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Shift in fish assemblage structure due to loss of seagrass Zostera marina habitats in Sweden

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Abstract

The areal extent of *Zostera marina* in the archipelago of the Swedish Skagerrak has decreased by 60% over two decades. To investigate the effects of *Z. marina* loss on the local fish assemblages, the fish fauna was compared between existing seagrass beds and sites where seagrass had vanished. A field study was carried out at four shallow locations in the outer archipelago of the coast in June 2004. Within each location two sites were sampled, one with an existing *Z. marina* bed and another where *Z. marina* had disappeared. Fish were sampled semi-quantitatively with a beach seine. Samples were taken during both day and night and captured fish were examined to species, enumerated and measured in the field, and released thereafter. The number of fish species was found to be significantly higher in *Z. marina* habitats compared to areas where seagrass was missing, and density and biomass of fish were generally lower in areas dominated by bare sediment compared to those in the seagrass habitats. Several species and groups of fishes (i.e., gadoids, labrids, syngnathids) were absent or occurred in low densities at sites where *Z. marina* was missing. For example, juvenile 0-group cod density was reduced by 96% at sites where *Z. marina* had disappeared. Such a reduction in recruitment of cod is in the same order of magnitude as the combined effect of seal predation and mortality due to by-catches in the eel fyke-net fishery estimated for the archipelago of the Swedish Skagerrak. Hence, the results clearly indicate a shift in the fish assemblage, including a loss of taxa at the family level as a result of degradation in habitat-forming vegetation.

Keywords: habitat loss; eutrophication; cod; plaice; Skagerrak

1. Introduction

Seagrass meadows provide habitat diversity in the coastal seascape worldwide. This habitat-forming vegetation creates a three dimensional architecture over soft bottoms, which stabilizes the sediment and reduces water movements. Seagrass meadows are known to harbour a diverse and abundant fauna of invertebrates and are generally considered as essential habitats for many fish species (Orth et al., 1984; Jenkins et al., 1997). Fish may spawn in seagrass beds or use the area as a nursery ground, where growth and survival of juvenile fish

* Corresponding author. E-mail address: leif.pihl@kmf.gu.se (L. Pihl). are considered to be higher compared to alternative habitats (Beck et al., 2001; Deegan et al., 2002).

The global loss of seagrasses from the mid-1980s to the mid-1990s has been estimated to be 12,000 km² (Short and Wyllie-Echeverria, 1996), which correspond to an overall reduction by about 7% of the total areal extent (Spalding et al., 2003). This fact has contributed to the listing of seagrass beds as habitats worthy of protection in the Rio-declaration (1992/93:13). The consensus from the report "World Atlas of Seagrasses" is that the main reasons for the decline, apart from natural threats such as storms and diseases, are anthropogenic (Green and Short, 2003). Most serious are the indirect effects of human activity. Increased turbidity and overgrowth by epiphytic algae reduce light penetration, resulting in subsequent loss of seagrass. Turbidity and surplus algal growth may

derive from physical disturbances on land or in the water, and from eutrophication combined with trophic cascades (e.g. effects of over-fishing) in the coastal ecosystem (Howarth et al., 2000; Jackson et al., 2001; Hughes et al., 2004). Direct disturbances such as dredging and benthic trawling in seagrass will most likely cause drastic local effects, but are probably of less importance on a larger scale compared to more diffuse, indirect anthropogenic affects (Hily et al., 2003).

Zostera marina is the dominant seagrass species in Swedish coastal waters. Along the Skagerrak-Kattegat coast, it occurs in semi-exposed and protected areas within water depths of 0.5-6 m (Baden and Boström, 2001). These Zostera beds have been shown to support a high production of benthic fauna as well as epibenthic invertebrates and fish (Baden and Pihl, 1984; Möller et al., 1985), and to serve as nursery and feeding grounds for more than 40 fish species (Pihl and Wennhage, 2002; Wennhage and Pihl, 2002). Over the last two decades, a 60% reduction in distribution of the Z. marina has been observed in the Swedish Skagerrak archipelago (Baden et al., 2003). Along most sections of the coast both the upper and the lower depth distributions of seagrass have been reduced, resulting in a narrowing of meadows, but in some areas seagrass meadows have disappeared completely. The lost Z. marina is commonly replaced by a bare sediment bottom, but in some areas the sediment is partly covered by filamentous green algae or patches of Fucus spp., attached to shells and stones. The reason for the degradation of the seagrass habitat in the Skagerrak is not known, but coastal eutrophication and/ or over-fishing have been suggested as plausible causes. In addition, altered water exchange due to construction of road banks and leisure boat harbours could have reduced the distribution of seagrass in the coastal Skagerrak.

Historical distribution maps of seagrass from Scandinavia are few, but extensive Danish investigations dating back to 1900 reveal that only about 25% of the former areal extension remained in 1990 (Petersen, 1914). This large areal reduction is partly attributed to losses of deep eelgrass stands as a consequence of impoverished light conditions and partly to the slow recovery after the seagrass disease in the 1930s. Between 1900 and 1990, maximum colonisation depths decreased from 5-6 m in estuaries and 7-8 m in open waters, to 2-3 m and 4-5 m, respectively (Boström et al., 2003).

The change in habitat structure following the loss of a *Zostera marina* bed is likely to shift the local system into an alternative state. Primarily, the loss of the habitat-forming species *Z. marina* will alter habitat complexity, changing the structure of associated fauna assemblages. In a review of the extensive literature testing the importance of seagrass meadows as nursery areas for juvenile fish and invertebrates, Heck et al. (2003) found that their abundance, growth and survival were generally higher in seagrass compared to unstructured habitats, but similar to other structured habitat, indicating that habitat complexity may be more important to fish diversity than the type of structures present. There are also a few studies more specifically reporting changes in species composition following large-scale losses of seagrass beds. Historical comparisons without appropriate controls are, however, hard to evaluate and there may be alternative explanations for the changes observed (Orth et al., 1996; Browder et al., 1999). To our knowledge there is only one study comparing areas with extant and lost seagrass habitats (Hughes et al., 2002). The study, performed in estuaries along the NW Atlantic Coast, reported that the abundance, biomass and species richness of fish were lower in areas where seagrass beds had disappeared, but the generality of these findings for other coastal areas are not known.

The aim of this study was to investigate the effects of losses of *Zostera marina* on the local fish assemblages on the Swedish west coast. This was carried out by comparing the fish fauna in existing seagrass beds with sites where seagrass has vanished over the last two decades. The main purpose was to document shifts in fish assemblages through measurements of species numbers, densities and biomass. By comparing the utilization by fish of *Z. marina* beds and alternative habitats, changes in the ecological function of coastal areas with loss of seagrass could be evaluated.

2. Methods

This field study was carried out in the outer archipelago of the Swedish Skagerrak coast ($58^{\circ} 14-22'N$; $11^{\circ} 23-32'E$) (Fig. 1) between 8 and 20 June 2004. The archipelago consists of islands of varying size, and a shoreline characterized by a mixture of rocky and soft-bottom substrata. On soft bottoms *Zostera marina* is the dominating vegetation within the depth range of 1-5 m (Baden et al., 2003). This coastal region is micro-tidal with a tidal amplitude of around 0.2 m. Mean surface water temperatures usually range from 5 to 15 °C in spring and autumn and from 15 to 20 °C during the summer (Pihl and Rosenberg, 1982). Surface water salinity typically fluctuates between 20 and 25 psu in the summer.

June was selected for sampling in this investigation because previous studies on seasonal dynamic of the fish community had shown that the highest species richness, abundance and biomass occurred at that time of the year (Pihl and Wennhage, 2002). In June most of the fish are recruited to the coastal habitats, giving a full representation of age-classes in the fish community. The investigated coastal region represents one of five areas where Zostera marina has been observed to decrease significantly in its distribution over the last two decades (Baden et al., 2003). Within this region four locations were chosen at random and two sites were selected in each: one with an existing Z. marina bed and another where Z. marina had disappeared (Fig. 1). Sites with existing seagrass were chosen in close vicinity (about 500 m) to the sites without seagrass. At the seagrass sites each Z. marina bed had a spatial distribution of more than 10 ha, covering 60-100% of the bottom area within the depth range of 1-4 m. At sites where Z. marina had disappeared compared to the 1982 distribution, the bottom sediment was generally free of vegetation, except from sparse occurrence of Z. marina shoots and small patches of Fucus spp. stands. Vegetation cover at these sites was 1-15% of the bottom area.



Fig. 1. Map of the investigated area in the archipelago of the Swedish Skagerrak. Sampling locations indicated by open circles.

A sampling area of 5 ha was designated in the centre of each selected site. Fish were sampled semi-quantitatively with a beach seine according to Tveite (1984), a method most commonly used to study fish communities in the littoral zone. The method has the advantage of allowing for estimates of the area being sampled; a feature not shared by some other methods in use (e.g. gillnets and fyke-nets). Methodological studies have shown that benthic species and small-size individuals may hide within substrata having a high complexity or escape underneath the foot-rope of the seine (Parsley et al., 1989). Beach seines may also have selectivity towards small-sized species, at least in comparison to other methods (Pierce et al., 1990; Weaver et al., 1993). However, the beach seine maintains its performance better than visual sensing techniques when macrophyte cover increases (Brind'Amour and Boisclair, 2004). The seine was 40 m long, 3 m high, had a mesh opening of 10 mm in the arms and 5 mm in the "cod end" and was towed by 30 m long ropes. The gear was deployed from a small boat in a rectangular shape with its deepest part at around 3 m depth. It was pulled shoreward 33 m by four people 15 m apart until reaching a water depth of 1 m, giving an effective fishing area of approximately 500 m^2 . One haul was taken during daytime (12-13 hours) and one

haul during the night (24-01 hours) in each of the investigated sites. Sampling order was randomly allocated between sites and over time to avoid introduction of systematic errors. Day and night samples were taken at random in the designated area, and \geq 50 m apart within a site. Captured fish were examined to species, enumerated and measured (total length, mm) in the field, and released thereafter. Some fish from three large samples collected at night were brought to the laboratory for further analysis. Estimates of the biomass (wet wt.) for all individual fishes were derived from established length-weight relationships. In addition to fish, macro-crustaceans (mainly shrimps and crabs) were also collected. Numbers and pooled biomass (wet wt.) for each species of invertebrates were recorded for each sample in the laboratory.

Shoot density, mean and maximum length and biomass of *Zostera marina* were estimated in the four seagrass beds. Three quantitative samples were taken by a diver using a net-bag (mesh opening 1 mm) connected to a bottom metal ring (diameter of 35 cm). Samples were allocated randomly in the centre of the *Z. marina* bed at approximately 2 m depth. Percentage cover of *Z. marina* was visually assessed by a diver, swimming over the investigated area. At sites where *Z. marina* had disappeared, the vegetation cover was assessed visually

from the boat before sampling. To characterize the sediment substrate three quantitative sediment cores were collected randomly by a diver in each of the study sites (1-3 m water depth) for analysis of organic content. Samples of the upper 2 cm of the sediment core were dried at 60 °C for 24 h and combusted for 4 h at 450 °C, and organic content was measured by weight loss.

Fish assemblage structure was compared between samples by using Bray-Curtis similarity indices, as described in the PRIMER package (Field et al., 1982). Fish abundance data were log(X + 1) transformed to weigh the relative numerical importance of common and rare species in the analysis. Bray-Curtis similarity indices were computed and the resulting similarity matrix was used to perform non-metric Multi-Dimensional Scaling (MDS). An analysis of similarities (ANOSIM) was used to test for differences in assemblage structure between the two habitat types, and to compare day and night samplings (method in Clarke, 1993). The proportional contribution of different fish species to the dissimilarity between groups was investigated using SIMPER (method in Clarke and Warwick, 1994). Fish abundance, biomass and number of species in the two habitat types were compared using two-way ANOVAs, with habitat and time of day as factors. Non-transformed data used as variances were shown to be homogenous according to Cochran's test.

3. Results

3.1. Vegetation

In three out of four Zostera marina beds investigated the vegetation had a homogenous density with full cover of the sediment. Only at one site, Lindholmen (location 2), the Z. marina had a patchy distribution covering approximately 60% of the sediment. Mean shoot density was estimated to be 100-380 shoots m^{-2} in the four Z. marina beds, the lowest densities occurring at the site where the bed had a patchy distribution (Table 1). The mean blade length varied from 22 to 47 cm at the four sites, and maximum length was about double the mean length at all sites (Table 1). Blade biomass of Z. marina was found to be between 44 and 172 g dw m^{-2} at the study sites, with the lowest values in the beds having either low mean blade length or a patchy distribution. At the four sites where Z. marina beds had disappeared over the last two decades the sediment was mainly free of vegetation. At one site (the exposed area Finsbo, location 3) a few remaining shoots of Z. marina were found covering around 1% of the bottom (Table 1). The other three sites had patches of Fucus spp. growing on stones and shells of blue mussels with an approximate cover of between 5 and 15% of the bottom sediment.

3.2. Sediment

Two of the investigated locations (Brofjorden and Lindholmen) were situated in an enclosed part of the archipelago and were protected from exposure to wind and waves. Of the other

Table 1

Shoot density, blade length and biomass (wet wt.) of *Zostera marina*, and cover of *Z. marina* and *Fucus* spp., as well as sediment organic content (%) in the eight sample sites

	Brofjorden	Lindholmen	Finnsbo	Gåsö
Zostera marina sites				
Cover of Zostera (%)	100	60	100	100
Number of shoots				
Mean (g dw m^{-2}) ($n = 3$)	230	100	380	250
SE	36	21	21	50
Blade length				
Mean (cm) $(n=3)$	47.2	30.1	22.1	39.8
SE	4.6	2.3	1	3.9
Max (cm)	104	67	39	66
Blade biomass				
Mean (g dw m^{-2}) ($n = 3$)	172.2	43.5	71.2	141.2
SE	13.8	21.5	11.3	31.4
Sediment org. content				
Mean (%) $(n = 3)$	16.6	14.5	1.7	13.6
SE	1.3	0.6	0.1	0.8
Non-Zostera marina sites				
Cover of <i>Zostera</i> (%)	0	0	1	0
Cover of Fucus spp. (%)	5	10-15	0	5-10
Sediment org. content				
Mean (%) $(n = 3)$	5.4	3.3	1	1.3
SE	0.5	0.4	0.06	0.06

two areas, one was considered as semi-exposed (Gåsö) and one had a high physical exposure (Finnsbo). In the protected and semi-exposed areas, content of organic matter in *Zostera marina* beds varied between 13.6 and 16.6%, whereas the exposed *Z. marina* bed had a sandy sediment with only 1.7% organic content (Table 1). At the sampled sites mainly free of vegetation content of organic matter in the sediment was estimated to be between 1.0 and 5.4%, with the highest value in the protected areas (Table 1). Thus, organic content in the sediment was 2–10 times higher in *Z. marina* beds compared to unvegetated sites, but inter-location differences could be important due to variation in exposure.

3.3. Fish

Altogether, 33 fish species belonging to 15 families were identified in this investigation (Table 2). Twenty-eight species were found in the *Zostera marina* beds, of which nine were exclusive to this habitat. At the sites where *Z. marina* had disappeared 19 fish species were found, and five of these species were only found here. When comparing *Z. marina* and non-seagrass sites in pairs for each location, the number of fish species was in all cases higher in the *Zostera* habitat (Fig. 2). Overall the number of fish species was significantly higher (p < 0.005) in *Z. marina* beds than at non-seagrass sites, but no difference was observed between day and night samplings (Table 3). The mean number of individuals sample⁻¹ exhibited a large variation between locations and sites (Fig. 2). Generally, the numbers of individuals were higher in catches from

Table 2

Family	Fish species	Numbers		Biomass	
		Zostera marina	Non-Zostera marina	Zostera marina	Non-Zostera marina
Anguillidae	Anguilla anguilla	12	23	456.4	1436.7
Gobiidae	Aphia minuta	1423	169	4705.5	261.0
Callionymidae	Callionymus lyra	0	1	0.0	11.5
Clupeidae	Clupea harengus	1	84	2.6	157.4
Labridae	Ctenolabrus rupestris	272	2	2062.8	17.7
Syngnathidae	Entelurus aequoreus	16	0	70.1	0.0
Gadidae	Gadus morhua	146	12	947.1	1142.7
Gasterosteidae	Gasterosteus aculeatus	1164	916	1781.7	1527.6
Gobiidae	Gobius niger	738	304	4605.1	924.1
Gobiidae	Gobiusculus flavescens	264	0	137.3	0.0
Pleuronectidae	Limanda limanda	5	0	228.3	0.0
Gadidae	Merlangius merlangus	16	0	482.1	0.0
Cottidae	Myoxocephalus scorpius	22	2	868.9	81.6
Syngnathidae	Nerophis lumbriciformis	1	1	2.6	5.5
Syngnathidae	Nerophis ophidion	32	4	25.1	2.3
Pholidae	Pholis gunnellus	3	0	42.5	0.0
Pleuronectidae	Platichthys flesus	11	37	2206.6	1835.4
Pleuronectidae	Pleuronectes platessa	21	143	74.8	310.8
Gadidae	Pollachius virens	4	0	11.0	0.0
Gobiidae	Pomatoschistus microps	0	90	0.0	85.1
Gobiidae	Pomatoschistus minutus	30	72	75.6	178.6
Gobiidae	Pomatoschistus pictus	16	18	23.6	23.5
Salmonidae	Salmo trutta	9	4	785.4	777.8
Bothidae	Scophthalmus rhombus	0	1	0.0	0.2
Soleidae	Solea solea	0	1	0.0	48.8
Gasterosteidae	Spinachia spinachia	2	0	8.4	0.0
Labridae	Symphodus melops	4	0	62.8	0.0
Syngnathidae	Syngnathus acus	35	0	179.2	0.0
Syngnathidae	Syngnathus rostellatus	33	23	38.0	27.3
Syngnathidae	Syngnathus typhle	129	37	135.2	52.6
Cottidae	Taurulus bubalis	7	7	204.8	120.6
Gadidae	Trisopterus esmarkii	5	1	6.0	0.5
Zoarcidae	Zoarces viviparus	82	57	1648.0	474.5
		4503	2009	21,877.5	9503.7

Number of individuals and biomasses (wet wt.) of fishes recorded in beach-seine samples. Pooled data of day and night samples from four Zostera marina sites, and from four sites where Z. marina has disappeared

Z. marina beds compared to catches from areas where seagrass had disappeared when sites were compared in pairs. However, overall no significant difference in fish density could be detected between habitats or between day and night samplings (Table 3). Except for one sample in the *Z. marina* bed at location 4 (Gåsö), the fish biomass was generally low during daytime sampling, especially at non-seagrass sites (Fig. 2). Night fish biomass was generally higher than daytime biomass, and similar total fish weights were recorded in the two habitat types. Overall, a trend toward higher fish biomass was recorded in *Z. marina* beds, although the difference from non-seagrass sites was not significant (p = 0.10; Table 3).

MDS ordination based on a Bray-Curtis similarity matrix showed that the fish assemblages were mainly structured according to habitat type, whereas time of the day was of less importance for the structure of the fish assemblages (Fig. 3). An ANOSIM-test revealed a significant difference (Global R = 0.37; p = 0.01) between the fish assemblage structure in *Zostera marina* beds and non-seagrass habitat, but the test failed to show any difference (Global R = -0.07; p = 0.74) between day and night samplings. Furthermore, of the two habitat types, *Z. marina* sites were more closely clustered in the analysis than bare sediment sites, indicating a higher similarity of the fish assemblages in *Z. marina* beds.

An SIMPER-analysis revealed that the distribution of 10 species explained about 70% of dissimilarity between the two habitat types (Table 4). Of these species, eight had higher densities in *Zostera marina* beds and two were more abundant in non-seagrass habitats. The high affinity of several fish species to the *Zostera* habitat is further emphasised by the fact that 10 out of the 20 most abundant fish species were almost exclusively caught in the seagrass beds. Gadoids (*Gadus morhua, Merlangius merlangus* and *Pollachius virens*) labrids (*Ctenolabrus rupestris* and *Symphodus melops*), syngnathids (*Syngnathus acus* and *Entelurus aequoreus*) and *Gobiusculus flavescens* were predominantly found in *Z. marina* beds, whereas flatfishes such as *Pleuronectes platessa*, *Platichthys flesus* and *Solea solea* mainly occurred on bottoms dominated by bare sediment.

Cod (Gadus morhua) and plaice (Pleuronectes platessa) are the most important species of commercial interest that



Fig. 2. Number of species, individuals and biomass of fish captured during day and night samplings at four Zostera marina and four non-Z. marina sites in the archipelago of the Swedish Skagerrak.

occurred in high densities in this investigation. They both utilize the coastal zone as a nursery and juveniles may stay in shallow (<10 m) waters for about two years after settlement to the benthic habitat (Pihl, 1989; Pihl and Ulmestrand, 1993). From analysis of length distribution it was obvious that 0-group juvenile cod mainly utilized the *Zostera marina* beds as a nursery, whereas 1-group cod were equally represented in both habitats (Fig. 4). In the *Z. marina* beds cod

Table 3 Two-fixed-factor ANOVA-modes. Number of species, density and biomass of fish as a function of habitat (*Zostera*, no *Zostera*) and time (day, night)

Source of variation	SS	df	MS	F	р
Number of fish specie	es				
Habitat	203.1	1	203.1	21.8	0.005
Time	39.1	1	39.1	4.2	0.063
Habitat \times Time	1.6	1	1.6	0.2	0.692
Residual	111.8	12	9.3		
Density of fish					
Habitat	388,752	1	388,752	2.58	0.134
Time	133,225	1	133,225	0.88	0.365
Habitat \times Time	49,952	1	49,952	0.33	0.575
Residual	1,805,974	12	150,497		
Biomass of fish					
Habitat	9,571,289	1	9,571,289	3.91	0.099
Time	2,051,340	1	2,051,340	0.68	0.424
Habitat \times Time	2,133,790	1	2,133,790	0.71	0.415
Residual	3.6E+07	12	2,996,293		



Fig. 3. Similarities in fish assemblage structure between day and night samplings in four *Zostera marina* and four non-*Z. marina* sites, based on Multi-Dimensional Scaling (MDS) ordination.

Table 4

Fish species most responsible for the difference in assemblage structure between *Zostera marina* and non-*Zostera marina* habitats, listed in the order of their contribution to the average Bray–Curtis dissimilarity. Abundance is mean individuals $sample^{-1}$

Rank	Fish species	Abundan	ice	% Contribution	
		Zostera	Non-Zostera		
1	Aphia minuta	177.8	21.1	11.1	
2	Gasterosteus aculeatus	145.5	114.5	8.4	
3	Gobiusculus flavescens	33.0	0	8.2	
4	Gadus morhua	18.3	1.5	5.9	
5	Gobius niger	92.3	38.0	5.4	
6	Syngnathus typhle	16.1	4.6	5.4	
7	Zoarces viviparus	10.3	7.1	5.3	
8	Ctenolabrus rupestris	34.0	0.3	5.0	
9	Pleuronectes platessa	2.6	17.9	4.5	
10	Pomatoschistus minutus	3.8	9.0	4.4	
11	Nerophis ophidion	4.0	0.5	3.3	
12	Syngnathus rostellatus	4.1	2.9	3.2	
13	Pomatoschistus microps	0	11.3	3.1	
14	Syngnathus acus	4.4	0	2.7	
15	Pomatoschistus pictus	2.0	2.3	2.6	
16	Anguilla anguilla	1.5	2.9	2.5	
17	Platichthys flesus	1.4	4.6	2.5	
18	Myoxocephalus scorpius	2.8	0.3	2.5	
19	Merlangius merlangus	2.0	0	2.1	
20	Entelurus aequoreus	2.0	0	2.0	
21	Taurulus bubalis	0.9	0.9	1.7	
22	Salmo trutta	1.1	0.5	1.7	
23	Clupea harengus	0.1	10.5	1.3	
24	Trisopterus esmarkii	0.6	0.1	0.9	
25	Pollachius virens	0.5	0	0.7	
26	Limanda limanda	0.6	0	0.7	
27	Symphodus melops	0.5	0	0.7	
28	Nerophis lumbriciformis	0.1	0.1	0.6	
29	Pholis gunnellus	0.4	0	0.6	
30	Spinachia spinachia	0.3	0	0.5	
31	Solea solea	0	0.1	0.3	
32	Callionymus lyra	0	0.1	0.3	
33	Scophthalmus rhombus	0	0.1	0.3	

were caught both during day and night, but in the non-seagrass habitats cod only appeared in night samples. In contrast to cod, juvenile 0-group plaice were almost exclusively caught at sites dominated by bare sediment (Fig. 5). They occurred on bare sediment both during day and night. Only a few individuals of 1-group plaice were captured in this study. They appeared in both habitats, but were only caught during night sampling.

In an attempt to analyze possible relationships between the structure of *Zostera marina* and the fish assemblages (although based on a small sample size) density, length and biomass of vegetation were compared to species, density and biomass of fish (Table 5). Highest number of fish species and biomass was observed in the two *Z. marina* beds having the greatest blade length and the largest biomass of vegetation. These two beds also had the largest geographical extension of the four investigated *Z. marina* sites.

3.4. Macro-crustaceans

In addition to fish, nine species of macro-crustaceans were found in samples from the sites dominated by bare sediment and six species were found in Zostera marina habitats (Table 6). Carcinus maenas, Crangon crangon, Palaemon adspersus and Palaemon elegans were the dominant species in both habitats. There was a trend towards higher densities and biomasses in non-seagrass compared to Z. marina sites, however, the differences were not significant (p > 0.05). Catches were higher during the night, with significant larger biomass (p = 0.005) at night compared to day samples in both habitats.

4. Discussion

The main purpose of this study was to document shifts in the assemblages of fish as a direct consequence of loss of the habitat-forming vegetation, Zostera marina, in shallow soft-bottom areas. It would be expected that species richness and composition of fish species would change when vegetation disappears as a result of lower habitat complexity (Jackson et al., 2001; Hughes et al., 2002; Lazzari, 2002), but the density of fish does not necessarily decrease, since shallow soft bottoms are known to host large abundances of small fishes (Edgar and Shaw, 1995). The archipelago of the area investigated consists of a mosaic of rocky- and soft-bottom habitats that are to a varying degree covered by vegetation, thereby offering a suite of alternative habitats with different complexity that could be utilized by littoral fish. When seagrass disappears from an area, fish could either concentrate in alternative vegetated habitats or stay in the altered habitat dominated by bare sediment. Therefore, as pointed out in previous studies comparing fish in seagrass and bare sediment (Ferrell and Bell, 1991), it is important to consider the size of the area where seagrasses have been lost and the distance to other alternative habitats. In our study, the areas where seagrass had disappeared had a size of several hectares and the distance to vegetated habitats, in this case other seagrass beds or belts of macroalgae, was between 200 and 500 m. Despite the close proximity to complex habitats, a significant reduction in fish species and change in species structure were observed in areas where seagrass had vanished. Thus, there is a clear indication of a shift in the fish assemblage, including a loss of taxa at the family level as a result of degradation in habitat-forming vegetation at the observed scale.

In our study, fish biomass was generally higher during night in habitats both with and without *Zostera marina*. The high biomass was partly due to the larger size of individual fish captured during the night. This indicated that fish migrate into shallow water at night, and these areas may function as a night-time feeding ground for both types of habitat. Such nocturnal shoreward migration has previously been described for the two dominating commercial species in the area, cod and plaice (Pihl, 1982; Gibson et al., 1998). In other investigations it has been shown that fish migrate from seagrass into open sediment habitats at night for foraging (Gotceitas et al., 1997).

Different fish species may show different degrees of dependency on vegetation. Syngnathids is a group of fish species that are adapted to seagrass by their body shape. The habitat



Fig. 4. Number of individuals per length-class of 0- and 1-group juvenile cod (Gadus morhua) at Zostera marina and non-Z. marina sites.

dependence may vary for this group of fishes, but most species are found among vegetation. Six species of syngnathids were found in this study, of which four species occurred in both habitat types and two species were caught exclusively in *Zostera marina* beds. Altogether, over 80% of the individuals and biomass of this group of fish were found in the *Z. marina*. The reason that cryptic species like the syngnathids occupy the bare sediment habitat is probably because the missing *Zostera* beds had partly been replaced by *Fucus* spp. that could give sufficient camouflage for these fishes.

Gobies are important components in the food web of littoral fish assemblages, occurring in vegetated as well as unvegetated habitats. They are typically small-sized fish with a short life span and high production (Fonds, 1973). In temperate waters, gobies utilize shallow water for growth during the summer, but usually migrate to deeper water in wintertime where they comprise an important food resource for demersal



Fig. 5. Number of individuals per length-class of juvenile plaice (*Pleuronectes platessa*) at *Zostera marina* and non-*Z. marina* sites.

fish (Arntz, 1973). In this way, gobies provide an important energy link from the highly productive shallow coastal system to fish living in deeper less productive water (Möller et al., 1985). In our study, five species of gobies together contributed 30% of the numbers and 15% of the biomass of the total fish assemblage at sites dominated by bare sediment. In *Zostera marina* beds, the corresponding figures for gobies were 55 and 45%, respectively. The total density of gobies was four times higher in *Z. marina* beds compared to non-seagrass sites, and biomass was more than six times higher. Thus, *Z. marina* beds seem to have a considerably higher capacity for production of gobies that provides an essential energy transfer link to fish during the winter season of low productivity.

Some fish species may vary in their utilization of habitats over different time scales. The affinity to vegetation may change during ontogeny, as for example, early stages of juvenile cod are more habitat-specific and remain stationary in vegetation compared to older juveniles (Borg et al., 1997). Cod uses *Z. marina* beds as a nursery ground and immigrate to these coastal habitats by larval transport. Juveniles settle in the seagrass by active selection usually avoiding open bare sediment, and consequently the availability of seagrass beds may be considered as a bottleneck in the recruitment process due to the specific habitat requirement of the early benthic

Table 5

Density (individual m⁻²), length (cm) and biomass (g wet wt. m⁻²) of *Zostera* marina blades (n = 3), and number of species, density (individuals sample⁻¹) and biomass (g wet wt. sample⁻¹) of fish (n = 2) at four *Z. marina* sites

Zostera marina sites	Zostera			Fish		
	Density	Length	Biomass	Species	Density	Biomass
Brofjorden	230	47	172	21	463	1937
Lindholmen	100	30	44	20	785	1086
Finnsbo	380	22	71	20	207	1133
Gåsö	250	40	141	24	797	2260

Table 6

Density (individuals sample⁻¹) and biomass (g wet wt. sample⁻¹) of macrocrustaceans at *Zostera marina* and non-*Zostera marina* sites during day and night samplings

Sites	Zostera r	narina	Non-Zostera marina		
	Day	Night	Day	Night	
Density					
Athanas nitescens			0.8	1.3	
Carcinus maenas	11.3	24.0	29.8	26.8	
Crangon crangon	11.3	33.3	53.3	171.8	
Gammaridae	0.0	0.0	1.5	1.3	
Macropodia rostrata	20.0	12.8	0.3	2.5	
Mysidae	0.3	0.0	9.3	1.5	
Palaemon adspersus	24.0	134.3	155.8	236.0	
Palaemon elegans	17.0	75.8	113.3	86.3	
Pagurus bernhardus	0.0	0.0	0.5	0.0	
Total density	83.8	280.0	364.3	527.3	
Biomass	0.0	0.0		0.0	
Athanas nitescens	0.0	0.0	0.1	0.3	
Carcinus maenas	62.0	339.5	120.3	254.0	
Crangon crangon	6.3	17.8	22.8	76.5	
Gammaridae	0.0	0.0	0.1	0.1	
Macropodia rostrata	14.8	7.8	0.1	2.8	
Mysidae	0.0	0.0	0.7	0.3	
Palaemon adspersus	12.7	64.5	57.4	153.6	
Palaemon elegans	6.0	45.1	45.3	49.5	
Pagurus bernhardus	0.0	0.0	1.0	0.0	
Total biomass	101.8	474.6	247.6	536.9	

stages. Other gadoids, such as *Merlangius merlangus* and *Pollachius virens*, may also use vegetated coastal habitats as nursery grounds, and in our study juvenile of these two species were exclusively found in *Z. marina* beds. Thus, *Z. marina* beds are essential habitats during the recruitment process for gadoids, and losses of seagrass will most likely reduce the nursery function of the coastal zone for these commercial important species.

In an attempt to make a rough estimate of the potential effect of loss of seagrass on cod recruitment the following example is given: the present (2003-2004) spatial extent of Zostera marina in the Swedish Skagerrak archipelago has been assessed to be around 130 km⁻² (Johan Stål, personal communication). According to Baden et al. (2003) the distribution of Z. marina decreased by 60% over the last two decades, which would equal a total loss of 190 km^{-2} (from 320 to 130 km^{-2}) of the seagrass habitat. In our study, mean density of juvenile (0-group) cod was estimated to be 17 individuals per 500 m^{-2} haul in Z. marina meadows. At non-Zostera sites, densities were estimated to be 0.6 individual per haul. Hence, using the difference in density of juvenile cod (16.4 individuals per haul) between Zostera and non-Zostera habitats, the loss in Z. marina meadows over the last two decades could have resulted in a reduction in recruitment of 6.3 million juvenile cod each year. This is of the same order of magnitude as the estimated combined effect of seal predation and mortality due to by-catches in the commercial eel fyke-net fishery (Mats Ulmestrand, personal communication) in the archipelago of the Swedish Skagerrak.

This investigation included areas with different characteristics in terms of exposure, sediment type and vegetation structure. However, organic content of the sediment, as well as Zostera shoot density, blade length and biomass, of the studied Zostera marina beds in 2004 were within the range of what has previously (1982-1990) been reported for the Swedish coastal region (Baden and Pihl, 1984; Baden and Boström, 2001). Thus, there are no indications that the characteristics of the extant Z. marina meadows have changed over the last two decades. The number of species and density of fish recorded in this study are also in accordance with what have previously been found in surveys of Z. marina beds on the Swedish Skagerrak coast. Investigations carried out during June between 2000 and 2004, including 18 Z. marina beds from three costal regions of the Swedish west coast, estimated number of species and densities of fish per standard haul to 14.3 and 643, respectively (Anders Svenson, personal communication). The corresponding figures for number of species and density of fish in the present study was 16.2 and 389, respectively. Therefore, the result from this study concerning both vegetation and fish could be considered representative for Z. marina beds in the archipelago, and the findings would be expected to be generally applicable for the Swedish west coast.

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