities. However, as the role of biological interactions and their importance for community structure are still so unpredictable in a special area, it is still a field of work. Manipulative experiments seem to be a suitable tool to test the conflicting hypotheses of different models (see Underwood, 1985; Underwood & Fairweather, 1986).

This study deals with the rocky shore communities at the northeastern intertidal of

the island of Helgoland. Descriptive ecological publications for this study site on the algal and faunal communities and their distribution are already available (i.e. Lüning, 1970; Kornmann & Sahling, 1977; Gillandt, 1979; Janke, 1986), but there is little information about colonization, succession of the communities, and the importance of biological interactions for their development and maintenance. Only Markham & Munda (1980) and Munda & Markham (1982) studied the seasonal colonization of algae and their productivity at the nearby "Westwatt" (Fig. 1), but they ignored the possible effects of biological interactions on the development of communities at this study site.

I have focussed on the following general question: Do biological interactions play an important role in the development and maintenance of the rocky shore communities at the island of Helgoland, and in which way do they change and control the community structure? To give an answer to this I drew attention to the following problems in detail:

(1) Colonization and development of communities on cleared grounds at the beginning of a succession period.

(2) Development and maintenance of undisturbed and established long-term communities, and the importance of biological interactions regarding changes within the populations of settling organisms.

(3) Changes in the importance of biological interactions for the community structure along the vertical shore gradient.

This investigation was started as a pilot project to create a substantial framework for more quantitative studies on the special controlling effects that littoral organisms may exert on the community and environment in which they live.

STUDY SITE

Location, morphology and distribution of organisms

The island of Helgoland represents the only rocky shore in the southeastern part of the North Sea. For detailed information about the geomorphology, geography and genesis see Hagmeier (1930), Schmidt-Thomé (1937), Wurster (1962), Krumbein (1975, 1977) and Binot (1988). Today, the only authentic area of this highly erosive red sandstone shore is the northern site of the island (Fig. 1). All other parts were changed or separated from the sea by anthropogenous activities. In the west and north, the island is surrounded by an eroded flat rocky terrace which represents the base of the formerly larger island. The level of this terrace ("Felswatt"; Hagmeier, 1930; Fig. 1) slopes down within a distance of 300 to 400 m from mean high water level (MHW) to about mean low water line (MLW; difference in vertical level: 2.4 m). The morphology of the surface is structured in heterogeneous patterns (Hagmeier, 1930; Janke, 1986) that provide many niches and microhabitats for communities of high diversity (Janke, 1986). North of the island, the terrace is separated by a large mole ("Nordwest-Mole", Fig. 1). Access to the western part ("Westwatt") is restricted to just a few days within a month, whereas access to the "Nordost-Felswatt" (Figs 1, 2) is possible nearly every day in the year (except during storm periods). Thus the "Nordost-Felswatt" was chosen for the experimental studies. This part of the terrace is sheltered from storms and high wave exposure by the long mole. Thus the algal and faunal communities show the typical patterns of a "very sheltered" community (Ballantine, 1961; Dalby et al. 1978; Janke, 1986). There are three

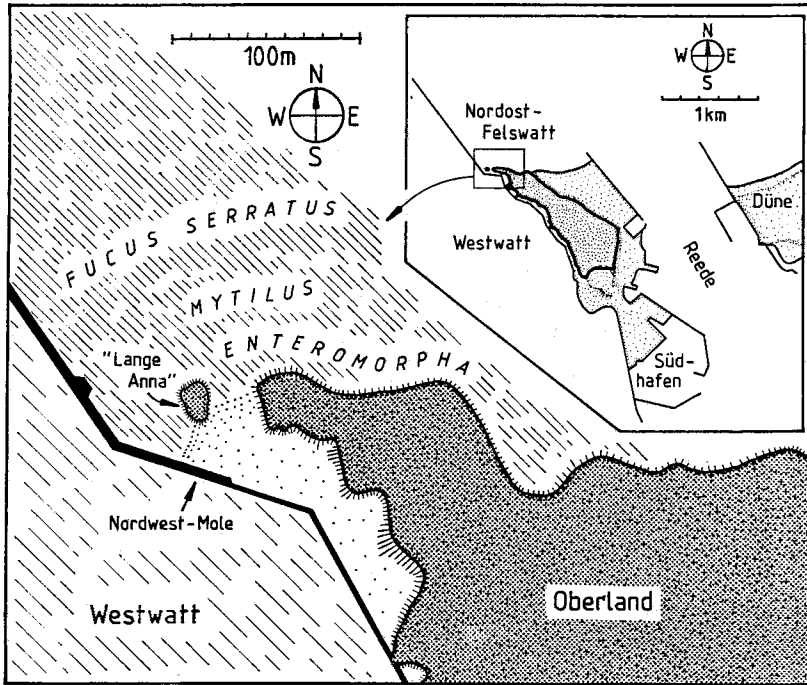


Fig. 1. Study site at the island of Helgoland (North Sea, German Bight)

distinct vertical belts within the intertidal. Each of them is characterized by a distinct community.

The upper intertidal is dominated by the green algae *Enteromorpha* spp. Link (see Kornmann & Sahling, 1977). These annual algae totally cover the upper part of the intertidal from mid spring to late autumn and then regularly disappear during the winter season. The green algal canopy is accompanied by small populations of *Fucus* spp. L., especially *F. spiralis* L. Animals in this zone are the herbivorous periwinkles *Littorina saxatilis* (Oliv) (up to the supralitoral) and *L. littorea* (L.) (in the lower part; Fig. 2). The lower limit of the upper intertidal is marked by a clear line where the growth of *Enteromorpha* stops abruptly.

The mid intertidal is dominated by *Littorina littorea* and also by beds of blue mussels (*Mytilus edulis* (L.)) in the mid and lower region. Algal growth is represented by *Fucus* spp. settling on the red sandstone rock surface and on the mussel shells, and the red alga *Chondrus crispus* (Stackh) growing only on the rock. During the time of submersion, this zone is visited by *Carcinus maenas* (L.) which feeds on the dense populations of mussels and periwinkles. As soon as this zone becomes emersed during ebb tide, they return to deeper parts of the "Felswatt".

The lower intertidal is characterized by the dense canopy of *Fucus serratus* L. and many seasonal or perennial undercover algae [*Monostroma* spp. (Wittr.), *Petalonia fascia* (O. F. Müller), *Cladophora sericea* (Huds.), *Acrosiphonia arcta* (Dillw.) and *Cladophora rupestris* (L.), *Chondrus crispus*, *Corallina officinalis* (L.), crustose red algae].

The lower intertidal is also intensively colonized by high numbers of sublittoral species that survive under the canopy of *F. serratus* (Janke, 1986) providing a moist and shaded microclimate. This zone is mainly occupied by *L. littorea* (grazing on both rock and kelp) and *L. mariae* Sacchi & Rastelli (grazing only on *Fucus* blades, see Goodwin & Fish, 1977; Janke, 1986). Predators are represented by the highly abundant *Carcinus* (Fig. 2) that migrate up into the intertidal from the beginning of June to the end of September/beginning of October.

For a more detailed description of the "Nordost-Felswatt", the settling organisms and their distribution, see Janke (1986).

In contrast to other very sheltered shores, in Great Britain or Norway, that are also dominated by fucoids, the communities at Helgoland lack typical species like *Ascophyllum nodosum* (L.), *Pelvetia canaliculata* (L.) and *Patella* spp. (L.). The predatory dogwhelk *Nucella lapillus* (L.) is very rare. According to the abundance and distribution of the key-species and to Lewis' universal "model" (Lewis, 1964, p. 320), it seems very likely that *Littorina* spp., *Mytilus* and *Carcinus* are the key organisms for the intertidal community structure at Helgoland. A model of this hypothesis is given in Figure 2 B. This does not reflect the relative importance of biological interactions in correlation to the vertical shore gradient.

Abiotic factors

The island of Helgoland is situated in the boreal region of the northern hemisphere. Annual fluctuations of water temperature and salinity are high because of the influence of the estuaries of River Elbe and Weser. For detailed data see Figure 3. The data reflect a very harsh winter in 1986/87 and an extremely mild winter 1987/88. Water temperature and salinity were measured once a day at the "Reede" (see Fig. 1), whereas air temperature was taken every hour. Wave exposure at the study site was estimated as "sheltered" to "very sheltered" (Ballantine, 1961; Dalby et al., 1978; Janke, 1986). Range between MLW and MHW is 2.4 m (DHI, 1987). The mean period of emersion during one tide is about 6 hours for the *Enteromorpha*-zone, 4 hours for the *Mytilus*-zone and about 2.5 hours for the *Fucus-serratus*-zone.

EXPERIMENTAL DESIGN AND METHODS OF DATA COLLECTION

The most effective way to answer the questions given above are manipulative field experiments (Underwood, 1985). Cages (0.5 m × 0.5 m × 0.1 m, nylon-mesh size 4 mm, plexiglas on top) were established in the upper, mid and lower intertidal for enclosure and/or enclosure of a controlled amount of organisms (Fig. 4). For estimates of caging effects, communities in areas covered by open cages and those in control areas without cages were compared. Data on both sessile faunal and algal cover were collected with a frame (0.5 m × 0.5 m) divided into 25 little quadrats of 10 cm length, thus representing 4 % of the observed experimental area. For each small quadrat, cover was estimated between 0/< 50 %/> 50 % (see Braun-Blanquet, 1964; Jones et al., 1980; Baker & Wolff, 1987). Mean deviation using this method is about ± 2 % total cover of the experimental area. Periwinkles and crabs were counted. Seasonal migrating behaviour of crabs was simulated by excluding them from the experimental areas during the months they stay in the subtidal. *Carcinus maenas* (mean carapace width: 50 ± 4 mm, only male) was

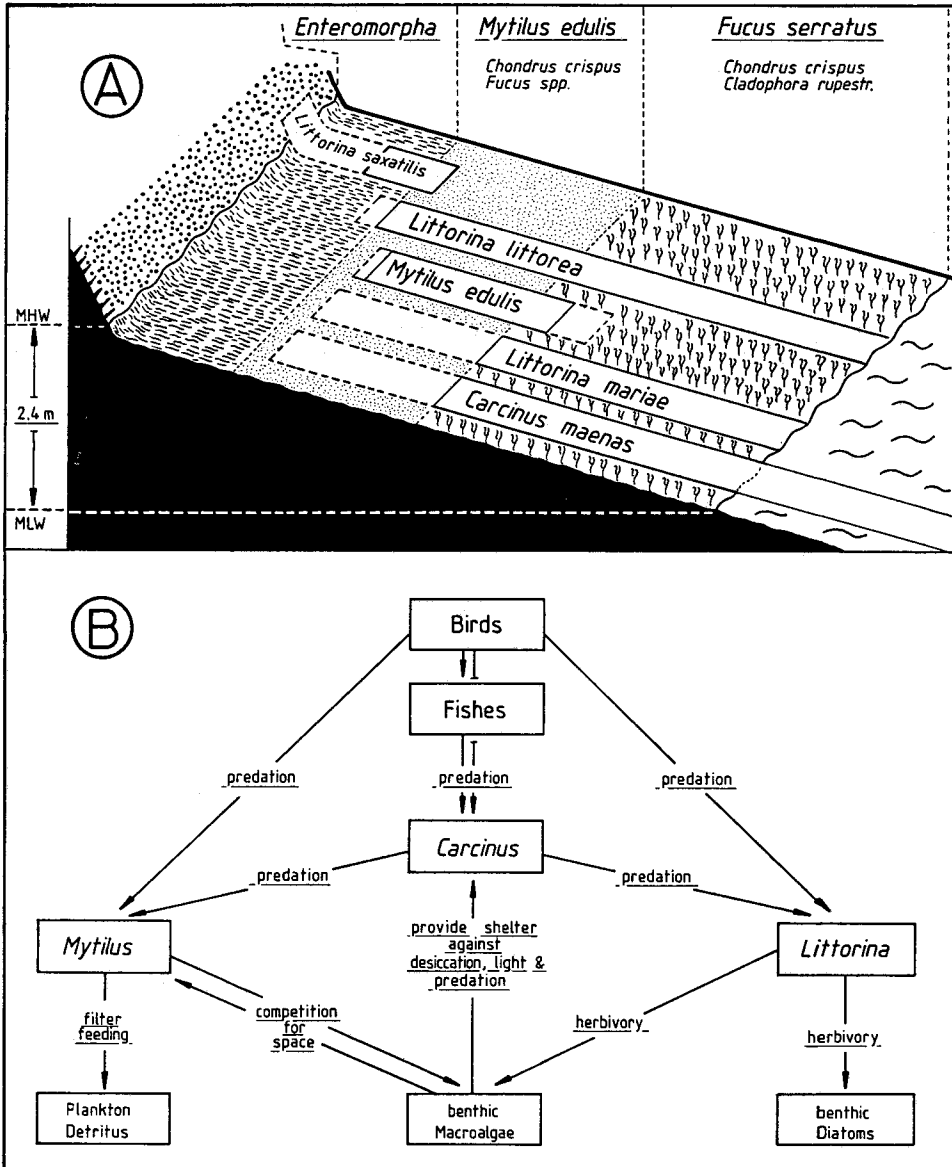


Fig. 2. Macrofauna of the rocky northeastern intertidal ("Nordost-Felswatt") of Helgoland. (A) Vertical zonation of dominant species (simplified after Janke, 1986). (B) Presumed biological interactions amongst dominant settlers and visitors

included between the beginning of June up to the end of September or beginning of October. Periwinkles consumed by *Carcinus* during enclosure were replaced at the beginning of the succession periods to simulate natural conditions. Experimental areas, for a new succession were mechanically cleared with a steel brush and then burnt with a

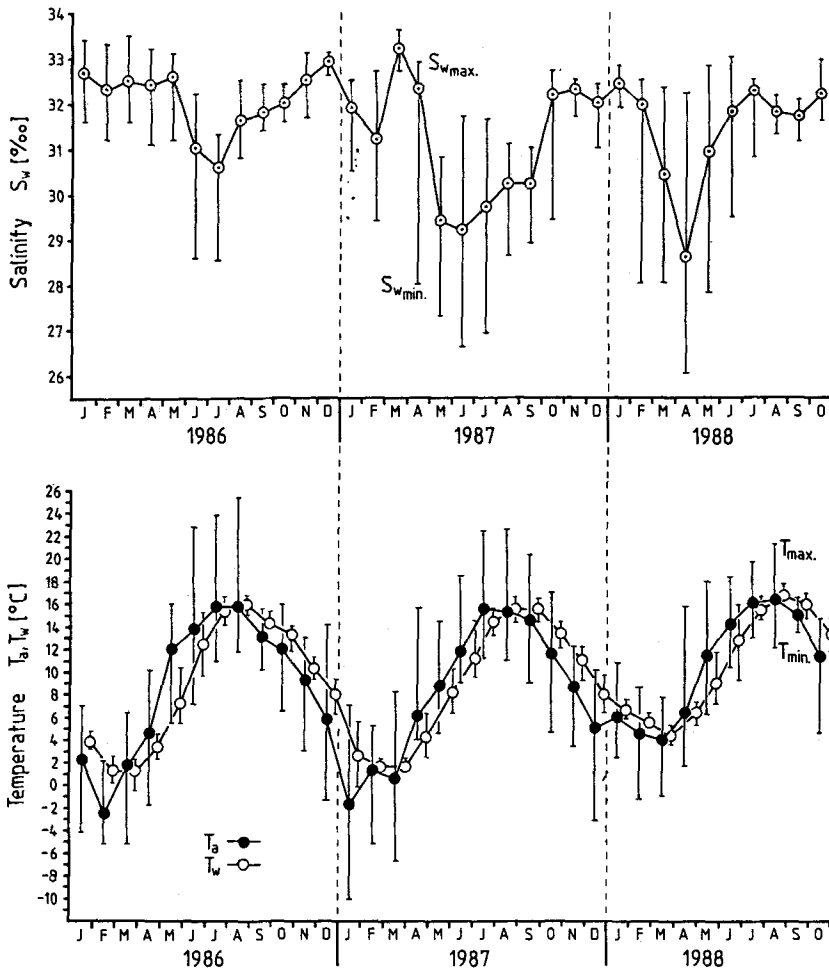


Fig. 3. Seasonal fluctuations of seawater salinity (S_w), seawater temperature (T_w) and air temperature (T_a) at Helgoland Reede [unpublished data provided by Biologische Anstalt Helgoland (T_w) and Wetterwarte Helgoland (T_a)]

portable cooker flame. Whenever possible (weather!) data were collected monthly, during winter every six weeks. At the beginning of the experiments, data were taken over fortnightly periods to document short seasonal changes of the community structure.

For calculations on the accuracy of representative area size and community diversity, 30 randomly chosen areas ($0.5 \text{ m} \times 0.5 \text{ m}$) each in mid and lower and 15 in the upper intertidal were monitored to document the mean densities of abundant sessile settlers (for method see above). Data of these pre-investigations are listed in Table 1. To estimate the accuracy of the abundance minimal areas for each of the three shore levels, Kulczynski-indices (I_k ; see Kronberg, 1987) were calculated (see also Table 1). For the definition of the abundance minimal area, Weinberg (1978) assumed a quantitative similarity of $I_k =$



Fig. 4. Field experiments in the northeastern rocky intertidal ("Nordost-Felswatt") of Helgoland. Cages for manipulative inclusion/exclusion experiments of organisms (size $0.5 \text{ m} \times 0.5 \text{ m} \times 0.1 \text{ m}$; plexiglas on top, 4 mm nylon gauze at the sides)

0.70 as satisfactory. In all of the three vertical shore levels, I_k was higher than 0.70 (see Table 1). Thus for the sessile components of the communities on the experimental areas, the size of the experimental field design ($0.5 \text{ m} \times 0.5 \text{ m}$) was large enough.

It was not appropriate to consider abundances of mobile species (*Littorina* spp., *Carcinus*) for this calculation. As they move around, distribution patterns change according to the tides, light and other abiotic factors (Crothers, 1967, 1968; Elner, 1978; Elner & Hughes, 1978; Underwood, 1979; Hawkins & Hartnoll, 1983). For instance, *Carcinus* is restricted to crevices and areas covered by the algal canopy during time of emersion, whereas it spreads around all over the place during submersion. Mid intertidal is visited by the crabs only during submersion. At ebb tide they migrate into the lower intertidal or upper subtidal to escape from desiccation. Thus to simulate natural populations of both crabs and periwinkles in the experimental areas, mean densities of species were enclosed in the cages (see Table 1). As crabs rarely appear in the mid intertidal during emersion, the mean density could only be estimated. To provide a good comparison for data, population density of *Carcinus* in the mid intertidal was assumed to be the same as in the lower intertidal ($= 5 \text{ ind. } 0.25 \text{ m}^{-2}$, see Table 1).

Experimental areas were divided into two classes: (1) Experimental caged areas for recruiting communities including one of the hypothetical key-species in natural population density; (2) Experimental caged areas including a representative established settlement, but excluding one of the hypothetical key-species.

In the upper intertidal, experiments on the established communities were not conducted because of total annual community recruitment during spring time. As mussels and crabs do not appear in this zone (Janke, 1986), studies on their importance for community structure in this zone were omitted.

Table 1. Mean population densities of dominant key-species in the northeastern rocky intertidal of Helgoland. \bar{N} = individuals $\times 0.25 \text{ m}^{-2}$; x = cover (%) $\times 0.25 \text{ m}^{-2}$; s = standard deviation; I_k = Kulczynski-Index (see Kronberg, 1987). For further information see text

Upper intertidal: <i>Enteromorpha</i> -zone:	(15 samples)	$I_k = 0.988$
<i>Enteromorpha</i> spp.	$x = 90.0$	$s = 14.5$
<i>Littorina saxatilis</i>	$\bar{N} = 15.3$	$s = 13.0$
<i>Littorina littorea</i>	$\bar{N} = 10.3$	$s = 8.4$
Mid intertidal: <i>Mytilus</i> -zone:	(30 samples)	$I_k = 0.782$
<i>Fucus</i> spp.	$x = 20.1$	$s = 9.6$
<i>Littorina littorea</i>	$\bar{N} = 24.9$	$s = 5.7$
<i>Mytilus edulis</i>	$x = 52.8$	$s = 26.7$
Lower intertidal: <i>Fucus-serratus</i> -zone:	(30 samples)	$I_k = 0.962$
<i>Fucus serratus</i>	$x = 97.5$	$s = 8.0$
<i>Littorina littorea</i>	$\bar{N} = 25.3$	$s = 17.6$
<i>Littorina mariae</i>	$\bar{N} = 24.2$	$s = 14.9$
<i>Carcinus maenas</i>	$\bar{N} = 5.1$	$s = 5.0$

A survey of the experimental areas and the organisms excluded or included is given in Table 2.

Some critical notes must be mentioned concerning the experimental plan and design. First of all there were no replicates; the site of each of the experimental areas was, however, large enough to allow trend observations and conclusions. Thus, there was no pseudoreplication. Hurlbert (1984) suggested one should prefer unreplicated large-size field experiments to replicated, but small-dimensional ones. Secondly, data for tests on statistical significance could not be provided. Thus, only obvious and drastic changes within the communities were used for inferring causes and mechanisms of change in community structure.

RESULTS

Upper intertidal: *Enteromorpha*-zone

As mentioned above, only experiments on recruiting communities (2 controls, recruitment with enclosure of herbivores, see Table 2) were conducted in the upper intertidal (Fig. 5).

Controls. On both open and caged control areas *Enteromorpha* spp. became the spatial dominant. Recruitment and rapid growth of the algae always occurred during March to April, whereas population decline started in October and became most obvious between January and March. Green algal populations showed a typical seasonal growth pattern. In all of the three periods of vegetation observed, *Enteromorpha* spp. attained total cover and declined drastically during the winter. Besides green algae, *Fucus* spp. settled on both control areas but did not cover more than 40% (Fig. 5 B, July 1987). In addition, the caged control area was colonized by the sedentarian polychaete *Fabricia sabella* (Ehrenberg) for periods of up to three months. These worms regularly produce large cushions of tubes made of detritus, slime and mud, thus promoting sedimentation of

Table 2. Biological interactions in the rocky intertidal of Helgoland. Studies of inclusion and exclusion of key-species (*Littorina* spp., *Mytilus edulis*, *Carcinus maenas*) on experimental areas. Following biological interactions were taken into consideration: competition for space, herbivory, predation. For further explanations see text

Intertidal level Dominant species	Recruiting Communities		
	Upper <i>Enteromorpha</i> spp.	Mid <i>Mytilus edulis</i>	Lower <i>Fucus serratus</i>
Control with cage	yes	yes	yes
Control without cage	yes	yes	yes
Inclusion of competitors for space	no	50% <i>Mytilus</i>	no
Inclusion of predators	no	5 × <i>Carcinus</i>	5 × <i>Carcinus</i>
Inclusion of herbivores	15 × <i>L. saxatilis</i> 10 × <i>L. littorea</i>	25 × <i>L. littorea</i>	25 × <i>L. littorea</i> / <i>L. mariae</i> (each) 15/25/50 × <i>L. littorea</i> controls with/without cages
Inclusion of herbivores and predators	no	no	25 × <i>L. littorea</i> / <i>L. mariae</i> (each) 5 × <i>Carcinus</i>
Intertidal level Dominant species	Upper <i>Enteromorpha</i> spp.	Mid <i>Mytilus edulis</i>	Lower <i>Fucus serratus</i>
Control with cage	no	yes	yes
Control without cage	no	yes	yes
Exclusion of competitors for space	no	25 × <i>L. littorea</i> 5 × <i>Carcinus</i>	100% <i>Fucus serratus</i> 25 × <i>L. littorea</i> / <i>L. mariae</i> (each) 5 × <i>Carcinus</i>
Exclusion of predators	no	50% <i>Mytilus</i> 25 × <i>L. littorea</i>	100% <i>Fucus serratus</i> 25 × <i>L. littorea</i> / <i>L. mariae</i> (each)
Exclusion of herbivores	no	50% <i>Mytilus</i> 5 × <i>Carcinus</i>	100% <i>Fucus serratus</i> 5 × <i>Carcinus</i>

small particles. Within a few weeks, *Fabricia* cushions occupied up to 76% of the experimental area (Fig. 5B, August 1987). Increase of worm cushions was always correlated with a decline of *Enteromorpha* spp. Periwinkles were not observed on either of the control areas during the time of data collection.

Inclusion of herbivores. All periwinkles enclosed survived the whole term of study. *Enteromorpha* settled in spring and increased very rapidly up to total or nearly total cover of the area (1986: 96% in May and June; 1987: 100% in July; 1988: 90% in May). Compared to the control areas, succession of *Enteromorpha* was slower, whereas decline was accelerated by herbivory of periwinkles. In contrast to both control areas, *Fucus* spp. did not grow at all. *Fabricia sabella* settled during summer for periods of up to

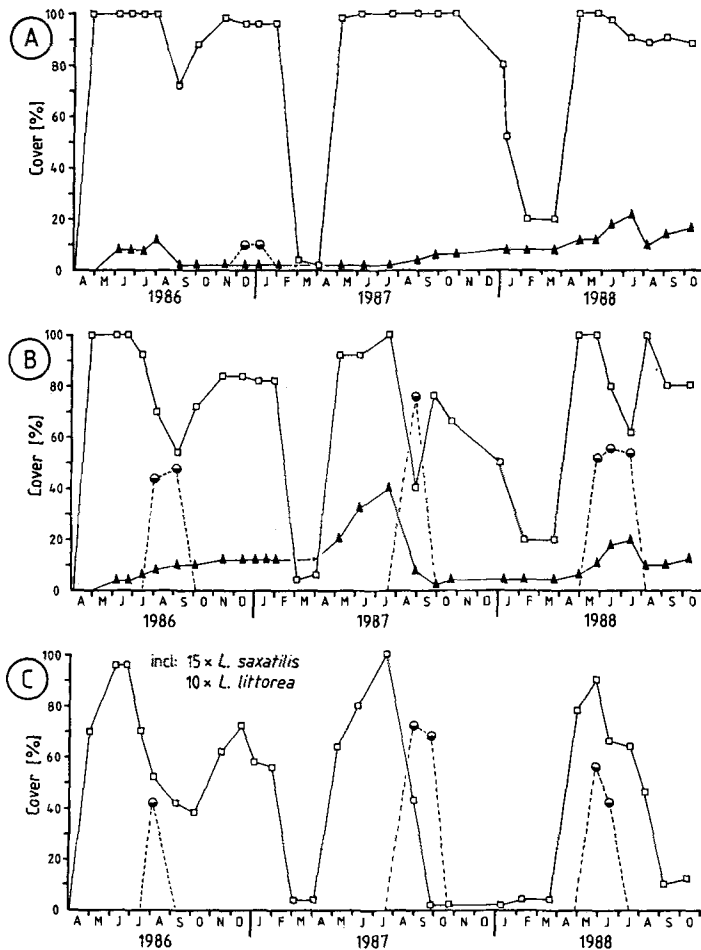


Fig. 5. Biological interactions in the upper intertidal of Helgoland. Experiments on recruiting communities. Ⓐ Control without cage (open). Ⓑ Control with cage (caged). Ⓒ Recruiting settlement including herbivores (15 × *Littorina saxatilis* and 10 × *L. littorea*). Fauna: ---○--- *Fabricia sabella*. Flora: -□- *Enteromorpha* spp., -▲- *Fucus* spp. All data given as degree of cover (%)

about three months and produced thick tube cushions. Increase of worm cushions was correlated with a decline of *Enteromorpha* spp.

Mid intertidal: *Mytilus*-zone

Recruiting communities in the mid intertidal

Controls. Both open and caged control areas were intensively visited and grazed by *Littorina littorea*. Only in February and March 1987 were no periwinkles observed during data collection. Mean densities of *Littorina*-populations were $\bar{N}(s) = 30.0$ (17.7) ind. 0.25 m^{-2} on the open control area and $\bar{N}(s) = 31.1$ (16.6) ind. 0.25 m^{-2} on the caged control area. *L. maria*e appeared with the establishment of *Fucus* spp. Space occupation by *Mytilus edulis* started with the succession period in spring 1987 (April and May) and stagnated during winter 1987/88. At the end of the experimental period, 20 % (open)/22 % (caged) of the ground were covered by mussels. Annual succession of algae started with seasonal species such as *Monostroma* spp., *Cladophora sericea* and *Dumontia incrassata* (O. F. Müller). Growth rates were very high in the beginning but they also decreased very quickly. None of these alga species reached more than 28 % cover (*Monostroma* spp., Fig. 6 B, April 1988). With the onset of winter, all seasonal algae had disappeared. Succession of perennial algae started in July 1986 with *Fucus* spp. Standing crop increased up to September 1987 on both control areas (28 % cover for open control/16 % on caged control) but decreased during late autumn and winter. Succession of *Fucus* spp. started again in February 1988 and reached 26 % cover on open and 22 % on caged control areas. Another perennial species *Chondrus crispus* settled on both control areas in August 1986 and reached its maximum cover at 8 % on the open and 10 % on the caged ground (Fig. 6 A, B, both August 1987).

Inclusion of competitors for space. A mussel population of natural mean density (50 % cover) was enclosed in the experimental area (Fig. 7 A). As soon as the experiments were initiated, mussels started to occupy more space though not increasing in numbers. By June 1986, *Mytilus edulis* covered 74 % of the rock surface, but then kept constant cover up to March 1987. In spring 1987 many juvenile mussels (<4 mm) settled on top of the old ones or next to them. Cover increased up to 82 % in October 1988. Of the perennial algae, *Fucus* spp. appeared in May 1986 and grew up steadily both on mussel shells and rock, covering the whole experimental area between May to October 1988. Succession of seasonal algae started with *Monostroma* spp. in May 1986, which, however, was replaced within a month by *Ulva pseudocurvata* Koeman. *Ulva* showed a pronounced seasonal growth cycle, covering all or most of the ground during spring and summer and disappearing in winter. In spring and summer 1988, *Ulva* appeared with a maximum cover of only 6 %, settling exclusively on blades of *Fucus* spp.

Inclusion of predators. Predators in the mid intertidal were represented by the shore crab *Carcinus maenas*. Five individuals (estimated natural population density) were enclosed in a cage (Fig. 7 B). Recruitment of seasonal algae started in May 1986 with *Monostroma* spp. followed by *Ulva pseudocurvata* in June 1986. As described in the previous chapter, *Ulva* showed a very conspicuous seasonal growth cycle throughout the whole period of study, covering all or most of the ground during spring and summer and (nearly) disappearing in winter. The first of the perennial algae to settle was *Chondrus*

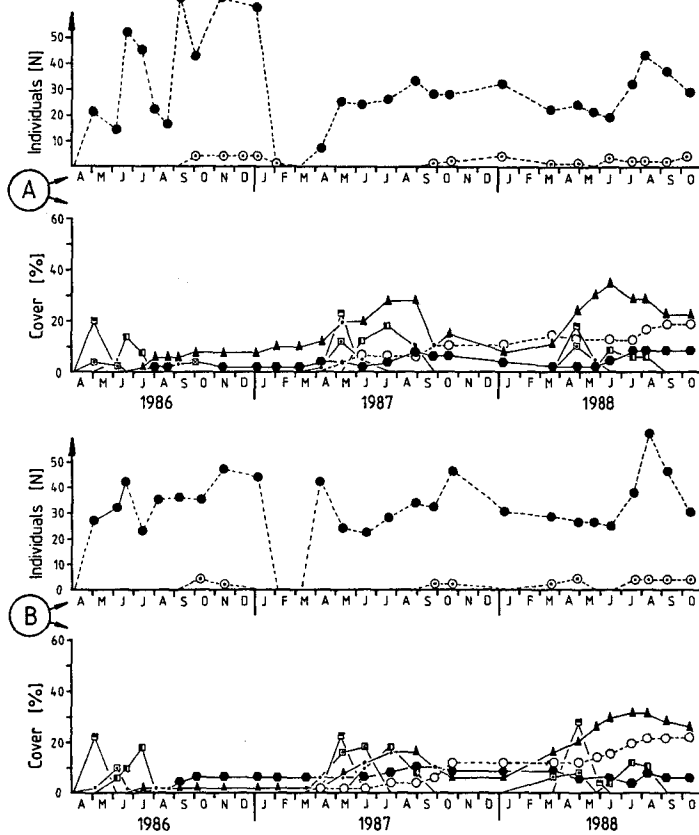


Fig. 6. Biological interactions in the mid intertidal of Helgoland. Experiments on recruiting communities. I. ① Control without cage (open). ② Control with cage (caged). Fauna: ●— *Littorina littorea*, ○— *L. mariae*, ○— *Mytilus edulis*. Flora: ■— *Cladophora sericea*, □— *Monostroma* spp., ▲— *Fucus* spp., ●— *Chondrus crispus*, □— *Dumontia incrassata*. All data given as degree of cover (%) or number of individuals (N)

crispus (May 1986) which grow up to 6% cover (July 1986). In April 1987, the *Chondrus* stock had disappeared. *Fucus* spp. settled in June 1987 and established a small stock (up to 8% cover in May/June 1987) until the end of the experimental period. *Fucus* blades were consumed by *Carcinus*. In October 1987, a small colony of juvenile *Mytilus* settled but was consumed within a month (May to June 1988) by *Carcinus*.

Inclusion of herbivores. Herbivores in the mid intertidal were represented by the periwinkle *Littorina littorea*. 25 individuals (estimated natural population density) were enclosed in the cage (Fig. 7 C). All periwinkles enclosed survived the whole term of data collection. Algal settlement was very low compared to ungrazed communities initiated at the same time (see Fig. 7 A, B). *Cladophora sericea* was the only seasonal alga that settled during all succession periods coming up between March and July and disappearing between August (1986) and October (1987). Highest degree of cover occurred in July 1988 (20%). Other seasonally growing algae were *Petalonia fascia*

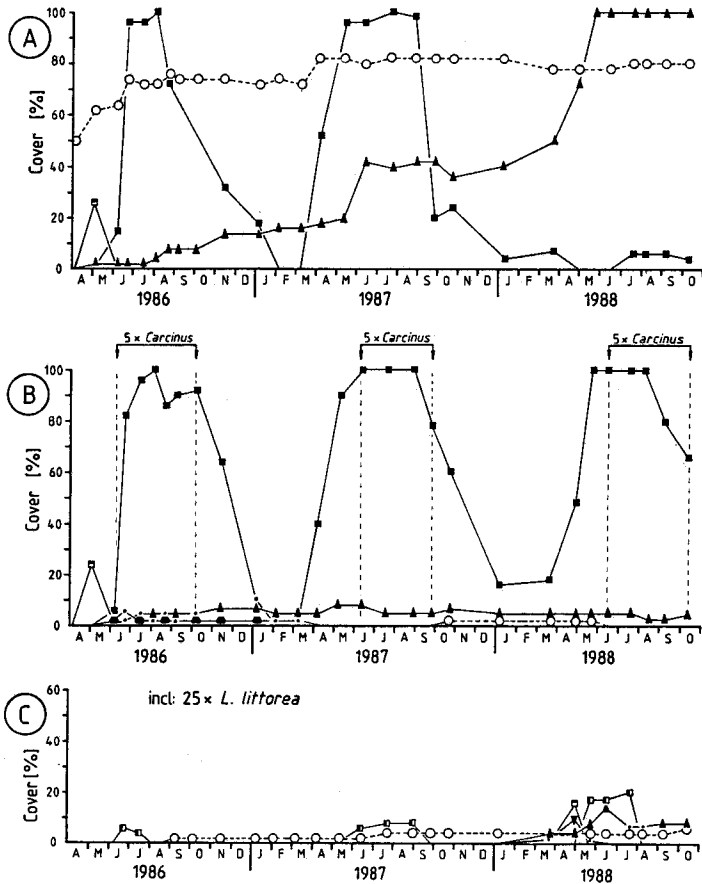


Fig. 7. Biological interactions in the mid intertidal of Helgoland. Experiments on recruiting communities. II. (A) Inclusion of competitors for space (*Mytilus edulis*). (B) Inclusion of predators (*Carcinus maenas*). (C) Inclusion of herbivores (*Littorina littorea*). Fauna: --○-- *Mytilus edulis*. Flora: --□-- *Cladophora sericea*, --■-- *Monostroma* spp., --■-- *Ulva pseudocurvata*, --▲-- *Fucus* spp., --▼-- *Petalonia fascia*, --●-- *Chondrus crispus*. All data given as degree of cover (%)

(March to May 1988) and *Monostroma* spp. (April 1988). The first perennial alga to establish itself was *Fucus serratus* (March 1988), reaching highest cover in June (14%). Space was occupied by, besides algae, juvenile *Mytilus edulis* which first settled in August 1986, growing up to final cover of 6%. Recruitment by invasion of juvenile mussels happened in July 1987 and August 1988, leading subsequently to increased occupation of space either immediately (1987) or during the following months (in 1988). Space occupation also increased with the growth rate of established mussels.

Established communities in the mid intertidal

Controls. Both open and caged control areas were intensively visited and grazed by *Littorina littorea* (Fig. 8). Only in February and March 1987 were no periwinkles

observed during data collection. Mean densities of *Littorina* populations were $\bar{N}(s) = 23.9$ (8.5) ind. 0.25 m^{-2} on the open control area and $\bar{N} = 27.3$ (9.4) ind. 0.25 m^{-2} on the caged control area. In addition, *L. mariae* sporadically appeared on *Fucus* spp. Seasonal macroalgae settling on control areas were *Cladophora sericea*, *Petalonia fascia* and *Dumontia incrassata*. None of these algae reached more than 10% cover. *Fucus* spp. dominated algal vegetations on both open and caged control areas and doubled their canopy from 18% (20% on the caged control) to 40% (42%). A sudden decrease on the

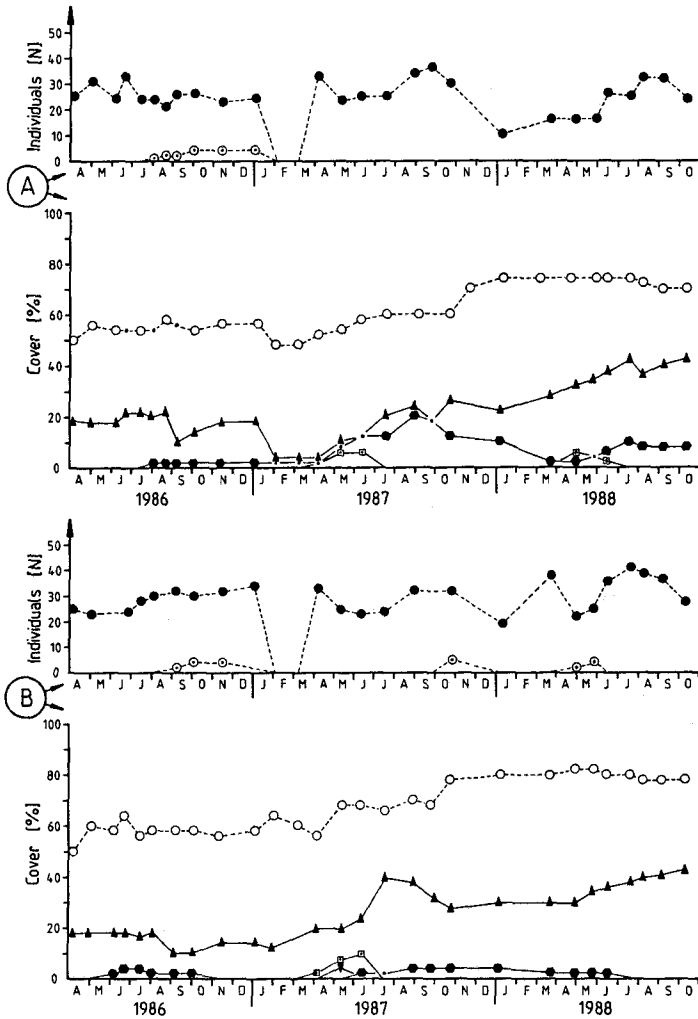


Fig. 8. Biological interactions in the mid intertidal of Helgoland. Experiments on established communities. I. Ⓐ Control without cage (open). Ⓑ Control with cage (caged). Fauna: --●-- *Littorina littorea*, --○-- *L. mariae*, --□-- *Mytilus edulis*. Flora: --▲-- *Fucus* spp., --▼-- *Petalonia fascia*, --●-- *Chondrus crispus*, --□-- *Dumontia incrassata*. All data given as degree of cover (%) or number of individuals (N)

open control area between February and March 1987 was followed by a period of accelerated growth. Besides *Fucus* spp., the only perennial alga to settle on the control areas was *Chondrus crispus*. On the open control area it grew up to 20 % cover but did not exceed more than 4 % on the caged control area. Mussel beds on control areas expanded steadily during the period of study. As soon as the experiments had started, *Mytilus edulis* began to occupy more space (maximum 6 %) though not increasing in numbers. From July to October 1986 many juvenile mussels settled on adult ones. During the two following succession periods, they changed position and occupied new space on the ground.

Exclusion of competitors for space. At the beginning of the experiment, algae and mussels were removed from the experimental area. Mean population densities of *Littorina littorea* (25 individuals) and *Carcinus maenas* (5 individuals) were kept enclosed in the experimental area (Fig. 9A). Periwinkles consumed by crabs were replaced at the beginning of the succession periods to simulate natural conditions. Seasonal algal settlers at the beginning of the succession period were *Monostroma* spp., *Dumontia incrassata* (observed in all years) and *Petalonia fascia* (only in spring 1988). There was no continuous establishment of perennial macroalgae. *Fucus* spp. settled in June 1986 but disappeared again in September 1987, not exceeding more than 10 % cover. Second recruitment of this alga occurred in May 1988. This little stock stayed until October 1988 reaching 4 % cover. *Chondrus crispus* also settled in June 1986 but disappeared in October 1987 not exceeding a maximum cover of 8 % during the summer. *Littorina* was reduced by *Carcinus*. The crabs consumed 52 % of the periwinkles in 1988 and 28 % in both 1986 and 1987.

Exclusion of predators. At the beginning of the experiment, crabs were removed from the experimental area. Mean population densities of *Littorina littorea* (25 individuals), *Mytilus edulis* (cover of 50 %) and perennial macroalgae (*Fucus* spp., cover 20 %) were enclosed in the cage (Fig. 9B). Settlement of seasonal macroalgae was very sparse. Only *Cladophora sericea* settled during June and July of 1986 reaching a maximum cover of 4 %. *Fucus* spp. showed high stability during the whole period of study with a slight tendency towards expansion. Maximum cover was reached in August 1988 (28 %). Space occupied by mussels expanded steadily during the period of study. As soon as the experiments had started, *Mytilus* began to occupy more space (maximum 6 %) though not increasing in numbers. During all the summer periods observed, many juvenile mussels settled on the established adults but migrated to free ground space in spring of the following year, thus leaving new ground to a new invasion of juveniles on the older parts of the mussel beds. At the end of the study term, the mussel bed covered 80 % of the ground.

Exclusion of herbivores. At the beginning of the experiment, periwinkles were removed from the experimental area. A mean population density of *Mytilus edulis* (cover of 50 %), *Carcinus maenas* (5 individuals) and perennial macroalgae (*Fucus* spp., cover 18 %) was enclosed in the experimental area (Fig. 9C). While herbivores were excluded, macroalgae became very abundant settlers. Succession of seasonal algae started in May 1986 with *Monostroma* spp. reaching a maximum cover of 20 %. It was followed by *Ulva pseudocurvata* in June. *Ulva* showed a distinctive seasonal growth cycle throughout the whole study term, covering all or most of the ground during spring and summer of 1986 and 1987 and (nearly) disappearing in winter. In spring and summer

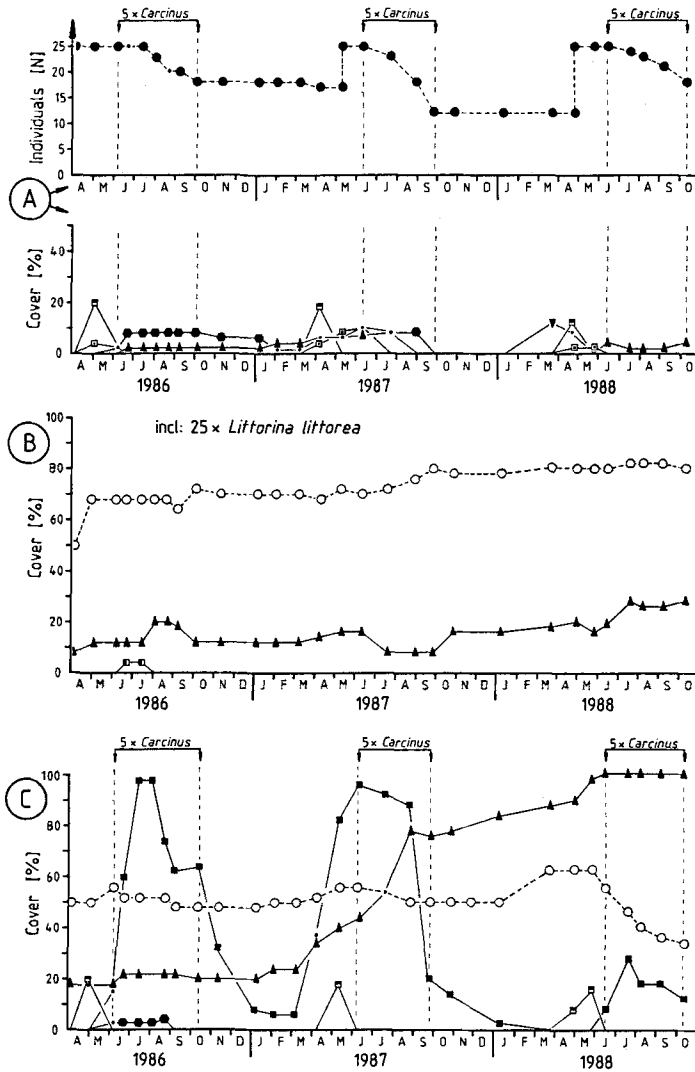


Fig. 9. Biological interactions in the mid intertidal of Helgoland. Experiments on established communities. II. (A) Exclusion of competitors for space (*Mytilus edulis*). (B) Exclusion of predators (*Carcinus maenas*). (C) Exclusions of herbivores (*Littorina littorea*). Fauna: --●-- *Littorina littorea*; --○-- *Mytilus edulis*. Flora: --□-- *Cladophora sericea*, --■-- *Monostroma* spp., --▲-- *Ulva pseudocurvata*, --▼-- *Fucus* spp., --▽-- *Petalonia fascia*, --●-- *Chondrus crispus*. All data given as degree of cover (%) or number of individuals (N)

1988, *Ulva* appeared with a maximum cover of only 28%. In contrast to earlier observations, *Ulva* did not grow on mussel shells and rock but exclusively on blades of *Fucus* spp.

Perennial algae (i.e. *Fucus* spp.) increased steadily from 18% cover in April 1986 to 100% in March 1988, thus covering the whole experimental area and settling on both mussel shells and rock. *Chondrus crispus* settled between June and September 1986

reaching a maximum cover of 4%. Mussels constantly occupied about half of the experimental area but were always preyed upon by *Carcinus* during summer months. The crabs reduced *Mytilus* populations by 14% in 1986 and 11% in 1987. The recruitment rate of the mussels compensated for the loss by predation caused by *Carcinus* between autumn and spring until May 1988, when *Mytilus* covered 64%. Predation activity of *Carcinus* during the summer 1988 was higher than during the previous summers (47% reduction). At the end of the study term, *Mytilus* covered only 34% of the experimental area.

Lower intertidal: *Fucus-serratus*-zone

Recruiting communities in the lower intertidal

Controls. Both open and caged control areas were intensively visited and grazed by *Littorina* spp. Only in February and March 1987 were no periwinkles observed during data collection. Highest densities of *L. littorea* populations observed were 26 individuals on the open control area and 34 individuals on the caged control area (both June 1988; Fig. 10 A,B). *L. mariae* appeared in August 1986 following the establishment of *Fucus serratus*. Mean densities of periwinkles on control areas are listed in Table 3.

Table 3. Recruiting communities in the lower intertidal. Mean densities of *Littorina littorea* and *L. mariae* on control areas between April 1986 and October 1988 (\bar{N} = individuals \times 0.25 m⁻²; s = standard deviation)

Species	Open control area	Caged control area
<i>Littorina littorea</i>	\bar{N} = 9.9 (s = 8.3)	\bar{N} = 19.6 (s = 11.4)
<i>Littorina mariae</i>	\bar{N} = 10.0 (s = 9.0)	\bar{N} = 12.0 (s = 10.0)

Of the seasonal algae, *Ullothrix* spp. Kützting was the first to occupy free space and this grew up to 50% cover on both control areas (May 1986, Fig. 10 A, B). In June/July, it was replaced by *Ulva pseudocurvata*. Maximum cover of *Ulva* was reached at the beginning of August 1986 (46% on open control area, 92% on caged control area) and disappeared between November and January. Other seasonal algae appearing for short periods during the summer were *Cladophora sericea* and *Dumontia incrassata* (Fig. 10 A, B). *F. serratus* as the most obvious perennial alga species appeared on open control areas in May and June 1986 growing up very fast and covering the whole experimental area between April 1987 and October 1988. In May 1987, *Spirorbis spirorbis* (L.) settled on blades of *F. serratus* on the caged control area and occupied more than 70% of the blade surface by October 1988. *Fucus* blades on the open control area were not settled by this polychaete. Other perennial algae appearing in 1986 were *Chondrus crispus* and *Cladophora rupestris*. In contrast to the settlement on the open control area, both of them did not establish on the caged control area until the end of the study term. *Chondrus crispus* reached maximum cover in August 1986 (28% on open control, 18% on caged control; Fig. 10). The only perennial macrofauna species settling on the ground was *Balanus crenatus* Bruguière which first appeared in September 1987. The little stock was spread around all over the surface reaching a maximum cover of 6% on both control areas.

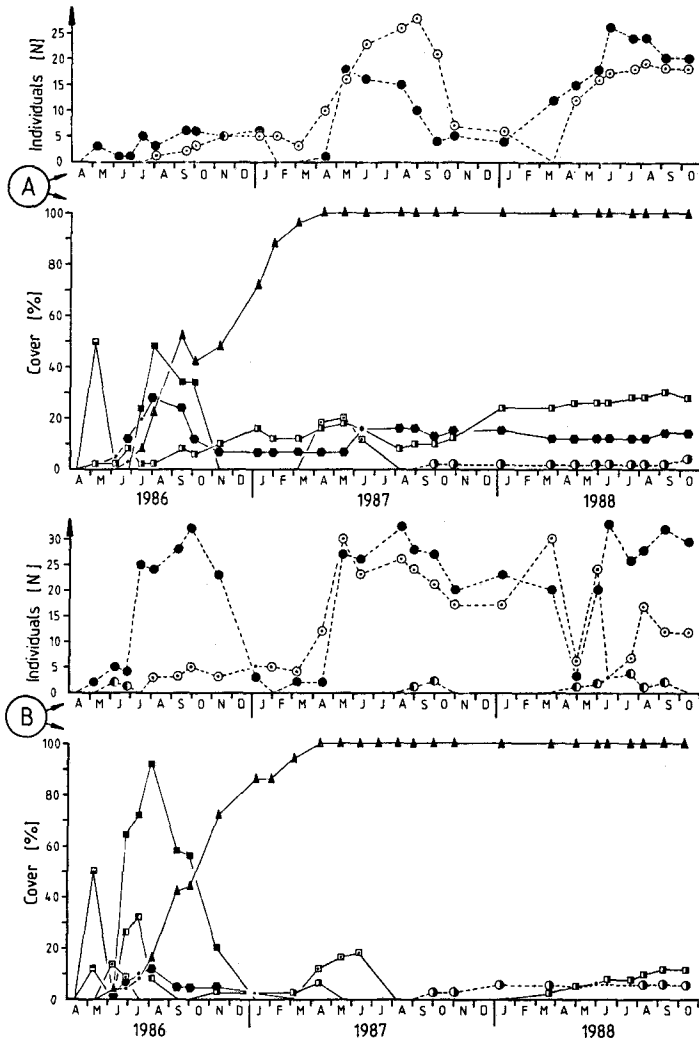


Fig. 10. Biological interactions in the lower intertidal of Helgoland. Experiments on recruiting communities. I. (A) Control without cage (open). (B) Control with cage (caged). Fauna: --●-- *Littorina littorea*, --○-- *L. mariae*, --○-- *Balanus crenatus*, --●-- *Carcinus maenas*. Flora: --■-- *Cladophora rupestris*, --□-- *Cladophora sericea*, --□-- *Monostroma* spp., --□-- *Ulothrix* spp., --■-- *Ulva pseudocurvata*, --▲-- *Fucus serratus*, --●-- *Chondrus crispus*, --□-- *Dumontia incrassata*. All data given as degree of cover (%) or number of individuals (N)

Inclusion of predators. Predators in the lower intertidal were represented by the shore crab *Carcinus maenas*. Five individuals (estimated natural population density) were enclosed in the experimental area (Fig. 11 A). Recruitment of seasonal algae started in May 1986 with *Ulothrix* spp. covering up to 24 % of the area. *Ulva pseudocurvata* appeared in June 1986 showing a distinctive seasonal growth cycle throughout the whole study term by covering all or most of the ground during spring and summer (up to 82 % in

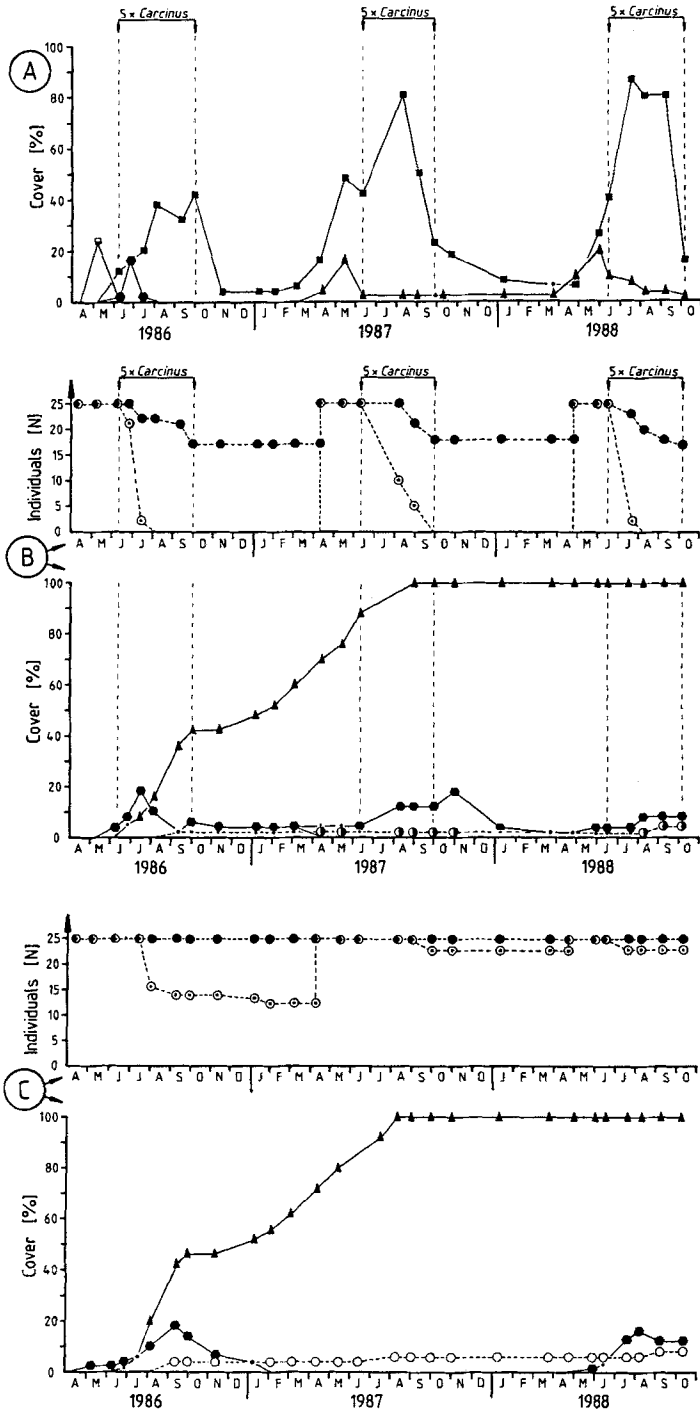
July 1988) and nearly disappearing in winter. *Chondrus crispus* settled in small stocks between May and July 1986. *Fucus serratus* first appeared in March 1987 reaching maximum cover in May 1988 (20%). *Fucus* blades were consumed by *Carcinus* during summer. The crabs caused characteristic lacerations of the blades while consuming them. Especially between October 1987 and May 1988, *F. serratus* recovered and grew up to 28% cover. After the crabs had been included *F. serratus* decreased down to a cover of 2% in October 1988.

Inclusion of predators and herbivores. Predators and herbivores in the lower intertidal are represented by *Carcinus maenas*, *Littorina littorea* and *L. mariae*. Five individuals of *Carcinus* (only during the summer season) and 25 individuals of both *Littorina* species were enclosed in the experimental area (Fig. 11 B). Periwinkles consumed by the crabs were replaced in the beginning of the succession period to simulate natural conditions. No seasonal algae were observed in this area during the period of study. The first perennial alga to appear was *Chondrus crispus* (beginning of June 1986), reaching a maximum cover in October 1987 (16%). *Fucus serratus* appeared at the end of June 1986 and became the dominant settler in this area, growing steadily to cover the whole ground between September 1987 and October 1988. *Balanus crenatus* settled in little patches in August 1986 covering a maximum of 4% of the ground in September and October 1988. Both *Littorina* species were preyed upon by *Carcinus*. Crabs consumed the whole population of *L. mariae* during the period of enclosure. The *L. littorea* population was reduced by a maximum of 32% (= 8 individuals, 1986 and 1988).

Inclusion of herbivores. Herbivores in the lower intertidal were represented by *Littorina littorea* (grazing on the rock and the blades of macroalgae) and *L. mariae* (grazing exclusively on blades of *Fucus* spp.). Experiments were divided into two sections: (1) Investigations on recruiting communities including natural populations of herbivores, and (2) parallel investigations on recruiting communities including populations of herbivores in lower, natural and double densities.

(1) Recruiting communities including a natural population of herbivores (Fig. 11 C). 25 individuals of both *Littorina* species were enclosed in the experimental area. Dead periwinkles were replaced in the beginning of the annual succession periods to simulate natural conditions (constant density of herbivores). All individuals of *L. littorea* survived during the whole period of study. In contrast, the population of *L. mariae* was reduced by 36% between July and August 1986. By the beginning of the next succession period, 52% (April 1987) of the populations had died. The mortality rate of *L. mariae* was lower during 1987 and 1988. The first alga species to settle was *Chondrus crispus*, appearing in May 1986 and reaching a maximum cover of 18%. In February 1987, *Chondrus* disappeared but settled again in April 1988 with maximum cover in August (16%). *Fucus serratus* first appeared in June 1986 and became the dominant alga on this experimental area. It grew up steadily reaching total cover of the ground in August 1987. Besides algae,

Fig. 11. Biological interactions in the lower intertidal of Helgoland. Experiments on recruiting communities. II. (A) Inclusion of predators (*Carcinus maenas*). (B) Inclusion of predators and herbivores (5 × *Carcinus maenas*, 25 × *Littorina littorea*, 25 × *L. mariae*). (C) Inclusion of herbivores (25 × *Littorina littorea*, 25 × *L. mariae*). Fauna: --●-- *Littorina littorea*, --○-- *L. mariae*, --○-- *Mytilus edulis*, --●-- *Balanus crenatus*. Flora: --■-- *Ulothrix* spp., --■-- *Ulva pseudocurvata*, --▲-- *Fucus* spp., --●-- *Chondrus crispus*. All data given as degree of cover (%) or number of individuals (N)



juvenile *Mytilus edulis* occupied free space in August 1986 (4 %) and established a small mussel bed by covering up to 8 % of the rock (September and October 1988).

(2) Recruiting communities including populations of herbivores either at lower, natural or double density. To study the importance of grazing pressure on algal succession, additional experiments were initiated in April 1987. Lower, natural and double densities of *Littorina littorea* were enclosed in cleared areas (Fig. 12).

Controls (Fig. 12 A, B). Both open and caged control areas were intensively visited and grazed by *L. littorea*. *Littorina mariae* appeared in August 1987 following the establishment of *Fucus serratus*. Mean densities of periwinkles on control areas are listed in Table 4. *Fucus serratus* appeared on the control areas in May and June 1987 growing

Table 4. Recruiting communities in the lower intertidal. Parallel inclusion of herbivores at different densities. Mean densities of *Littorina littorea* and *L. mariae* on control areas between April 1986 and October 1988 (\bar{N} = individuals \times 0.25 m⁻²; s = standard deviation)

Species	Open control area	Caged control area
<i>Littorina littorea</i>	$\bar{N} = 17.6$ (s = 9.1)	$\bar{N} = 25.7$ (s = 13.7)
<i>Littorina mariae</i>	$\bar{N} = 7.2$ (s = 5.9)	$\bar{N} = 6.2$ (s = 5.7)

up to cover the whole ground of control areas in May 1988. Perennial undercover algae (*Chondrus crispus* and *Cladophora rupestris*) settled in May 1987. *Chondrus crispus* reached maximum cover in September 1987 (46 % on open/22 % on caged control) and then slowly decreased until October 1988. *Cladophora rupestris* showed slower but more constant growth rates reaching a seasonal peak on the caged control area in June 1988 (30 %). Settlement of seasonal algae was sparse. Only *Dumontia incrassata* appeared (March 1988, on both control areas) reaching maximum cover at the end of May (22 %/34 %; Fig. 12 A, B).

Recruiting communities including herbivores at lower, natural and higher densities. (Fig. 12 C, D, E). Community succession on areas grazed by different numbers of periwinkles showed a distinctive difference in recruiting pattern. Succession on areas enclosing a lower density (15 individuals of *Littorina littorea*) started in June with the appearance of both seasonal (*Cladophora sericea*, *Ulva pseudocurvata*) and perennial algae (*Fucus serratus*, *Cladophora rupestris*, *Chondrus crispus*). Up to October, seasonal vegetation dominated the ground, but then disappeared. Afterwards *F. serratus* grew up very fast covering the whole experimental area at the end of May 1988. The only seasonal alga settling in spring of 1988 was *Dumontia incrassata* reaching a maximum of cover (18 %) at the end of May. The area enclosing a natural density of herbivores (25 individuals of *L. littorea*) lacked settlement of seasonal algae. Settlement of undercover perennial algae was lower than in the experiment described before, but *F. serratus* developed in nearly identical patterns (cf. Fig. 12 C, D). Succession on the area including double herbivore density (50 individuals of *L. littorea*) was characterized by a lack of rich settlement of both seasonal and perennial macroalgae. Only *Chondrus crispus* appeared, reaching a maximum cover of 10 %. On all

three experimental areas, juvenile *Mytilus edulis* settled between August and September 1987 establishing small mussel beds. These mussel beds survived until the end of the experiment while constantly occupying more space. Maximum cover on all experimental areas was reached in October 1988 (6%/6%/10%; Fig. 12 C, D, E).

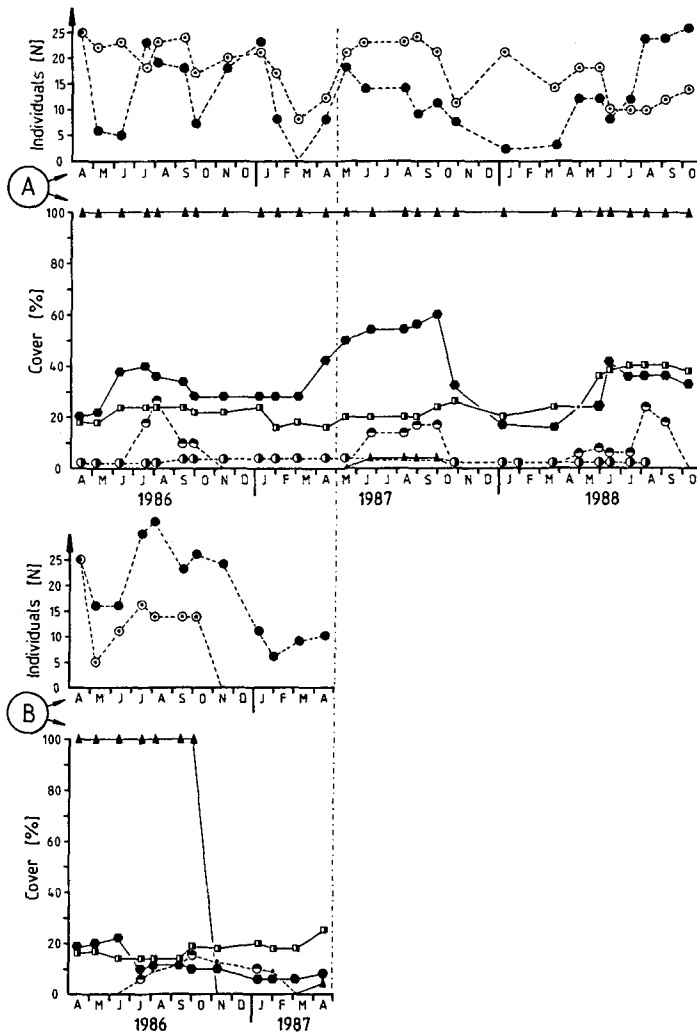


Fig. 12. Biological interactions in the lower intertidal of Helgoland. Experiments on recruiting communities. III. Ⓐ Control without cage (open). Ⓑ Control with cage (caged). Ⓒ Inclusion of herbivores at lower density ($15 \times L. littorea$). Ⓓ Inclusion of herbivores at natural density ($25 \times L. littorea$). Ⓔ Inclusion of herbivores at double density ($50 \times L. littorea$). Fauna: --●-- *Dynamena pumila*, --●-- *Littorina littorea*, --○-- *L. mariae*, --○-- *Mytilus edulis*. Flora: --■-- *Cladophora rupestris*, --□-- *Cladophora sericea*, --■-- *Ulva pseudocurvata*, --▲-- *Fucus serratus*, --●-- *Chondrus crispus*, --□-- *Dumontia incrassata*. All data given as degree of cover (%) or number of individuals (N)

Established communities in the lower intertidal

Controls. Results of community succession on both control areas are shown in Figure 13 A and B. In contrast to the open control area, data on the caged control area were collected only between April 1986 and April 1987. Both open and caged control areas were intensively visited and grazed by *Littorina littorea* and *L. mariae*. Herbivores were found neither on the caged control area in February 1987 nor on the open control area between November 1987 and April 1988. Mean densities of periwinkles on both control areas are listed in Table 5. Seasonal macroalgae did not settle on either of the

Table 5. Established communities in the lower intertidal. Mean densities of *Littorina littorea* and *L. mariae* on control areas between April 1986 and October 1988 (\bar{N} = individuals \times 0.25 m⁻²; s = standard deviation)

Species	Open control area	Caged control area
<i>Littorina littorea</i>		
IV 1986–IV 1987	\bar{N} = 13.4 (s = 8.5)	\bar{N} = 19.0 (s = 9.0)
IV 1986–X 1988	\bar{N} = 13.1 (s = 7.8)	no data
<i>Littorina mariae</i>		
IV 1986–IV 1987	\bar{N} = 19.2 (s = 5.1)	\bar{N} = 7.9 (s = 8.5)
IV 1986–X 1988	\bar{N} = 13.1 (s = 7.8)	no data

control areas. *Fucus serratus* dominated the control areas, covering all of the ground between April and October 1986. In November 1986, all stipes of *Fucus* plants on the caged control areas broke at the bases and were washed away. In April 1987 young shoots of *F. serratus* appeared again. Established undercover algae like *Chondrus crispus* and *Cladophora rupestris* showed either drastic seasonal growth rates and decline (*Chondrus crispus*) or also less fluctuating population changes (*Cladophora rupestris*). Mean densities of *Chondrus crispus* and *Cladophora rupestris* on both control areas are listed in Table 6. Besides algal vegetation, hydrozoan colonies of *Dynamena pumila* (L.) settled on both control areas during periods of succession. On caged control areas the hydrozoans survived the winter season 1986/87 and disappeared in March 1987.

Table 6. Established communities in the lower intertidal. Mean cover of dominant perennial undercover algae (*Cladophora rupestris*, *Chondrus crispus*) on control areas between April 1986 and October 1988 (\bar{x} = cover % \times 0.25 m⁻²; s = standard deviation)

Species	Open control area	Caged control area
<i>Cladophora rupestris</i>		
IV 1986–IV 1987:	\bar{x} = 20.8 (s = 3.4)	\bar{x} = 16.5 (s = 1.9)
IV 1986–X 1988:	\bar{x} = 25.9 (s = 8.3)	no data
<i>Chondrus crispus</i>		
IV 1986–IV 1987:	\bar{x} = 31.0 (s = 7.0)	\bar{x} = 11.9 (s = 5.5)
IV 1986–X 1988:	\bar{x} = 33.8 (s = 13.1)	no data

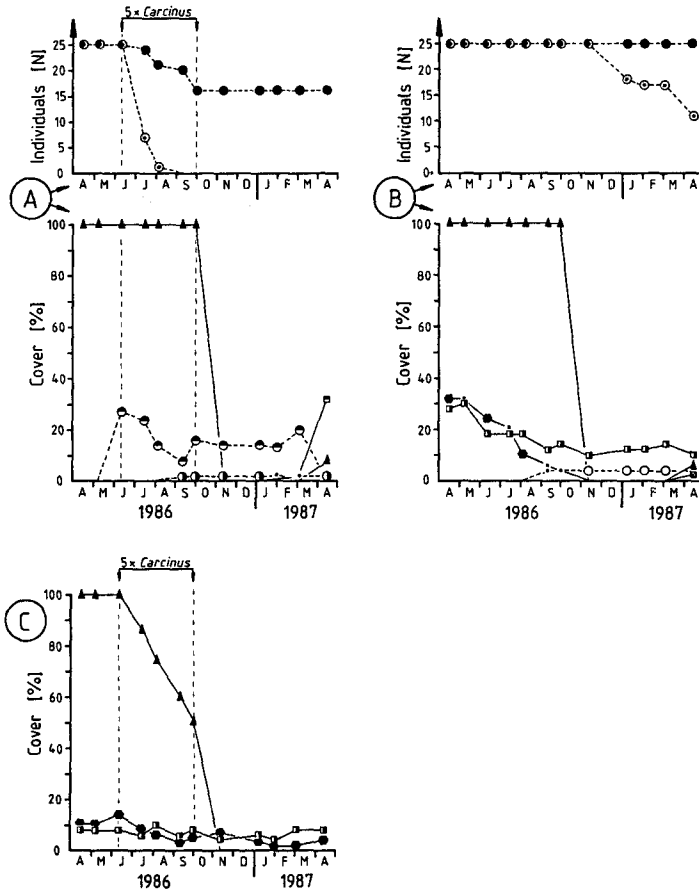


Fig. 13. Biological interactions in the lower intertidal of Helgoland. Experiments on established communities. I. Ⓐ Control without cage (open). Ⓑ Control with cage (caged; data collection stopped in April 1987). Fauna: --○-- *Dynamena pumila*, --●-- *Littorina littorea*, --□-- *L. mariae*, --△-- *Balanus crenatus*. Flora: --■-- *Cladophora rupestris*, --▲-- *Fucus serratus*, --△-- *Laminaria digitata*, --●-- *Chondrus crispus*. All data given as degree of cover (%) or number of individuals (N)

Exclusion of competitors for space. At the beginning of the experiment all sessile species (algae, barnacles, mussels and hydrozoans) except *Fucus serratus* were removed from the experimental area. Mean population densities of *Littorina littorea* and *L. mariae* (25 individuals of each species) and *Carcinus maenas* (5 individuals) were enclosed on the experimental area (Fig. 14 A). Both *Littorina* species were reduced by *Carcinus*. Crabs consumed the whole population of *L. mariae* during the periods of enclosure. The *L. littorea* population declined by 36% (= 9 individuals). In November 1986 all stipes of *Fucus* plants on the caged control area broke at the bases. In April 1987, juvenile plants of *F. serratus* appeared again (8%). *Monostroma* spp. was the only seasonal alga to grow, appearing in March 1987 and reaching maximum cover in April 1987 (32%). Free space was also occupied by *Dynamena pumila* and *Balanus crenatus*.

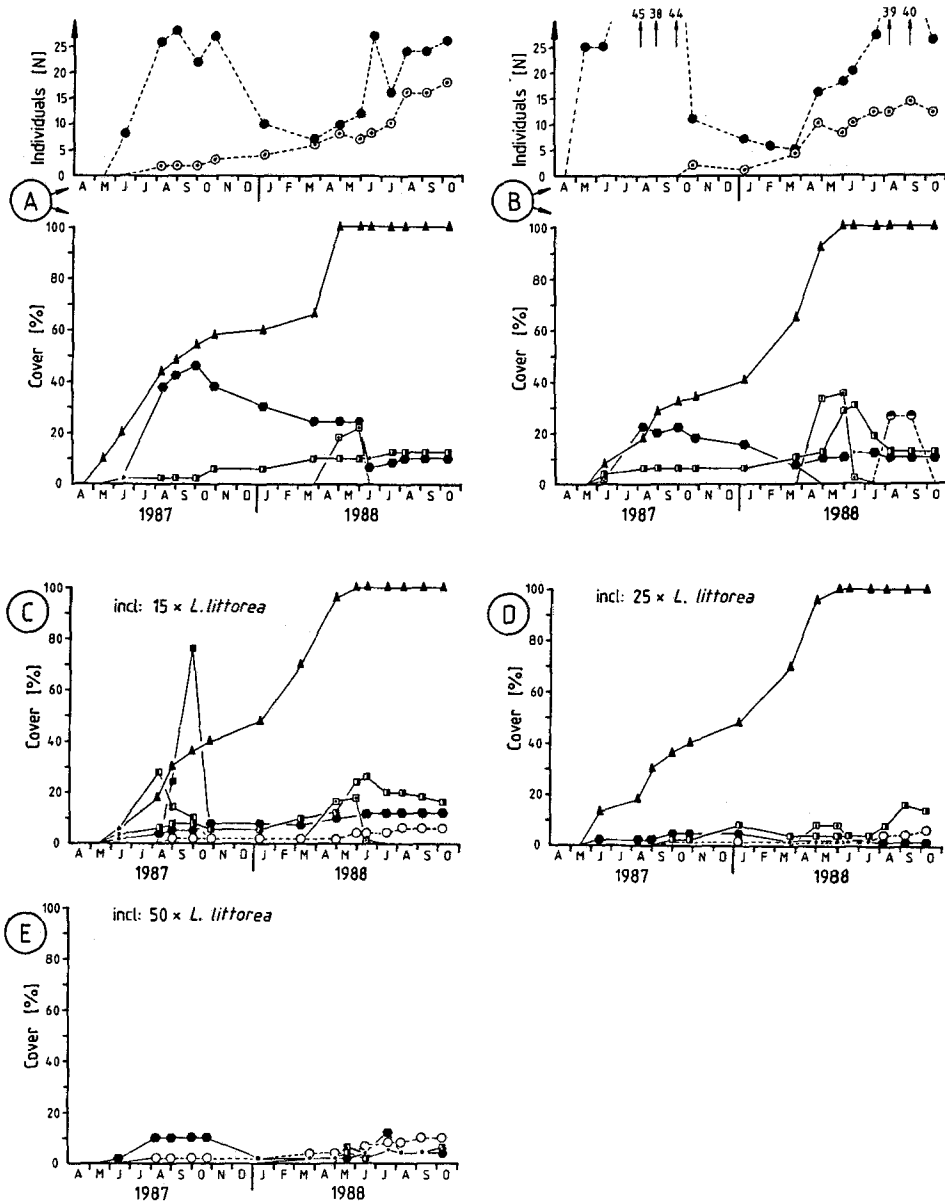


Fig. 14. Biological interactions in the lower intertidal of Helgoland. Experiments on established communities. II. (A) Exclusion of competitors for space (*Mytilus edulis*, macroalgae). (B) Exclusion of predators (*Carcinus maenas*). (C) Exclusion of herbivores (*Littorina littorea*). Fauna: --○-- *Dynamena pumila*, --●-- *Littorina littorea*, --○-- *L. mariae*, --○-- *Mytilus edulis*, --○-- *Balanus crenatus*. Flora: --■-- *Cladophora rupestris*, --□-- *Monostroma* spp., --▲-- *Fucus serratus*, --●-- *Chondrus crispus*. All data given as degree of cover (%) or number of individuals (N)

Hydrozoan colonies first appeared in June 1986 reaching a maximum cover of 26 % (June 1986) and mean cover density of about 16 %. *B. crenatus* settled in September 1986 occupying 2 % of the ground until the end of the study term in April 1987.

Exclusion of predators. At the beginning of this experiment, crabs were removed from the experimental area. Mean population densities of both *Littorina littorea* and *L. mariae* (25 individuals each) and perennial macroalgae (*Fucus serratus*, 100 %; *Cladophora rupestris*, 28 %; *Chondrus crispus*, 32 %) were kept enclosed in the cage (Fig. 14 B). All individuals of *L. littorea* survived during the whole period of study. 56 % of *L. mariae* died between November 1986 and April 1987. *F. serratus* covered all of the ground between April and October 1986. In November 1986, all stipes of *Fucus* plants on the caged control area broke at the bases. In April 1987, juvenile plants of *F. serratus* appeared again (6 %). Perennial undercover algae decreased during the period of study. *Chondrus crispus* disappeared in November 1986, but settled again in April 1987. *Cladophora rupestris* remained until April 1987 but decreased down to 10 % cover (= 36 % of cover in April 1986). Besides algae, juvenile *Mytilus edulis* occupied free space in September 1986 (4 %) and established a small mussel bed.

Exclusion of herbivores. At the beginning of this experiment periwinkles were removed from the experimental area. Mean population density of *Carcinus maenas* (5 individuals), *Fucus serratus* (cover 100 %) and also small stocks of *Cladophora rupestris* (10 %) and *Chondrus crispus* (12 %) were enclosed in the experimental area (Fig. 14 C). *F. serratus* covered all of the ground between April and June 1986 and then decreased, disappearing in November 1986. Most of the stock was reduced by *Carcinus*. The crabs reduced *F. serratus* by 50 % between June and the beginning of October 1986. In November 1986 all stipes of *Fucus* plants remained broken at the bases. *Chondrus crispus* decreased down to 4 % cover in April 1987, but reached a maximum cover of 14 % in June 1986. Cover by *Cladophora rupestris* remained nearly constant during the period of study.

DISCUSSION

Biological interactions in the rocky intertidal of Helgoland

The results of the experiments presented above confirm that biological interactions play an important role in the rocky intertidal community structure at Helgoland. Figure 15 summarizes schematically the changes of the relative importance of competition for space, of herbivory, and of predation in relation to the vertical shore level and some other factors.

Upper intertidal

Data collected in the upper intertidal reveal *Enteromorpha* spp. as dominant competitors for space. It became obvious that herbivores cannot inhibit the settlement and dominant occupation of space by *Enteromorpha* spp., but they did both slow down algae growth and accelerate its seasonal decline. *Fabricia*-cushions caused a distinctive decrease of *Enteromorpha* cover, as they promoted sedimentation of mud and detritus. Aggregations of these polychaetes are well known from the "Westwatt"-intertidal (Fig. 1), where they locally exclude mats of green algae from the rock. In the intertidal of "Nordost-Felswatt" they are very sparse. As *Fabricia*-cushions were not observed around the experimental area, their appearance is very likely caused by "caging-effects" and

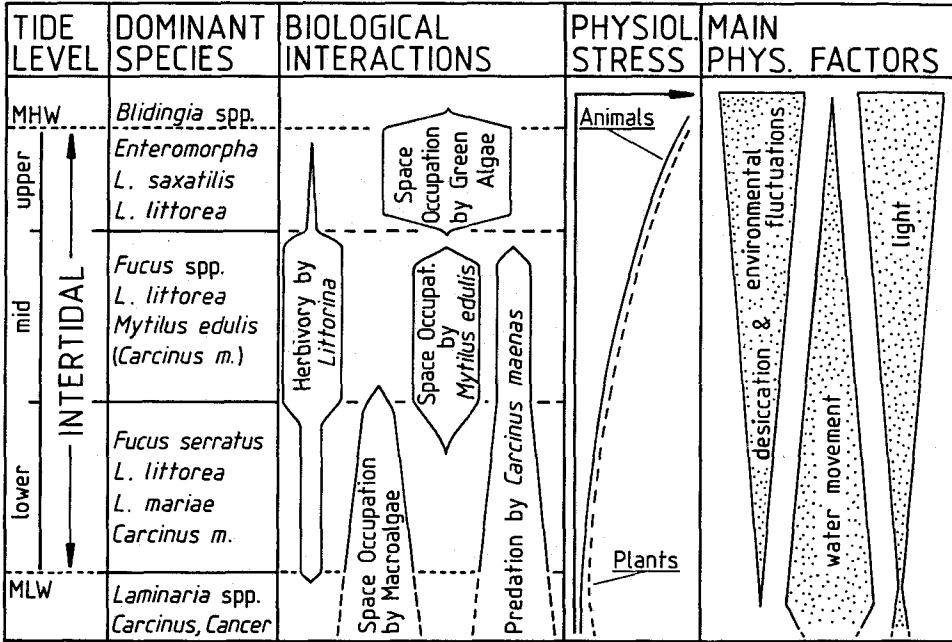


Fig. 15. Factors controlling the community structure along the vertical shore gradient in the rocky intertidal of Helgoland. All factors are not shown to scale but to relative degree of importance (redrawn and transposed to the communities found at Helgoland after Hawkins & Hartnoll, 1983)

thus do not represent natural conditions. Usually, they do not play an important role in the community pattern in the upper intertidal at "Nordost-Felswatt".

Following Remmert's definition (Remmert, 1984, p. 260) the simple structured community in the *Enteromorpha*-zone can be characterized by low constancy, low stability but high resilience (Fig. 16). According to Remmert, communities of high stability withstand disturbances from outside without changing community structure; communities that do not change their structure during the seasons are of high constancy; if communities change because of disturbances from outside and reach again very quickly their former climax they are characterized by high resilience.

Unexpected or seasonal disturbances (storms followed by large amounts of kelp washed ashore) cause total decline of the vegetation but recruitment in spring, summer or early autumn happens within a few days or weeks. Disturbances in late autumn or winter are not followed by recruitment of the community because of unfavourable climatic conditions.

Mid intertidal

The results presented here confirm the hypothesis that biological interactions play an important role in community structure in the mid intertidal of Helgoland. A comparison of the environmental controls shows no distinctive differences in community development and maintenance. Thus, possible "caging effects" were of minor importance for the community structure on experimental fields. An explanation is needed for the lack of *Littorina littorea* on the control areas in February and March 1987. This phenomenon was

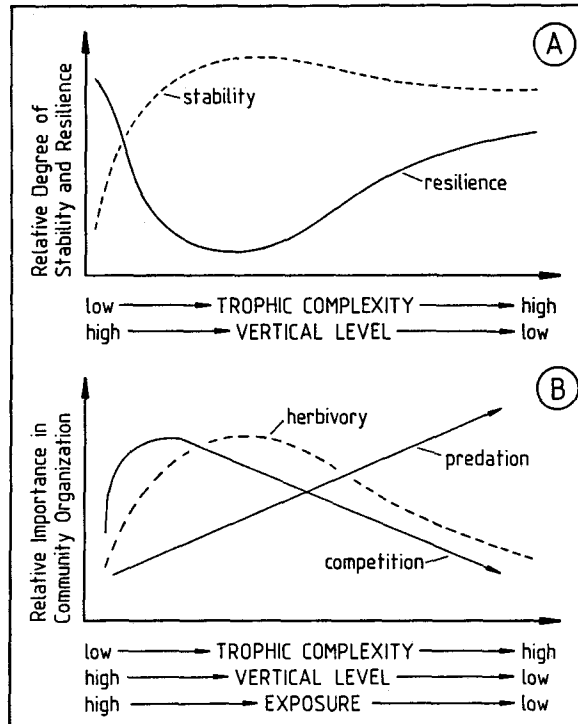


Fig. 16. Stability, resilience and biological interactions in the intertidal of Helgoland. Ⓐ Relative degree of stability and resilience (for definition see Remmert, 1984) compared to trophic complexity and vertical level. Ⓑ Relative degree in community organization of competition for space, herbivory and predation compared to trophic complexity, vertical shore level and degree of wave exposure (changed after Menge & Sutherland, 1976)

obviously caused by very low air temperatures that changed the behaviour of the periwinkles. To escape from death by frost they all moved to rockpools when emerged and waited for the oncoming high tide, continuing grazing activities when submerged. This behaviour does not exclude the possibility of grazing activity on the control areas during February and March 1987.

Competition for space. Competitors for space could be divided into two groups: (1) perennial species (i.e. *Mytilus edulis*, *Fucus* spp., *Chondrus crispus*) and (2) seasonal species (i.e. *Ulva pseudocurvata*, *Monostroma* spp., *Cladophora sericea*, *Petalonia fascia*, *Dumontia incrassata*). At the beginning of the succession periods, the vegetation was generally dominated by seasonal species (i.e. green algae). Fast decline of these species in summer or autumn was obviously caused by fluctuations in seasonal climatic factors but not influenced by settlement of perennial species. For instance, see development and decline of *Ulva* and *Monostroma* spp. (Figs 7, 9). Whenever present, *Mytilus* became the dominant competitor for space, excluding algae from the rock but also providing free space for settlement on its shells. The dominant competitor amongst the perennial algae was *Fucus* spp. Whenever herbivores were excluded, *Fucus* spp.

settled in high densities and outcompeted all other algae within two vegetation periods. Even fast growing seasonal species like *Ulva pseudocurvata* were prevented from settlement on rocks and mussel shells. Instead, space for settlement was provided on *Fucus* blades. On this substratum, *Ulva* blades showed heavy laceration caused by mutual friction and mechanical stress of the blades during floatation. Seasonal algae were not outcompeted whenever *Fucus* spp. occurred at natural densities (about 20 % cover). *Fucus* spp. growing on the ground were outcompeted by *Mytilus*, but the mussels provided new space for settlement on their shells. In contrast to the rock surface, mussel shells do not provide secure holdfast for many years. Occasionally, *Fucus* plants decreased the population density of *Mytilus*, especially when algae became very large and promoted removal of the mussels by water turbidity. Such events reduced mussel beds on control areas in the mid intertidal (Figs 6, 8).

Predation. Compared to experiments on the importance of competition for space or herbivory, studies on predation were carried out only during summer to simulate natural conditions. Predation by crabs is also restricted to periods of submersion. Thus, effects of predation were not that obvious. In fact there were some changes in community structure caused by crab predation. Results showed that mussels were reduced by *Carcinus maenas*. Broken shells in the cages showed the cause of the decline of mussels. During the period of study, the growth rate of mussel beds compensated the loss by predation, but in the experiment *Carcinus* reduced *Mytilus edulis* by 57 % within one summer (see Fig. 9 C, June to October 1988). Thus, it is very likely that *Carcinus* prevents recruitment of mussels on free space. Whenever *Mytilus* settled within cages including crabs, they were consumed within very short periods (for instance see Fig. 7 B). *Carcinus* also reduced established mussel beds on all experimental fields, when they were enclosed together (see Figs 7 B, 9 A and C; mentioned before also by Crothers, 1967; Ropes, 1968; Reise, 1977, 1978). If crabs were excluded from the experimental areas, *Mytilus* established and grew up at low but constant growth rates (see Figs. 7 A and C, 9 B). These results and interpretations do not explain the growth of mussel beds observed on control areas occupied by established communities (Fig. 8). Development of *Mytilus* stock on these areas indicate that the *Carcinus* density (5 individuals) enclosed in the cages was probably much higher than in natural populations in the mid intertidal.

The results also indicate the controlling effects of predation by *Carcinus maenas* on populations of herbivores (*Littorina littorea*). Broken *Littorina* shells in the cages showed that even adult periwinkles (up to 4 cm in shell height) were consumed by the crabs. Reduction of *L. littorea* (28 % in 1986 and 1988, 52 % in 1987) did not promote algal settlement or growth rates. Obviously, predation pressure of crabs on periwinkles did not cause such a distinctively low rate of herbivory that could cause a more intensive algal settlement.

Results in Figure 7 B show a negative correlation between *Carcinus maenas* and *Fucus* spp. This phenomenon can be interpreted as a caging effect. Crabs usually prefer predation to herbivory, but they accept *Fucus* for food, if nothing else is offered. Experiments in the laboratory could verify this hypothesis and the results in this cage experiment in the lower intertidal (Fig. 11 B). In fact, this constellation does not reflect natural conditions in the intertidal of Helgoland. Unlike *Fucus serratus*, *Ulva pseudocurvata* was not consumed by the crabs and thus could establish in typical seasonal pattern. Other predators (such as fish and birds) were not included in this study although they

possibly play an important role. Up to now there have been no special investigations about this problem in the rocky intertidal of Helgoland that provide data for serious estimations (see Vauk & Prüter, 1987; Krüß, 1988).

Herbivory. Compared to all other manipulative experiments in the mid intertidal, the enclosure/enclosure-experiments with herbivory showed the most obvious and distinctive changes in community succession and maintenance. Results clearly demonstrate that herbivores control both seasonal and perennial algal growth and settlement. Thus, they limit high cover by algae in the *Mytilus*-zone. Whenever *Littorina littorea* was excluded, seasonal green algae (i.e. *Monostroma* spp., *Ulva pseudocurvata*) grew very quickly showing a typical seasonal growth pattern (cover of more than 90 % in summer) and (sometimes total) decline. In the surrounding open field, on control areas and on experimental areas including periwinkles, *Ulva* did not occur. Growth rates of *Ulva* were also limited by the occurrence of perennial algae (*Fucus* spp.) if they came to cover most or all of the ground. *L. littorea* also limited succession and growth rates of *Fucus* spp. On experimental areas excluding periwinkles, growth rates of *Fucus* spp. accelerated rapidly to reach total cover of the ground within 26 months.

Summarizing these results and the biological structure found in the mid intertidal before experiments were started (see Fig. 2 A), the mid intertidal community is dominated by perennial species such as *Littorina littorea*, *Mytilus edulis* and *Fucus* spp. Following Remmert's definition (Remmert, 1984, p. 260), the *Mytilus*-zone community is characterized by high stability (probably high constancy) and low resilience (see Fig. 16). Major unexpected or seasonal disturbances causing a serious decline of dominant sessile species may have an important effect on the community structure for a long period as the recruitment rates of the dominant settlers (e.g. *Mytilus*) will take at least more than three periods of succession (probably many more) to reach the former community pattern.

Lower intertidal

The results presented here demonstrate that biological interactions play an important role in the community structure in the lower intertidal of Helgoland. Unfortunately, a comparison of the controls shows distinct differences in community development and maintenance (see Figs 10, 13). Thus "caging effects" definitely played an important role in community structure on the experimental fields. These "caging effects" make it difficult to interpret the results on experimental areas, but they also indicate a probable importance of abiotic factors, the influence of which on community has so far been neglected. An explanation is needed for the lack of *Littorina littorea* on the control areas in February 1987.

Competition for space. The competitors for space observed during the period of study could be divided into two groups: (1) perennial species (i.e. *Fucus serratus*, *Cladophora rupestris*, *Chondrus crispus*, *Mytilus edulis*, *Balanus crenatus*) and (2) seasonal species (i.e. *Ulva pseudocurvata*, *Monostroma* spp., *Cladophora sericea*, *Petalonia fascia*, *Dumontia incrassata*, *Dynamena pumila*). As in the mid intertidal, the beginning of succession periods were generally dominated by seasonal species (i.e. green algae). Fast decline of these species in summer or autumn was obviously caused by fluctuations in seasonal climatic factors but not influenced by settlement of perennial species. For instance, see development and decline of *Ulva pseudocurvata* and *Monostroma* spp. These patterns were suppressed whenever *Fucus serratus* reached a high

percentage of cover. As this dominant and fast-growing species covered the whole ground within one year after total clearance, settlement and development of seasonal species including typical patterns of seasonal growth and decline were only observed during the first period of succession (1986). If succession and growth of *F. serratus* were controlled and limited (by *Carcinus*, see Fig. 11 A), seasonal species (i.e. *Ulva*) became dominant competitors for space and showed characteristic seasonal patterns of occurrence. Settlement of *Mytilus edulis* played only a subordinate role in competition for space. Mussel beds could only establish if *Carcinus maenas* was excluded. At the end of the studies, *Mytilus* reached a maximum cover of 10 % on experimental fields, indicating that growth rates of mussel beds in the mid and lower intertidal were about the same during the first period of colonization. Neither perennial nor seasonal algae were outcompeted by *Mytilus* in the lower intertidal as the growth rate of mussels was not high enough to enable the mussels to become the dominant competitor for space. *Chondrus crispus* and *Cladophora rupestris* did not settle on mussel shells. Caging effects stopped growth and further establishment of *Fucus serratus* on some experimental areas. This effect was observed whenever the plants had grown to a length of about 35 cm. Two months before *F. serratus* broke at the bases, the thalli became rough, dry and partly lacerated. Phylloids were intensively settled by epibionts (i.e. *Spirorbis spirorbis*, *Flustrellidra hispida*, *Elachista fucicula*) and covered by about 70 % before the stipes broke away. This effect was very likely promoted by the flat cages because the algae could not float within them. Thus, epibionts were not wiped away mechanically by neighbouring plants. Intensive growth of epibionts on *F. serratus* is a typical phenomenon in the "Nordost-Felswatt" especially at very sheltered areas next to the mole (see Fig. 1). It did not seem sensible to continue data collection on those experimental areas where *Fucus* had been eliminated by caging effects. Those experiments were stopped at the beginning of new succession periods in spring (April). *F. serratus* was also eliminated by *Carcinus maenas* whenever the crabs had nothing else to consume. This must also be interpreted as a caging effect (see above).

Predation. Predation by *Carcinus maenas* plays an important role in the community structure in the lower intertidal. Populations of herbivores were either heavily reduced (*Littorina littorea*) or totally extinguished (*L. mariae*). Crabs first preferred the smaller and more delicate *L. mariae* but changed their feeding habits after having extinguished them to consume *L. littorea*. Population decrease of the herbivores caused by *Carcinus* did not initiate a higher growth rate of macroalgae. Thus, it seems very likely that the establishment and growth of *Fucus serratus* is not controlled by periwinkles (see Figs 14 A, B; see also below). Continuous reduction of *Littorina* spp. might not cause any further change in the growth of *F. serratus*, as the young sporelings settle during those periods of the year (winter and spring) when predation activity in the intertidal is very low. Thus, the young plants will be reduced by populations of herbivores that are temporarily not controlled by predators during the "sensitive" periods of the year.

Herbivory. The activity of herbivores for the control of macroalgae seems to play a less important role in the community structure in the lower than in the mid intertidal. Natural densities of *Littorina* spp. could neither prevent the settlement nor reduce the growth rate of *Fucus serratus*. Even when the population of *L. littorea* was reduced by 40 % there were no enhanced settlement and growth rates of *F. serratus*. Growth of macroalgae slowed down if the population of *L. littorea* was doubled. Under this

circumstance, settlement of fucoids was totally inhibited. Extremely high herbivore population densities, as described before, occurred in the field in small patches, especially at those locations where drift ice had eroded and cleared the rock of algae. In fact, regular observations showed that those patches remained open for more than two years. Settlement and growth of seasonal algae were strongly controlled by *L. littorea*. *Monostroma* spp. and *Ulva pseudocurvata* could only grow, if periwinkles were either excluded or reduced. Recruitment by perennial undercover algae (*Cladophora rupestris*, *Chondrus crispus*) was not significantly slowed down by herbivores. Their populations fluctuated and suffered very obviously from the lack of *Fucus* floatation within the cages. *L. mariae* as a characteristic settler on *Fucus* blades did not play an important role in the settlement and growth of macroalgae on the ground. Reduction of the *L. mariae* population was high if *F. serratus* was absent, but the death rate became smaller as soon as the fucoids had settled and grown. Decrease of these algae led to a decline of the population of *L. mariae*. These observations support previous results by Barkman (1955), van Dongen (1956), Bakker (1959) and Underwood (1972, 1979) that showed the essential dependence of *L. obtusata* (= *L. littoralis* L.) on fucoid algae. The authors of these publications did not (could not) divide their populations of periwinkles into those of *L. obtusata/littoralis* on the one hand and the sympatric *L. mariae* on the other hand (see Goodwin & Fish, 1977). In contrast, *L. littorea* is not confined to special grounds. Around Helgoland and the German North Sea shore, this prosobranch lives both on muddy and sandy bottoms, on moles, rocks and macroalgae (Reise, 1985; Janke, 1986). However, there seems to be a preference for hard bottom underground (personal observation, unpubl.). Settlement and growth of epibionts on *F. serratus* (i.e. *Ceramium rubrum*, *Spirorbis spirorbis*, *Flustrellidra hispida* (Fabricius), *Dynamena pumila*) did not significantly reduce *L. mariae* as has been described before by Stebbing (1973) for *L. obtusata*. Instead, mechanical rub-down caused by blades of neighbouring plants and water turbulence seem to play a more important role. Whenever free floatation of the plants was limited (in the cages), epibionts settled in large number and grew up very quickly to occupy up to about 70 % of the blade surface.

Settlement and growth of juvenile *Mytilus edulis* were not prevented or reduced by activities of herbivores. A reason for this is that the size of the mussel brood at the time of settlement is already too large to be consumed by the periwinkles. Settlement of *Balanus crenatus* and juvenile colonies of *Dynamena pumila* were also not influenced by periwinkles.

In contrast to observations in the mid intertidal, recruitment and total ground cover by *Fucus* spp. are completed much faster (within about a year) followed by the settlement of perennial undercover algae in the shade of the *Fucus* canopy. Also, fluctuations of the algal stock within established communities seem to be low.

Summarizing these results and the biological structure found in the lower intertidal before experiments were started (see Fig. 2A), the lower intertidal community seems likely to be dominated by perennial species like *Littorina littorea*, *Fucus* spp. and perennial undercover algae. Following Remmert's definition (Remmert, 1984, p. 260), the community in the *Fucus-serratus*-zone can be characterized by a stability nearly as high as in the *Mytilus*-zone (probably high constancy) but with higher resilience (see Fig. 16). Unexpected or seasonal disturbances causing serious decline of dominant sessile species may cause highly significant changes within community structure, but as the recruitment

rates of dominant (and also perennial) species are high, reinstatement of the former community structure may not take more than about a year after the beginning of the following succession period. Thus, the degree of resilience of the community is higher than in the mid intertidal, but not as high as in the upper intertidal.

Biological interactions within sheltered rocky intertidal communities: competition for space, predation, and herbivory

There is no doubt that biological interactions play an important role in the structure of the intertidal rocky shore community at the Island of Helgoland. The relative degree of importance of each competition for space, predation and herbivory changes according to the vertical level on the shore. The following conclusions on their importance and change along the vertical shore gradient are compared with literature previously published.

Competition for space

Competition for space is a very important factor in controlling the community structure in rocky intertidal communities, especially at high shore levels and wave exposed sites (see Menge & Sutherland, 1976). In the upper unertidal of Helgoland, the most successful competitors are green algae (*Enteromorpha* spp.). They dominate over perennial fucoids (i.e. *Fucus spiralis*, *F. vesiculosus*), as they overgrow most of their sporelings and prevent them from growing up. If sporelings of *Fucus* spp. survive and grow to a certain size they become dominant competitors to the green algae, but this seems to occur rarely. Abiotic factors, especially desiccation, may also play an important role in the numbers of species that can occur as competitive settlers. For instance, *Mytilus edulis* beds are outcompeted from upper intertidal zones because of constant desiccation stress (Seed, 1969a, 1969b; Suchanek, 1985). Other competitive macroalgae usually found in upper intertidal zones (e.g. *Pelvetia canaliculata*) do not occur around Helgoland as most of them may not withstand the high annual fluctuations of temperature (Lüning, 1985) and the highly erosive rock of the island. Lubchenco (1983) has already investigated competition for space between *F. vesiculosus* and seasonal green algae (*Enteromorpha* spp., *Ulva* spp.), but her results were based on populations in rockpools. She also described green algae as more competitive to fucoids, as long as there were no grazing periwinkles. But if the green algae were consumed by *Littorina littorea*, *F. vesiculosus* could settle and establish constantly. Thus Lubchenco (1983) demonstrated exemplarily that competition for space can have the function of a mechanism controlling community structure within a rocky intertidal. There are many indications that her observations also reflect the controlling mechanism in the upper intertidal at Helgoland. Small patches of *Fucus* spp. spread around all over the *Enteromorpha*-zone showing that *Fucus* spp. is able to withstand constant stress caused by abiotic factors (see also Schonbeck & Norton, 1978, 1980), but dominance of *Enteromorpha* spp. restricts the distribution of fucoids.

In the mid intertidal where physiological stress decreases (for marine species), the importance of competition for space becomes more obvious as a controlling factor. At Helgoland, *Mytilus edulis* becomes the most dominant competitor for space excluding both seasonal (*Dumontia incrassata*) and perennial macroalgae (*Fucus* spp., *Chondrus crispus*) from rocky surfaces. Correspondingly, mussels provide new space on the surface

of their shells, which is used by *Fucus* spp. Thus, fucoids are not excluded by the mussels but are very likely limited by grazing activities of periwinkles (see below). These observations correspond with conclusions of Suchanek (1985). He found out that mussels may play an important role worldwide as dominant competitors for space within sheltered rocky intertidal zones as long as they do not have to suffer from predation pressure of large or very effective predator populations such as starfish, crabs or carnivorous prosobranchs. In contrast, Hartnoll & Hawkins (1980, 1985) have demonstrated during long-term studies that successful competitors for space can be outcompeted within long periods by other competitive species. For instance, in the rocky mid intertidal of British shores, populations of dominant competitors such as fucoids and barnacles oscillate over many years. This phenomenon seems to be influenced by herbivory of *Patella vulgata* showing exemplarily interactions between two different types of biological factors causing drastic changes within the community structure.

Community structure changes drastically at Helgoland within the fringe between mid and lower intertidal. *Mytilus edulis* disappears and *Fucus serratus* becomes the dominant competitor for space. The intense occupation of space by the macroalgae can be explained by high activity of crabs preying on the mussels and thus promoting other competitors for space. *F. serratus* appears as the most competitive algae species within the lower intertidal. During the first season of succession, seasonal green algae dominate the algal community but with the beginning of the second period of growth, a canopy of *F. serratus* completely covers the ground promoting perennial undercover algae (e.g. *Cladophora rupestris*, *Chondrus crispus*).

Exclusion experiments have revealed competition for space as an important factor in controlling the community structure of rocky intertidal communities. The relative degree of its importance changes with the vertical level on the shore and the relative degree of importance of both predation and herbivory (see below) and, of course, with abiotic factors. Development and maintenance of littoral hard bottom communities and the importance of competition for space to control the community patterns have not yet led to a generalizing model (see Menge & Sutherland, 1976, 1987; Connell & Slatyer, 1977; Sutherland & Karlson, 1977; Paine, 1984). There are many factors that may play an important role in the succession of a cleared rock surface. Besides biological interactions and fluctuations of abiotic factors, there are other circumstances to be considered to understand succession and the patterns of how organisms occupy free space (Osman, 1977). There are for example: (a) seasonal effects on larval recruitment; (b) larval selectivity for different substrates, specific growth rates and mechanisms of competition between solitary and colonial species; (c) rates and seasonal aspects of reproduction; (d) size of the substrate free for occupation.

Despite a general high variability of recruitment pattern of littoral hard bottom communities there is an amazing correspondence of the results presented here with conclusions of investigations carried out under similar conditions (Southward & Southward, 1978; Markham & Munda, 1980). The results support the hypothesis that free space will first be occupied by seasonal green algae but without excluding further settlement and growth of perennial species. If predation pressure is low, at least mussel beds settle and outcompete algae from the rock, but they provide a secondary substrate for algal settlement. Ignoring the hypothetical influences of predation and herbivory on community structure the succession of free space within the mid and low intertidal can be

characterized by three phases: seasonal green algae > perennial algae > mussel beds. In fact this predictable development will usually be disturbed and changed by other biological interactions and/or abiotic factors thus preventing a possible "climax" of succession, dominated by the influence of competition for space. At sites exposed to wave action, the development of the communities changes drastically. Mostly they are dominated by barnacles, but seasonal aspects are important in the prediction of species that will become the dominant competitor (Caffey, 1985). For smaller habitats cleared of organisms (like experimental plates, shells of mussels, boulder fields) other sequences of succession could be demonstrated (e.g. Sousa, 1979; Kay & Keough, 1981): serpulid worms > bryozoans > sponges > ascidians > destruction (winter).

Again, abiotic factors and biological factors can change the development and pattern of the community. Menge & Sutherland (1976, 1987) have proposed a model suggesting that the influence of herbivory and (especially) predation on the community structure will increase with the complexity of the community and therefore weaken the relative importance of competition for space as a controlling factor. The results presented here support their view. In contrast to the upper intertidal where competition for space seems to be the only biotic factor controlling community pattern, the mid and lower intertidal community patterns are also highly influenced by herbivory and predation.

Predation

From the beginning of the experiments, it was obvious that experiments on the importance of predation on the community structure would become the most problematical part of this investigation. One reason for this is that not all presumable predators such as fish and birds (see Gibson, 1982; Feare & Summers, 1985; Marsh, 1986; Vauk & Prüter, 1987; Prüter, 1988) could be included in the investigations. Another problem was the high mobility of the *Carcinus maenas*, which made it very difficult to estimate the natural population density especially in the mid intertidal. Changes in the community structure caused by the crabs were limited because of their seasonal occurrence in the intertidal (only 4 months a year). Nevertheless, predation by *Carcinus* plays an important role in the community structure in lower parts of the intertidal by reducing populations of periwinkles and mussels. In the mid and lower intertidal, predation on *Littorina littorea* did not promote algal growth, but a control of the population density of the periwinkle seems to be very likely. In the mid intertidal, loss of mussels caused by crab predation or/and environmental stress is compensated by the growth and recruiting rates of *Mytilus edulis*. In the lower intertidal *Carcinus* excludes the mussels from settlement, thus indirectly promoting growth of *Fucus serratus* and other macroalgae. Therefore, the importance of predation as a controlling factor of community pattern increases from mid to lower intertidal. Other investigations (e.g. Kitching et al., 1959; Elner, 1978; Elner & Hughes, 1978) have also demonstrated the importance of *Carcinus* for the community structure in the lower intertidal. Following Suchanek (1985) they are a decisive factor in controlling the lower limits of distribution of mussel beds. This opinion is supported by the results presented here. Petraitis (1987) did not agree with this opinion. His experiments, performed in New England, USA, under similar climatic conditions, demonstrated that the occurrence of mussels in a sheltered bay was not due to lack of predators. These could be seen commonly at the study sites. He considered (1) a possible dominance of mussels caused by occasional initiations of new beds, or (2) expansions of existing beds. It

is most likely that successful initiations of new beds would be very rare but recruitment of and into existing beds should lead to maintenance and expansion of existing beds. The experiments carried out at Helgoland reveal that predation by *Carcinus* can prevent successful initiation of new beds, but it seems very unlikely that the crabs can completely displace existing beds.

Another important predator on mussels (and barnacles) in boreal rocky intertidal communities is the dog whelk *Nucella lapillus* (syn. *Thais lapillus*). The predation activity of *Nucella* has already been intensively studied, showing significant changes in barnacle populations but smaller reduction rates on mussel beds compared to *Carcinus maenas* or starfish (Connell, 1961; Menge, 1972, 1976, 1978a, 1978b, 1983; Barnett, 1979; Hughes & Dunkin, 1984a, 1984b; Crothers, 1985; Hughes & Drewett, 1985; West, 1986). On Helgoland, *N. lapillus* is rare, but personal communications with senior scientists revealed that this species once was more abundant. Today, *Nucella* has little effect on mussel and barnacle populations. Menge (1972, 1976, 1983) analysed the importance of physical factors to describe the relationship between predators and their prey. Following his arguments, the predation intensity of *N. lapillus* decreases with the exposure to wave action (Menge, 1983; see also Underwood, 1985). Canopy macroalgae (fucoids, laminarians) mainly occurring on sheltered shores provide a moist and favourable microclimate for dogwhelks promoting higher rates of predation. This opinion is in contrast to the development of *Nucella* populations at Helgoland. Although the Nordwest-Mole has sheltered the Nordost-Felswatt (built in 1940), *Nucella* populations have decreased there, whereas they have been able to keep up a significantly higher population density in the wave exposed "Westwatt" (Janke, not publ.). *Carcinus* prefers sheltered and moist microhabitats. The crabs are obviously more sensitive to wave exposure and physiological stress (e.g. desiccation) than *Nucella* as their patterns of distribution show (Southward, 1958; Lewis, 1964; Stephenson & Stephenson, 1972; Dalby et al., 1978). Whenever different groups of predators (crabs, starfish, carnivore prosobranchs) occur at one site in the rocky intertidal, crabs are the most effective consumers (Menge, 1983). Menge (1983) also proposed that the general predation pressure increases with an increasing number of predator groups, especially when morphologically different types occur consuming different resources. Menge & Sutherland (1976, 1987) have proposed that, in general, predation activity increases from upper to lower parts of the shore and thus with increasing complexity of the shore. The results of the experiments presented here support this opinion. The relative importance of predation by *Carcinus maenas* as a controlling factor for the community structure increases drastically in the lower intertidal. There are few data available that describe the importance of predation by birds as a controlling factor, although these can be important consumers. Especially periwinkles are eaten by birds in large numbers (Pettitt, 1975; Marsh, 1986). On Helgoland, seagulls (*Larus* spp.) and waders (e.g. *Haematopus ostralegus*) partly take their food from the rocky intertidal preferring periwinkles, mussels, polychaetes and crabs (pers. observation, unpubl.). As there are not many birds in the intertidal zone, predation pressure caused by birds is presumably low. Only a few pairs of oystercatchers breed during summer, and most of the migrating birds pass through after/before the crabs have migrated down to/up from the sublittoral region. In addition to the crabs, mussels and periwinkles are consumed by seagulls and oystercatchers throughout the year. There are some quantitative data concerning the food spectrum of Laridae around Helgoland (Vauk & Prüter, 1987; Prüter,

1988), but it does not seem to be meaningful to include them in this discussion as they do not comprise special data on bird predation in the intertidal zone.

Herbivory

Herbivory causes the most striking changes in the community structure of the rocky intertidal at Helgoland. The relative importance again changes with the vertical level on the shore as was demonstrated before for competition for space and predation. The influence in the upper intertidal is very low. Increase and decline of *Enteromorpha* populations can be slowed down and accelerated a little, respectively, by *Littorina* spp., but the algae are not prevented from covering the whole ground, thus promoting other species to settle and compete with *Enteromorpha* spp. Obviously, physical stress is too high for the periwinkles. Consequently, they react with lower grazing activity and a reduced physiological turnover rate (see Underwood, 1972, 1979; Newell, 1979; Hawkins & Hartnoll, 1983; Heil & Eichelberg, 1983; Kronberg, 1983). Investigations performed at the American Atlantic coast (e.g. Menge 1976; Lubchenco, 1978, 1980, 1982, 1983; Lubchenco & Menge 1978) and British coast (Hartnoll & Hawkins, 1985) support the low ability of herbivores to control algae (e.g. green algae) in upper intertidal areas. In contrast, Lein (1980) could demonstrate that *L. littorea* controls the populations of *Blidingia* and *Enteromorpha* in the inner Oslofjord (Norway). He observed the phenomenon of characteristic periwinkle frond-grazing which reduces the algae at the edges. These observations seem to contradict the results collected at Helgoland but can be described by differences in the environment. In the inner Oslofjord, the vertical level between MHW and MLW is very small and the green algae are situated in a lower vertical level than at Helgoland. Consequently, periwinkles do not suffer that much from physiological stress and find more favourable conditions to graze on the algae. Robles & Cubit (1981) described reductions of green algae in the upper intertidal zone caused by grazing activities of dipteran insect larvae. These results cannot be compared with those from Helgoland although these herbivorous dipteran larvae (*Clunio marinus* Haliday) do occur (especially in the "Westwatt"; Caspers, 1951) but only in small numbers (Janke, 1986). In the mid intertidal of Helgoland, herbivory by *Littorina* causes striking changes in the community pattern. The periwinkles exclude seasonal green algae (*Ulva pseudo-curvata*, *Monostroma* spp.) and reduce the settlement and growth of *Fucus* spp. from 100% cover down to about 20%. Control of *Fucus* populations caused by periwinkle grazing activity has also previously been described by Petraitis (1987). In contrast, others have reported that *L. littorea* is unable to prevent furoid establishment (Sundene, 1973; Menge, 1976; Lubchenco, 1978; 1982, 1983; Lubchenco & Menge, 1978; Keser et al., 1981; Keser & Larson, 1984). Petraitis (1987) has also reported that mussel recruitment can be influenced by intense herbivory. Periwinkles indirectly depress their establishment by reducing densities of juvenile barnacles and cyprid larvae which in turn promote mussel recruitment. These results are not relevant to the communities at Helgoland which lack large populations of barnacles (see Janke, 1986).

In Great Britain, wave-exposed sites are colonized by barnacles [*Chthamalus* spp. (L.), *Elminius modestus* Darwin and *Semibalanus balanoides* (L.)], limpets (*Patella vulgata*) and fucoids (*Fucus* spp.). Within this system, the grazing activity of *Patella* controls the settlement and growth of the algae and thus influences the competition for space between algae and barnacles (Hawkins & Hartnoll, 1983). During a long-term

study, Hartnoll & Hawkins (1983) could show that herbivory can have the function of an important regulative factor that causes recurrent oscillations in community structure.

The influence of predation and herbivory on the intertidal hard bottom community structure belongs to those phenomena which are easy to predict, replicate and verify (see Underwood, 1980, 1985; Lubchenco & Gaines, 1981; Underwood & Jernakoff, 1981; Gaines & Lubchenco, 1982; Hawkins & Hartnoll, 1983; Lubchenco et al., 1984; Underwood & Denley, 1984). At Helgoland, the importance of herbivory for community structure decreases from the mid to lower intertidal. Especially the settlement and growth of *Fucus serratus* are not controlled by natural densities of herbivores, as even a drastically decreased population density of herbivores does not promote fucoid growth (but settlement of seasonal green algae, as long as they are not overgrown by *F. serratus*). Thus, reduction of *Littorina* spp. by *Carcinus maenas* does not cause a distinctive change in community structure in the lower intertidal. It has previously been shown that the significant decrease of *Littorina* spp. below the *Fucus-serratus*-zone is not caused mainly by predation but by their physiology and behaviour (see Evans, 1948; Newell, 1979; Underwood, 1979; Branch, 1981; Heil & Eichelberg, 1983), especially patterns of behaviour adapted to tidal rhythms (see Underwood, 1972; Hawkins & Hartnoll, 1983; Hartnoll & Hawkins, 1985). Lubchenco (1978) demonstrated that selective herbivory of *L. littorea* can be a controlling factor for algal diversity. Following her observations, there are two main factors controlling the vegetation pattern: (1) preference of periwinkles for dominant species, and (2) the intensity of herbivory on the algal community. For rockpool communities on the New England rocky shore she found out that the highest species diversity occurred at intermediate *Littorina* densities as long as the snails preferred competitive dominant algae (here *Fucus* spp.). As soon as the preferred food was competitively inferior, *L. littorea* decreased algal diversity. Thus Lubchenco (1978) concluded that the effect of consumers on plant species diversity depended on the relationship between herbivore food preference and competitive abilities (and adaptations) of the plants. Her results also indicated that herbivores (and also predators) do not only increase or decrease species diversity of their food but are potentially able to cause both. Lubchenco also provided a list of algae that are either preferred or neglected by *L. littorea*. *Fucus serratus*, *Cladophora rupestris* and *Chondrus crispus* belong to the latter group, thus being indirectly promoted by the periwinkles. Previous investigations (e.g. van Alstyne, 1988) have indicated some reasons for the behaviour of the periwinkles. The experiments demonstrated that fucoid plants are able to produce polyphenolic substances in order to avoid being consumed when attacked by herbivores. *Cladophora rupestris* is rejected because it contains sulphuric acid. *Chondrus crispus* might be neglected because of its leathery consistency (Lubchenco & Menge, 1978). These results may explain both the dominance of *Fucus serratus* as the competitive dominant canopy algal species and *Chondrus crispus* and *Cladophora rupestris* as dominant undercover algae in the lower intertidal at Helgoland. Lubchenco & Cubit (1980) also demonstrated that intertidal algae may change their stature and growth during periods of high herbivory. However, these considerations derived from observations in warm temperate regions are probably not relevant to the community at Helgoland.

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LITERATURE CITED

- Alstyne, K. L., van, 1988. Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. – *Ecology* 69, 655–663.
- Anonymus, 1981. Amoco Cadiz. Fates and effects of the oil spill. Proceedings of the international symposium, Brest November 19–22, 1979. Centre national l'exploitation des océans, Paris, 882 pp.
- Baker, J. M. & Wolff, W. J. (Ed.), 1987. Biological surveys of estuaries and coasts. Cambridge Univ. Press, Cambridge, 449 pp.
- Bakker, K., 1959. Feeding habits and zonation in some marine snails. – *Archs néerl. Zool.* 13, 230–257.
- Ballantine, W. J., 1961. A biologically defined exposure scale for the comparative description of rocky shores. – *Fld Stud.* 1, 1–19.
- Barkman, J. J., 1955. On the distribution and ecology of *Littorina obtusata* and its subspecific units. – *Archs néerl. Zool.* 11, 22–86.
- Barnett, B. E., 1979. A laboratory study of predation by the dogwhelk *Nucella lapillus* on the barnacles *Elminius modestus* and *Balanus balanoides*. – *J. mar. biol. Ass. U.K.* 59, 299–306.
- Bertness, M. D., Yund, P. O. & Brown, A. F., 1983. Snail grazing and the abundance of algal crusts on a sheltered New England shore. – *J. exp. mar. Biol. Ecol.* 71, 147–164.
- Binot, F., 1988. Strukturentwicklung des Salzkissens Helgoland. – *Z. dt. geol. Ges.* 139, 51–62.
- Branch, G. M., 1981. The biology of the limpets: physical factors, energy flow and ecological interactions. – *Oceanogr. mar. Biol.* 19, 235–380.
- Braun-Blanquet, J., 1964. Pflanzensoziologie. Springer, Wien, 865 pp.
- Caffey, H. M., 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. – *Ecol. Monogr.* 55, 313–332.
- Caspers, H., 1951. Rhythmische Erscheinungen in der Fortpflanzung von *Clunio marinus* (Dipt. Chiron.) und das Problem der lunaren Periodizität der Organismen. – *Arch. Hydrobiol.* 18, 415–594.
- Connell, J. H., 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. – *Ecol. Monogr.* 31, 61–104.
- Connell, J. H., 1964. The influence of interspecific competition and other factors on the barnacle *Chthamalus stellatus*. – *Ecology* 42, 710–723.
- Connell, J. H., 1970. A predator-prey system in the marine intertidal region. – *Ecol. Monogr.* 40, 49–78.
- Connell, J. H., 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: *Ecology and evolution of communities*. Ed. by M. L. Cody & J. M. Diamond. Belknap Press, Cambridge, Maine, 460–490.
- Connell, J. H., 1985. The consequences of variation in initial settlement vs. post settlement mortality in rocky intertidal communities. – *J. exp. mar. Biol. Ecol.* 93, 11–45.
- Connell, J. H. & Slatyer, R. O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. – *Am. Nat.* 111, 1119–1144.
- Creese, R. G. & Underwood, A. J., 1982. Analysis of inter- and intraspecific competition amongst intertidal limpets with different methods of feeding. – *Oecologia* 53, 337–346.

- Crothers, J. H., 1967. The biology of the shore crab, *Carcinus maenas* (L.). I. The background – anatomy, growth and life history. – *Fld Stud.* 2, 407–434.
- Crothers, J. H., 1968. The biology of the shore crab, *Carcinus maenas* (L.) II. The life of the adult crab. – *Fld Stud.* 2, 579–614.
- Crothers, J. H., 1985. Dogwhelks: An introduction to the biology of *Nucella lapillus* (L.). – *Fld Stud.* 6, 291–360.
- Cubit, J. D., 1984. Herbivory and seasonal abundance of algae on a high intertidal rocky shore. – *Ecology* 65, 1904–1917.
- Dalby, D. H., Cowell, E. B., Syratt, W. J. & Crothers, J. H., 1978. An exposure scale for marine shores in western Norway. – *J. mar. biol. Ass. U.K.* 58, 975–996.
- Dayton, P. K., 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. – *Ecol. Monogr.* 41, 351–389.
- Dayton, P. K., 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. – *Ecol. Monogr.* 45, 137–159.
- DHI, 1987. Hoch- und Niedrigwasserzeiten für die Deutsche Bucht und die oberen Flußgebiete 1988. DHI, Hamburg, 112 pp.
- Dongen, A., van, 1956. The preference of *Littorina obtusata* L. for Fucacea. – *Archs néerl. Zool.* 11, 373–386.
- Doty, M. S., 1946. Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast. – *Ecology* 27, 315–328.
- Elnor, R. W., 1978. The mechanisms of predation by the shore crab, *Carcinus maenas* (L.) on the edible mussel, *Mytilus edulis* L. – *Oecologia* 36, 333–344.
- Elnor, R. W. & Hughes, R. N., 1978. Energy maximisation in the diet of the shore crab, *Carcinus maenas*. – *Ecology* 47, 103–116.
- Evans, R. G., 1948. The lethal temperatures of some common molluscs. – *J. Anim. Ecol.* 17, 165–173.
- Feare, C. J. & Summers, R. W., 1985. Birds as predators on rocky shores. In: *The ecology of rocky coasts*. Ed. by P. G. Moore & R. Seed. Hodder & Stoughton, London, 249–264.
- Fletcher, W. J. & Creese, R. G., 1985. Competitive interactions between co-occurring herbivorous gastropods. – *Mar. Biol.* 86, 183–191.
- Gaines, S. D. & Lubchenco, 1982. A unified approach to marine plant herbivore interactions. II. Biogeography. – *A. Rev. Ecol. Syst.* 13, 111–138.
- Gillandt, L., 1979. Zur Ökologie der Polychaeten des Helgoländer Feislitorals. – *Helgoländer wiss. Meeresunters.* 32, 1–35.
- Gibson, R. N., 1982. Recent studies on the biology of intertidal fishes. – *Oceanogr. mar. Biol.* 20, 363–414.
- Goodwin, B. J. & Fish, J. D., 1977. Inter- and intraspecific variation in *Littorina obtusata* and *Littorina mariae* (Gastropoda). – *J. moll. Stud.* 43, 241–254.
- Hagmeier, A., 1930. Die Besiedelung des Felsstrandes und der Klippen von Helgoland. I. Der Lebensraum. – *Wiss. Meeresunters. (Abt. Helgoland)* 15 (18a), 1–35.
- Hartnoll, R. G. & Hawkins, S. J., 1980. Monitoring rocky shore communities: a critical look at spatial and temporal variation. – *Helgoländer Meeresunters.* 33, 484–494.
- Hartnoll, R. G. & Hawkins, S. J., 1985. Patchiness and fluctuations on moderately exposed rocky shores. – *Ophelia* 24, 53–63.
- Hawkins, S. J. & Hartnoll, R. G., 1983. Grazing of intertidal algae by marine invertebrates. – *Oceanogr. mar. Biol.* 21, 195–282.
- Heil, K. P. & Eichelberg, D., 1983. Untersuchungen zum Harnsäuremetabolismus von *Littorina littorea* (Gastropoda). – *Helgoländer Meeresunters.* 36, 465–472.
- Hughes, R. N., 1985. Rocky shore communities: catalysts to understand predation. In: *The ecology of rocky coasts*. Ed. by P. G. Moore & R. Seed. Hodder & Stoughton, London, 223–233.
- Hughes, R. N. & Drewett, D., 1985. A comparison of the foraging behaviour of dogwhelks, *Nucella lapillus* (L.), feeding on barnacles or mussels on the shore. – *J. moll. Stud.* 51, 73–77.
- Hughes, R. N. & Dunkin, S. de B., 1984a. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels *Mytilus edulis* L. in the laboratory. – *J. exp. mar. Biol. Ecol.* 77, 45–68.
- Hughes, R. N. & Dunkin, S. de B., 1984b. Effect of dietary history on selection of prey and foraging

- behaviour among patches of prey, by the dogwhelk, *Nucella lapillus* (L.). – *J. exp. mar. Biol. Ecol.* **79**, 159–172.
- Hurlbert, S. H., 1984. Pseudoreplication and the design of ecological field experiments. – *Ecol. Monogr.* **54**, 187–211.
- Jackson, J.B.C., 1977a. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. – *Am. Nat.* **111**, 743–767.
- Jackson, J. B. C., 1977b. Habitat area, colonization and development of epibenthic community structure. In: *Ecology of benthic organisms*. Ed. by B. F. Keegan, P. O. Ceidigh & J. P. S. Boaden. Pergamon Press, New York, 349–358.
- Janke, K., 1986. Die Makrofauna und ihre Verteilung im Nordost-Felswatt von Helgoland. – *Helgoländer Meeresunters.* **40**, 1–55.
- Jernakoff, P., 1985a. Interactions between the limpet *Patelloida latistrigata* and algae on an intertidal rock platform. – *Mar. Ecol. Prog. Ser.* **23**, 71–78.
- Jernakoff, P., 1985b. An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. – *J. exp. mar. Biol. Ecol.* **88**, 287–302.
- Jones, W. E., Beveridge, S., McConnell, B., Mark-Smith, S., Mitchell, J. & Fletcher, A., 1980. Methods of data collection and processing in rocky intertidal monitoring. In: *The shore environment. I. Methods*. Ed. by J. H. Price, D. E. G. Irvine & W. Farnham. Acad. Press, London, 137–170.
- Kay, A. M. & Keough, M. J., 1981. Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. – *Oecologia* **48**, 123–130.
- Keser, M. & Larson, B. R., 1984. Colonization and growth dynamics of three species of *Fucus*. – *Mar. Ecol. Prog. Ser.* **15**, 125–134.
- Keser, M., Vadas, R. L. & Larson, B. R., 1981. Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting regimes in Maine, U.S.A. – *Botanica mar.* **24**, 29–38.
- Kitching, J. A., Sloane, J. F. & Ebling, F. J., 1959. The ecology of Lough Ine. VIII. Mussels and their predators. – *J. Anim. Ecol.* **28**, 331–341.
- Kitting, C. L., 1980. Herbivore plant interactions of individual limpets maintaining a mixed diet of intertidal marine algae. – *Ecol. Monogr.* **50**, 527–550.
- Kornmann, P. & Sahling, P. H., 1977. Meeresalgen von Helgoland. – *Helgoländer wiss. Meeresunters.* **29**, 1–289.
- Kronberg, I., 1983. Ökologie der Schwarzen Zone im marinen Felslitoral. Monographie eines extremen Lebensraumes. Diss., Univ. Kiel, 237 pp.
- Kronberg, I., 1987. Accuracy of species and abundance minimal areas determined by similarity area curves. – *Mar. Biol.* **96**, 555–562.
- Krüß, A., 1988. Die benthische Fischfauna des Helgoländer Felssockels. Ein Beitrag zur Biologie und Ökologie der häufigen Arten. Dipl.-Arb., Univ. Karlsruhe, 172 pp.
- Krumbein, W. E., 1975. Verwitterung, Abtragung und Küstenschutz auf der Insel Helgoland. – *Abh. Verh. naturwiss. Ver. Hamburg*, **18/19**, 5–31.
- Krumbein, W. E., 1977. Zur Frage der Verwitterung der Felsmasse der Insel Helgoland. – *Abh. Verh. naturwiss. Ver. Hamburg* **20**, 5–11.
- Lein, T. E., 1980. The effects of *Littorina littorea* (Gastropoda) grazing on littoral green algae in the inner Oslofjord, Norway. – *Sarsia* **65**, 87–92.
- Levin, S. A. & Paine, R. T., 1974. Disturbance, patch formation and community structure. – *Proc. ntn. Acad. Sci. U.S.A.* **71**, 2744–2747.
- Lewis, J. R., 1961. The littoral zone on a rocky shore – a biological or a physical entity? – *Oikos* **12**, 280–301.
- Lewis, J. R., 1964. *The ecology of rocky shores*. Engl. Univ. Press, London, 323 pp.
- 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*. Ed. by B. F. Keegan, P. O. Ceidigh & P. J. S. Boaden. Pergamon Press, New York, 417–424.
- Lubchenco, J., 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algae competitive abilities. – *Am. Nat.* **112**, 23–29.
- Lubchenco, J., 1980. Algae zonation in the New England rocky intertidal community: an experimental analysis. – *Ecology* **61**, 333–344.

- Lubchenco, J., 1982. Effects of grazers and algal competition on fucoid colonization in tide pools. – *J. Phycol.* 18, 544–550.
- Lubchenco, J., 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity and plant escapes during succession. – *Ecology* 64, 1116–1123.
- Lubchenco, J. & Cubitt, J. D., 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. – *Ecology* 61, 676–686.
- Lubchenco, J. & Gaines, S. D., 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. – *A. Rev. Ecol. Syst.* 12, 405–437.
- Lubchenco, J. & Menge, B. A., 1978. Community development and persistence in a low rocky intertidal zone. – *Ecol. Monogr.* 48, 67–94.
- Lubchenco, J., Menge, B. A., Garrity, S. D., Lubchenco, P. J., Ashkenas, L. R., Gaines, S. D., Emlet, R., Lucas, J. & Strauss, S., 1984. Structure, persistence and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). – *J. exp. mar. Biol. Ecol.* 78, 23–73.
- Lüning, K., 1970. Tauchuntersuchungen zur Vertikalverteilung der sublitoralen Helgoländer Algenvegetation. – *Helgoländer wiss. Meeresunters.* 21, 271–291.
- Lüning, K., 1985. Meeresbotanik. Thieme, Stuttgart, 375 pp.
- Mann, K. H. & Clark, R. B., 1978. Session III. Summary and overview: long-term effects of oil spills on marine intertidal communities. – *J. Fish. Res. Bd Can.* 35, 791–795.
- Markham, J. W. & Munda, I. M., 1980. Algal recolonization in the rocky eulittoral of Helgoland. – *Aquat. Bot.* 9, 33–71.
- Marsh, C., 1986. Rocky intertidal community organization: the impact of avian predators on mussel recruitment. – *Ecology* 67, 771–786.
- Menge, B. A., 1972. Foraging strategies of a starfish in relation to actual prey availability and environmental predictability. – *Ecol. Monogr.* 42, 25–50.
- Menge, B. A., 1976. Organisation of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. – *Ecol. Monogr.* 46, 355–393.
- Menge, B. A., 1978a. Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. – *Oecologia* 34, 1–16.
- Menge, B. A., 1978b. Predation intensity in a rocky intertidal community. Effect of an algae canopy, wave action and desiccation on predator feeding rates. – *Oecologia* 34, 17–34.
- Menge, B. A., 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. – *Oecologia* 58, 141–155.
- Menge, B. A. & Lubchenco, J., 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. – *Ecol. Monogr.* 51, 429–450.
- Menge, B. A. & Sutherland, J. P., 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. – *Am. Nat.* 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. – *Am. Nat.* 130, 730–757.
- Munda, I. M. & Markham, J. W., 1982. Seasonal variations of vegetation pattern and biomass constituent in the rocky eulittoral of Helgoland. – *Helgoländer wiss. Meeresunters.* 35, 131–151.
- Newell, R. C., 1979. Biology of intertidal animals. Mar. Ecol. Surv. Ltd, Faversham, 781 pp.
- Ortega, S., 1985. Competitive interactions among tropical intertidal limpets. – *J. exp. mar. Biol. Ecol.* 90, 11–25.
- Osman, R. W., 1977. The establishment and development of a marine epifaunal community. – *Ecol. Monogr.* 47, 37–63.
- Paine, R. T., 1966. Food web complexity and species diversity. – *Am. Nat.* 100, 65–75.
- Paine, R. T., 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. – *Oecologia* 15, 93–120.
- Paine, R. T., 1976. Size limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. – *Ecology* 57, 858–873.
- Paine, R. T., 1984. Ecological determinism in the competition for space. – *Ecology* 65, 1339–1357.
- Paine, R. T. & Vadas, R. L., 1969. The effect of grazing by sea urchins, *Strongylocentrotus* spp. on benthic algal populations. – *Limnol. Oceanogr.* 14, 710–719.
- Petratits, P. S., 1987. Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. – *J. exp. mar. Biol. Ecol.* 109, 117–136.

- Petratis, C. W., 1989. The effects of the periwinkle *Littorina littorea* (L.) and of intraspecific competition on growth and survivorship of the limpet *Notacmaea testudinalis* (Müller). – J. exp. mar. Biol. Ecol. 125, 99–115.
- Pettitt, C. W., 1975. A review of the predators of *Littorina*, especially those of *L. saxatilis* (Olivi) (Gastropoda, Prosobranchia). – J. Conch., Lond. 28, 343–357.
- Prüter, J., 1988. Weitere Untersuchungen zur Ernährung von Mantel- (*Larus marinus*) und Silbermöwe (*Larus argentatus*) bei Helgoland im Winterhalbjahr. – Seevögel 9 (Sonderbd.), 79–91.
- Quinn, G. H. & Ryan, N. R., 1989. Competitive interactions between two species of intertidal herbivorous gastropods from Victoria, Australia. – J. exp. mar. Biol. Ecol. 125, 1–12.
- Reise, K., 1977. Predator exclusion experiments in an intertidal mud flat. – Helgoländer wiss. Meeresunters. 30, 263–271.
- Reise, K., 1978. Experiments on epibenthic predation in the Wadden Sea. – Helgoländer Meeresunters. 31, 55–101.
- Reise, K., 1985. Tidal flat ecology. Springer, Stuttgart, 192 pp.
- Remmert, H., 1984. Ökologie – ein Lehrbuch. Springer, Berlin, 334 pp.
- Robles, C. D. & Cubit, D., 1981. Influence of biotic factors in an upper intertidal community: dipteran larvae grazing on algae. – Ecology 62, 1536–1547.
- Ropes, J. W., 1968. The feeding of the green crab *Carcinus maenas* (L.). – Fish. Bull. U.S. 67, 183–203.
- Scheltema, R. S., 1974. Biological interactions determining larval settlement of marine invertebrates. – Thalassia jugosl. 10, 263–296.
- Schmidt-Thomé, P., 1937. Der tektonische Bau und die morphologische Gestaltung von Helgoland. – Abh. Verh. naturw. Ver. Hamburg 1, 215–249.
- Schonbeck, M. & Norton, T., 1978. Factors controlling the upper limits of furoid algae on the shore. – J. exp. mar. Biol. Ecol. 31, 303–313.
- Schonbeck, M. & Norton, T., 1980. Factors controlling the lower limits of furoid algae on the shore. – J. exp. mar. Biol. Ecol. 43, 131–150.
- Seed, R., 1969a. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed shores. I. Breeding and settlement. – Oecologia 3, 277–316.
- Seed, R., 1969b. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed shores. II. Growth and mortality. – Oecologia 3, 317–350.
- Sousa, W. P., 1979. Disturbance in marine boulder fields: the non-equilibrium maintenance of species diversity. – Ecology 60, 1225–1239.
- Southward, A. J., 1958. The zonation of plants and animals on rocky sea shores. – Biol. Rev. 33, 137–177.
- Southward, A. J., 1964. Limpet grazing and the control of vegetation on rocky shores. In: Grazing in terrestrial and marine environments. Ed. by D. J. Crisp. Blackwell Scientific Publications, Oxford, 265–273.
- Southward, A. J. & Southward, E. C., 1978. Recolonization of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon spill. – J. Fish. Res. Bd Can. 35, 682–706.
- Stebbing, A. R. D., 1973. Competition for space between the epiphytes of *Fucus serratus* L. – J. mar. biol. Ass. U.K. 53, 247–261.
- Stephenson, T. A. & Stephenson, A., 1949. The universal features of zonation between tidemarks on rocky coasts. – J. Ecol. 37, 289–305.
- Stephenson, T. A. & Stephenson, A., 1972. Life between tidemarks on rocky shores. Freeman, San Francisco, 425 pp.
- Steneck, R. S., 1982. A limpet coralline alga association: adaptations and defences between a selective herbivore and its prey. – Ecology 63, 507–522.
- Suchanek, T. H., 1985. Mussels and their role in structuring rocky shore communities. In: The ecology of rocky coasts. Ed. by P. G. Moore & R. Seed. Hodder & Stoughton, London, 70–96.
- Sundene, O., 1973. Growth and reproduction in *Ascophyllum nodosum* (Phaeophyceae). – Norw. J. Bot. 20, 249–255.
- Sutherland, J. P. & Karlson, R. H., 1977. Development and stability of the fouling community at Beaufort, North Carolina. – Ecol. Monogr. 47, 425–466.
- Underwood, A. J., 1972. Tide model analysis of the zonation of intertidal prosobranchs. Four species of *Littorina* (L.). – J. exp. mar. Biol. Ecol. 9, 239–255.

- Underwood, A. J., 1979. The ecology of intertidal gastropods. – *Adv. mar. Biol.* 16, 111–210.
- Underwood, A. J., 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. – *Oecologia* 46, 201–213.
- Underwood, A. J., 1984a. Vertical and seasonal patterns in competition between intertidal gastropods. – *Oecologia* 64, 211–222.
- Underwood, A. J., 1984b. Microalgal food and the growth of the intertidal gastropods *Nerita atramentosa* Reeve and *Bembicium nanum* (Lamarck) at four heights of the shore. – *J. exp. mar. Biol. Ecol.* 79, 277–291.
- Underwood, A. J., 1985. Practical factors and biological interactions: the necessity and nature of ecological experiments. In: *The ecology of rocky coasts*. Ed. by P. G. Moore & R. Seed. Hodder & Stoughton, London, 372–389.
- Underwood, A. J. & Denley, E. J., 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In: *Ecological communities: conceptual issues and the evidence*. Ed. by D. Strong, D. Simberloff, L. G. Abele & A. B. Thistle. Princeton Univ. Press, Princeton/N. J., 151–180.
- Underwood, A. J. & Fairweather, P. G., 1986. Intertidal communities: do they have different ecologies or different ecologists? – *Proc. ecol. Soc. Aust.* 14, 7–16.
- Underwood, A. J. & Jernakoff, 1981. Effects of interaction between algae and grazing gastropods on the structure of a low shore intertidal algal community. – *Oecologia* 48, 221–233.
- Vauk, G. & Prüter, J., 1987. *Möwen*. Niederelbe-Verl., Otterndorf, 303 pp.
- Weinberg, S., 1978. The minimal area problem in invertebrate communities of Mediterranean rocky substrata. – *Mar. Biol.* 49, 33–40.
- West, L., 1986. Interindividual variation in prey selection by the snail *Nucella* (= *Thais*) *emarginata*. – *Ecology* 67, 798–809.
- Wurster, P., 1962. Geologisches Portrait Helgolands. – *Die Natur* 70, 135–150.