



Changes in depth distribution and biomass of sublittoral seaweeds at Helgoland (North Sea) between 1970 and 2005

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ABSTRACT: Recent investigations of the intertidal macrophyto- and zoobenthos of the island of Helgoland (North Sea) revealed that species composition and spatial extent of communities have changed within the last century. To evaluate the situation in the subtidal, a diving study from the late 1960s was repeated with comparable methods in 2005 and 2006. Along 2 vertical transects, the cover of dominant brown seaweeds, *Fucus serratus*, *Laminaria digitata*, *L. hyperborea*, *Saccharina latissima* (= *Laminaria saccharina*), *Sargassum muticum* and *Desmarestia aculeata*, was semi-quantitatively assessed to define vegetation zones. Within each zone, all macroalgal species were estimated quantitatively in 3 to 6 random 1 m² quadrats. Additionally, a replicated biomass survey was performed at 6 depths (0.5, 2, 4, 6, 8 and 10 m below mean low water spring tide [MLWS]). Comparison of recent and historical data showed some characteristic changes. The previously dominant brown seaweed *S. latissima* showed a decline in the northern part of the island, but is still present at other sites. *S. muticum* invaded the kelp forest, but is not dominant within this vegetation. The vertical distribution of *L. hyperborea* increased, and its lower depth limits as well as those of various understory seaweeds deepened by about 2 to 8 m. Biomass data followed this trend. The maximum biomass of *L. hyperborea* shifted from 2 m below MLWS in 1967 to 4 m below MLWS in 2005. The overall downward extension of the *Laminaria* forest is concordant with the increase in water transparency observed around Helgoland since 1975.

KEY WORDS: Biomass · Change · Depth limit · Macroalgae · *Laminaria* · *Saccharina* · Helgoland · North Sea

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1. INTRODUCTION

Brown seaweeds of the order Laminariales (kelps) are the major structuring element of temperate to polar coastal kelp beds worldwide (Kain 1962, Lüning 1990). A change or loss of these kelp beds would drastically affect coastal ecosystems as they provide habitat and shelter for epibionts and rich invertebrate and fish fauna (Schultze et al. 1990). They also have a wave dampening effect which is important for coastal protection (Dubi & Tørum 1995). Since the late 1980s, there have been increasing and alarming reports of changes in the quantitative patterns of kelp communities along European coastlines and elsewhere. Eutrophication, sedimentation, invasion of foreign species

and the global warming trend have been implicated but unequivocal evidence is missing (Givernaud et al. 1991, Cosson 1999, Moy et al. 2003). In the Baltic, where the ecological role of dominant kelps is taken by species of the genus *Fucus*, several studies revealed a decrease in the depth distribution of *Fucus vesiculosus* and of algal depth limits in general. This was regarded as an indirect consequence of eutrophication due to reduced light availability (Kautsky et al. 1986, Pedersen & Snoeijs 2001).

The seaweed vegetation of Helgoland (North Sea) has been intensively studied during the past century. The investigations focused on the intertidal and were mostly descriptive or qualitative (Bartsch & Kuhlenskamp 2000 and citations therein). Quantitative

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investigations of the intertidal marine flora at Helgoland are few (den Hartog 1959, Markham & Munda 1980, Munda & Markham 1982, Reichert et al. 2008). The first, and so far only, quantitative sublittoral study was conducted by Lüning, who described sublittoral algal zonation and depth limits (Lüning 1970) and biomass as well as morphometric parameters such as stipe length and leaf area index of major kelp species (Lüning 1969). More than 25 years later, de Kluijver (1997) added information on sublittoral faunistic communities, partly extending knowledge of algal depth distribution at Helgoland.

Although regular monitoring of benthic flora and fauna was not conducted on Helgoland before 2000, changes in abundances and recent species immigrations have been documented (e.g. Bartsch & Tittley 2004, Franke & Gutow 2004, Reichert & Buchholz 2006). Detailed analysis of abiotic factors at Helgoland (1962–2001) taken every working day revealed 3 major trends: (1) mean sea surface water temperature increased significantly by 1.13 to 1.33°C, (2) phosphate concentration decreased by $>0.3 \mu\text{mol l}^{-1}$ and (3) Secchi depth increased by 1 m between 1975 and 2001 (Wiltshire & Manly 2004, Wiltshire et al. 2008). Mean yearly salinity between 1975 and 2001 varied between ~31 and ~33 PSU, but without a significant trend (Wiltshire et al. 2008). Unpublished data show an increase in storminess since 1989 and a change in storm direction from predominantly W-SW to additional dominance of S-SW and E-SE (I. Bartsch pers. comm.). Furthermore, there were indications that *Saccharina latissima* (formerly *Laminaria saccharina*) stands are being lost and kelp zonation patterns are changing (I. Bartsch pers. obs.). To quantify anticipated changes in algal zonation patterns, algal depth limits and kelp biomass, the diving investigations of Lüning (1969, 1970) were repeated in 2005 and 2006.

2. MATERIALS AND METHODS

Methods used were adapted from the investigations of Lüning (1969, 1970) to make the datasets comparable.

2.1 Investigation area and diving procedure

Two sublittoral transects that had been investigated ~40 years earlier by Lüning (1970) were traversed

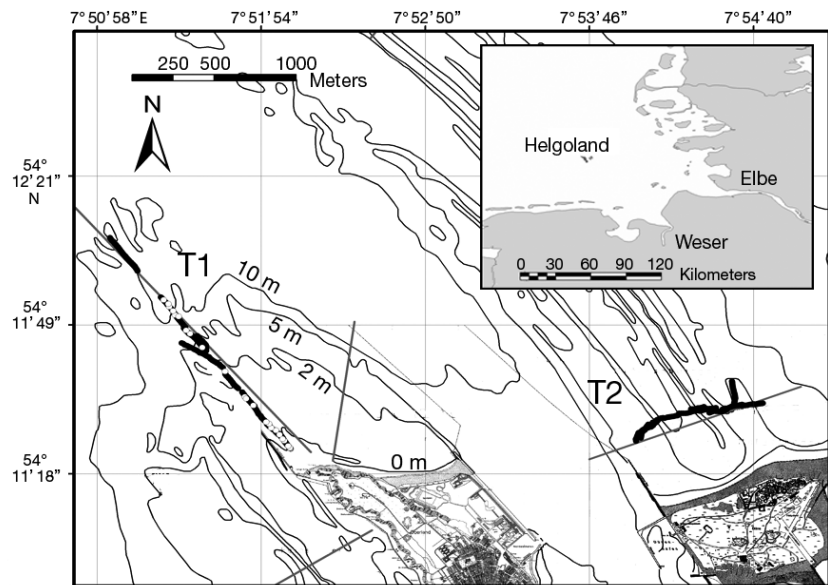


Fig. 1. Transect T1 (2005) in the north of the main island of Helgoland and Transect T2 (2006) in the north of the island Dune. Black lines: adjacent locations of 5 m intervals; white dots: locations of quadrats; straight lines: transects of Lüning (1970). Depth contour lines indicate 0, 2, 5 and 10 m below mean low water spring tide (MLWS)

again in this study (Fig. 1). Transect T1 in the North of Helgoland has a total length of ~1580 m and represents Transect P3 of Lüning (1970). It follows the depth gradient along the red sandstone platform of the main island for 1300 m in a northwesterly direction (bearing 320°). As the transect becomes much deeper after 1300 m, carrying predominantly faunistic communities which were not in the scope of the investigation, the transect was interrupted for ~220 m. It was then continued for ~280 m over chalk cliffs, after which depths increase again and support predominantly algal communities (diving profile: Fig. 9 in Lüning 1970). Transect T2 in the north of Dune Island has a total length of 845 m and represents Transect P1 of Lüning (1970). It crosses the chalk and limestone cliffs, perpendicular to their depth gradients, in an east-northeasterly direction (bearing 80°).

As no coordinates were available for the P1 and P3 transects of Lüning (1970), their location was calculated as follows: Fig. 1 in Lüning (1970) was scanned (Mustek Scan Express 6000P, Mustek Optic-Computer & Communication International) and geo-referenced point by point with the help of an orthophoto of Helgoland (Land Surveying Office, Schleswig-Holstein, Germany) and the GIS Software ArcGIS 9.1 (ESRI). The start and end coordinates were determined and used as reference points for Transects T1 and T2 of the present investigation.

Fifty-one dives were carried out (T1: April 21 to August 22, 2005; T2: June 8 to July 31, 2006). Under-

water bearings were taken with a compass (Seemann Sub). For depth determination, a digital depth gauge was used (Seemann Sub; precision: 40 cm). The exact local time was logged simultaneously. The measured depth was corrected with tide level records of the tide gauge 'Helgoland Südhafen' (Water and Shipping Authority, Tönning, Germany) as had been done by Lüning (1970). To locate the present transects, the diver signaled the diving boat by tugging a cord connecting him and a surface marker buoy every 25 to 35 m. The diving boat approached the buoy as close as possible and took a GPS reading (Magellan GPS 320, Magellan Corporation; precision: 25 m). These readings were used to locate transects on a digital map (ArcGIS 9.1). Intermediate points without GPS readings were calculated in ArcInfo 9.1.

2.2. Estimation of dominant brown seaweeds and definition of vegetation zones

Presence/absence and percentage cover classes of the dominant brown seaweeds *Desmarestia aculeata* (only transect T2), *Fucus serratus*, *Sargassum muticum*, *Laminaria digitata*, *L. hyperborea* and *Saccharina latissima* were noted along a 3 to 5 m broad corridor (H. Kautsky pers. comm.) in increments of 5 m along T1 and T2. *L. digitata* and *L. hyperborea* were differentiated by their stipe morphology: adult *L. digitata* have flexible, flattened and smooth stipes with no or just few epiphytes whereas *L. hyperborea* have stiff, round and rough stipes with many epiphytes. *L. digitata* thalli lie near the substrate while *L. hyperborea* thalli are upright. Although these characteristics are distinct, misidentification in a few cases cannot be discounted. Cover estimation of the dominant brown seaweeds followed a modified semi-quantitative scale (Braun-Blanquet 1951, modified) with 6 cover classes (Table 1). At the beginning of each 5 m interval, para-

Table 1. Semi-quantitative cover classes (Braun-Blanquet 1951, modified)

Class	% Cover	Description
0	0	Not present
5	1–10	One or few individuals present with sparse ground coverage
25	11–40	Clearly <50% of ground covered, but species common
50	41–60	Coverage ~50%
75	61–90	Cover clearly >50%, but <100%
100	91–100	Dense coverage, only few and small gaps in canopy present

meters such as depth, time, substratum (red sandstone, shell limestone, chalk) and topography (solid rock, boulders, stones, gravel and shell) were recorded in addition to presence/absence and cover data. The total number of 5 m intervals investigated along T1 and T2 were 272 and 235, respectively.

From the data obtained, vegetation zones were defined. As Lüning (1970) did not define his 'pure' and 'mixed' vegetation stands precisely, we used the following criteria: (1) 'pure' vegetation stands, named after the dominant brown seaweed species, are those dominated by just one brown algal species with cover of 41 to 100%, or with cover <41% but without other co-occurring brown seaweeds; (2) 'mixed' stands or transition zones, named after the co-occurring dominant brown seaweeds, are comprised of 2 brown algal species in variable abundances between 11 and 90%; and (3) 'red algal zones' have only foliose and filamentous red algae present. In total, 9 zones were defined (Table 2).

2.3. Percentage cover of macrophytes

In each vegetation zone, the percentage cover and 'rooted' local frequency (cf. Greig-Smith 1983) of all noncrustose macrophytes and all epiphytes in 3 random samples (6 in pure *Laminaria hyperborea* stand; see Table 2) were quantified with the help of a 1 m² quadrat with 16 subdivisions. Each zone was divided into 5 m intervals (based on the diving segments) and numbered using GIS. Random sites were chosen by picking random numbers from these intervals. Their

Table 2. Vegetation zones of Transects T1 and T2 adopted from Lüning (1970). LAI: leaf area index; ID: identification letter for the respective zone, see Fig. 4

Zone	Description	Transect	ID
Fser	Pure <i>Fucus serratus</i> stands	T1	A
Fser-Ldig	Mixed <i>F. serratus</i> and <i>Laminaria digitata</i> stands	T1	B
Ldig	Pure <i>L. digitata</i> stands	T1, T2	C
Ldig-Lhyp	Mixed <i>L. digitata</i> and <i>L. hyperborea</i> stands	T1, T2	D
Lhyp	Pure <i>L. hyperborea</i> stands	T1, T2	E
Lhyp-Slat	Mixed <i>L. hyperborea</i> and <i>Saccharina latissima</i> stands	T2	–
Slat	Pure <i>S. latissima</i> stands	T2	–
Lhyp-park	Pure <i>L. hyperborea</i> stand with LAI ≤ 1	T1	F
Red algae	Red algal zone without dominant brown seaweeds	T1	G

coordinates were determined and the diving boat was positioned at each of these locations in the field. At each location, a diver dived straight down and positioned the quadrat on the bottom. In each quadrat, percentage cover over ground of each species and the percentage of free substrate were estimated. Local time and depth were also noted (see above).

2.4. Biomass survey

All *Laminaria* individuals were quantitatively harvested from 3 random 1 m² quadrats at each of 6 depths (0.5, 2, 4, 6, 8 and 10 m below mean low water spring tide [MLWS]) along T1. All other foliose and filamentous algae within a 0.25 m² subquadrat (central 4 of 16 subdivisions) of each 1 m² quadrat were harvested. To locate the random quadrats at each depth, a 20 m rope was placed perpendicular to the transect. The rope was numbered at every meter and the 3 collecting sites were randomly chosen beforehand. Fresh weights (FW) of species were determined with a Sartorius 1574 MP 8-2 (Data Weighing Systems; precision: ±0.01 g) after removal of epiphytes and shaking off excess water twice. Dry weights (DW) were determined after drying individual specimens at 100°C for 24 h. With longer drying time, no further significant weight loss was attained. Stipe lengths of *Laminaria* were measured before drying. The leaf area index (LAI) was determined by taking size-calibrated digital photographs (Olympus C-8080 WZ, Olympus) of each *Laminaria* blade (FW > 100 g). The blade area was then calculated with an image analysis program (WinFOLIA 2001a, Régent Instruments).

2.5. Data analysis

Quantitative data were tested for homogeneity of variance (Cochran's C-test). ANOVA was performed on homogeneous data or a Kruskal-Wallis ANOVA on heterogeneous data. Post hoc tests (Tukey's honestly significant difference [HSD] or multiple comparisons of mean ranks of all groups) were performed to discriminate differences between groups (Statistica 5.0, 6.0 and 8.0). To compare 2005 and 1969 data (Lüning 1969), effect size was calculated (Underwood 1997). A negative or a positive value of the effect size, with a CI not crossing the x-axis, indicates a significant decrease or increase in the tested variable, respectively. The similarity of

the vegetation zones was investigated by nonparametric multidimensional scaling (n-MDS; Bray-Curtis similarity index, square-root transformation of percentage cover data; Primer 5.1).

3. RESULTS

3.1. Vertical distribution of dominant brown seaweeds

The relative presence (RP) of *Laminaria hyperborea*, *L. digitata*, *Saccharina latissima*, *Desmarestia aculeata* (only in T2), *Fucus serratus* and *Sargassum muticum* in different cover classes (%) normalised to all investigated 5 m intervals per transect is shown in Table 3. *L. hyperborea* dominated T1 and T2 with respective RPs of 77 and 71% followed by *L. digitata* with 31 and 16%. In T1, *S. latissima* only occurred in 12% of the 5 m intervals, with low densities (1 to 10%; cover class 5) and young thalli. In T2, it was present in 69% of the 5 m intervals with percentage cover (PC) values mostly between 1 to 40% (cover classes 5 and 25) and occasionally up to 91 to 100% (cover class 100). *D. aculeata*, which was only actively searched for in T2, occurred in nearly half of the investigated 5 m intervals, mostly with low coverages but sometimes with PC of up to 91 to 100%. *F. serratus* was mainly present in the middle and lower eulittoral zone of T1 with low PC of 1 to 10%. *S. muticum* was only present in T1 in 5% of the intervals, also with low PC of 1 to 10%.

The vertical distribution of vegetation zones along both transects is shown in Fig. 2. Pure stands of *Fucus serratus*, *Saccharina latissima*, *Laminaria digitata* and

Table 3. Relative presence (number of 5 m intervals with occurrence of respective species in different cover classes per total number of investigated 5 m intervals) of dominant brown seaweeds in Transects T1 and T2 (see Fig. 1). Cover classes described in Table 1. –: no data

Species	Transect	Relative presence per cover class (%)					Σ Relative presence (%)
		5	25	50	75	100	
<i>Laminaria hyperborea</i>	T1	7.8	12.1	9.3	22.2	25.7	77.0
	T2	13.7	13.7	14.1	13.3	16.1	71.0
<i>Laminaria digitata</i>	T1	4.7	3.1	6.6	8.1	8.1	30.6
	T2	5.1	5.1	3.5	1.2	1.2	16.1
<i>Saccharina latissima</i>	T1	11.6	0.4	0	0	0	12.0
	T2	27.4	25.1	12.2	5.9	0.8	68.6
<i>Desmarestia aculeata</i>	T1	–	–	–	–	–	–
	T2	21.6	14.5	6.3	6.3	0.8	49.4
<i>Fucus serratus</i>	T1	5.8	1.6	1.6	0.4	0	9.3
	T2	0	0	0	0	0	0
<i>Sargassum muticum</i>	T1	5.0	0	0	0	0	5.0
	T2	0	0	0	0	0	0.0

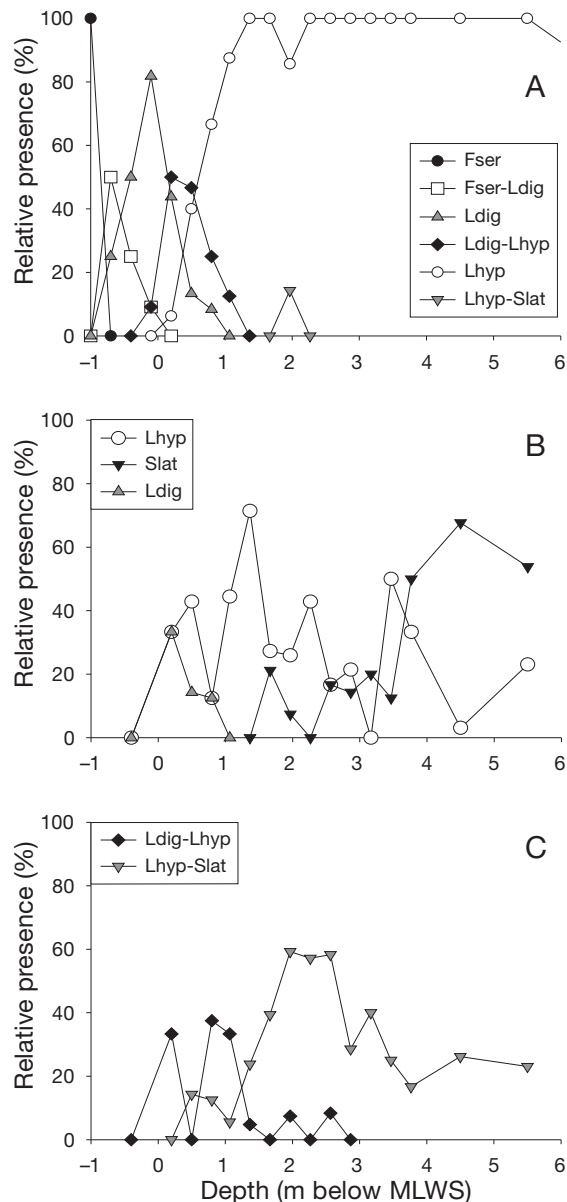


Fig. 2. Relative presence of vegetation zones dominated by single and/or mixed brown seaweeds at (A) transect T1 (2005) and (B,C) transect T2 (2006). Abbreviations of communities are explained in Table 2. For direct comparison to Lüning (1970; his Fig. 7) exact depth values of occurrence were transformed into depth classes (1 m above–3.8 m below MLWS: 30 cm classes; 4.5–13.5 m below MLWS: 1 m classes). MLWS is designated as depth 0. Exact values are given in Section 3.1

L. hyperborea alternated with mixed stands. In T1 (Fig. 2A), pure *F. serratus* stands (Fser) only grew in the intertidal at 1 m above MLWS. Pure *L. digitata* stands (Ldig) were common at a depth range of 0.7 m above MLWS and 0.9 m below MLWS and pure *L. hyperborea* (Lhyp) between 0.2 to 10.6 m below MLWS (data shown only down to 6 m below MLWS). Among these

zones were mixed stands of *F. serratus*/*L. digitata* (Fser-Ldig; 0.9 m above to 0.1 m below MLWS) and *L. digitata*/*L. hyperborea* (Ldig-Lhyp; 0 to 1 m below MLWS). *S. latissima* did not form pure stands along transect T1 and was only present at 2 m below MLWS in low quantities and in co-existence with *L. hyperborea* (Lhyp-Slat). *Desmarestia aculeata* was also present but not monitored or quantified in this transect.

Along T2 (Fig. 2B,C), *Fucus serratus* was absent because the entire transect was below MLWS except one point. Pure *Laminaria digitata* stands (Ldig) occurred between 0.3 and 0.6 m below MLWS, pure *L. hyperborea* stands (Lhyp) between 0.1 and 5.1 m below MLWS and pure *Saccharina latissima* (Slat) stands between 1.7 and 5.5 m below MLWS (Fig. 2B). The RP of pure *S. latissima* stands increased between 3.8 and 5.5 m below MLWS whereas the RP of pure *L. hyperborea* stands decreased at this depth range. Moreover, the RP of mixed *L. hyperborea*/*S. latissima* stands (Lhyp-Slat; Fig. 2C) at this depth range was also low. Pure stands of *Desmarestia aculeata* occurred between 1.5 and 5.5 m below MLWS, and mixed stands with *Laminaria* species between 1.3 and 5.4 m below MLWS. The RP of pure and mixed stands (maximum of 62 and 40%, respectively) increased between 4 and 5.5 m below MLWS (not shown). Transect T2 was never deeper than 5.5 m below MLWS.

3.2. Vertical distribution of all macroalgal species

Table 4 combines presence/absence data (epiphytic and/or epilithic occurrence) along the depth gradient and depth limits observed by analysing the 1 m² quadrats (n = 24) set along the vegetation zones and the 18 quadrats harvested along different depth levels for the biomass survey. Data were compared to the algal depth limits of Lüning (1970). In 2005, a total of 36 noncrustose algal species were recorded (4 Chlorophyta, 7 Phaeophyta, 25 Rhodophyta). A few species were only found as epiphytes (*Ceramium deslongchampsii*, *Cladophora sericea*, *Porphyropsis coccinea*) and 2 species (*Cladophora sericea* and *Sargassum muticum*) were not recorded by Lüning (1970). The number of recorded species per depth level was quite constant (17 to 21 species), except at 4 and 12 m below MLWS (13 species).

Eighteen out of 36 species (50%) were recorded at depths greater by 1.9 to 8.3 m and 16 out of 36 species (44%) were observed at approximately the same depth range (± 1.5 m) as those reported by Lüning (1970). One exception was *Rhodochorton purpureum*, a small filamentous red alga that is easily overlooked. Lüning (1970) reported *R. purpureum* at 8.0 m below MLWS, but it was found only at 0.4 m above MLWS in the pre-

Table 4. Occurrence and lower depth limits of macroalgae at Transect T1. Comparison of recent (2005 data) and previous (1966–1968 data) depth limits is given as ΔD (difference in depth distribution); -: not present; *: no comparable data; L: epilithic, P: epiphytic on *Laminaria* species

Species	Depth (m below MLWS)							Lower depth limits (m below MLWS)		
	0	2	4	6	8	10	12	1966–1968 ^a	2005 ^b	ΔD
<i>Ahnfeltia plicata</i>	L	L	–	–	–	–	–	2.7	2.0	–0.7
<i>Bonnemaisonia hamifera</i> ^c	–	–	–	L	L	L	L	12.0	12.5	0.5
<i>Brongniartella byssoides</i>	–	–	L	L	L	L	L	11.2	12.5	1.3
<i>Bryopsis plumosa</i>	–	–	–	–	L	L	–	10.6	10.0	–0.6
<i>Ceramium deslongchampsii</i>	–	P	–	–	–	–	–	0.0	2.0	2.0
<i>Ceramium virgatum</i>	L P	L	P	L	L	–	L	3.2	11.5	8.3
<i>Chaetomorpha melagonium</i>	P	L P	L P	–	–	L	–	7.3	9.6	2.3
<i>Chondrus crispus</i>	L	L P	L	–	–	L	–	2.4	9.6	7.2
<i>Cladophora rupestris</i>	L	–	–	–	–	–	–	1.3	1.6	0.3
<i>Cladophora sericea</i>	P	P	–	–	–	–	–	–	2.0	*
<i>Coccotylus truncatus</i>	–	–	–	–	L	L	–	7.4	10.0	2.6
<i>Corallina officinalis</i>	L	L	–	–	–	–	–	4.7	2.8	–1.9
<i>Cystoclonium pupureum</i>	–	–	–	L	L	L	L	3.2	11.5	8.3
<i>Delesseria sanguinea</i>	L	L P	L P	L P	L P	L	L	10.6	12.5	1.9
<i>Desmarestia aculeata</i>	L	L	L	L	–	L	L	6.0	11.5	5.5
<i>Desmarestia viridis</i>	–	–	–	L	–	L	–	7.4	9.3	1.9
<i>Erythrodermis traillii</i>	–	L	–	L	–	L	L	13.8	12.5	–1.3
<i>Fucus serratus</i>	L	–	–	–	–	–	–	1.2	1.6	0.4
<i>Halarachnion ligulatum</i>	–	–	–	–	–	L	L	7.0	12.5	5.5
<i>Laminaria digitata</i>	L	L	–	–	–	–	–	1.9	2.5	0.6
<i>Laminaria hyperborea</i>	L	L	L	L	L	L	L ^d	8.3	10.5 ^e	2.2 ^e
<i>Lomentaria clavellosa</i>	–	–	–	L	L	L	L	7.0	12.5	5.5
<i>Lomentaria orcadensis</i>	–	–	–	L	L P	L	L	8.3	12.5	4.2
<i>Membranoptera alata</i>	L P	L P	L P	L P	L P	–	–	5.9	8.0	2.1
<i>Phycodrys rubens</i>	–	L	–	L	–	–	–	7.5	6.0	–1.5
<i>Phyllophora pseudoceranooides</i>	L	L P	L	L	L	–	–	8.2	9.3	1.1
<i>Plocamium cartilagineum</i>	L	L	L P	L P	L	L	L	9.0	11.5	2.5
<i>Polyides rotundus</i>	–	L	–	–	–	–	–	3.2	1.9	–1.3
<i>Polysiphonia stricta</i>	P	L P	L P	L P	L P	L	L	9.6	12.5	2.9
<i>Porphyropsis coccinea</i>	–	–	P	–	P	–	–	8.6	9.3	0.7
<i>Pterothamnion plumula</i>	–	–	–	L	P	L	–	7.0	9.6	2.6
<i>Rhodochorton purpureum</i>	–	–	–	–	–	–	–	8.0	+0.4	–8.4
<i>Rhodomela confervoides</i>	L	–	–	–	L	L	–	7.3	10.2	2.9
<i>Saccharina latissima</i>	–	P	–	–	–	–	–	2.9	2.0	–0.9
<i>Sargassum muticum</i>	L	L	–	–	–	–	–	–	2.4	*
<i>Ulva</i> sp.	L P	L P	P	P	–	L	–	9.0	9.6	0.6
Total number of species	20	21	13	18	17	20	13			

^aData extracted from Lüning (1970); ^bthis study; ^c*Trailiella intricata*-phase; ^dyoung individuals; ^eadult plants

sent study. Another exception was *Corallina officinalis*, an easily identifiable conspicuous alga, which was only found 1.9 m shallower than in 1966–1968 (Lüning 1970). A few red algae (*Ceramium virgatum*, *Chondrus crispus*, *Cystoclonium pupureum*, *Halarachnion ligulatum*, *Lomentaria clavellosa*) and the brown alga *Desmarestia aculeata* occurred even 5.5 to 8.3 m deeper than in 1966–1968. The upper and lower limits of the dominant brown seaweeds *Fucus serratus*, *Laminaria digitata* and *Saccharina latissima* did not change, but adult *L. hyperborea* occurred 2.2 m deeper and 1 m shallower than in 1966–1968, thereby widening its zone of occurrence. Young thalli of the latter were found down to a depth of 12.5 m.

3.3. Biomass parameters of *Laminaria* spp. along the depth gradient

Biomass, LAI and stipe length of *Laminaria* spp. along the depth gradient are presented in Tables 5 & 6. All biomass parameters of *Laminaria* plants were high between 0.5 and 4 m below MLWS and significantly decreased between 6 and 8 m below MLWS. In contrast, the biomass of epilithic, understory, noncrustose algae showed a drastic but insignificant increase below 4 m (Table 5), decreasing again at 10 m below MLWS (data not shown).

The LAI of *Laminaria digitata* and *L. hyperborea* showed the same trend as their biomass: high values of

Table 5. *Laminaria hyperborea*. Biomass (kg m^{-2} ; total understory: g m^{-2}) along a depth gradient between 0.5 and 8 m below MLWS (mean of means \pm SD, $n = 3$) and comparison of recent (2005; this study) and previous (Lüning 1969) data. 2005 means followed by different letters (a,b,c or combination of these) are significantly different ($p < 0.05$). Fresh weight data from 1969 partially extracted from figures of Lüning (1969). Ldig: *L. digitata*; Lhyp: *L. hyperborea*; FW: fresh weight; DW: dry weight; nd: no data; (-) not included in statistical analyses. Total understory FW and mean blade DW: no significant differences (partially due to high SDs at 6 and 8 m)

Biomass	Year	Depth (m below MLWS)					
		0.5	0.5	2	4	6 ^a	8
	1969	Ldig	nd	Lhyp	Lhyp	Lhyp	nd
	2005	Ldig + Lhyp	Lhyp ^b	Lhyp	Lhyp	Lhyp	Lhyp
Whole plant FW	1969	5.6 \pm 0.9	nd	11.1 \pm 1.8	4.8 \pm 1.5	0.1	nd
	2005	6.6 \pm 0.3 ac	3.4 \pm 2.1 -	6.4 \pm 2.4 ac	9.9 \pm 2.6 a	3.2 \pm 0.8 bc	0.8 \pm 0.6 b
Whole plant DW	2005	1.6 \pm 0.3 a	0.9 \pm 0.6 -	1.8 \pm 0.4 a	1.9 \pm 0.4 a	0.7 \pm 0.2 b	0.2 \pm 0.0 b ^c
	1969	4.7	nd	7.1	nd	nd	nd
Blade FW	2005	5.3 \pm 0.5 a	2.5 \pm 1.5 -	3.8 \pm 1.1 ac	5.7 \pm 1.8 a	1.6 \pm 0.3 bc	0.6 \pm 0.5 b
	1969	nd	nd	0.260 \pm 0.053	0.292 \pm 0.091	nd	nd
Single blade FW	2005	0.138 \pm 0.047	0.313 \pm 0.028	0.232 \pm 0.028	0.255 \pm 0.244	0.117 \pm 0.025	0.116 \pm 0.021
Blade DW	1969	nd	nd	1.4	nd	nd	nd
	2005	1.3 \pm 0.2 a	0.8 \pm 0.5 -	1.2 \pm 0.3 a	1.2 \pm 0.3 a	0.4 \pm 0.1 b	0.2 \pm 0.0 b
Stipe FW	1969	0.9 \pm 0.2	nd	4.0 \pm 1.3	1.9 \pm 0.4	<0.1	nd
	2005	1.4 \pm 0.4 bc	0.9 \pm 0.6 -	2.6 \pm 1.3 ac	4.1 \pm 1.0 a	1.6 \pm 0.5 bc	0.3 \pm 0.2 b
Stipe DW	2005	0.3 \pm 0.1 bc	0.2 \pm 0.1 -	0.6 \pm 0.2 ac	0.7 \pm 0.1 a	0.3 \pm 0.1 bc	0.1 \pm 0.0 b
	Total understory FW	2005	84.6 \pm 51.0	nd	88.3 \pm 17.3	223.0 \pm 85.0	577.0 \pm 283.0

^aLüning (1969) refers to 5.5 m below MLWS; ^bLhyp data at 0.5 m are part of Ldig + Lhyp data at 0.5 m; ^cn = 2

Table 6. *Laminaria hyperborea*. Population density (ind. m^{-2}) and morphometric parameters along a depth gradient between 0.5 and 8 m below MLWS (mean of means \pm SD, $n = 3$). Comparison of recent (2005; this study) and previous (Lüning 1969) data. Data from 1969 partially extracted from figures of Lüning (1969). 2005 means followed by different letters (a, b, c, or combination of these) are significantly different ($p < 0.05$). Ldig: *L. digitata*, Lhyp: *L. hyperborea*, nd: no data. Stipe length: no significant differences due to high SDs at 2 m

Biomass	Year	Depth (m below MLWS)						
		0.5	0.5	2	3	4	6	8
	1969	Ldig	-	Lhyp	Lhyp	Lhyp	Lhyp	nd
	2005	Ldig + Lhyp	Lhyp ^a	Lhyp	nd	Lhyp	Lhyp	Lhyp
Density (ind. > 20 cm)	1969	nd	nd	27 \pm 5.7	13 \pm 6.7	10 \pm 1.4	0.9	nd
	2005	25.7 \pm 6.4 ab	6.3 \pm 7.5 -	31.0 \pm 21.1 ab	nd nd	35.3 \pm 7.2 a	15.3 \pm 6.0 ab	3.7 \pm 4.0 b
Leaf area index	1969	4.7 \pm 0.8	nd	4.1 \pm 0.3	2.3	1.6 \pm 0.5	nd	nd
	2005	5.3 \pm 0.9 a	2.6 \pm 1.5 -	3.3 \pm 1.1 ac	nd nd	4.4 \pm 0.9 a	1.3 \pm 0.5 bc	0.3 \pm 0.3 b
Stipe length (cm)	2005	31.6 \pm 4.9	46.1 \pm 6.0	54.5 \pm 52.1	nd	33.6 \pm 0.8	29.9 \pm 10.8	16.4 \pm 12.7

^aLhyp data at 0.5 m are part of Ldig + Lhyp data at 0.5 m
^bAs we did not measure total length of individuals (unlike Lüning 1969), but measured stipe length and leaf area index, we assumed that individuals with stipe length > 10 cm were comparable to those with a total length > 20 cm

3.3 to 5.5 occurred between 0.5 and 4 m below MLWS and significantly lower values of 1.3 and 0.3 were encountered at 6 and 8 m below MLWS, respectively (Table 6).

Maximum stipe lengths of up to 123 cm were present at 2 m below MLWS and then decreased with increasing depth (not shown). However, differences in mean stipe lengths at different depths were not significant (Table 6), although maximum stipe lengths indicated such a trend. In contrast, stipe biomass of *Laminaria hyperborea* was significantly higher at 4 m below MLWS than at 0.5, 6 and 8 m below MLWS (Table 5).

The mean population density of *Laminaria hyperborea* with stipe lengths ≥ 10 cm showed an insignificant increase from 25.7 ind. m^{-2} at 0.5 m below MLWS (here together with *L. digitata*) to 31.0 ind. m^{-2} at 2 m below MLWS and a maximum of 35.3 ind. m^{-2} at 4 m below MLWS. Below this depth, the mean density decreased to 15.3 ind. m^{-2} at 6 m and significantly to 3.7 ind. m^{-2} at 8 m below MLWS (Table 6). Although no *L. hyperborea* was found in the random quadrats at 10 m depth, they were observed at this depth.

The LAI, density and biomass (kg FW m^{-2}) of *Laminaria* species differed between 1969 and 2005 (Tables 5 & 6; Fig. 3). LAI at 4 m and density at 4 and 6 m below MLWS were significantly higher in 2005 than in 1969, whereas no significant differences were obvious at 0.5 and 2 m below MLWS. Similarly, biomass significantly increased at 0.5, 4 and 6 m below MLWS in 2005 compared to 1969, but significantly decreased at 2 m below MLWS.

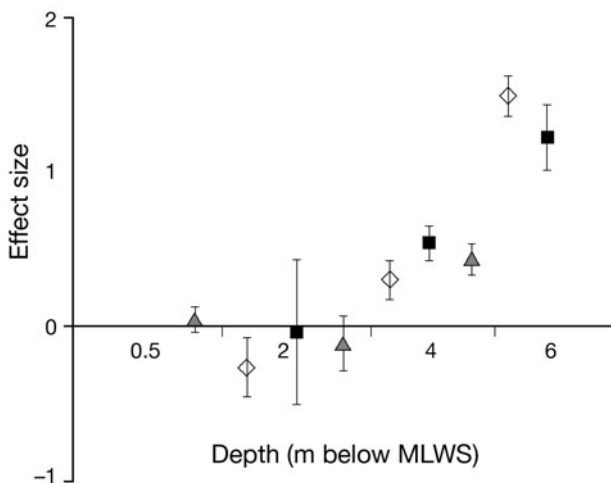


Fig. 3. *Laminaria hyperborea*. Effect size of (▲) LAI (leaf area index), (■) density of individuals (ind. m^{-2}) and (◇) biomass (kg FW m^{-2}) in relation to depth below MLWS (mean \pm 95% CI, $n = 3$). Positive values indicate an increase, negative values a decrease, of the measured parameter compared to those from Lüning (1969). Significance is indicated when whiskers of the CI do not cross the x-axis

4. DISCUSSION

The data presented reveal that the depth distribution of seaweeds and the biomass and structure of the kelp beds off Helgoland have significantly changed between 1966–1968 and 2005–2006. The most important changes are (1) ~2 to 8 m increase in the lower depth limits in 50% of the recorded noncrustose algal species, (2) a shift in the biomass maximum of *Laminaria hyperborea* from 2 to 4 m below MLWS, (3) significant increases in biomass, leaf area index and density of *L. hyperborea* at 0.5, 4 and 6 m below MLWS and extension of the dense *L. hyperborea* forest (LAI > 1) towards shallower and deeper areas; and (4) a change in the community structure of the kelp bed evident in the drastic decrease of the relative presence and abundance of the sugar kelp *Saccharina latissima* in the northern transect T1, the increase in its depth distribution in Transect T2, the widening of the *L. hyperborea* zone and invasion of the Sargasso weed *Sargassum muticum*.

4.1. Change in lower depth limits

The described ~2 to 8 m increase in the depth distribution ranges of sublittoral seaweed species around the island of Helgoland appears to reflect the increased water transparency reported for Helgoland. Mean yearly Secchi depths increased by 1 m between 1975 and 2001 (Wiltshire et al. 2008), increasing steadily over time. However, given that low yearly mean Secchi depths (< 3 m) were recorded only prior to 1984, there might have been a more rapid increase in water transparency since then. Although Secchi depths have been recorded every weekday since 1975, these have not yet been analysed by season, thus precluding more detailed analysis. The situation at Helgoland runs parallel to the general situation in the North Sea which has become less turbid in recent years (McQuatters-Gallop et al. 2007). Generally, the depth range of seaweeds corresponds to irradiance levels which are a function of water depth and Jerlov water types. At Helgoland, the water body is dominated by coastal Jerlov Water Type 7 (irradiance transmittance < 65%, maximal transmittance in green light between ~480 and 580 nm; Lüning 1981) during the main growth period from April to September. The total annual light received at the lower kelp limit corresponds to 0.7% of the surface irradiance at Helgoland and is generally set at ~1% of the surface irradiance for kelps and at 0.05 to 0.1% for other multicellular algae (Lüning & Dring 1979). The relationship between Secchi depths and underwater irradiance availability has been determined only once at Helgoland (Dring &

Lüning 1994). Two points have to be taken into account here: (1) Under conditions of identical light attenuation in the water column, the same Secchi depth may reflect different underwater irradiance regimes in summer than in winter as (2) there is considerable variability due to seasonal variation in incident light. This may result in Secchi depths with opposing trends between seasons, as has been observed in the southern North Sea (Cadée & Hegeman 2002). This certainly is also the case for Helgoland where underwater light is strongly reduced during winter months (Lüning & Dring 1979). However, correlation between seasonal Secchi depth changes and active growth periods of seaweeds is still missing. As turbidity is not only connected to eutrophication but also to wind stress and irradiance changes, the proportion of de-eutrophication and climate change effects that ameliorate underwater irradiance at Helgoland is yet unclear.

A decrease in depth limits has been variously reported (e.g. Pedersen & Snoeijs 2001) to be an indirect consequence of eutrophication that has degraded the light climate. However, depth limits for *Fucus vesiculosus* at some selected Baltic sites have recently increased (Torn et al. 2006). Secchi depths also explained most of the variation in the depth limits, but the observed trends in all investigated districts did not clearly follow reported changes in nutrient or light levels and are thus not attributable to de-eutrophication alone (Torn et al. 2006). Five red and one brown algal species at Helgoland shifted their maximum depths of occurrence by 5.5 to 8.3 m which exceeds the reported Secchi depth increase of 1 m as well as the methodological differences (number of transects, accuracy of depth gauge of both investigations) which could only account for ~1 m. Thus, the depth changes at Helgoland do not merely follow mean Secchi depths. Differences between species in algal depth changes have also been observed elsewhere (Pedersen & Snoeijs 2001). Species-specific seasonal growth patterns and different low-light acclimation potentials (e.g. Wiencke 1990) may interact in a still unknown manner with seasonal and long-term light availability.

A variety of species that were present between 10 and 13.5 m below MLWS in 2005 were not recorded by Lüning (1970) at these depths. Previously, crustose species and the small red algae *Erythrodermis traillii* and *Colaconema membranaceum* dominated at >10 m below MLWS (Lüning 1970), while another 11 algal species were recorded at this level in the present study. These include *Bonnemaisonia hamifera* (*Trilliella*-phase), *Brongniartella byssoides*, *Delesseria sanguinea*, *Halarachnion ligulatum*, *Lomentaria clavellosa* and *L. orcadensis*, most of them typical deep water species. The depth limit for crustose species had been 15 m below MLWS in 1966–1968 (Lüning 1970) with

occasional records at 21 m below MLWS (K. Lüning pers. comm.). This corresponds to observations of de Kluijver (1997) who reported crustose algae at 23 m below MLWS. In 2005 and 2006, this limit was not investigated.

In a few cases, obvious changes of upper depth limits were also observed. Most prominent is that of the deep red alga *Halarachnion ligulatum*. This species was only recorded between 9.6 and 12.5 m below MLWS in 2005 (Table 4), while it was restricted to 4.5 to 8.5 m below MLWS in 1966–1968 (Lüning 1970). This could either be a sampling artefact due to the reduced number of investigated quadrats in 2005 or may indicate susceptibility to higher irradiance. Pang et al. (2001) reported that UV radiation may limit the upper distribution of the deepwater species *Delesseria sanguinea*.

4.2. Change in the structure of the kelp bed

For comparative purposes, Lüning's concept of vegetation zones was adopted. Although it is generally accepted that there is zonation of dominant brown algae along the depth gradient in the sublittoral similar to the zonation of Fucales in the intertidal (Lüning 1990), there is some debate whether these zones represent distinct floristic communities or a continuum (see discussion in Kent & Coker 1992). The similarity analysis of quantitative percentage cover values of quadrats taken along the depth gradient and pre-classified to vegetation zones (see Table 2) revealed that these zones can only be partially separated (Fig. 4). Species composition and abundance in the mixed *Fucus serratus*/*Laminaria digitata* zone, the pure *L. digitata* zone and the mixed *L. digitata*/*L. hyperborea* zone are indistinguishable. The pure *F. serratus* zone is similar to this cluster, but separated. The pure *L. hyperborea* zone is clearly distinct from all other zones, while the *L. hyperborea*-park vegetation and red algal zone form a cline following the depth of occurrence. Thus, while these vegetation zones are only partially discrete entities, the widths and depths of occurrence of the dominant brown seaweeds nevertheless provide a good indication of stability or change within the kelp bed.

Although the number of investigated depths and 5 m intervals differed between the present study and that of Lüning (2005–2006: 2 transects; 607 5 m intervals, 0.9 m above to 13.5 m below MLWS vs. 1966–1968: 5 transects, 537 5 m intervals, 0.2 to 8.3 m below MLWS), major changes in zonation patterns and depth distribution were detected: the pure vegetation of *Fucus serratus* and *Laminaria digitata* was shifted into shallower areas around 1 m below MLWS in 2005. Furthermore, pure *Saccharina latissima* stands were no

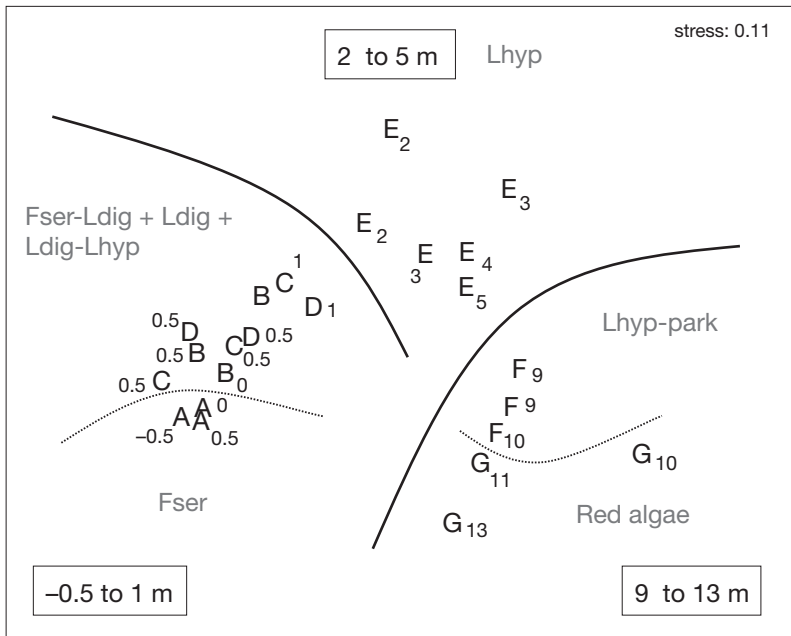


Fig. 4. Results of n-MDS analyses of quantitative percentage cover data (square root transformed) along Transect T1 with zone and depth classification. Letters refer to the predefined brown algal zones (see Table 2; also for abbreviations) and numbers beside letters indicate depth below MLWS

longer present in T1 in 2005, and had shifted to greater depths in T2 (in 2006). In 1966–1968, *L. digitata* and *S. latissima* together were the most important species of the upper sublittoral (0.4 to 1.3 m below MLWS), while presently this zone is mostly occupied by *L. digitata* alone. The mixed *L. digitata*/*L. hyperborea* vegetation did not exist previously and the pure *L. hyperborea* forest extended both shallower (at 1.3 m below MLWS in 2005 vs. 2.5 m below MLWS in Fig. 7 of Lüning 1970) and deeper (park vegetation at 10.5 m below MLWS in 2005 vs. 8 to 9 m below MLWS in 1966–1968). These distributional changes and the changes in biomass, density and LAI indicate that the *L. hyperborea* forest extended its range upwards and downwards; upwards most probably at the expense of *S. latissima* and *L. digitata* stands. Although pure *S. latissima* stands still occur at T2 north of Dune Island (Fig. 2), vegetation structure also changed here. Today, most pure *S. latissima* stands occur between 3.5 and 5.5 m below MLWS and therefore much deeper than reported in 1966–1968 (1.1 to 2 m below MLWS; Fig. 7 in Lüning 1970). Furthermore, mixed *S. latissima*/*L. hyperborea* stands which were not present in the late 1960s (Lüning 1970) presently occur between 0.5 and 5.5 m below MLWS. Old reports from Helgoland mentioned 4 m long thalli of *S. latissima* (Hallier 1863, Kuckuck 1897, Nienburg 1925, Lüning 1970) and noted the ubiquity of this species, which formed a closed girdle in the infralittoral zone around the entire island (Hallier 1863, Kuckuck

1894, Nienburg 1925). This situation has completely changed. At least since 1999 (I. Bartsch pers. obs.), no infralittoral fringe of *S. latissima* has been reported from the northern part of the island; mostly small and young individuals were found along T1 during the present investigation, but adult plants were still present in low quantities along T2. Similar drastic population losses of *S. latissima* have been reported from Norway (Moy et al. 2003) and France (Givernaud et al. 1991, Cosson 1999), for reasons that are still unknown.

The increased water clarity and therefore increased depth penetration of UV radiation and photosynthetically active radiation (PAR) may have affected the kelp population at Helgoland. Kelp zoospore photosynthesis is adapted to low irradiation conditions and in Helgoland, *Laminaria hyperborea* and *Saccharina latissima* zoospores are clearly more sensitive to higher photon flux rates than *L. digitata*

zoospores (Roleda et al. 2005). Young *S. latissima* sporophytes are more susceptible to UV radiation than those of *L. hyperborea* and *L. digitata* (Dring et al. 1996), but germination of zoospores of Helgolandic *S. latissima* and *L. digitata* have not been affected by UVA (Roleda et al. 2005). Arctic *S. latissima* zoospores are also more sensitive to UV radiation compared to 3 other Arctic kelp species (Roleda et al. 2006). These findings may partially explain the presently deeper distribution of *S. latissima* at Helgoland but does not explain the extension of *L. hyperborea* towards the water surface. Thus, the structural changes cannot be accounted for by improvement of water clarity alone. Another factor acting in the shallow sublittoral is wave exposure which is dependent on wind stress. *S. latissima* prefers more wave protected sites compared to *L. digitata* and *L. hyperborea* (Kain 1962). The increase in storm activity and extreme wave height over the southern North Sea between 1958 and 2001 (e.g. Weisse et al. 2005) may have affected the kelp population at Helgoland.

Finally, temperature increases affect the distribution of kelp species (Breeman 1988). Mean summer surface water temperatures at Helgoland were reported to be $\sim 18^{\circ}\text{C}$ (Lüning 1990) with maxima at 20°C but have been higher in recent years (K. H. Wiltshire unpubl. data); mean summer surface temperature has increased by 1.33°C in the last 40 yr (Wiltshire et al. 2008). Peak summer surface temperatures are close to

the survival limit of Helgolandic *Laminaria hyperborea*, *L. digitata* and *Saccharina latissima* (Fortes & Lüning 1980, tom Dieck 1992). Uppermost *L. digitata* in Helgoland (I. Bartsch pers. obs.) and *L. hyperborea* in Northern Spain (J. Rico pers. comm.) may suffer after hot summers, and spore germination of *L. digitata* is hampered even during 'normal' summers (J. S. Vogt & I. Bartsch pers. comm.). Evidence of negative effects of hot summers on the life cycle of *S. latissima* is yet missing. Nevertheless, migration of kelp species into deeper and somewhat cooler water is probable if water temperatures increase.

4.3. Change in biomass, LAI and population density

The biomass of *Laminaria* in general (overview in Bartsch et al. 2008) and specifically of *L. hyperborea* have been previously investigated (e.g. Lüning 1969, Gunnarsson 1991, Sjøtun et al. 2004). As biomass values are dependent on density of stands, season and latitude, the numbers available in the literature are difficult to compare. The biomasses of *L. hyperborea* and *L. digitata* stands vary between 5 to 40 kg FW m⁻² (see Lüning 1969, Gunnarsson 1991, Sjøtun et al. 2004). With a maximum of 9.9 ± 2.6 kg FW *L. hyperborea* m⁻² recorded within a dense undisturbed stand in August (the time period of its maximum blade size, Lüning 1979) (Table 5), Helgoland may thus be regarded as a mean to low production site.

Comparison of present and previous biomass, LAI and population density data from Helgoland confirm the trend in depth shift described above for the algal depth limits. Although the kelp biomass remained nearly constant at 0.5 and 2 m below MLWS, the species composition changed: in 1966–1968, *Saccharina latissima* was present at this depth, but it is partially replaced by *Laminaria hyperborea* today. The present-day 55% biomass increase from 2 to 4 m below MLWS contrasts with a 57% biomass decrease from 2 to 4 m below MLWS in 1966–1968. This may be explained by natural variability of population density and the sample size in this study. Two of the 3 quadrats at 2 m below MLWS showed relatively low biomass but high density values, being composed of relatively young specimens (<1 to 3 yr, only 9–27% of individuals older than 3 yr), while one quadrat showed the opposite (few old and heavy plants, 6 to 7 yr old; data not shown) and thus had comparable data as that of Lüning (1969). Due to this age variance of the algae in the investigated quadrats at 2 m below MLWS, the SD of all investigated parameters at this depth was very high, resulting in insignificant differences, although clear trends were visible. Comparing the SDs at 2 and 4 m below MLWS, it is also apparent that the *Laminaria*

forest is more stable at 4 m than at 2 m below MLWS. Hence, the extent of sampling should be increased in future studies. Despite the depth shift of 2 m, maximum biomass remained rather constant over time, as 2005 biomass data at 4, 6 and 8 m below MLWS corresponded to values at 2, 4 and 6 m below MLWS in 1969. However, total kelp biomass increased due to the expansion of the *L. hyperborea* forest.

In conclusion, this study shows that significant changes have occurred in the depth limits, community structure, and biomass of dominant brown seaweeds at Helgoland between 1966–1968 and 2005–2006. Most of these changes are probably attributable to the observed increase in water clarity, but changes in temperature and storminess may also have had an effect. As the reported increase in water transparency is accompanied by a decrease in phosphate concentration of 40% (Wiltshire et al. 2008), the observed changes in depth distribution and biomass of seaweeds may also reflect de-eutrophication. However, Wiltshire et al. (2008) assume that this situation reflects a hydrographic shift to more marine conditions at Helgoland correlated with increased southwesterly wind events. The same paper cites unpublished data by Stockmann and colleagues who showed a shift to a less coastally dominated system for Helgoland. De-eutrophication is normally correlated with a decrease in primary production and biomass (e.g. Cadée & Hegeman 2002) which has not been observed here and in phytoplankton systems in the North Sea (McQuatters-Gallop et al. 2007, Wiltshire et al. 2008). The probability of an altered circulation pattern with more inflow of clear Atlantic water during a positive phase of the North Atlantic Oscillation has been discussed in several papers (e.g. Ottersen et al. 2001, Edwards et al. 2002, McQuatters-Gallop et al. 2007). This and the observed changes in water clarity should be taken into consideration for the southern North Sea and Helgoland.

Acknowledgements. C.P. and I.B. thank the diving crew of the Biologische Anstalt Helgoland, especially C. Wanke and S. Brandt, for their invaluable help and constant support; the State Office for Nature and Environment (LANU), Schleswig-Holstein for partial financial support; P. Schubert and T. Kaschell for help with the field work; M. Molis for support in statistics and data evaluation; H. Pehlke and J. Bartsch for help with GIS topics; T. Schütte for collecting data for Transect T2; and J. Bartsch for correction of the manuscript. We also thank K. Lüning for providing us with his original material. This work was part of the M.Sc. thesis of C.P. at the University of Bremen, Germany. Publication content complies with German laws.

LITERATURE CITED

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

- Bartsch I, Tittley I (2004) The rocky intertidal biotopes of Helgoland: present and past. *Helgol Mar Res* 58:289–302
- Bartsch I, Wiencke C, Bischof K, Buchholz CM and 14 others (2008) The genus *Laminaria sensu lato*: recent insights and developments. *Eur J Phycol* 43:1–86
- Braun-Blanquet J (1951) *Pflanzensoziologie: Grundzüge der Vegetationskunde*. Springer, Wien
- Breeman AM (1988) Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. *Helgol Mar Res* 42:199–241
- Cadée GC, Hegeman J (2002) Phytoplankton in the Marsdiep at the end of the 20th century; 30 years monitoring biomass, primary production, and *Phaeocystis* blooms. *J Sea Res* 48:97–110
- Cosson J (1999) Sur la disparition progressive de *Laminaria digitata* sur les côtes du Calvados (France). *Cryptogam Algal* 20:35–42
- de Kluijver MJ (1997) Sublittoral communities of the North Sea hard-substrata. PhD thesis, University of Amsterdam
- den Hartog C (1959) The epilithic algal communities occurring along the coast of the Netherlands. *Wentia* 1:1–241
- Dring MJ, Lüning K (1994) Influence of spring-neap tidal cycles on the light available for photosynthesis by benthic marine plants. *Mar Ecol Prog Ser* 104:131–137
- Dring MJ, Wagner A, Boskov J, Lüning K (1996) Sensitivity of intertidal and subtidal red algae to UVA and UVB radiation, as monitored by chlorophyll fluorescence measurements, influence of collection depth and season, and length of irradiation. *Eur J Phycol* 31:293–302
- Dubi A, Tørum A (1995) Wave damping by kelp vegetation. In: Edge BL (ed) *Proc 24th Int Conf on Coastal Engineering*, Kobe, Japan, 22–28 Oct., 1994, American Society of Civil Engineers, p 142–156
- Edwards M, Beaugrand G, Reid PC, Rowden AA, Jones MB (2002) Ocean climate anomalies and the ecology of the North Sea. *Mar Ecol Prog Ser* 239:1–10
- Fortes MD, Lüning K (1980) Growth rates of North Sea macroalgae in relation to temperature, irradiance and photoperiod. *Helgol Mar Res* 34:15–29
- Franke HD, Gutow L (2004) Long-term changes in the macrozoobenthos around the rocky island of Helgoland (German Bight, North Sea). *Helgol Mar Res* 58:303–310
- Givernaud T, Cosson J, Givernaud-Mouradi A (1991) Étude des populations de *Sargassum muticum* (Yendo) Fensholt sur les côtes de Basse-Normandie (France). In: Elliott M, Ducrotony JP (eds) *Estuaries and coasts: spatial and temporal intercomparisons*. 19th ECSA Symp, Olsen & Olsen, Fredensborg, p 129–132
- Greig-Smith P (1983) *Quantitative plant ecology*. Studies in ecology, Vol 9, 3rd edn. Blackwell, Oxford
- Gunnarsson K (1991) Populations de *Laminaria hyperborea* et *Laminaria digitata* (Phéophycées) dans la Baie de Breidifjörður, Islande. *J Mar Institue Reykjavik* 12:1–148
- Hallier E (1863) *Vegetation auf Helgoland*. Otto Meißner, Hamburg
- Kain JM (1962) Aspects of the biology of *Laminaria hyperborea*, I. Vertical distribution. *J Mar Biol Assoc UK* 42:377–385
- Kautsky N, Kautsky H, Kautsky U, Waern M (1986) Decreased depth penetration of *Fucus vesiculosus* (L.) since the 1940's indicates eutrophication of the Baltic Sea. *Mar Ecol Prog Ser* 28:1–8
- Kent M, Coker P (1992) *Vegetation description and analysis*. A practical approach. Belhaven Press, London
- Kuckuck P (1894) *Bemerkungen zur marinen Algenvegetation von Helgoland*. *Wiss Meeresunter* 1:223–263
- Kuckuck P (1897) *Ueber marine Vegetationsbilder*. *Ber Dtsch Bot Ges* 15:441–447
- Lüning K (1969) Standing crop and leaf area index of the sublittoral *Laminaria* species near Helgoland. *Int J Life Oceans Coast Waters* 3:282–286
- Lüning K (1970) Tauchuntersuchungen zur Vertikalverteilung der sublittoralen Helgoländer Algenvegetation. *Helgol wiss Meeresunters* 21:271–291
- Lüning K (1979) Growth strategies of three *Laminaria* species (Phaeophyceae) inhabiting different depth zones in the sublittoral region of Helgoland (North Sea). *Mar Ecol Prog Ser* 1:195–207
- Lüning K (1981) Light. In: Lobban CS, Wynne MJ (eds) *The biology of seaweeds*. Blackwell, Oxford, p 326–355
- Lüning K (1990) *Seaweeds. Their environment, biogeography and ecophysiology*. Wiley, New York
- Lüning K, Dring MJ (1979) Continuous underwater light measurement near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. *Helgol Wiss Meeresunters* 32:403–424
- Markham JW, Munda IM (1980) Algal recolonization in the rocky eulittoral at Helgoland, Germany. *Aquat Bot* 9:33–71
- McQuatters-Gallop A, Raitso DE, Edwards M, Pradhan Y, Mee LD, Lavender SJ, Attrill MJ (2007) A long-term chlorophyll data set reveals regime shift in North Sea phytoplankton biomass unconnected to nutrient trends. *Limnol Oceanogr* 52:635–648
- Moy F, Aure J, Dahl E, Green N and 9 others (2003) Landtidsovervåking av miljøkvaliteten i kystområdene av Norge. *Årsrapport for 2002*, p 1–69
- Munda IM, Markham JW (1982) Seasonal variations of vegetation patterns and biomass constituents in the rocky eulittoral of Helgoland. *Helgol Mar Res* 35:131–151
- Nienburg W (1930) *Die Besiedelung des Felsstrandes und der Klippen von Helgoland, Teil II. Die Algen*. *Helgol Wiss Meeresunters* 15:1–15
- Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC (2001) Ecological effects of the North Atlantic oscillation. *Oecologia* 128:1–14
- Pang S, Gomez I, Lüning K (2001) The red macroalga *Delesseria sanguinea* as a UVB-sensitive model organism: selective growth reduction by UVB in outdoor experiments and rapid recording of growth rate during and after UV pulses. *Eur J Phycol* 36:207–216
- Pedersen M, Snoeijis P (2001) Patterns of macroalgal diversity, community composition and long-term changes along the Swedish west coast. *Hydrobiologia* 459:83–102
- Reichert K, Buchholz F (2006) Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002. *Helgol Mar Res* 60:213–223
- Reichert K, Buchholz F, Bartsch I, Kersten T, Giménez L (2008) Scale-dependent patterns of variability in species assemblages of the rocky intertidal at Helgoland (German Bight, North Sea). *J Mar Biol Assoc UK* (in press)
- Rolela MY, Wiencke C, Hanelt D, van de Poll WH, Gruber A (2005) Sensitivity of *Laminariales* zoospores from Helgoland (North Sea) to ultraviolet and photosynthetically active radiation: implications for depth distribution and seasonal reproduction. *Plant Cell Environ* 28:466–479
- Rolela MY, Hanelt D, Wiencke C (2006) Exposure to ultraviolet radiation delays photosynthetic recovery in Arctic kelp zoospores. *Photosynth Res* 88:311–322
- Schultze K, Janke K, Krüß A, Weidemann W (1990) The macrofauna and macroflora associated with *Laminaria digitata* and *Laminaria hyperborea* at the island of Helgoland (German Bight, North Sea). *Helgol Mar Res* 44:39–51

- Sjötun K, Olsen BR, Eggereide SF (2004) Biomassekartlegging av *Laminaria digitata* i Smøla-området - Biomass survey of *Laminaria digitata* in the Smøla area. *Fisken og havet* 11, p 20
- tom Dieck (Bartsch) I (1992) North Pacific and North Atlantic digitate *Laminaria* species (Phaeophyta): hybridization experiments and temperature responses. *Phycologia* 31: 147–163
- Torn K, Krause-Jensen D, Martin G (2006) Present and past distribution of bladderwrack (*Fucus vesiculosus*) in the Baltic. *Aquat Bot* 84:53–62
- Underwood JA (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge
- Weisse R, von Storch H, Feser F (2005) Northeast Atlantic and North Sea storminess as simulated by a regional climate model 1958–2001 and comparison with observations. *J Clim* 18:465–479
- Wiencke C (1990) Seasonality of red and green macroalgae from Antarctica — a long-term culture study under fluctuating Antarctic daylength. *Polar Biol* 10:601–607
- Wiltshire KH, Manly BFJ (2004) The warming trend at Helgoland Roads, North Sea: phytoplankton response. *Helgol Mar Res* 58:269–273
- Wiltshire KH, Malzahn AM, Wirtz K, Greve W and others (2008) Resilience of North Sea phytoplankton spring bloom dynamics: an analysis of long-term data at Helgoland Roads. *Limnol Oceanogr* 53:1294–1302

Submitted: October 18, 2007; Accepted: July 30, 2008

Proofs received from author(s): September 19, 2008