From flatfish to sticklebacks: assemblage structure of epibenthic fauna in relation to macroalgal blooms

H. Wennhage*, L. Pihl

Department of Marine Ecology, Kristineberg Marine Research Station, Göteborg University, 450 34 Fiskebäckskil, Sweden

ABSTRACT: On the Swedish west coast, blooms of green macroalgae have become a common feature over recent decades. Assemblage structure of epibenthic fauna was studied in randomly selected shallow soft substratum bays, with and without macroalgae, using quantitative sampling techniques. The study was performed biannually (June and August) over 4 yr in 4 regions along the coast. Mat-forming macroalgae on average covered 35 % of the surface area in vegetated bays, with an overall mean biomass of 100 g DW m^{-2}. The assemblage structure of epibenthic fauna was different in the presence of macroalgae, a pattern which was consistent over years and regions. Within the subset of bays containing vegetation, there were no bay-scale relationships between the biomass of algae and the abundance, biomass or number of species of epibenthic fauna. However, a detailed analysis revealed that the species had different responses to an increase in algal biomass at the scale of individual samples (0.5 m^2). The flatfish *Pleuronectes platessa* occurred predominantly in samples completely free of vegetation. The shrimp *Crangon crangon* and the gobies *Pomatoschistus* spp. were found most commonly in the open sand habitat, and rapidly decreased in abundance with increasing biomass of algae. *Gobius niger*, Mysidacea, *Anguilla anguilla*, *Sygnathus typhle* and *Palaemon* spp. were most prevalent at a low to moderate biomass of algae. Sticklebacks (*Pungitius pungitius* and *Gasterosteus aculeatus*) increased in abundance with increasing algal biomass, and remained dominant at the highest level of algal biomass recorded. Thus, macroalgal blooms have the potential to change the structure and function of shallow soft substratum habitats, lowering their value as nursery and feeding grounds for commercial fish species.

KEY WORDS: Habitat · Epibenthic predators · Green macroalgae · Biodiversity · *Pleuronectes platessa* · *Gasterosteus aculeatus* · Fish · Nursery ground

INTRODUCTION

Degradation or loss of shallow water habitats may cause drastic changes in the structure and function of coastal ecosystems. These changes are often caused by anthropogenic stressors, which transfer the system into an alternate state with new component organisms in the food web. An example is blooms of green macroalgae that have become a common feature in intertidal and shallow waters around much of the world's coastlines (reviewed in Raffaelli et al. 1998). Eutrophication is generally considered to have caused the increase in such habitat-forming macroalgae (e.g. Valiela et al. 1997). In shallow sandy areas, blooms of green algae may change the habitat characteristics dramatically, from bare sediment habitats to habitats with dense mats of green macroalgae that may extend from the bottom up to the water surface. Similar dramatic shifts in habitat complexity have been described in several other aquatic and terrestrial environments, leading to profound changes in the ecosystem structure and function (Scheffer et al. 2001). Aquatic examples where habitat-forming vegetation plays a key role in ecosystem shifts include eutrophication of lakes (e.g. Scheffer

et al. 1993), kelp deforestation (Steneck et al. 2002), and degradation of coral reefs (e.g. McCook 1999). Blooms of green macroalgae change not only the physical structure of shallow coastal areas dramatically, turning open sand substratum into densely vegetated habitats; they also reduce water circulation, which together with increased decomposition and respiration from the algae, may lead to oxygen depletion in the bottom water and sediment (e.g. Krause-Jensen et al. 1999). In addition, green macroalgae release exudates that may be toxic to animals (Johnson & Welsh 1985, Larson 1997). In concert, these changes in biotic and abiotic factors create a new environment with very different conditions for the animals living therein.

Macroalgal blooms are normally seasonal in temperate shallow coastal environments, with a proliferation of thalli in spring, development of mats in summer, followed by a decay of the mats in autumn (Pihl et al. 1996, Berglund et al. 2003, Nelson et al. 2003). The faunal assemblages occupying these waters are also highly dynamic. On the Swedish west coast, settlement of new recruits occurs predominantly during spring and summer, and established populations increase rapidly in biomass over the season (Möller et al. 1985). Motile species normally leave these habitats before the winter and return the following spring (Pihl & Rosenberg 1982). A large number of coastal fish species use the shallow habitat as nursery or feeding grounds during the productive part of the year (Pihl & Wennhage 2002, Wennhage & Pihl 2002). The fish assemblage includes recruits of commercially important species such as cod and flounder (Pihl 1982), and newly settled juveniles of plaice (Pihl & Rosenberg 1982). The motile fauna make use of the rich food production and predator refuge of the shallow habitat through seasonal and diurnal migrations (Gibson et al. 1998). Consequently, macroalgal blooms coincide with the seasonal peak in recruitment and production of the faunal assemblage in shallow soft substratum habitats.

Numerous studies have documented the ecological effects of macroalgal blooms on the benthic fauna found in the underlying sediment (reviewed in Raffaelli et al. 1998). A number of studies have also investigated the impact of blooms on the distribution and foraging success of wading birds (e.g. Lewis et al. 2003), and fish (e.g. Isaksson et al. 1994). These faunal groups, which constitute important prey and predators of the epibenthic fauna, generally show clear responses to the presence of algae. To our knowledge, the effect of macroalgal blooms on the assemblage of epibenthic fauna has not been studied in detail previously. A historical comparison of a bay that became increasingly covered with macroalgae over the years (Isaksson & Pihl 1992), did however, suggest that the presence of mat-forming algae results in pronounced differences in the structure of the epibenthic assemblage.

Shallow sandy habitats in the North Sea region have only a few epibenthic species occurring at high densities (e.g. Pihl & Rosenberg 1982, Burrows et al. 1994). They are all well adapted to the variable physical environment and use the soft sediment substratum for protection and food search. In shallow sandy bays on the Swedish west coast, the assemblage of epibenthic fauna typically consists of 5 to 10 species that are present in the habitat from spring to autumn. Two crustaceans *Crangon crangon* and *Carcinus maenas* and 4 fishes *Pleuronectes platessa*, *Platichthys flesus*, *Pomatoschistus minutus* and *P. microps* are the numerically dominant species in most areas (Pihl 1986). The total abundance of the assemblage fluctuates between 20 and 100 ind. m^{-2} during the summer, and the annual production amounts to approximately 5 g AFDW m^{-2} (Pihl & Rosenberg 1982).

In the present study, we report an extensive field study into the effects of green macroalgae on the assemblage structure of epibenthic fauna. The study was replicated in 4 regions along the Swedish west coast to establish general coast-wide patterns, and was repeated over 4 years to account for inter-annual variability in recruitment and survival of component species. Furthermore, we studied how abundance of epibenthic species is related to the biomass of algae at the scale of individual samples (metre scale).

MATERIALS AND METHODS

Study area and sampling design. This study was carried out along the Swedish west coast archipelago bordering the Skagerrak (Fig. 1). The archipelago is complex, with hundreds of islands of varying size forming a mosaic pattern of shallow soft substratum interrupted by rocky habitats. The habitats studied are small shallow bays (surface area from 2 to 5 ha), generally bordered by rocky areas and separated from deeper soft substratum by seagrass beds (*Zostera marina*) starting at approximately 0.7 m depth and extending towards 5 m depth. Such bays have a sandy-silt sediment structure with an organic matter content of 1 to 3% by weight where vegetation is absent. The tidal amplitude is small (0.2 m) and the coast is influenced by the Baltic current, which results in surface water salinities that normally fluctuate between 14 and 24 PSU during the summer. During the summer season, daily mean surface water temperature typically fluctuates between 17 and 20°C (Pihl & Rosenberg 1982). Sampling was performed in June and August over a 4 yr period (1999–2002). Sixteen bays were sampled within 12 d during any one of the sampling periods.

Information from aerial photographic surveys of the distribution of algal mats, repeated each year in June and August along the coast, was used to list available bays with vegetation (L. Pihl unpubl. data). Aerial pho-
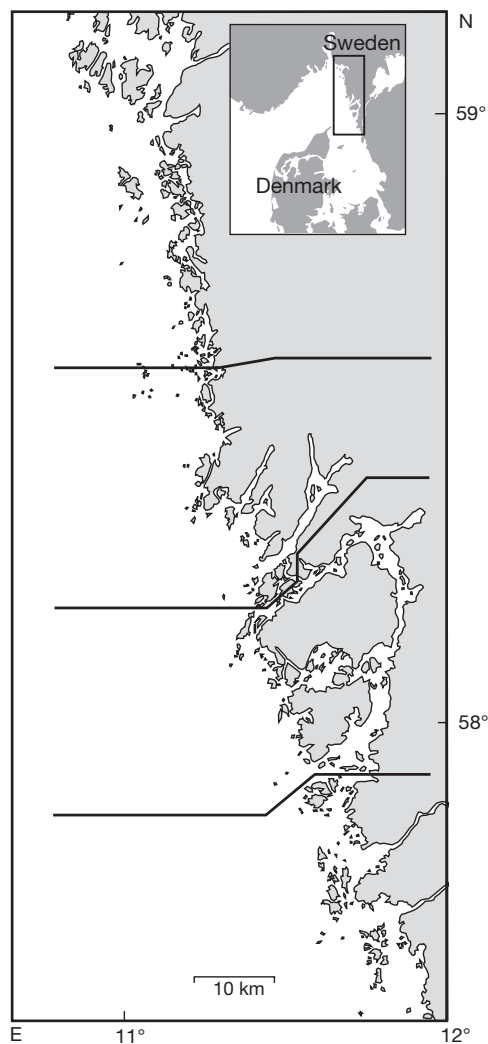

Fig. 1. Location of the study area in the Swedish west coast archipelago. The coastline was divided into 4 regions shown (reflecting catchment areas). Sampling was performed in bays randomly selected on each sampling occasion

tographs were analysed following methods evaluated by Pihl et al. (1999). The coastline was divided into 4 regions based on catchment areas used by the Swedish Meteorological and Hydrological Institute and an earlier study describing the distribution of green macroalgal mats (Pihl et al. 1999). Within each region, 2 bays where macroalgal mats had developed were chosen randomly on each sampling occasion from the list of available bays. For each vegetated bay, the closest similar bay without vegetation was chosen to represent the open sand habitat. Two bays with algae and 2 bays with open sand substratum were sampled within each of the 4 regions on each sampling occasion, resulting in 64 vegetated and 64 open sand bays being sampled. Ten drop-trap samples were randomly allocated within the depth range zero to 0.7 m in each bay. Drop-traps are square boxes that enclose 0.5 m^2 of the sediment and the overlying water. This sampling gear has been shown to be quantitative and close to 100 % efficient for the dominant species of epibenthic fauna on shallow soft substrata (Pihl & Rosenberg 1982, Wennhage et al. 1997). In bays with vegetation, sampling was restricted to areas covered with algae. Animals were subsequently hand-netted (2 mm mesh) out of the drop-traps and preserved in 70 % ethanol. All epibenthic fauna were determined to the lowest possible taxonomic level, enumerated and the wet weight (WW) biomass was estimated for each taxon within each sample.

Sediments and algae. Sediment characteristics were analysed from 5 random samples in all bays during the June sampling of each year. Samples were collected with a core sampler (5 cm^2) from the sediment surface to a depth of 2 cm. Sediment samples were transported on ice to the laboratory and were freeze-dried subsequently. Total carbon and nitrogen content (mg g^{-1} freeze-dried sediment) was estimated using an elemental analyzer (Fison Instruments). Mean total contents of carbon and nitrogen are given in Table 1.

Cover and biomass of macroalgae was estimated for all bays in the vegetated category. Cover of algae (%) in the bays was estimated from aerial photographs analysed through projection onto a digitising table

Table 1. Mean (SD) total content of carbon and nitrogen given as dry weight (DW) % in the upper 2 cm of sediment by habitat and region. n = 8

Habitat	Region								All regions	
	1		2		3		4			
Total carbon										
Algae	3.80	(2.94)	1.25	(0.95)	1.80	(1.20)	0.66	(0.41)	1.88	(2.02)
Sand	0.49	(0.29)	0.78	(0.76)	0.45	(0.24)	0.75	(0.56)	0.62	(0.52)
Total nitrogen										
Algae	0.41	(0.33)	0.13	(0.10)	0.19	(0.13)	0.07	(0.04)	0.20	(0.22)
Sand	0.04	(0.03)	0.08	(0.08)	0.05	(0.02)	0.08	(0.06)	0.06	(0.05)

(Sigma Scan software), and verified through ground truth visual inspections. Biomass of algae was estimated by taking 5 random samples in each bay with a cylindrical sampler (area: 0.035 m^2). The samples of algae were frozen. Samples of algae were subsequently thawed in the laboratory and cleaned of fauna and sediment. Dry weight (g DW; m^{-2}) of algae was obtained after drying to constant weight at 70°C. Qualitative field observations were made to establish the predominant growth form (thread/leaf-like) of algae and the dominant taxa within the mat. Additional small samples of algae (approx. 100 cm^3; n = 5) were taken in each bay to check the species composition. The smaller samples were checked in a binocular microscope to establish the presence/absence of different taxa of algae. In 2002, the biomass of algae was linked to individual drop-trap samples by taking samples of seaweeds next to each faunal sample in all vegetated bays (n = 160).

Statistical analysis. Assemblage structure of epibenthic fauna was compared using multivariate analyses within the PRIMER package. Abundance data were square root transformed to weigh the relative importance of common and rare species in the analyses. Bray-Curtis similarity indices were computed and the resulting similarity matrices were then used to perform non-metric Multi Dimensional Scaling (MDS). An analysis of similarities (ANOSIM) was used to test for differences in assemblage structure across habitats, regions, seasons and years (method in Clarke 1993). Vegetation biomass was superimposed on the 2 dimensional representation of the MDS to investigate relationships between the local vegetation biomass and the assemblage structure of epibenthic fauna. The proportional contribution of different taxa to the dissimilarity between groups was investigated using the SIMPER software within the PRIMER package. Abundance, biomass and number of species were compared using 2-factor ANOVA with habitat and region as factors. Normality of the data was checked with Kolmogorov Smirnov's test and homogeneity of variances using Levene's test. Biomass data were square-root transformed to remove heterogeneity of variances.

Table 2. Average cover (%) of macroalgae in the vegetated bays by region and year

Year	Region				All regions
	1	2	3	4	
1999	59.8	34.5	50.8	46.8	47.9
2000	31.3	26.3	45.0	25.0	31.9
2001	47.5	31.3	30.0	18.3	32.7
2002	68.3	24.3	9.8	12.3	28.6
All years	51.7	29.1	33.9	26.1	35.3

RESULTS

Macroalgal mats

The cover of macroalgae showed temporal (among years) and spatial (among regions) variation. The highest cover of algae in vegetated bays was found in 1999, with an average of 48% of the bay surfaces being covered by seaweeds (Table 2). From 2000 to 2002, the cover ranged from 29 to 33%. Region 1 had the highest average cover amounting to 52% of the surface area in the region. In regions 2 to 4 the average cover ranged from 26 to 34%.

The biomass of algae showed only a limited variation at the largest temporal (among years across regions) and spatial (among regions across years) scales (Table 3). The average biomass ranged from 108 ± 13 (SD) g DW m^{-2} in the north (Region 1) to 84 ± 15 (SD) g DW m^{-2} in the south (Region 4), and the yearly mean biomass varied from 73 to 123 g DW m^{-2}. The biomass of algae in individual vegetated bays ranged from 24 to 259 g DW m^{-2}, with an overall mean biomass of 100 ± 53 (SD) g DW m^{-2} during the investigation. There was no correlation between the cover and biomass of algae within bays (Fig. 2).

The macroalgal mats were generally made up of several taxa, with a maximum of 7 taxa in an individual bay. Members of the genera *Ulva* and *Cladophora* were present in all vegetated bays, and they commonly dominated the samples of algae. *Ulothrix*, *Rhizoclonium*, *Lyngbya*, *Percursaria* and *Chaetomorpha*

Table 3. Biomass of macroalgae (g DW m^{-2}; SD in parentheses) in the vegetated bays by region and year

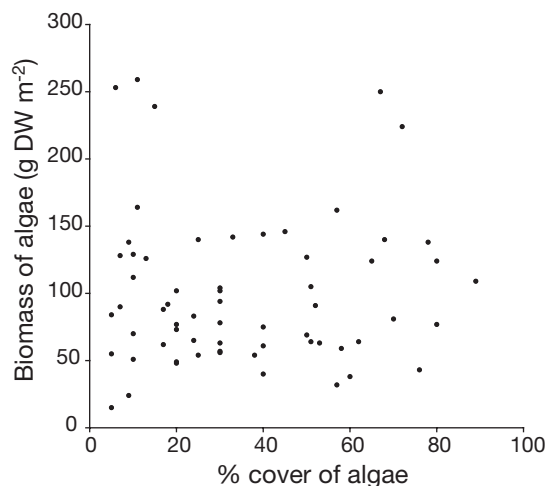| Year	Region								All regions
	1		2		3		4		
1999	113.8	(40.8)	126.0	(82.3)	91.5	(46.4)	69.5	(14.5)	100.2
2000	95.5	(36.5)	50.5	(7.4)	72.5	(7.7)	71.8	(55.8)	72.6
2001	99.5	(33.0)	140.5	(67.2)	68.3	(26.4)	100.3	(46.6)	102.1
2002	124.3	(93.6)	110.0	(27.0)	165.5	(112.5)	93.3	(34.1)	123.3
All years	108.3		106.8		99.4		83.7		99.5

Fig. 2. Relationship between cover (% of surface area) and biomass of macroalgae (g DW m^{-2}) in the vegetated bays. No significant relationship was found (n = 64, p > 0.05, R^2 = 0.0012)

were present in more than 40% of the bays, but only rarely dominated the algal samples. *Pilayella*, *Ectocarpus*, *Oedogonium* and *Ceramium* were encountered in less than 10% of the bays. Visual examination in the field showed that *Ulva* and/or *Cladophora* were indeed dominant taxa in the mats in all of the bays. All of the algal mats in the vegetated bays were categorised as thread-like in their growth form.

Abundance, biomass and species of epibenthic fauna

Bare sediment and vegetated substrata differed in both the total density and biomass of animals as well as in the proportional contribution of different species within the assemblages. The open sand habitat had an average of 24.4 ± 24.3 (SD) ind. m^{-2}, which was significantly lower (Table 4) than the density of animals in the vegetated habitat (53.7 ± 65.1 [SD] ind. m^{-2}). Total biomass of epibenthic fauna differed (Table 4) between the 2 habitats and was estimated to be 4.5 ± 3.9 (SD) g m^{-2} and 8.3 ± 6.8 (SD) g m^{-2} in the vegetation free and vegetated bays, respectively. The average number of epibenthic species encountered in the bare sediment bays (6.7 ± 2.3 [SD] species per bay) did not differ significantly (Table 4) from the number of species (7.3 ± 2.6 [SD]) in the vegetated bays. In total, 15 taxa of epifauna were recorded, and all taxa were common to both habitats.

Spatial and temporal patterns in faunal assemblage structure

The multivariate analyses performed to investigate temporal and spatial patterns in assemblage structure

were based on abundance data of the different species of epibenthic fauna. There was no evidence of differences among years (ANOSIM: Global R = 0.021, p > 0.05) or among regions (ANOSIM: Global R = 0.020, p > 0.05) in the composition of epibenthic fauna (Fig. 3a,b). All 4 years and 4 regions were therefore pooled in the analyses of seasonal patterns and patterns related to habitat structure.

Habitat type (bare sand versus vegetated substratum) had a significant effect on faunal assemblage structure (ANOSIM: Global R = 0.751, p < 0.001; Fig. 3c). The 2 species of sticklebacks and *Palaemon adspersus* had dramatically higher densities in the vegetated habitat, whereas *Crangon crangon*, together with *Pleuronectes platessa* showed the opposite pattern with more than a magnitude higher abundances on sand (Table 5). The assemblage structure of epibenthic fauna, however, did not show any clear pattern in relation to the differences in biomass of algae among vegetated bays (Fig. 3d).

There was a significant effect of season (June versus August) on the assemblage structure of epibenthic fauna (ANOSIM: Global R = 0.114, p < 0.01; Fig. 3c). Visual inspection of the MDS plot suggested that the effect of season was more pronounced in the open sand habitat than in the vegetated habitat (Fig. 3c), and the effect of season was therefore reanalysed within the 2 habitats separately. In the open sand habitat, there was a significant effect of season on the faunal assemblage structure (ANOSIM: Global R = 0.372, p < 0.001). This difference was caused mainly by an increase in the abundance of *Crangon crangon*, *Carci-*

Table 4. Two-factor ANOVA for effects of habitat and region on number of animal species, animal density and animal biomass. **Bold** p values were significant at <0.05 after Bonferroni correction for multiple pairwise testing

Source	df	MS	F	p
Number of species				
Habitat	1	11.28	2.00	0.160
Region	3	26.20	4.65	**0.004**
H × R	3	4.70	0.83	0.478
Residual	120	5.63		
Density				
Habitat	1	27372.00	10.82	**0.001**
Region	3	54.64	0.02	0.996
H × R	3	117.84	0.05	0.987
Residual	120	2530.55		
Biomass[a]				
Habitat	1	16.03	19.91	**<0.001**
Region	3	2.38	2.95	0.035
H × R	3	1.00	1.24	0.300
Residual	120	0.81		
[a]Square-root transformed to remove heterogeneity of variances				

nus maenas, Mysidacea and *Pomatoschistus* spp. from June to August (Table 6). In the vegetated habitat there was also a significant effect of season (ANOSIM: Global R = 0.106, p < 0.05), but the low R value sug-
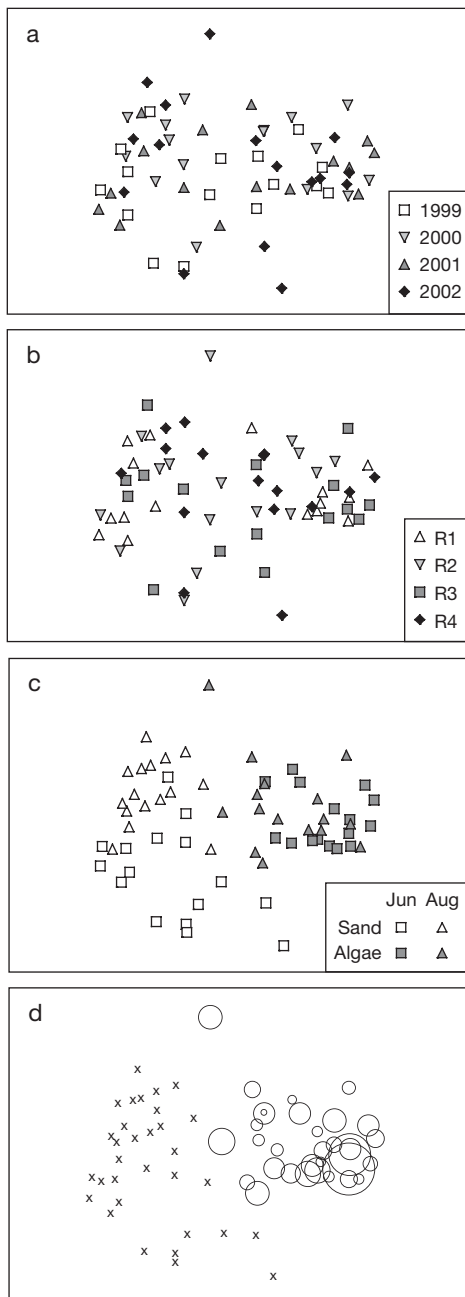
gests that differences were small in relation to the variation within season. A decrease in the abundance of the 2 stickleback species together with an increase in the abundance of Mysidacea and *Pomatoschistus* spp. caused the main seasonal difference in assemblage structure observed in the vegetated habitat (Table 6).

Brown shrimp *Crangon crangon*, shore crabs *Carcinus maenas*, and mysids Mysidacea were the numerically dominant species in the open sand habitat (Fig. 4a). In the vegetated habitat, 3-spined stickleback *Gasterosteus aculeatus*, 9-spined stickleback *Pungi-*

Fig. 3. MDS ordination of epibenthic fauna assemblage data, based on a Bray-Curtis similarity matrix of square-root transformed abundance data for all species encountered (stress value 0.15). (a) Bays contrasted by year, (b) bays contrasted by region (Fig. 1), (c) bays contrasted by habitat and season, (d) biomass of algae superimposed with the diameter of circles being proportional to the biomass value and × denoting bays without vegetation

Table 5. Abundances of taxa (N m^{-2}) most responsible for the differences in assemblage structure of epibenthic fauna between the vegetated and sand habitats, listed in the order of their contribution to the average Bray-Curtis dissimilarity

Species	Average abundance	
	Algae	Sand
Gasterosteus aculeatus	17.2	0.8
Pungitius pungitius	10.79	0.1
Crangon crangon	1.19	13.42
Palaemon adspersus	4.99	0.48
Mysidacea	5.07	2.92
Carcinus maenas	2.83	3.64
Pomatoschistus microps	2.13	1.16
Pomatoschistus spp. (juvenile)	0.84	0.73
Palaemon elegans	0.86	0.48
Pomatoschistus minutus	0.59	0.47
Pleuronectes platessa	0.03	0.45

Table 6. Abundances of animal taxa (N m^{-2}) most responsible for the change in assemblage structure from June to August in the sand and vegetated habitat, listed in the order of their contribution to the average Bray-Curtis dissimilarity

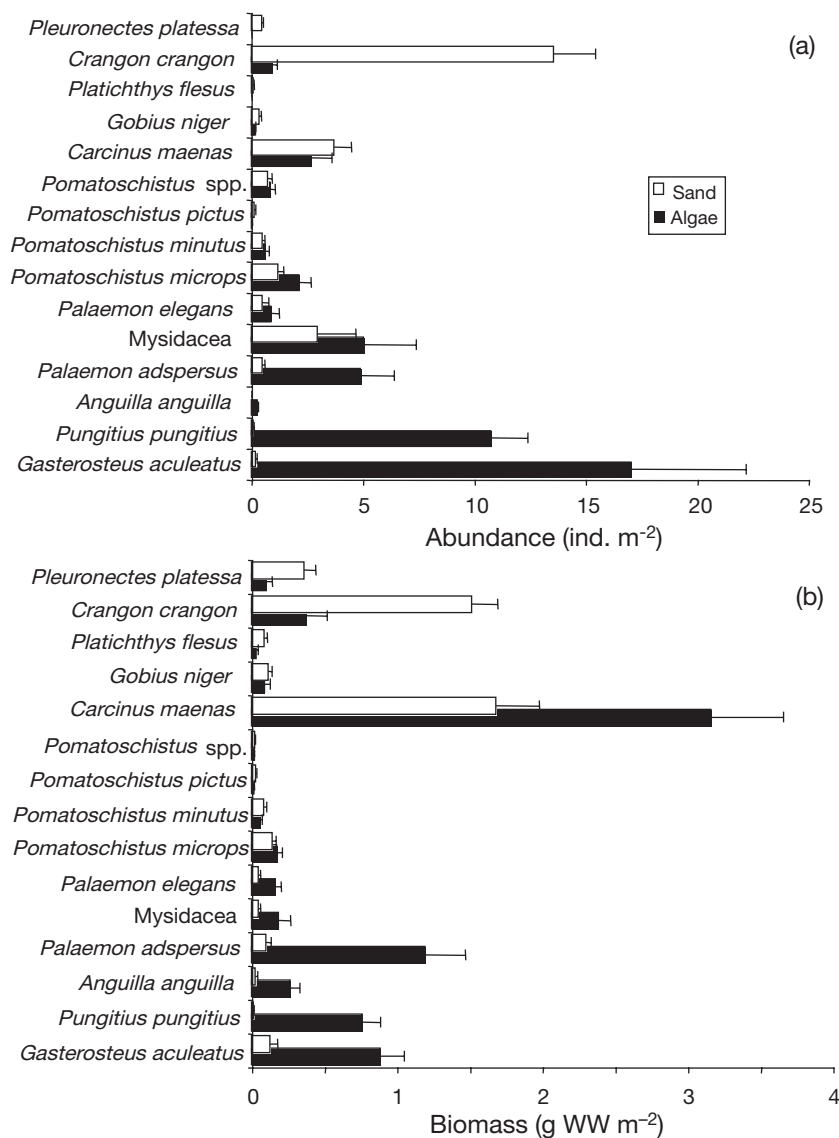| Species	Average abundance	
	June	August
Sand habitat		
Crangon crangon	5.56	21.28
Carcinus maenas	1.49	5.79
Mysidacea	0.68	5.16
Pomatoschistus microps	0.36	1.96
Pomatoschistus spp. (juvenile)	0.44	1.02
Gasterosteus aculeatus	0.38	1.23
Pomatoschistus minutus	0.23	0.71
Palaemon adspersus	0.51	0.44
Pleuronectes platessa	0.59	0.31
Vegetated habitat		
Gasterosteus aculeatus	26.62	7.78
Pungitius pungitius	12.89	8.7
Mysidacea	3.38	6.76
Pomatoschistus microps	0.94	3.32
Palaemon adspersus	2.97	7.01
Carcinus maenas	1.48	4.19
Crangon crangon	0.46	1.92
Pomatoschistus spp. (juvenile)	0.25	1.43
Palaemon elegans	0.56	1.17

Fig. 4. Comparison of epibenthic fauna found in algal mats and in bays without vegetation. (a) Density of animals m^{-2}, (b) wet weight (WW) biomass of animals m^{-2} (n = 64, +SE)

than in the open sand habitat (1.8 vs. 0.2%). In terms of biomass, the shore crab *C. maenas* was an important species in both habitats. Shore crabs made up 32.1% (1.68 g m^{-2}) of the biomass in the sand habitat and 34.8% (3.16 g m^{-2}) in the vegetated habitat (Fig. 4b). In the sand habitat, *C. crangon*, *P. platessa* and *P. flesus* together made up 47% of the total biomass, and in the vegetated habitat *G. aculeatus*, *P. pungitius* and *P. adspersus* dominated in terms of biomass, contributing 46% of the total weight.

Community parameters versus biomass of algae

Within the vegetated habitat, patterns in species richness, abundance and biomass of the epibenthic fauna were investigated in relation to the biomass of macroalgae. There were no significant correlations (p > 0.05; n = 64) between the fauna in the different bays in terms of number of species, abundance and biomass, and the biomass of algae within the corresponding bays (Fig. 5a–c).

Small-scale effects of algae on faunal distribution

The grouping of drop-trap samples by the biomass of algae in individual sampling plots revealed several different patterns of association between fauna and biomass of algae. Among the common species, *Pleuronectes platessa* occurred only in samples completely free of vegetation. *Crangon crangon* and the gobies *Pomatoschistus* spp. were found predominantly in the open sand habitat or in sparse vegetation (0 to 60 g DW m^{-2}), and rapidly decreased in numbers with increasing biomass of algae (Fig. 6). *Carcinus maenas*, *Gobius niger* and mysids were common in both the open sand habitat and at low to moderate levels of algal biomass (0 to 240 g DW m^{-2}). Another group, including *Anguilla anguilla*, *Syngnathus typhle* and the grass shrimps (*Palaemon elegans* and *P. adspersus*) was found mainly in vegetated habitats with an intermediate biomass of algae (60 to 240 g DW m^{-2}), but was rare on open sand, and rare or absent in dense vegetation (>240 g DW

tius pungitius and grass shrimp *Palaemon adspersus* were the most commonly occurring species. *C. crangon* made up 48.4% of the individuals in the open sand habitat, but only 3.4% of the animals in the vegetated habitat. The 2 species of sticklebacks *G. aculeatus* and *P. pungitius* together made up 53.6% of the individuals in the vegetated habitat compared to 4.7% in the bare sand habitat. The remaining taxa exhibited varying degrees of habitat affinity. The 2 flatfish species were found mainly in the open sand habitat. *P. platessa* made up 4.3 versus 0.1%, and flounder *P. flesus* 1.2 versus 0.1% of the individuals in the open sand and vegetated habitats, respectively. Eels *Anguilla anguilla* were more prevalent in the vegetated habitat

m^{-2}). Two species of sticklebacks *Pungitius pungitius* and *Gasterosteus aculeatus* were found to be at the other end of the habitat affinity spectra. The density of sticklebacks was low (< 0.4 ind. m^{-2}) in the open sand habitat, gradually increased with increasing biomass of algae and remained high (8 to 15 ind. m^{-2}) at the

highest levels of algal biomass recorded (> 360 g DW m^{-2}). At the small scale of individual drop-traps, total abundance and biomass of epibenthic fauna peaked at intermediate levels of algal biomass (Fig. 7).

DISCUSSION

Areas with macroalgae were found to have higher abundance and biomass of epibenthic fauna compared to bare sediment areas, whereas species richness was similar for the vegetated and open sand habitats. The same findings were inferred in an earlier study that compared the fauna over time (a decade) in a bay that became covered by macroalgae (Isaksson & Pihl 1992). The present study therefore supports the hypothesis that the historical change in epibenthic fauna observed by Isaksson & Pihl (1992) is linked to the simultaneous increase in macroalgal blooms. In observational studies such as the present work there could, however, always be other factors beside the presence of macroalgal blooms, which cause the patterns observed. Other shallow vegetated habitats are commonly reported to have higher abundance of fish and epibenthic macrofauna than adjacent unvegetated areas (e.g. Sogard & Able 1991), and there are indications that structure per se, rather than type of vegetation is the most important factor determining the density of some recruiting species (Heck et al. 2003). In addition, eutrophication, which is considered to favour macroalgal blooms, may initially increase the trophic state of coastal ecosystems before adverse effects on system functioning become evident (reviewed in Cloern 2001). Therefore, the high abundance and biomass of epibenthic fauna in the seaweed beds occurring in Swedish west coast bays may be attributed to increased habitat structural complexity and augmented levels of carbon and nutrients provided by the algae. From the small-scale observations of epibenthic fauna in relation to algal biomass, it is evident that the majority of animal taxa were most abundant at intermediate levels of seaweed abundance (see Fig. 6). This is also reflected in the peak in total abundance and biomass of the faunal assemblage at intermediate algal biomass levels together with a tendency towards higher average number of species per sample (see Fig. 7).

The other major difference observed between the bare sand and vegetated state was related to the assemblage structure of epibenthic fauna. Bays with green macroalgal mats differed in the assemblage structure of epibenthic fauna, shown as a clear difference in species dominance. Brown shrimp *Crangon crangon*, shore crabs *Carcinus maenas*, and mysids (Mysidacea) dominated in the open sand habitat. The 2
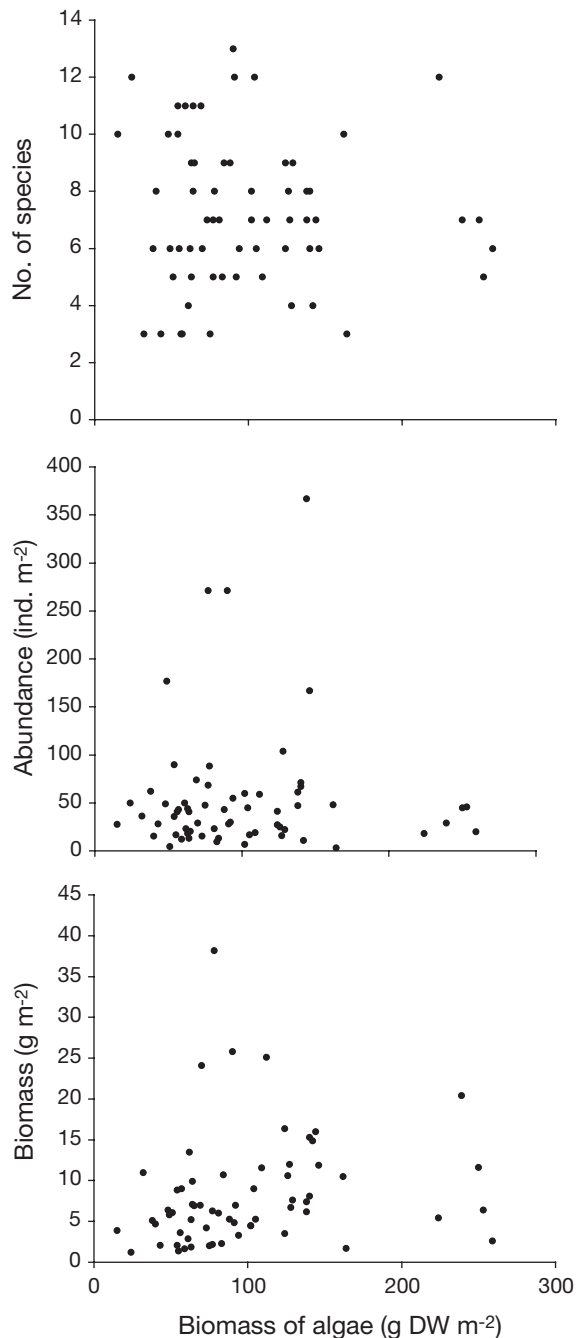

Fig. 5. Number of species, abundance and biomass of epibenthic fauna in vegetated bays in relation to the average biomass of algae. No significant relationships were found (n = 64, p > 0.05)
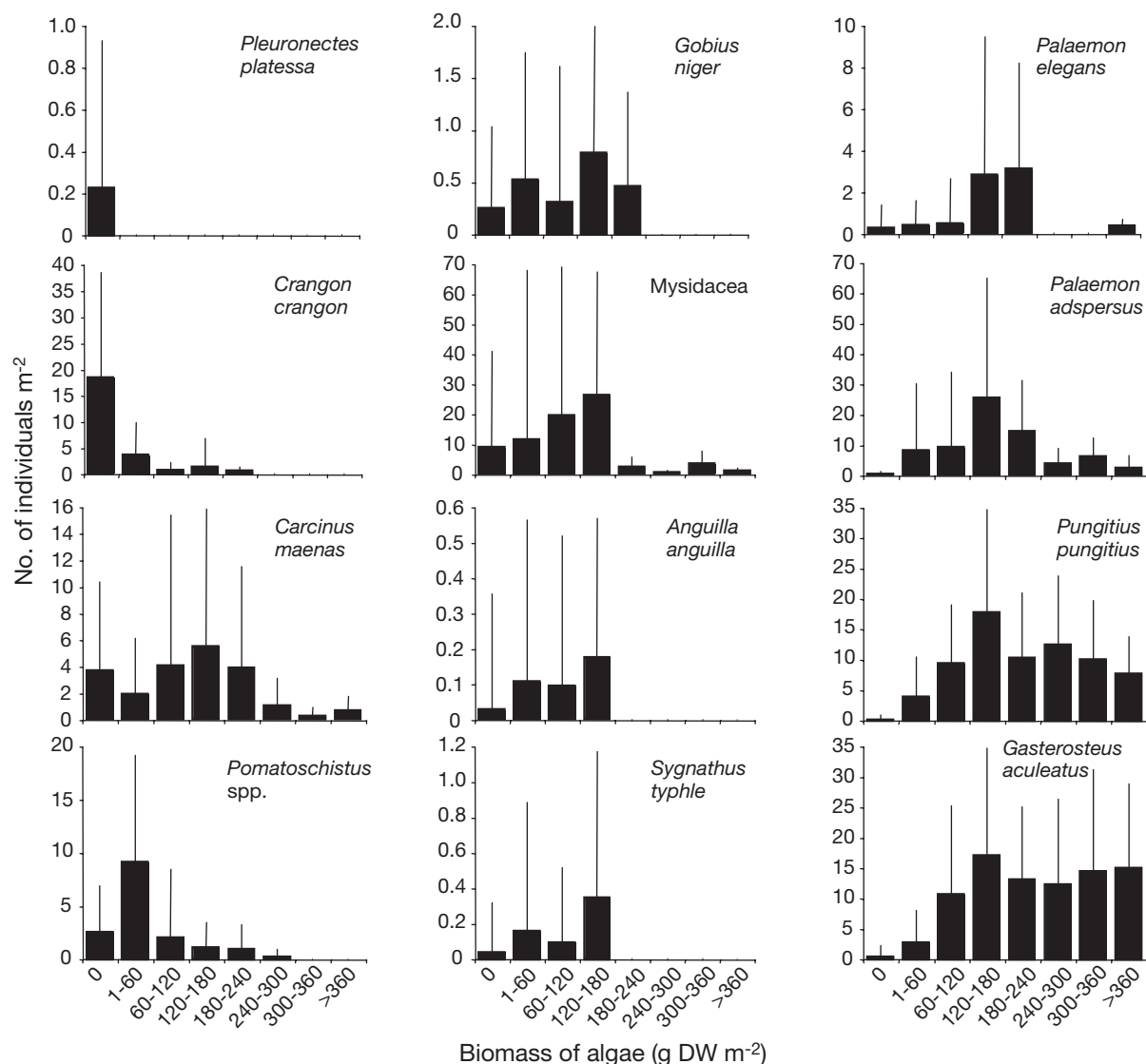
Fig. 6. Abundance (ind. m^{-2} +SD) of epibenthic faunal taxa in relation to the biomass of algae (g DW m^{-2}) in individual drop-trap samples. Samples were divided into algal biomass classes (60 g DW) resulting in n = 150, 38, 64, 23, 13, 8, 8 and 6 for the biomass classes 0, 1–60, 60–120, 120–180, 180–240, 240–300 and 300–360 g, respectively

flatfish species were not as numerically abundant, but were strongly associated with the open sand habitat. Plaice *Pleuronectes platessa* and flounder *Platichthys flesus* were rarely found in the vegetated habitat, and their densities were an order of magnitude less than in the bare sand habitat. In the vegetated habitat, 3-spined stickleback *Gasterosteus aculeatus*, 9-spined stickleback *Pungitius pungitius* and grass shrimp *Palaemon adspersus* were the most commonly occurring species. Eels *Anguilla anguilla* were also more prevalent in the vegetated habitat than in the open sand habitat. Spatial replication among regions and temporal replication among years suggest that the observed patterns could be generalised for the Swedish west coast archipelago.

Macroalgal blooms are commonly more variable in their spatial and temporal distribution than other vegetated shallow water habitats (e.g. sea grass and kelp beds). There is a strong seasonal component in bloom formation, with an initiation of growth in spring, a peak in cover and biomass during summer and a decay during autumn (Pihl et al. 1996). Algal mats seem to be absent during the winter in temperate areas where ice cover occurs, such as the Swedish west coast (H. Wennhage pers. obs.). Macroalgal mats may reach a peak in biomass and cover only 6 wk after initiation of growth, and the mats may be displaced suddenly or disappear after storm events (Pihl et al. 1996). There is also a considerable difference among years in maximum cover and number of bays affected by algae (Pihl
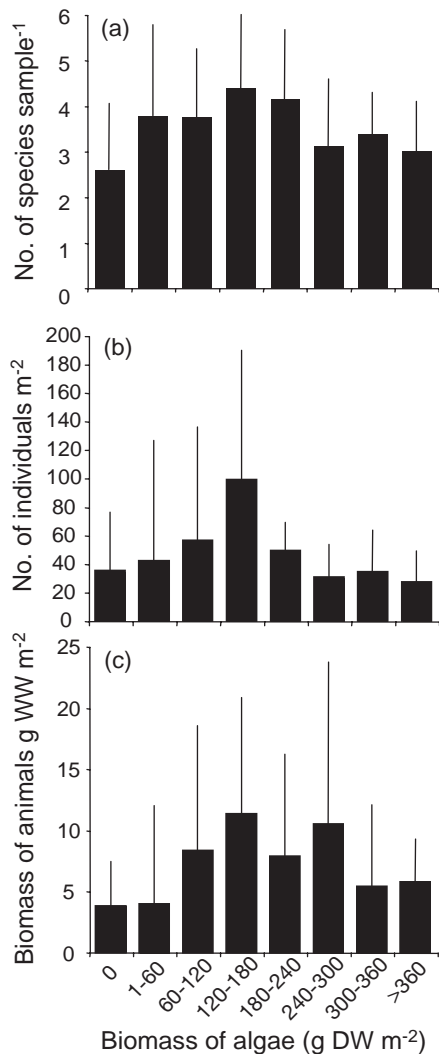
Fig. 7. Epibenthic fauna in relation to biomass of algae (g DW m^{-2}) in individual drop-trap samples. (a) Richness (no. of species sample^{-1} +SD), (b) abundance of epibenthic fauna (no. of individuals m^{-2} +SD), (c) biomass of epibenthic fauna (g WW m^{-2} +SD). Biomass classes of algae and number of samples as in Fig. 6

et al. 1999). In the large data set (128 bays) presented here, it can therefore be expected that some bays would have experienced a recent change in habitat characteristics. The results from the multivariate analyses were, however, very consistent in separating vegetated and bare sand bays in 2 groups on the basis of faunal assemblage. This consistency indicates that the epibenthic species have a high degree of motility and are able to redistribute rapidly following proliferation or loss of macroalgae. In addition, detached benthic macroalgae can act as a dispersal mechanism for coastal fauna (Holmquist 1994). In contrast, studies on the response of benthic fauna to macroalgal blooms commonly report long lasting effects on the community

structure following the disturbance by algae (reviewed in Raffaelli et al. 1998).

The epibenthic faunal assemblage structure underwent a seasonal change (from June to August) in both habitats. This change can be attributed to the recruitment of epibenthic species during the summer, resulting in marked changes in local population size for the species under study (Pihl & Rosenberg 1982). However, the difference in assemblage structure that could be attributed to the occurrence of algae was obvious, even with the large seasonal changes in assemblage structure that are normally present in the system. A plausible explanation for this would be that recruits of the different species settled and survived in relation to their habitat affinity, reinforcing the difference in assemblage structure.

There was no clear correlation between the biomass of algae and the assemblage structure of epibenthic fauna at the bay scale. However, when relating fauna and algae at the scale of individual samples, the different epibenthic species showed distribution patterns that were correlated to the biomass of algae in those samples. Earlier studies suggest that the epibenthic fauna in a bare sediment bay is confined to that particular bay during the summer (Pihl & Rosenberg 1982), but that animals redistribute themselves within the bay in relation to gradients in biotic and abiotic factors (Modin & Pihl 1996, Gibson et al. 1998). The rapid growth and loss of algal mats may not give the animals time to redistribute according to their habitat preferences over larger spatial scales.

Previous studies have shown that macroalgal blooms have a strong structuring effect on faunal groups other than epibenthic fauna, such as benthic infauna and avian predators (reviewed in Raffaelli et al. 1998), causing an ecosystem shift in shallow coastal waters. The underlying cause of ecosystem shifts may often be a gradual change in a variable or a disturbance regime (e.g. nutrient load, climate, biological exploitation). Rather than showing a gradual response, the ecosystems may exhibit resilience to changes until a threshold is reached causing the ecosystem to shift to an alternate state (Scheffer et al. 2001). The alternate state is generally undesirable from a conservation perspective, affecting biodiversity and the value of ecosystem services provided by the habitat (Troell et al. 2005, www.ecologyandsociety.org/vol10/iss1/art30/). In the case of macroalgal mats, there are indications that the vegetated alternate state is resilient to change. Benthic regeneration of nutrients from previous algal mats may support new blooms even at low external input of nutrients (Sundback et al. 2003).

Shallow coastal ecosystems have a large number of ecological functions providing important ecosystem goods and services. New habitat-forming species,

together with the newly associated fauna that become established after the structural shift are likely to change the function of the ecosystem. In our study a dramatic difference in the composition of fish species was found between the sandy sediment and the macroalgal habitat. Coastal sandy beaches are known to be important as nursery grounds for flatfish (Zijlstra 1972) and feeding grounds for several juvenile fish species like cod, whiting and sea trout (Wennhage & Pihl 2002). The shallow sandy areas are considered essential habitats, as they are crucial in the life cycle of several fish species. Flatfishes adapted to an open sandy substratum will avoid algae or die among the thalli (Wennhage & Pihl 1994, Wennhage 2002), and areas covered with algae will therefore lose their function as nursery areas for these species. As an example of this, a net loss of 30 to 40% (a reduction with up to 46×10^6 individuals) of the output of 0-group plaice has been assessed for the Swedish Skagerrak archipelago (the area investigated in this study) as a consequence of algal mats covering 30 to 50% of the sediment in plaice nursery grounds (Pihl et al. 2005).

Gobies of the genus *Pomatoschistus*, together with the crustaceans *Crangon crangon* and *Carcinus maenas*, are the main prey for several fish species that utilize shallow sediment habitats as feeding grounds (Pihl 1982, Wennhage & Pihl 2002). These prey species bury in the sediment as a means of avoiding predators (Gibson & Robb 1992). *Pomatoschistus* spp. and *C. crangon* were found mainly on bare sand or in areas with low algal biomass, whereas *C. maenas* occurred in habitats ranging from bare sand to areas with moderate biomass of algae (Fig. 6). The abundance of important prey species, such as gobies and *C. crangon*, will probably decrease with increasing growth of algal mats. In addition, algal mats in sandy bays will affect predators of epifauna. Experiments have shown that a 30% cover of green macroalgae on the sediment results in a significantly lower foraging success of juvenile (1-group) cod when feeding on their natural prey *C. crangon* and *C. maenas* (Isaksson et al. 1994).

In the algal habitat, sticklebacks mainly replaced flatfish and gobies. These small-sized fishes are generalised carnivores and different populations show a wide range of specialisations for different prey types (Hart & Gill 1994). An earlier study on the Swedish west coast, however, identified the sticklebacks as mainly planktivorous, not utilizing the rich benthic production of shallow bays (Wennhage & Pihl 2002). Further, sticklebacks are not known as an important prey species for the 15 most abundant fish species of the littoral zone in the Skagerrak archipelago (Wennhage & Pihl 2002). Therefore, sticklebacks do not replace flatfish, gobies or epibenthic crustaceans like *Crangon crangon* in the food web of shallow bays.

These findings suggest that when shallow sediment substratum shifts into a vegetated state, the system will lose the important function of energy transfer from the highly productive shallow sediment to higher trophic levels of the coastal ecosystem.

In conclusion, the abundance and biomass of epibenthic fauna in shallow bays of the Swedish west coast was higher in areas with macroalgal mats compared to open sand areas. The average number of species was similar in the 2 habitats, but there was a clear difference in species dominance. The present study adds to the list of ecological impacts likely to occur during green macroalgal blooms by suggesting a dramatic shift in the assemblage structure of epibenthic fauna. Blooms of macroalgae are known to be ephemeral and seasonal in nature, but may have a large effect on the epibenthic macrofauna coinciding with the peak in recruitment and production of these species. The ecological function and value as nursery and feeding ground for commercial fish will be reduced when sandy areas shift into a vegetated state.

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