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Seaweed of the littoral zone at Cove Island in Long Island Sound: annual variation and impact of environmental factors

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Abstract A site in the western part of Long Island Sound was monitored from January 2000 to May 2002. The littoral was divided into five different zones from the supra-littoral fringe (A) to the infra-littoral fringe (E). The midshore was dominated by *Fucus vesiculosus* L. and the sublittoral fringe by *Chondrus crispus* Stackh. There was a significant change in community structure over the years and the predominant change occurred between 2001 and 2002. The alternation in community structure was caused by an increase in abundance of species like *Porphyra suborbiculata* Kjellm., *Porphyra leucosticta* Type A and C (Neefus et al. 2000), *Ceramium virgatum* Roth, and *Codium fragile* subsp. *tomentosoides* (van Goor)Silva and a decrease in abundance in *Fucus vesiculosus*, *Blidingia minima* (Nägeli ex Kütz.) Kylin and *Ulva lactuca* L. The changes in community structure coincided with the change in environmental conditions. Air temperature as well as surface seawater temperature (depth <2 m) were the most important factors of those analyzed. Temperature seems to be the bottom-up force regulating the community structure.

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Keywords Community structure · New England · Temperature · Salinity · Nutrients · *Porphyra* spp

Introduction

Population and communities in the littoral zone can be complex and are influenced by various biotic and abiotic factors like climate, nutrient availability, predation, grazing, competition, symbionts, parasites, substrate characteristics, exposure and tidal variation. Species living in the littoral zone are exposed to an extreme environment.

Littoral communities have been extensively studied over centuries. Several studies of the community structure in the intertidal have focused on the coast from Rhode Island and up to Maine (Bertness and Leonard 1976; Leonard 2000; Lubchenco 1980, 1983; Mathieson et al. 1976, 1981a, b; Mathieson and Penniman 1986; Menge 1976, 1991; Petraitis 1987). However, very few studies have been published on the littoral assemblages in Long Island Sound (LIS), even though sites in the vicinity of Dominion Nuclear Power Station (Niantic, CT) have been thoroughly monitored for over 20 years (Keser et al. 2003, 2005).

The main factors regulating the littoral community structure in New England are exposure and top-down regulations such as predation and grazing pressure (Hunter and Price 1992). The main predators are *Nucella lapillus* L. and *Asterias* spp., while periwinkles are the main grazers (mainly *Littorina littorea* L.) (Dudgeon et al. 1999; Lubchenco 1983; Menge 1976, 1978a, b, 1983; Petraitis 1987). The intertidal zone is dominated by fucoids (*Fucus vesiculosus* and *Ascophyllum nodosum* (L) Le Jol.), and in the infra-littoral fringe Irish moss (*Chondrus crispus*) is the most abundant. In highly exposed areas, the mussel

(*Mytilus edulis* L.) outcompetes *Chondrus crispus* as predation pressures are reduced.

Studies have recently focused on the importance of bottom-up regulation. These factors, i.e. variation in nutrient and other environmental conditions, have been associated with changes in algal cover, usually in larger spatial scales (10–100 km) (Menge 2000). Other bottom-up processes like recruitment, congestion for space, nutrient and food abundance (POC, PON and chlorophyll-a) have also been shown to have a bottom-up effect on the community structure (Bertness et al. 1999a, b; Menge et al. 1999; Menge 2000). However, a recent study demonstrated that a bottom-up process interact with top-down forces in the regulation of community structure locally in the littoral zone in New England (Leonard et al. 1998).

Apart from fucoids and Irish moss which are the key algal species in the two main zones on these shores, several species of *Porphyra* are also frequently found in the littoral zone along New England's shores (Sears 1998). However, the genus *Porphyra* contains several species that are difficult to identify (Brodie et al. 1998; Broom et al. 2002; Lindstrom and Cole 1993; Neefus et al. 2000, 2002; Nelson et al. 2001) since their morphologies are very similar (Nelson et al. 2000). As several *Porphyra* are of great importance in aquaculture, especially in Korea, China and Japan (Oohusa 1992; Tseng and Fei 1987), domestic species have gained attention in recent years as potentially valuable resources, and several studies have recently been initiated (Carmona et al. 2001; Chopin et al. 2001a, b, c; Levine 1998; Yarish et al. 1997, 1998, 1999). As a part of this new interest in *Porphyra* in New England, this study aimed to gain information on the spatial and temporal occurrence of *Porphyra* species in LIS. However, the main goal of this study was to test the importance of climatic factors as bottom-up forces in regulating the community structure of the shore line.

Materials and methods

A site at Cove Island, Stamford, CT (41°2.644′N, 73° 30.133′W) (Fig. 1) was surveyed 23 times over a period of 2 years, from February 2000 to March 2002. The mid-littoral zone was divided into five vertical zones, from supra-littoral fringe (A) to the infra-littoral fringe (E) (classification of vertical zonation according to Hiscock and Mitchell 1980). The procedure of dividing the phytal zone into five different zones was based on biological as well as physical differences between the zones. The upper zone A represented the supra-littoral zone and extended into the upper part of the balanoid/fucoid belt in the mid-littoral zone. The extensive fucoid belt, present at the time, was divided into two zones, B and C. The two zones were

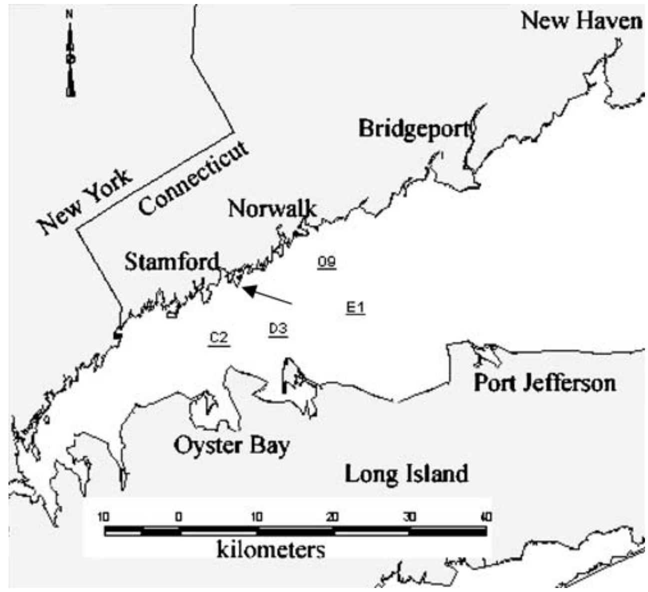

Fig. 1 NOAA's hydrographical stations in Long Island Sound, used to calculate average values for environmental variables (modified after NOAA's station map). *Arrow* points at Cove Island

thought to response differently to prolonged periods of abnormal environmental conditions. The two lower zones had a smaller angle of inclination than the above fucoid zones. They were separated into two zones. Zone D, just above the infra-littoral fringe, was flat with a few fucoids but periodically with high abundance of *Codium fragile.* The flats were occasionally covered with sediments and were daily exposed to air due to tidal fluctuations as opposed to the lowest zone (E) within the infra-littoral fringe which was only exposed to air a few days every month. The horizontal elevation from the Mean Lower Low Water (MLLW) was measured by laser level. MLLW was set to 0 m depth and the zones represented the following depth intervals (cm above MLLW) A=270–220 cm, B=220–150 cm, C=150–50 cm, D=50–0 cm and E=0 to −40 cm.

The dominating species in the lowest zone was also different from the above. It was also assumed that zone D would be more exposed to sedimentation than the above fucoid belt. The species occurring within each zone were recorded by placing a frame (0.5 × 0.5 m) subdivided into smaller (10×10 cm) squares randomly within the zones during each registration. Each sub-square represented 4% cover and enabled us to add up better the percentage cover of each species. Five replicate frames were recorded within each zone. All species were registered as percentage cover at low tide. The registrations were based on non-destructive sampling. However, small pieces of those species hard to identify in the field were collected either within or outside the frames for further identification in the laboratory.

Low taxonomic resolution reflected environmental pollution gradients even more clearly than did higher taxonomic levels (Gray et al. 1990; Olsgard et al. 1998; Olsgard and Somerfield 2000), especially when trying to relate community structure to environmental data (Clarke and Ainsworth 1993; Terlizzi et al. 2002). Hence, running multivariate analysis of the community structure of Cove Island included grouping of species into higher taxa. This was done to compensate for the existence of species difficult to distinguish and identify in the field. It has been shown that grouping species into higher taxa does not alter the main outcome and can sometimes improve the results of multivariate analysis of community structure (Clarke 1993; Gray et al. 1990; Lasiak 2003; Olsgard et al. 1997; Terlizzi et al. 2003; Warwick 1988).

Small inconspicuous species (<1–3 mm or microscopic) were not included. Species of similar morphology difficult to differentiate in the field, such as species from the genera *Ectocarpus* and *Pilaiella* as well as species within the *Ceramium*, *Polysiphonia, Neosiphonia*, *Enteromorpha* and *Cladophora* genera, were grouped for statistical analysis. Sedimentation was measured on a semi-quantitatively scale from 0 to 4, where 0=no obvious sedimentation, 1=ca. 1 mm, 2=ca. 3 mm, 3=ca. 4 mm and 4 severe sedimentation of > 5 mm.

Data for temperature, nitrate and salinity from LIS were obtained from National Oceanic and Atmospheric Administration (NOAA). These were obtained from NOAA's hydrographical stations 09, C2, D3 and E1 (Fig. 1) and averaged across a 1 month period prior to the dates when community structure were registered. Monthly values for nitrate (μM), salinity (ppt) and temperature (°C) were averaged for each season (i.e., winter, spring, summer and fall). Winter included the months December to March, spring from April to May, summer from June to September and fall from October to December. Missing values for temperature in February and May of 2001, nitrate + nitrite and salinity for May 2001, were interpolated based on the previous and the following months. Differences among environmental data were tested with two-sample *t* tests or paired *t* tests where applicable. To test the influence of climatic factors on the community structure, a dataset was obtained from the National Climate Data Center at NOAA for Stamford, CT, including: DPNT (departure from normal monthly temperature), DT00 (number of days with minimum air temperature less than or equal to –17.8°C), DT32 (number of days with minimum air temperature less than or equal to 0°C), DT90 (number of days with maximum air temperature greater or equal to 32°C), DX32 (number of days with maximum air temperature less than or equal to 0°C), EMNT (extreme minimum air temperature for the month), EMXT (extreme maximum air temperature for the month), EMXP (extreme maximum daily precipitation in the month), MMNT (monthly mean minimum air temperature), MMXT (monthly mean maximum air temperature) and MNTM (monthly mean air temperature).

Multidimensional scaling (MDS) was used to analyze quantitative data on species and taxa abundances over time. MDS is an ordination method and will present temporal differences in community structure in a graphical plot. The longer the distance between two samples, the greater is the difference in community structure between the samples. Due to the high number of quadrats recorded, the five replicate quadrats within each zone were averaged prior to the multivariate analysis. This was done to reduce number of permutation and make the computations possible to execute. Bray–Curtis similarity index was used in calculating the species similarity matrix. Prior to analysis, the species data were transformed by a fourth root transformation to make the datasets more similar to a normal distribution. The similarity matrices were input for MDS analysis. The same similarity matrices were used for hierarchical agglomerative clustering using group average linkage to cross-check the results obtained via MDS analysis, when the stress factor approached 0.2 (Clarke 1993). One-way ANOSIM permutation test (which is a simulated ANOVA, PRIMER ver. 5) was used to test differences between the species composition at different years, zones and seasons. SIMPER (Similarity percentage procedure) was used on the abundance data matrices to test the different species contribution to the Bray–Curtis dissimilarities between years, zones and seasons, i.e. the analysis ranks and quantify the importance of each species which causes the differences among the samples in the MDS plot. Similarity matrices of the environmental data, i.e. temperature, salinity and nitrate concentration in 2 m water depth in LIS and climate data from Stamford, were based on normalized Euclidean distance as opposed to a Bray–Curtis similarity matrices for the biological datasets. Principal component analysis (PCA) of environmental data from LIS and climate data from Stamford were plotted in two dimensions. To compare the environmental data and climate datasets against biological datasets, BIO-ENV (PRIMER ver.5) was used. These procedures compare the environmental matrices (environmental data matrix from LIS and climate data matrix from Stamford as well as a combination of them) against the biota matrices within each zone. BIO-ENV calculates a measure of agreement between the two dissimilarity matrices by rank correlation of the matching elements in the two matrices. The coefficient of agreement used was a Spearman rank correlation coefficient ρ which ranges from –1 complete discordance between ranked values) and +1 (complete concordance).

Results

Environmental conditions

The average temperature (at 2 m depth) in Long Island Sound off the study site, varied from 0.5°C in January to 23°C in August/September (Fig. 2). In 2002, the average temperature (T) in the coldest winter months was twice as high as in 2000 and 2001, 4.5°C as opposed to 1.8°C and 1.7°C, respectively. No difference was detected between summer temperatures in 2000 and 2001.

Nitrate (=NO_3+NO_2) concentration (N) in the upper water column varied dramatically over the year with low N in the summer months and high in the winter months. Figure 2 shows that N dropped dramatically from February to March in 2000 and from January to February in 2001. However, in 2002, high N was observed into May.

The salinity (S) at 2 m depth in the inner part of LIS varied between 25.4 and 29.1 psu (Fig. 2). S was lower during the spring/summer months than during winter presumably due to runoff from land during spring. S during the summer months in 2000 and 2001 varied from 25.4 to 26.8 psu, while the average S in the winter months from November 2000 to March 2001 (27.5 psu) was significantly lower than in the same period during the 2001/2002 winter (28.9, p<0.001) (Fig. 2).

Principal Component Analysis (PCA) of the environmental data placed the samples as shown in Fig. 3. The data analyzed are monthly average values for S, N and T concentration from the inner part of LIS. It shows that the conditions follow a cyclic pattern and that conditions varied more in late winter/early spring than in late fall/early winter. Conditions in January and February 2002 were quite different from the previous 2 years. PC 1 explained more than 50% of the variation (Fig. 3; Table 1) and was mainly represented by differences in N at the different sampling occasions (0.701 in Table 2). The relative importance of T represented almost all of the 34.6% variation explained by PC2 (0.967) (Tables 1 and 2). S was the least influential environmental factor of the three (Fig. 3; Tables 1 and 2).

Climate data from National Climate Data Center at NOAA also shows that the climate in January in 2000 and 2001 as well as December in 2000 was different from the same periods in 2002. The constellation of stations in Fig. 4 A, B was mainly due to the mean monthly minimum and maximum temperatures (MMNT, MMXT), monthly mean temperature (MNTM) and extreme temperatures in winter and summer months (EMNT, EMXT) (Table 4). Departure from normal monthly temperature (DPNT) gave the best discrimination along PC2 where it explained 0.62 of the variation.

The annual variation in climate over the monitored period showed that 2002 was a warmer year than the previous two years (Fig. 2). No days during 2002 had maximum temperature below 0°C whereas 2000 and 2001 had 13 and 5 days, respectively. The winter temperature in surface waters (>2 m) was much higher during 2002 than the previous two years (Fig. 2). This was due to an air temperature that was higher than normal from August 2001 until April 2002. During this period the temperatures were on average 2.4°C above the normal (based on 30 years variation, NOAA-datasets). The previous winter temperatures were not different from the 30-year range. DPNT (departure from normal monthly temperature) was the factor that best described the variation over PC2 as well as other temperature factors as DT00 and DX32 (Tables 3 and 4).

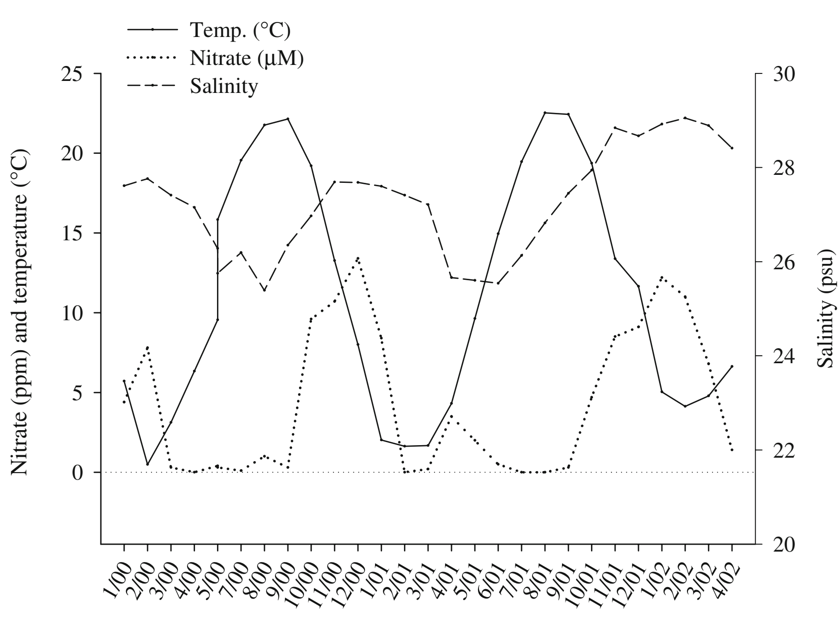

Fig. 2 Average nitrate concentrations, temperature and salinity at 4 stations (NOAA) in LIS from January 2000 to April 2002. (Note that values for June 2000 are missing.)

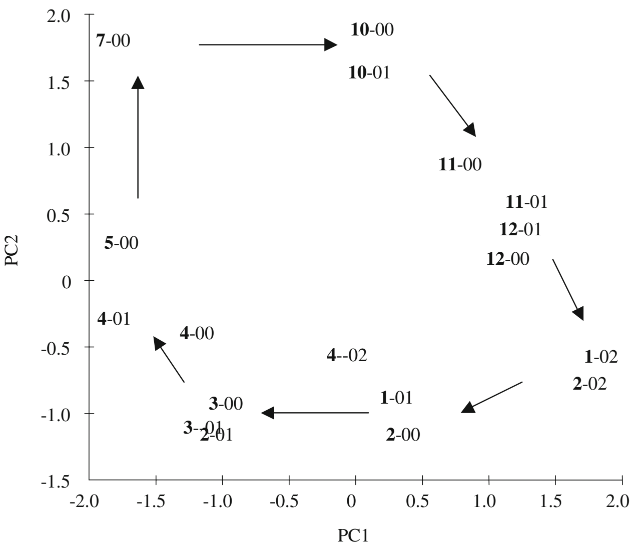

Fig. 3 PCA of the environmental conditions in the inner part of LIS during the period February 2000 to April 2002. The *arrows* indicate succession in environmental condition during the years. The labels on the x-axis are in month-year format

Biological succession at Cove Island, LIS

The intertidal zone at Cove Island was dominated by *Fucus vesiculosus* with a total average annual cover of 34%, followed by *Chondrus crispus* (19%) and *Semibalanus* sp. (11%) (Table 5). The occurrence varied within the five different zones and, although *F. vesiculosus* was found in all five zones, it was most pronounced in the intermediate zones B (68%), C (55%) and D (37%) (Table 5; Fig. 5). *Fucus vesiculosus* is a perennial, but the percentage cover varied both seasonally and annually. During 2000 and until May 2001, the average cover (5 replicates) within each zone were fairly stable. However, during summer 2001, the percentage cover dropped significantly in all zones (two-sample *t* test: $p<0.05$,; Fig. 5a).

Chondrus crispus dominated in the sublittoral fringe, zone E, and the percentage cover was stable over the years. There was a drop in cover in spring 2000 which coincided with an increased cover of *Ulva lactuca* in the same zone (Fig. 5d). *Ulva lactuca* was epiphytic on *C. crispus* and concealing it. Hence, *C. crispus* coverage was underestimated.

Green algae like *Ulothrix* spp. and *Urospora* spp. (combined in the analysis) showed the same pattern as *Ulva lactuca*, with a significantly ($p<0.01$) higher occurrence in winter/spring of year 2000 than in 2001 and 2002. *Codium fragile* subsp. *tomentosoides*, introduced in LIS in 1956 (cited in (Sears 1998), showed opposite trends than the other green algae by having a significant higher percentage cover (in zone D) in 2002 than the previous years ($p<0.01$; Fig. 5c). Another green alga that occurred early spring, sometimes in very high percentage cover, was *Blidingia minima*. However, *B. minima* showed high occurrence only in 2001 in the upper two zones, A and B (Fig. 5b).

Table 1 Eigenvalues and explained variation on 3 PC-axis in Fig. 3

PC	Eigenvalues	Variation (%)	Cumulative variation (%)
1	1.55	51.8	51.8
2	1.04	34.6	86.5
3	0.41	13.5	100.0

Table 2 Eigenvectors representing the relative importance of the three variables *N* (nitrate + nitrite), *T* (temperature) and *S* (salinity) in describing the variation along the different PC-axis

Variable	PC1	PC2	PC3
N	0.710	0.150	-0.688
T	0.038	0.967	0.250
S	0.703	-0.203	0.682

Among the red alga, *Ceramium virgatum* varied over the period with low percentage cover in 2000 and a slight increase in 2001. In 2002, the increase in percentage cover of *C. virgatum* was significantly higher than the previous years ($p<0.01$; Fig. 5e) similar to *Codium fragile* subsp. *tomentosoides* and *Neosiphonia harveyi* (Bailey) Kim, Choi, Guiry & Saunders. Three different species of *Porphyra* spp. were found at the site. They occurred most frequently in winter/spring, but their occurrence varied significantly over the years. *Porphyra suborbiculata*, which is easily identified by peripheral 2–4 cell teeth along the edge of the thallus in young sporophytes, was first observed in October and increased with a peak in late March. The teeth did, however, disappear later in spring and on older individuals. The round to oval thallus varied in thickness between 23–30 µm, but was usually found to be about 25 µm. Older sporophytes formed numerous endosporangia (Figs. 5–10 in Nelson et al. 1998) in March/April and these individuals were still found in late June, but not in August. The overall percentage cover of *P. suborbiculata* increased significantly from 2000 to 2001 ($p<0.05$) and slightly from 2001 to 2002 (n.s.; Fig. 5f). However, the increase was different within each zone and most pronounced in zones A and C. *Porphyra leucosticta* Thur. is a difficult taxa to identify and there may be five or more cryptic species behind this designation (Neefus et al. 2000). The types found at Cove Island resembled Type A and Type C in Neefus et al. (2000). *Porphyra leucosticta* Type A occurs epiphytic on *C. crispus* in the period January–May in the lower intertidal to shallow subtidal in LIS (zones D and E; Fig. 5g). The Type A strain has a lanceolate blade with ruffled margins and were between 1–5 cm wide and 5–12 cm long. The thallus thickness ranged from 18–24 µm.

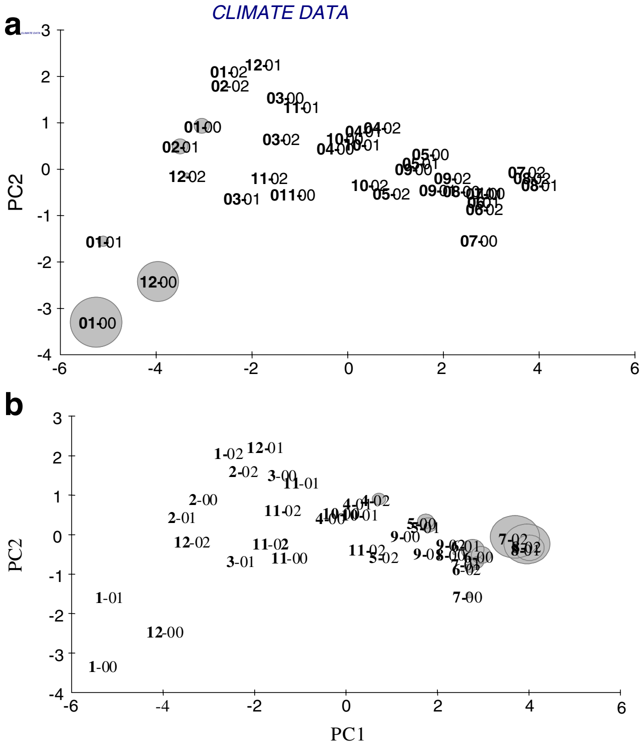

Fig. 4 PCA of the climate data from Stamford, CT, during 2000, 2001 and 2002. The labels on the x-axis are in month-year format. **a** Values for number of days with maximum temperatures below 0°C are superimposed on plot. **b** Values for number of days with maximum temperature above 32°C are superimposed on the plot

Porphyra leucosticta Type A increased over the years from 0.5% cover in zone D in 2000 to 5.5% cover in 2002 (n.s.). Type C of *P. leucosticta* was found epiphytic on different algae or epilithic in the mid-littoral zone from November to May (Fig. 5h). It was mainly ovate with ruffled edges of 3–8 cm wide and 5–10(–15) cm long. The thallus thickness varied between 30–40 µm (21–50 µm) in thickness. It was found in all zones at Cove Island from A to E as opposed to Type A found exclusively in zones D and E. In general, all types of *Porphyra* spp found at the site increased in percentage coverage from 2000 to 2002 as did *Ceramium virgatum, Neosiphonia harveyi* and *C. fragile* subsp *tomentosoides*.

Table 3 Eigenvalues and explained variation on 5 PC-axis in Fig. 4

PC	Eigenvalues	Variation (%)	Cumulative variation (%)
1	6.86	62.4	62.4
2	1.35	12.2	74.6
3	1.08	9.8	84.4
4	0.73	6.6	91.0
5	0.49	4.4	95.5

Multivariate analysis of community structure

Average percentage cover for all species was compared for all sampling dates. The community structure shows that some zones form more distinct group than others (A+B+C and D and E) (Fig. 6). Zones B and C show less separation than others and are also indicated with the lowest pairwise *r*-value between zones (B and C in Table 6). There are significant differences between all zones (one-way ANOSIM, $p<0.001$; Table 6). The community structure of upper three zones (A, B, C) are more alike as opposed to the well separated two lower zones (Fig. 6; Table 6). In zones A–D, the occurrence of *F. vesiculosus* contributed most to the zones' characteristics (25–34%) as did *C. crispus* in zone E (39%). The species that contributed most in separating the zones are listed in Table 7. Other important species in separating the different zones were *Blidingia minima, Mytilus edulis* L. and balanoids which were abundant in the upper zones, *Enteromorpha spp* in the intermediate zones and *U. lactuca*, *Ceramium virgatum, Polysiphonia stricta* (Dwil.) Grev. and *Codium fragile* subsp. *tomentosiodes* in the lower two zones. All contributed from 4 to 15% in separating the different zones (Table 7).

To check the effect of redundancy in the dataset, MDS, SIMPER and ANOSIM were performed on the same dataset excluding *F. vesiculosus*, which was the dominating species in the upper four zones. The MDS plot did not change dramatically and still showed distinct zones significantly different from each other ($p<0.001$). However, excluding *F. vesiculosus* resulted in even less separation of zones A, B and C (smaller *r*-values). Several species had different abundances over the period monitored. Figure 7 shows the total community structure as in Fig. 6, but with years superimposed on the samples. *Fucus vesiculosus*,

Table 4 Eigenvectors representing the relative importance of the 11 variables (coefficients in the linear combinations of variables making up PC's)

Variable	PC1	PC2	PC3	PC4	PC5
DPNT	0.009	0.620	0.424	0.612	−0.106
EMNT	0.371	−0.086	0.023	−0.017	0.031
EMXP	0.152	−0.371	−0.446	0.764	0.112
EMXT	0.364	0.003	0.112	0.040	−0.058
MMNT	0.377	−0.089	0.022	−0.034	−0.056
MMXT	0.376	−0.064	0.077	−0.044	−0.135
MNTM	0.378	−0.076	0.051	−0.039	−0.098
DT00	−0.186	−0.444	0.496	0.117	−0.601
DT90	0.252	−0.085	0.510	−0.025	0.644
DT32	−0.363	0.015	0.028	0.087	0.316
DX32	−0.224	−0.499	0.306	0.117	0.256

See Materials and methods for abbreviations

Table 5 Average (plus minimum and maximum) percentage cover of species and taxa within the zones used in the analysis of community structure at Cove Island, LIS during January 2000 to May 2002

Species	Zones (depth)					
	Sum all 5 zones (0–310 cm) Av. (min–max)	A (0–50 cm) Av. (min–max)	B (50–120 cm) Av. (min–max)	C (120–220 cm) Av. (min–max)	D (220–270 cm) Av. (min–max)	E (270–310 cm) Av. (min–max)
Algae						
Agardhiella subulata	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)
Ascophyllum nodosum	1 (0–30)	0 (0–0)	0 (0–0)	0 (0–6)	2 (0–30)	0 (0–1)
Erythrocladia irregularis	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)	0 (0–0)
Audouniella daviesii	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)	0 (0–1)
Bangia atropurpurea	1 (0–15)	2 (0–15)	1 (0–15)	0 (0–0)	0 (0–0)	0 (0–0)
Blidingia minima	5 (0–63)	14 (0–63)	7 (0–63)	3 (0–10)	0 (0–1)	0 (0–0)
Bryopsis plumose	0 (0–2)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–2)	0 (0–2)
Ceramium virgatum	2 (0–35)	0 (0–0)	0 (0–0)	0 (0–1)	5 (0–35)	2 (0–16)
Chondrus crispus	19 (0–98)	0 (0–0)	0 (0–0)	0 (0–2)	17 (0–39)	78 (0–98)
Chorda filum	0 (0–2)	0 (0–0)	0 (0–0)	0 (0–2)	0 (0–0)	0 (0–0)
Cladophora sp.	0 (0–3)	0 (0–0)	0 (0–0)	0 (0–1)	0 (0–3)	0 (0–1)
Codium fragile subsp. *tomentosoides*	3 (0–43)	0 (0–0)	0 (0–0)	0 (0–0)	13 (0–43)	1 (0–3)
Dasya baillouviana	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)
Desmarestia viridis	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)
Colonial Diatoms	2 (0–62)	0 (0–1)	0 (0–0)	1 (0–5)	7 (0–62)	2 (0–22)
Ectocarpales indet.	2 (0–48)	0 (0–0)	1 (0–8)	1 (0–4)	3 (0–23)	5 (0–48)
Elachista fucicola	1 (0–6)	0 (0–0)	1 (0–4)	1 (0–5)	1 (0–6)	0 (0–0)
Enteromorpha linza	3 (0–40)	2 (0–40)	3 (0–28)	8 (0–37)	3 (0–10)	0 (0–3)
Enteromorpha prolifera	2 (0–30)	1 (0–14)	3 (0–30)	6 (0–27)	2 (0–13)	0 (0–1)
Fucus vesiculosus	34 (0–90)	8 (0–23)	68 (0–86)	55 (0–90)	37 (0–71)	1 (0–10)
Hildenbrandia rubra	1 (0–10)	0 (0–2)	0 (0–2)	2 (0–10)	1 (0–5)	0 (0–0)
Laminaria juv.	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)
Laminaria saccharina	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)	0 (0–0)
Petalonia fascia	0 (0–2)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–2)	0 (0–1)
Polysiphonia fucoids	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)	0 (0–1)
Neosiphonia harveyi	1 (0–11)	0 (0–0)	0 (0–0)	0 (0–0)	1 (0–10)	2 (0–11)
Polysiphonia nigrescens	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)
Polysiphonia urceolata	0 (0–4)	0 (0–0)	0 (0–0)	0 (0–1)	1 (0–2)	1 (0–4)
Porphyra suborbiculata	1 (0–8)	2 (0–8)	1 (0–7)	1 (0–7)	0 (0–0)	0 (0–0)
Porphyra leucosticta A	0 (0–5)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–2)	1 (0–5)
Porphyra leucosticta C	1 (0–10)	0 (0–3)	1 (0–10)	1 (0–5)	1 (0–8)	0 (0–2)
Scytosiphon lomentaria	0 (0–2)	0 (0–0)	0 (0–2)	0 (0–0)	0 (0–0)	0 (0–1)
Sphacelaria sp.	0 (0–6)	0 (0–0)	0 (0–0)	0 (0–0)	1 (0–6)	0 (0–1)
Sphacelaria plumosa	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)	0 (0–1)
Spongomorpha pallida	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)
Ulothrix/Urospora spp.	3 (0–66)	11 (0–66)	2 (0–7)	3 (0–11)	1 (0–8)	0 (0–0)
Ulva lactuca	3 (0–47)	0 (0–0)	0 (0–0)	2 (0–9)	6 (0–18)	9 (0–47)
Fauna						
Alcyonidium undet.	0 (0–7)	0 (0–0)	0 (0–0)	0 (0–0)	1 (0–7)	2 (0–6)
Balanoids undet.	11 (0–97)	18 (0–97)	20 (1–43)	19 (0–50)	0 (0–2)	0 (0–0)
Bryozoa undet.	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–1)	0 (0–1)
Crepidula fornicate	0 (0–2)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–2)	0 (0–0)
Littorina obtusata	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)
Littorina spp.	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–0)
Mytilus edulis	1 (0–10)	0 (0–3)	4 (0–10)	1 (0–7)	0 (0–0)	0 (0–0)
Ostrea sp.	0 (0–2)	0 (0–1)	1 (0–2)	0 (0–2)	0 (0–0)	0 (0–0)
Porifera undet.	0 (0–8)	0 (0–0)	0 (0–0)	0 (0–0)	0 (0–8)	0 (0–2)
Sediment: unclassified	3 (0-	0 (0–0)	0 (0–2)	2 (0–14)	10 (0–51)	1 (0–5)

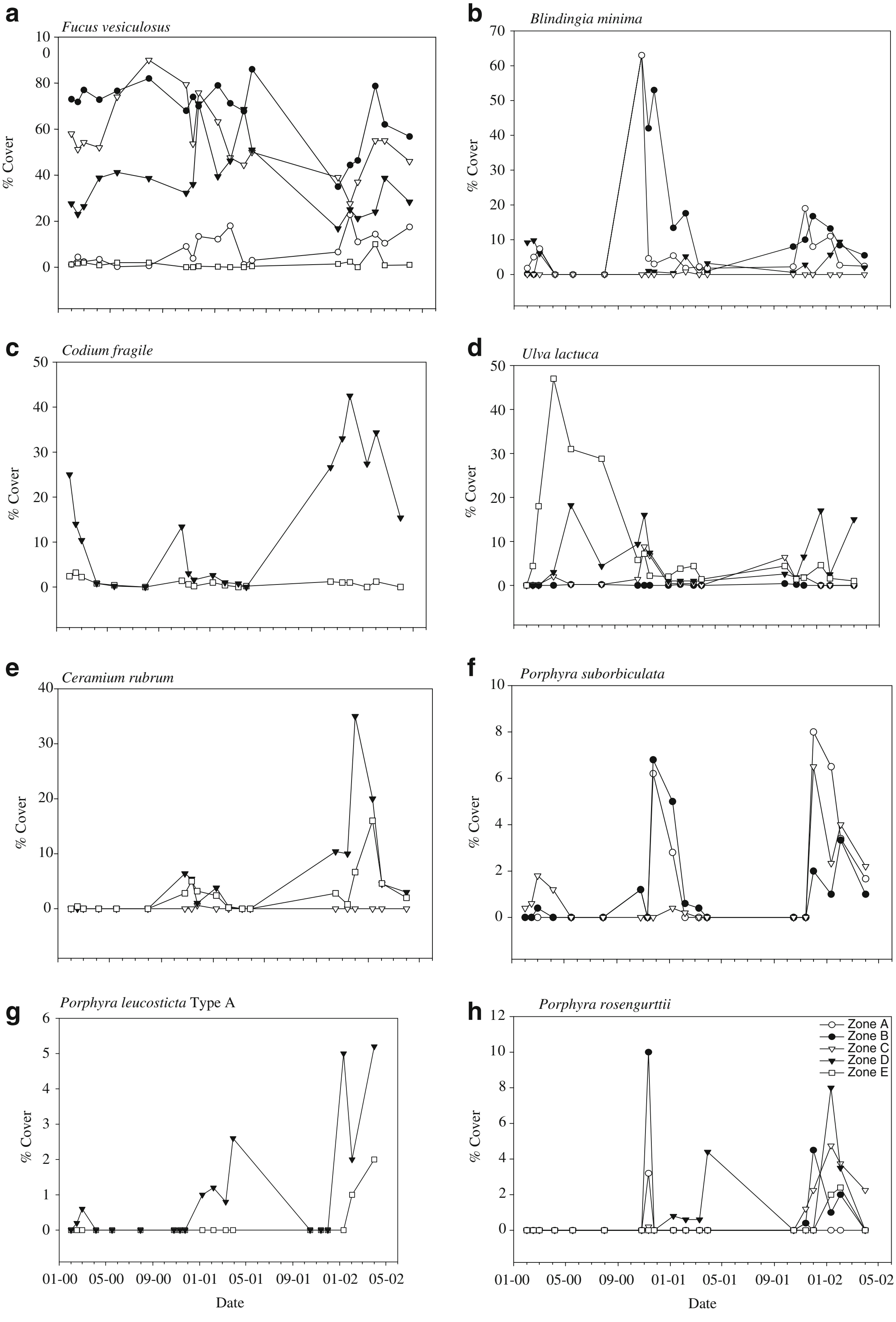

Fig. 5 Difference in percentage cover of 8 important species in the littoral zones (**a**–**h**) at Cove Island, LIS. Note different scale of percentage cover axis. (Note that data between June and September 2001 are missing.)

Ulothrix/Urospora and *U. lactuca* decreased from January 2000 to May 2002, whereas other species like the *Porphyra* spp., *C. virgatum, N. harveyi* and *C. fragile* subsp. *tomentosiodes* increased in abundance over the 2 years. Two-way crossed simulated ANOVA's (ANOSIM) were used to test for differences between years (averaged across all zones) and a two-way nested ANOSIM tested for differences between seasons (averaged across zone groups) as well as among zones across seasons groups. Both analysis showed that all years were significantly different from each other (global $r=0.23$, $p<0.001$) and that all zones were significant different (Table 8). Differences between seasons were even more distinct from each other than years (global $r=0.32$, $p<0.001$) and the difference between zones became even more evident (Table 9).

Correlation between biological and environmental/climate data

BIO-ENV (for explanation see Materials and methods) between N, S and T at 2 m depth in the inner part of LIS, and the observed community structure at the respective sampling occasions, resulted in an average correlation coefficient among all depth interval of $r=0.37$. Even though it is a positive correlation, the coefficient is not significant as the numbers of variables are only three. Salinity and nitrogen concentrations gave the best correlation coefficient between the two matrices.

Best correlation coefficients were obtained when running BIO-ENV on the combined matrices for environmental data from LIS and climate data from Stamford, against the biological data matrix. The Spearman rank correlation coefficient was significant at the 5% level for zones A, B and C ($r=0.54$ when $\rho=0$,;Table 13 in Pearson and Hartley 1966) but not for D and E. The average correlation coefficient (r) for all zones was 0.39, but this is not significant.

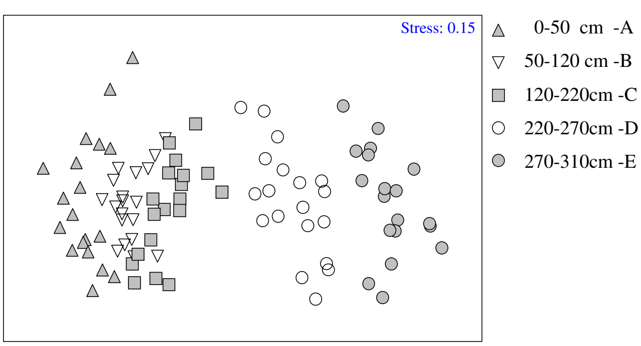

Fig. 6 Multidimensional Scaling of the community structure at Cove Island from January 2000 to May 2002. The *symbols* represent the different zones from upper littoral fringe down to the sublittoral fringe. 270 cm is Mean Lower Level Water

Table 6 Result of a simulated one-way ANOVA (ANOSIM) on the community structure with zones (A–E) as factors (ref. Fig. 6)

Groups	Pairwise tests	
	R statistic	Significance level %
A, B	0.418	0.1
A, C	0.477	0.1
A, D	0.969	0.1
A, E	0.999	0.1
B, C	0.233	0.1
B, D	0.949	0.1
B, E	1.000	0.1
C, D	0.755	0.1
C, E	0.995	0.1
D, E	0.531	0.1

Global $R=0.712$ ($p<0.001$)
Number of permutations: 999 (random sample from a large number)
Number of permuted statistics greater than or equal to Global R: 0

Discussion

Community characteristics

The most abundant species occurring in the zones, from 50 to 220 cm (B, C, D) above the MLLW at Cove Island, was bladder wrack *Fucus vesiculosus* with its peak in zone B, closely followed by zone C. In the sublittoral fringe, *Chondrus crispus* was the main species with an overall average cover of 78%. Such a zonal pattern was also found earlier in the intertidal zone along the New England coast (Lubchenco and Menge 1978; Lubchenco 1980; Menge 1976). Other studies found that, at more exposed coasts, barnacles and the mussel *Mytilus edulis* were more dominant (Lubchenco and Menge 1978; Menge 1976).

By recording percentage cover at low tide by placing a frame randomly on top of the algae cover underestimates the abundance or percentage cover of many species. Underestimation is especially the case for understory flora and fauna, as well as for thin filamentous and membranous algae. In the fucoid belt, periwinkles and small predators, as well as other species of algae, might have been hidden under the fucoids. It was, however, easier to detect such species in the *Chondrus* belt at MLLW due to the upright shape of the Irish moss. *Porphyra* spp. were especially problematic to estimate at low tide. Thin membranous species will collapse and percentage cover will be significantly reduced. Hence, the maximum percent cover of *Porphyra* spp. and herbivores like periwinkles, were underestimated at low tide, but the consistency in the method made registrations applicable in the analysis.

The *Porphyra* species occurring at Cove Island varied in abundance within the zones, and also their occurrences peaked at different times during fall to spring. Thallus thickness of *P. leucosticta* Type C, which occurred in all

Table 7 Average abundance (percentage cover) and contribution of the 7 most important species/taxa groups to the distribution of samples within each zone in the MDS analysis (Fig. 6)

Species	Av. abund.	Av. abund.	Contrib. %	Cum. %	Species	Av. abund.	Av. abund.	Contrib. %	Cum. %
	Zones A and B: average dissimilarity=50.21					Zones C and D: average dissimilarity=63.12			
	Zone A	Zone B				Zone C	Zone D		
Fucus vesiculosus	8.18	68.03	12.46	12.46	*Chondrus crispus*	0.19	17.24	8.81	8.81
Mytilus edulis	0.27	4.5	9.96	22.42	Balanoids	18.99	0.29	7.91	16.72
Balanoids	18.16	19.61	9.17	31.6	*Codium fragile*	0	13.26	7.6	24.32
Ulothrix/Urospora	10.98	1.93	8.99	40.59	*Blidingia minima*	2.95	0.04	4.48	28.8
Blidingia minima	13.75	7.44	8.57	49.16	*Enteromorpha linza*	7.67	2.89	4.47	33.27
Enteromorpha linza	2.4	2.62	6.95	56.11	*Ceramium rubrum*	0.03	5.26	4.25	37.52
Porphyra suborbiculata	1.57	1.14	6.21	62.32	*Hildenbrandia rubra*	2.45	0.59	4.21	41.73
	Zones A and C: average dissimilarity=56.66					Zones A and E: average dissimilarity=91.39			
	Zone A	Zone C				Zone A	Zone E		
Fucus vesiculosus	8.18	55.42	9.69	9.69	*Chondrus crispus*	0	77.61	15.15	15.15
Enteromorpha linza	2.4	7.67	8.52	18.22	*Ulva lactuca*	0	8.99	7.66	22.81
Blidingia minima	13.75	2.95	8.15	26.37	Balanoids	18.16	0	7.32	30.12
Balanoids	18.16	18.99	7.87	34.24	*Blidingia minima*	13.75	0	7.2	37.33
Ulothrix/Urospora	10.98	2.79	7.69	41.93	*Ulothrix/Urospora*	10.98	0.06	5.69	43.02
Hildenbrandia rubra	0.29	2.45	6.35	48.28	*Fucus vesiculosus*	8.18	1.38	4.32	47.33
Ulva lactuca	0	1.61	6.18	54.46	*Polysiphonia urceolata*	0	1.44	4.23	51.56
	Zones B and C: average dissimilarity=42.89					Zones B and E: average dissimilarity=89.34			
	Zone B	Zone C				Zone B	Zone E		
Enteromorpha linza	2.62	7.67	8.36	8.36	*Chondrus crispus*	0.01	77.61	12.46	12.46
Mytilus edulis	4.5	1.23	7.72	16.08	*Fucus vesiculosus*	68.03	1.38	9	21.46
Blidingia minima	7.44	2.95	7.02	23.1	Balanoids	19.61	0	8.36	29.82
Hildenbrandia rubra	0.42	2.45	6.54	29.64	*Ulva lactuca*	0.06	8.99	5.63	35.44
Ulothrix/Urospora	1.93	2.79	6.44	36.08	*Mytilus edulis*	4.5	0	5.62	41.07
Ostrea sp	0.67	0.21	6.35	42.43	*Blidingia minima*	7.44	0	5.34	46.4
Enteromorpha prolifera	3.03	5.75	6.35	48.78	*Polysiphonia urceolata*	0	1.44	3.53	49.94
	Zones A and D: average dissimilarity=79.44					Zones C and E: average dissimilarity=82.81			
	Zone A	Zone D				Zone C	Zone E		
Chondrus crispus	0	17.24	9.17	9.17	*Chondrus crispus*	0.19	77.61	12.67	12.67
Codium fragile	0	13.26	7.3	16.47	*Fucus vesiculosus*	55.42	1.38	8.88	21.55
Blidingia minima	13.75	0.04	6.82	23.29	Balanoids	18.99	0	8.17	29.72
Balanoids	18.16	0.29	6.09	29.38	*Enteromorpha linza*	7.67	0.34	4.68	34.41
Ulva lactuca	0	5.67	5.96	35.34	*Hildenbrandia rubra*	2.45	0	4.11	38.51
Ulothrix/Urospora	10.98	1.19	4.82	40.16	*Blidingia minima*	2.95	0	4.01	42.52
Enteromorpha linza	2.4	2.89	4.68	44.84	*Ulva lactuca*	1.61	8.99	3.96	46.49
	Zones B and D: average dissimilarity=70.2					Zones D and E: average dissimilarity=57.79			
	Zone B	Zone D				Zone D	Zone E		
Chondrus crispus	0.01	17.24	8.56	8.56	*Fucus vesiculosus*	36.53	1.38	9.58	9.58
Balanoids	19.61	0.29	7.86	16.43	*Chondrus crispus*	17.24	77.61	6.31	15.89
Codium fragile	0	13.26	6.95	23.38	*Codium fragile*	13.26	0.91	5.33	21.22
Mytilus edulis	4.5	0	6.17	29.55	*Enteromorpha linza*	2.89	0.34	5.18	26.4
Blidingia minima	7.44	0.04	5.71	35.26	*Ceramium rubrum*	5.26	2.47	4.81	31.21
Ulva lactuca	0.06	5.67	5.11	40.37	Ectocarpaceae	2.68	5.17	4.8	36.01
Ceramium rubrum	0	5.26	3.9	44.27	*Ulva lactuca*	5.67	8.99	4.13	40.14

zones from A to E, seemed to increase the higher it was found in the mid-littoral. The same pattern has been found for species of *Porphyra* occurring in China (personal communication). This might be due to the specimens different exposure to desiccation. Thick cell walls might preserve water better during period of desiccation than thin specimens, hence the gradient in thickness. The thinnest *Porphyra* sp was *P. leucosticta* Type A which was found in

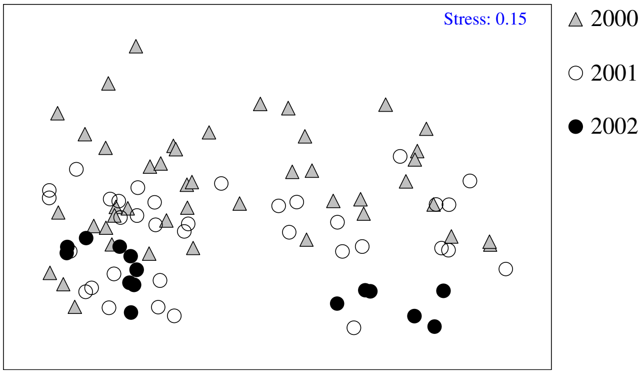

Fig. 7 Multidimensional Scalingof the community structure at Cove Island from January 2000 to May 2002 with years as overlay

the infra-littoral fringe and thereby less exposed to desiccation.

At Cove Island, *C. cripsus* was the dominating species around MLLW and beyond (−40cm). A top-down regulation was suggested to promote establishment of *C. crispus* in sheltered areas in New England; predators like starfish (*Asteria forbesi* and *Asterias vulgaris*), dogwinkles (*Nucella lapillus*) and periwinkles (*Littorina littorea*) have been shown to prevent establishment of the competitive dominant *Mytilus edulis* in mid- and lower mid-littoral zones (Lubchenco and Menge 1978; Menge 2000; Petraitis 1983, 1987). Periwinkles (*Littorina littorea, L. obtusata* L. and small *Littorina* sp.) were observed within the frames among *F. vesiculosus* at Cove Island, but their abundance was low (average < 0.4%). A top-down regulation suggested by Lubchenco (1983) explains to some extent the main zonation pattern at Cove Island. A mid-littoral zone consisting of more or less small rocks and pebbles next to the study site (2–3 m) was dominated by periwinkles. Very little vegetation was found here and the periwinkles most probably prevented all recruitment of alga by heavy grazing, hence supporting a potential impact at our study site.

Table 8 Result of a two-way crossed ANOVA (ANOSIM) on the community structure between years and between zones with years as samples

Groups	Pairwise tests	
	R statistic	Significance level %
A – B	0.405	0.1
A – C	0.633	0.1
A – D	0.978	0.1
A – E	0.998	0.1
B – C	0.351	0.1
B – D	0.952	0.1
B – E	1	0.1
C – D	0.786	0.1
C – E	0.993	0.1
D – E	0.559	0.1

Tests for differences between Year groups (averaged across all Zone groups): Global test; sample statistic (Global *R*): 0.226 ($p<0.001$)
Tests for differences between Zone groups (averaged across all Year groups): Global test; sample statistic (Global *R*): 0.743 ($p<0.001$)

Table 9 Result of two-way nested ANOVA (ANOSIM) on community structure between seasons and between zones with season groups as samples. (A-E are the different zones in the intertidal)

Groups	Pairwise tests	
	R statistic	Significance level %
A – B	0.854	2.9
A – C	0.844	2.9
A – D	1.000	2.9
A – E	1.000	2.9
B – C	0.927	2.9
B – D	1.000	2.9
B – E	1.000	2.9
C – D	1.000	2.9
C – E	1.000	2.9
D – E	0.969	2.9

Global R=0.324, $p<0.001$ for tests between season groups (averaged across zone groups)
Global R=0.942, $p<0.001$ for test between zone groups (using season groups as samples)

Climate and environmental data

The environmental factors salinity, temperature and nitrate-nitrite concentration in the surface water (<2 m depth) clearly showed a natural seasonal pattern (Fig. 2), and when run in a PCA the seasonal pattern resulted in a cyclic pattern (Fig. 3). The reduction in nutrients during spring of the respective years indicates that the spring bloom started earlier in 2001 than the other years, and in 2002 the seawater was still not nitrate-depleted in April. The bacterial remineralization of organic matter to nitrate and nitrite started in September–October. The PCA showed that January and February 2002 did separate from the same periods the previous years (Fig. 3), and do to some extent coincide with the configuration in the PCA for climate data (Fig. 4). The position of December 2001, February 2002 and especially January 2002 were placed farthest off on PC2 with respect to these months in 2000 and 2001, showing the climate influence on the surface water environment in LIS (Fig. 4).

Multivariate analysis of community structure

The MDS plot of the biological data (Fig. 6) showed that the community structure formed distinct zones, and they were placed in the MDS plot according to the order in which they formed the littoral zone from the upper zone A to the lowest zone E. The zones were significantly different from each other (Table 6). As shown in Table 8, *F. vesiculosus* dominated in the middle zones B, C and D, and *C. crispus* was irrefutably the dominant species in the sublittoral fringe (zone E). These patterns coincide with the structure found in the littoral shores of protected and semi-protected shores in New England (Lubchenco 1980, 1983; Menge 1976).

The community structure from January to April was different in 2002 than in the two previous years. This corresponds with differences in environmental data from LIS (Fig. 3) and climate data from Stamford (Fig. 4), where the winter months were plotted far from each other. High temperature in LIS and in the air during the winter 2001/2002 coincided with the changes in species abundances during same period. High temperature significantly promoted the occurrence of *Codium fragile, Porphyra* spp. and other red alga like *Ceramium virgatum* ($p<0.01$) at the sacrifice of *Blidingia minima, Fucus vesiculosus* and *Ulva lactuca.*

Statistically comparing biological and environmental data

BIO-ENV was used to test the concordance between environmental (including climate) data and biological data. One might expect that EMNT (Extreme minimum air temperature of the month) would be more important in zones A and B than further down on the shoreline, as A and B are the zones mostly exposed to air. The water temperature will reflect air temperatures, but at a much slower and delayed response and less fluctuating patterns. This was also the case in our findings.

Our analysis includes a limited numbers of environmental factors. PAR (photosynthetically active radiation) is an important environmental factor for structuring communities and algal growth, but it has not been recorded here. Hence, one cannot conclude that the combination of environmental factors resulting in a significant concordance with the biological matrices in this paper are the only factors determining the community structure. However, correlations found here between community structure and environmental factors are indications that the factors are important in regulating the community structure at our site at Cove Island.

In general, the community structure at Cove Island was similar to other shorelines described for medium to sheltered New England shorelines, with a dominating zone of *F. vesiculosus* in mid-littoral zone and a luxurious *C. cripus* belt in the upper infra-littoral zone (Bertness and Leonard 1976; Leonard 2000; Lubchenco 1980, 1983; Mathieson et al. 1976, 1981a, b; Mathieson and Penniman 1986; Menge 1976, 1991; Petraitis 1987). Three *Porphyra* spp were recorded and they all occurred in the fall to spring period, although with spatial and temporal differences in peak abundances. The different species showed a conspicuous variation among the years and all seem to increase during the unusually warm winter of 2001/2002.

Significant annual variation in different environmental factor was reflected in differences in community structure between 2001 and 2002 as documented in this paper. Of the environmental factors tested, temperature was shown to be the most important factor. The most prominent responses to increase in temperature were increases in several Rhodophytes and decline in the Fucoids population. A decline in *Ascophyllum nodosum* populations as a response to an increase in water temperature (Keser et al. 2005) for the eastern LIS, coincides with the results in this paper. The unusual high temperature during winter/spring 2002 turned back to normal temperatures in fall 2002. We have no data on the community structure in late 2002 and winter 2003, but one would expect the community structure during fall and winter 2002/2003 to oscillate back to similar assemblages occurring in 2000–2001. The community structure at Cove Island is most probably regulated both by top-down forces like grazing by periwinkles as suggested by several authors (Dudgeon et al. 1999; Lubchenco 1983; Menge 1976, 1978a, b, 1983; Petraitis 1987) but also as shown in this paper, from bottom-up regulating forces (Bertness et al. 1999a, b; Menge et al. 1999; Menge 2000) like air and seawater surface temperatures (depth <2 m) in LIS.

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