Habitat choice by juvenile cod (*Gadus morhua* L.) on sandy soft bottoms with different vegetation types

Å. Borg, L. Pihl & H. Wennhage

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

ABSTRACT: Habitat choice by juvenile cod (*Gadus morhua* L.) on sandy bottoms with different veg-etation types was studied in laboratory. The experiment was conducted day and night in flow-through tanks on two different size-classes of cod (7–13 and 17–28 cm TL). Four habitats, typical of shallow soft bottoms on the Swedish west coast: *Fucus vesiculosus, Zostera marina, Cladophora* sp. and bare sand, were set up pair-wise in six combinations. The main difference between habitats in this study was vegetation structure, since all parameters except vegetation type was considered equal for both sides of the experimental tanks and natural prey was eliminated. The results showed a difference in habitat utilization by juvenile cod between day (light) and night (dark). During day time the fishes showed a significant preference for vegetation, while nocturnally no significant choice of habitat was made. Both size-classes preferred *Fucus*, considered the most complex habi-tat in this study, when this was available. The smaller size-class seemed to be able to utilize the other vegetation types as well, always preferring vegetation over sand. Larger juvenile cod, on the other hand, appeared to be restricted to *Fucus*. This difference in habitat choice by the two size-classes might be due to a greater dependence on shelter from predation by the smaller juveniles, causing them to associate more strongly with vegetation. The larger juveniles avoided *Cladophora*, since they might have difficulties in entering the compact structure of this filamentous algae. Availability of vegetation at day time, as a predation refuge, as well as of open sandy areas for feeding during night, thus seems to be important for juvenile cod. It is concluded that eutrophication-induced chan-ges in habitat structure, such as increased dominance by filamentous algae, could alter the availa-bility of predation refuges and foraging habitats for juvenile cod.

INTRODUCTION

Preferential habitat choice of an organism is dependent on a combination of factors such as habitat structure and availability, food supply, predation and inter- and intraspe-cific competition (Gjøsæter, 1987a; Menge & Sutherland, 1987). The choice of habitat may vary depending on what requirement is to be satisfied, e.g. shelter from predation, for-aging or finding a mate (Adams, 1976). Habitat choice has also been shown to vary with season and life stage of the organism (Jansson et al., 1985; Clark & Green, 1990).

In many studies a strong linkage between vegetation and faunal community struc-ture has been shown (Wheeler, 1980; Carr, 1989; Sogard & Able, 1991; Isaksson & Pihl, 1992; Kingsford, 1992; Sogard, 1992). For example, seagrass meadows support a denser and richer fauna of vertebrates and invertebrates than adjacent unvegetated areas (Orth et al., 1984). Fish biomass has also been found to be highest when seagrass or kelp algae biomass is at a maximum (Adams, 1976; Pihl et al., 1994). Vegetation increases the

complexity of a habitat, thereby providing a higher availability and variability of micro-habitats, enabling a more diverse fauna to establish (Wheeler, 1980). Vegetation provides a higher availability of predation refuges, thus increasing survival, especially in species under high predation pressure (Wheeler, 1980; Gotceitas & Brown, 1993). Fish, and other macrofaunal organisms, utilizing vegetation as a shelter from predation often resemble the surrounding vegetation in colour and/or body form (Wheeler, 1980), indicating the importance of these refuges for survival of vegetation-associated species.

Important factors determining the potential of a vegetation type as a shelter from predation are, for example, substrate type, vegetation density, plant biomass and architecture (Orth et al., 1984; Pihl et al., 1994). Plant growth form influences foraging behaviour in fish by changing prey visibility and association to plants and also fish foraging manoeuvres (Dionne & Folt, 1991).

Many marine animals, both benthic and pelagic, use shallow coastal areas as nursery and feeding grounds (Wheeler, 1980; Pihl & Rosenberg, 1982; Gibson et al., 1993). The shallow soft bottom with its patches of vegetation among sandy open areas provides an ideal refuge from predation (Orth et al., 1984). Finding a suitable habitat for settling might be crucial for the survival of newly recruited juveniles, and both quantity and quality of the recruitment habitat may be a limited resource, i.e. being a decisive factor for the carrying capacity of an area (Gotceitas & Brown, 1993; Carr, 1994; Gibson, 1994). Another factor which makes shallow coastal habitats favourable as a nursery area is the high productivity of benthos that can be utilized as food resource by both permanent and temporary inhabitants (Pihl & Rosenberg, 1982; Baden & Pihl, 1984; Jansson et al., 1985). This dependence on shallow bottoms in many juvenile marine species makes them vulnerable to several threats, including the loss of habitat and feeding areas (Elliott et al., 1990).

During the last decades increasing amounts of nutrients have reached estuaries and coastal waters leading to eutrophication of these areas (Rosenberg, 1985; Reise et al., 1989; Rosenberg et al., 1990; Nixon, 1995), resulting in an expansive growth of opportunistic plant species, giving the observed effects of phytoplankton blooms and proliferation of filamentous algae (Breuer & Schramm, 1988; Raffaelli et al., 1989; Bonsdorff, 1992; Isaksson & Pihl, 1992; Reise & Siebert, 1994; Pihl et al., 1995). Mats of filamentous algae can cover formerly open sandy habitats or occur as epiphytes on seagrass and kelp algae resulting in a change of the habitat structure, thereby affecting the species composition of associated fauna (Reise, 1983; Raffaelli et al., 1991; Isaksson & Pihl, 1992; Pihl et al., 1995). These mats can act as a physical barrier to epibenthic predators, thus reducing predation and increasing survival of prey species able to cope with the conditions under the mats (Hull, 1987; Isaksson et al., 1994). There is also a risk of hypoxia, due to the increase in organic input from decaying algae and decreased water exchange below algal mats (Rosenberg, 1985; Hull, 1987; Bonsdorff et al., 1995; Norkko & Bonsdorff, 1996). This can be devastating for the benthic organisms, resulting in migration of mobile animals, while sessile forms eventually die (Menge & Sutherland, 1987; Baden et al., 1990; Isaksson & Pihl, 1992).

Cod (*Gadus morhua* L.) is one of the most important species of the commercial fisheries off the west coast of Sweden. Exploited populations of adult cod in the open ocean are dependent upon the recruitment of juvenile fishes in shallow coastal areas (Zijlstra, 1972). Juvenile cod remain within the coastal zone during their first two years (Pihl & Ulmestrand, 1993), where they undertake nocturnal migrations and utilize the rich food re-

sources of shallow (1–2 m) soft bottoms (Pihl, 1982). Structural changes of these habitats might affect the distribution and survival of newly recruited juveniles, consequentially influencing the standing stock of adult fishes. It is therefore imperative to evaluate habitat selection by juvenile cod in order to assess any potential alterations of habitat type.

In this study habitat choice of juvenile cod was investigated on sandy soft bottoms with different vegetation types, in absence of prey, predators and competitors. It was hypothesized that the choice would differ between day and night, with a preference for the most complex habitat during day and an open habitat during night. These expectations were based on results from other studies, where juvenile cod was found to associate with habitats providing shelter from predation during daytime (Gjøsæter, 1987b; Keats et al., 1987; Gotceitas et al., 1995). During nighttime, juvenile cod has been found to migrate to open habitats, to feed on mobile epifauna, mainly crustaceans (Pihl, 1982; Clark & Green, 1990).

MATERIALS AND METHODS

Juvenile cod from the size-classes 7–13 cm TL (0-group) and 17–28 cm TL (1-group) (referred to as small and large, respectively) were used in this experiment. The fish were caught by beach seine (both size-classes) and fyke net (17–28 cm) during September and October 1995 at the Bökevik in the mouth of the Gullmarsfjord (58° 15' N; 11° 27' E), on the west coast of Sweden (Fig. 1). They were kept in flow-through holding tanks without natural substratum, supplied with surface water from the Gullmarsfjord. The fish were allowed to acclimate to laboratory conditions for at least 24 h before being used in experiments. The different size-classes were held separately, and fed a diet of mussels *(Mytilus edulis)*, shrimps *(Crangon crangon, Palaemon adspersus* and *Pandalus borealis)*, and small herring *(Clupea harengus)*.

The experiments were conducted in six flow-through tanks (1 x 1 x 0.45 m), with a water depth of 0.38 m. A layer of 2–3 cm of sandy sediment, collected from the shore and sieved in a 5 mm sieve, covered the bottoms of the tanks. The tanks were divided in two halves with one habitat in each half. Inflow and outflow were situated at opposite sides of the tanks (Fig. 2). The inflow (approx. 0.07 l/s) was T-shaped to ensure that the two sides of the tanks were supplied with equal amounts of water. Surface water from the Gullmarsfjord was used in the experimental tanks, and water temperature and salinity (7.8–13.1 °C and 32–34 ‰ respectively) followed that of the water in the Gullmarsfjord during the experimental period. Fluorescent tubes, suspended 1.5 m above the water surface provided illumination, in daylight wavelengths, at a 12 h light : 12 h dark regime, with a light intensity measured to 5 μmol/s^{-1} m^{-2} PAR at the water surface (LiCOR Quantum meter, model LI-190 SA). Oxygen saturation (about 90 %, oxygen meter YSI, model 57) did not differ between the tanks or the different habitats.

The four different habitats used were brown seaweed *(Fucus vesiculosus)*, eelgrass *(Zostera marina)*, filamentous algae *(Cladophora* sp.*)* and bare sand, all representative habitats of the sandy bottoms in Bökevik. They were set up pair-wise in six combinations in the experimental tanks: sand/*Fucus*, sand/*Zostera*, sand/*Cladophora*, *Zostera/Fucus*, *Cladophora/Fucus* and *Cladophora/Zostera*. Vegetation was, like the fish, collected at the Bökevik during September and October, except for the filamentous algae which was collected in another nearby bay, Rågårdsvik. All vegetation was cleared of natural prey by soaking in fresh water and manual removal of animals and epiphytic vegetation. In
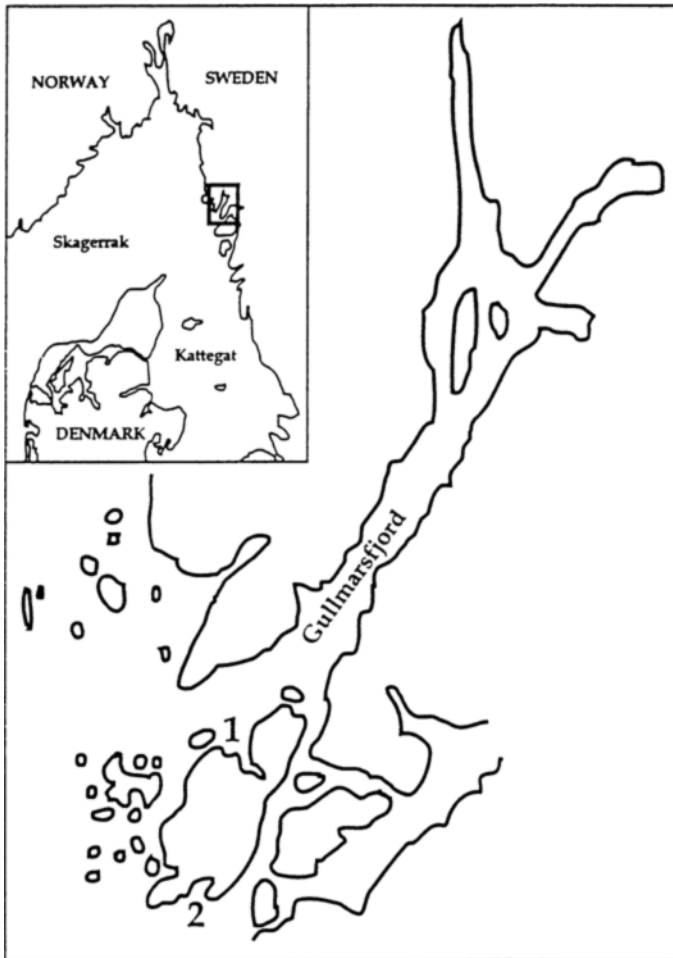
Fig. 1. Map of the Swedish west coast with the Gullmarsfjord area. 1: Bökevik; 2: Rågårdsvik

the experimental tanks, *Fucus* was attached to stones covered with sand, while *Zostera* and *Cladophora* were planted in the sand. The vegetation was planted in as natural densities as possible, while at the same time providing comparable cover of the substratum between treatments (Table 1).

Initially, habitat combinations were randomly allocated between tanks, but stationary over the experimental period. Effects of shading could not be ignored, but light intensity at the water surface, oxygen conditions and water-flow were the same for both sides of all tanks. Thus, the greatest difference was the structure of the different habitats, i.e. morphology of the vegetation types. Furthermore, all habitat types were represented on both sides (left and right), although in different experimental tanks and combinations; significant choices appeared nevertheless.

In a pilot study fish activity was assessed by putting a fish of the large size-class in
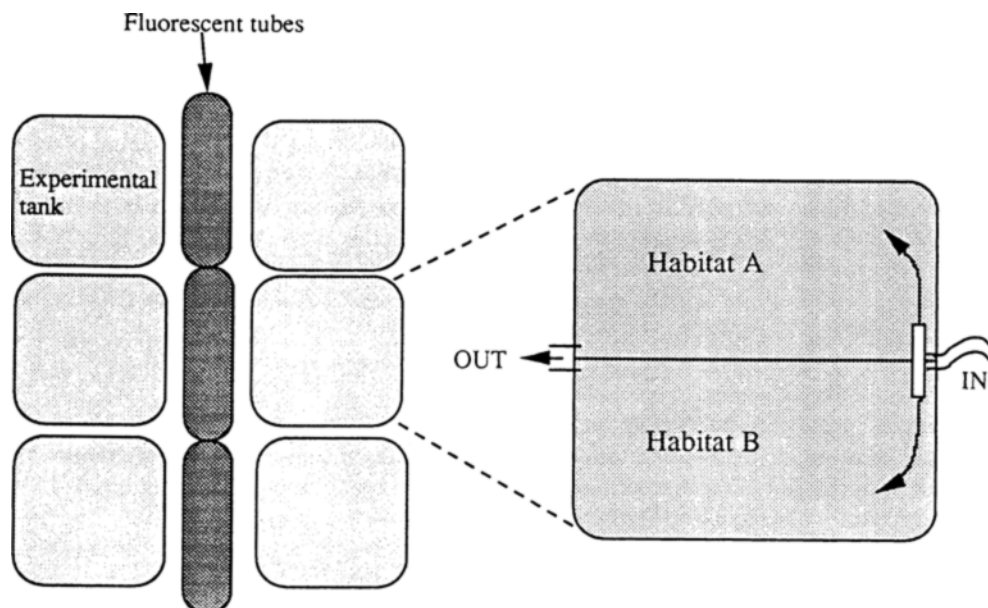
Fluorescent tubes

Fig. 2. The experimental apparatus in the two-choice experiments on habitat selection by juvenile cod. Four habitats were tested against each other resulting in six different combinations. The habitats used were *Fucus vesiculosus*, *Zostera marina*, *Cladophora* sp. and bare sand. Dimensions of the experimental tanks were 1 x 1 x 0.45 m

each of the six experimental tanks and recording the position of each fish in relation to the two habitats every 10 min for five hours. In five out of six habitat combinations the fish seemed to stabilize their response after one hour. These results indicate that an acclimation period of one hour should be sufficient since most of the fishes made a choice before this time had passed, if making a choice at all.

The experiments on habitat choice by both size-classes of juvenile cod was conducted between 10th October and 6th November 1995. Experiments were replicated five (small juveniles) and seven (day) or six (night) times (large juveniles), respectively. The length of each fish was measured as total length to the nearest cm. One fish was subsequently introduced to each tank and allowed to acclimate for one hour. Observations were made

Table 1. Biomass of vegetation used in the experiments of habitat choice in juvenile cod. Natural biomass of the vegetation as found in the literature (Pihl et al., 1994[*]; Baden & Pihl, 1984[**]; Pihl et al., 1995[***])

Vegetation type	Wet weight (g/m^2)	Dry weight (g/m^2)	Natural biomass (dry weight in g/m^2)
Fucus vesiculosus	2025 ± 27	610 ± 8	42–416[*]
Zostera marina	883 ± 141	107 ± 17	>50–>100[**]
Cladophora sp.	1424 ± 85	331 ± 51	20–500[***]

by carefully entering the experimental room and recording the position of the fish at ten minutes intervals over a 2 h observation period. Experimental tanks were occasionally monitored by a video camera to evaluate if the fishes were affected by the observational procedure. Since no disturbance was detected, the procedure was considered acceptable. During the night experiments a torch was used to locate the fish. To ensure that observation of one tank did not disturb the fishes in the other tanks, the torch was only lit for a short period and restricted to the tank observed. The experiments were conducted at the same time each day to prevent any influence of the time of day; 11–15 hrs and 21–01 hrs for experiments in light and in the dark, respectively. Different fish were used in all experiments, thus no individual was used more than once. After each experiment the tanks were emptied of water to prevent potential stimuli from previous fishes affecting the next trial. The vegetation was left undisturbed between trials, but the filamentous algae was substituted when it was no longer buoyant.

Habitat preference by the fish was tested separately for the six habitat combinations. The two habitats in each combination were first assigned either 0 or 1 (e.g. sand = 0, *Fucus* = 1 for the sand/*Fucus* treatment), and a mean of recorded positions of the fish for each replicate was calculated. This gave a ratio for every replicate during the observation period, which was used to evaluate whether the fish exhibited a habitat preference. A two-tailed t-test was used for this, comparing the observed ratio to an expected ratio of 0.5 (random distribution). Size-classes and day and night experiments were tested separately.

Differences between the two size-classes, as well as between day and night experiments, were tested for each habitat combination with a two-factor ANOVA, after testing for homogeneous variance using Cochran's test. Where an interaction occurred, a post-hoc test (Student-Newman-Keuls) was conducted. Activity (expressed as the number of shifts between habitats recorded over the observational period) comparing day and night, habitat combinations and the two size-classes, was tested in a three-factor ANOVA. All replicates were used in the t-test, whereas five randomly chosen replicates from each treatment were used to produce balanced ANOVA's.

RESULTS

Both size-classes of juvenile cod made a choice in most of the habitat combinations during the day experiments, while no such choice was seen during night (Tables 2, 3). For small cod there was a significant habitat preference in four habitat combinations during daytime (Table 2); all vegetation types *(Fucus, Zostera* or *Cladophora)* were chosen in combinations with sand, and *Fucus* was selected when combined with *Cladophora.* No significant choice was found in the *Zostera/Fucus* and *Cladophora/Zostera* combinations for this size-class. In contrast, the larger size-class of juvenile cod made only one significant choice in the combinations with sand during day experiments, where *Fucus* was preferred to sand (Table 2). On the other hand, significant habitat choice was found in all the combinations with the three different vegetation types, with a preference for *Fucus* when available, and for *Zostera* rather than *Cladophora.*

In the night experiments no significant difference was found between the expected ratio from the null-hypothesis (0.5) and the observed ratios for either size-class of juvenile cod (Table 3). However, there was a tendency of a choice among larger juveniles,

Table 2. Habitat choice by juvenile cod during day experiments: mean ratio and results from t-test for the different habitat combinations, the two size-classes shown separately. A low ratio indicates a preference for the first habitat, while a high ratio represents a choice favouring the second habitat and a ratio around 0.5 appears when no choice has been made. Number of replicates was 5 for the small and 7 for the large juveniles (df = 4 and 6, respectively). Significance levels: ns = no significance, $*$ = p < 0.05, $**$ = p < 0.01, $***$ = p < 0.001

Treatment	Mean	Standard deviation	t-value	Probability	Significance level
Small (7–13 cm TL)					
Sand/*Fucus*	0.87	± 0.22	3.77	0.020	$*$
Sand/*Zostera*	0.97	± 0.046	22.86	0.0001	$***$
Sand/*Cladophora*	0.95	± 0.11	9.00	0.0008	$***$
Zostera/*Fucus*	0.67	± 0.24	1.62	0.18	ns
Cladophora/*Fucus*	0.88	± 0.14	6.15	0.0036	$**$
Cladophora/*Zostera*	0.33	± 0.38	−0.98	0.38	ns
Large (17–28 cm TL)					
Sand/*Fucus*	0.75	± 0.15	4.35	0.0048	$**$
Sand/*Zostera*	0.48	± 0.26	−0.12	0.91	ns
Sand/*Cladophora*	0.68	± 0.26	1.84	0.18	ns
Zostera/*Fucus*	0.71	± 0.15	3.74	0.0096	$**$
Cladophora/*Fucus*	0.80	± 0.30	2.66	0.038	$*$
Cladophora/*Zostera*	0.83	± 0.15	5.80	0.0012	$**$

Table 3. Habitat choice by juvenile cod during night experiments: mean ratio and results from t-test for the different habitat combinations, the two size-classes shown separately. A low ratio indicates a preference for the first habitat, while a high ratio represents a choice favouring the second habitat and a ratio around 0.5 appears when no choice has been made. Number of replicates was 5 for the small and 6 for the large juveniles (df = 4 and 5, respectively). Significance levels: ns = no significance, $*$ = p < 0.05, $**$ = p < 0.01, $***$ = p < 0.001

Treatment	Mean	Standard deviation	t-value	Probability	Significance level
Small (7–13 cm TL)					
Sand/*Fucus*	0.68	± 0.31	1.33	0.25	ns
Sand/*Zostera*	0.45	± 0.45	−0.25	0.81	ns
Sand/*Cladophora*	0.58	± 0.32	0.59	0.59	ns
Zostera/*Fucus*	0.37	± 0.47	−0.64	0.56	ns
Cladophora/*Fucus*	0.65	± 0.39	0.85	0.44	ns
Cladophora/*Zostera*	0.70	± 0.30	1.50	0.21	ns
Large (17–28 cm TL)					
Sand/*Fucus*	0.58	± 0.20	1.04	0.35	ns
Sand/*Zostera*	0.35	± 0.33	−1.15	0.30	ns
Sand/*Cladophora*	0.39	± 0.30	−0.92	0.40	ns
Zostera/*Fucus*	0.67	± 0.21	1.94	0.11	ns
Cladophora/*Fucus*	0.72	± 0.25	2.22	0.077	ns
Cladophora/*Zostera*	0.47	± 0.11	−0.60	0.58	ns

where *Fucus* was preferred when combined with *Zostera* or *Cladophora*. The larger juveniles also displayed a general preference for the sand habitat rather than vegetation during night.

There were no significant differences in habitat choice between the two size-classes or time of day for the combinations with *Fucus* in the two-factor ANOVA (Fig. 3a, d and e), which indicates that the choice in these combinations was independent of both size and time of day. The significant difference ($F = 5.39$, df = 4, $p = 0.0034$) between size-classes in the sand/*Zostera* combination, on the other hand, reflects the strong habitat choice for *Zostera* made by the small fish during day experiments, while the larger fish did not prefer any habitat in this combination (Fig. 3b). Although not obvious from the ANOVA results, the Student-Newman-Keuls test gave a significant difference in choice between the two size-classes during day time ($p < 0.01$), as well as for the small fishes between day and night experiments ($p < 0.05$) (Fig. 3b). In the combination with sand and *Cladophora* there was a significant difference between size-classes ($F = 4.99$, df = 4, $p = 0.040$), as well as between day and night experiments ($F = 9.60$, df = 4, $p = 0.0069$), but no interaction (Fig. 3c). Thus, the cod had chosen differently during day and night and the behaviour also differed for the two size-classes, in that the smaller juveniles made a habitat choice while the larger did not, although the response pattern was the same for both size-classes. The combination with *Cladophora* and *Zostera* gave a rather different result in the ANOVA (Fig. 3f); neither size nor time of day was a significant factor but there was an interaction ($F = 8.44$, df = 4, $p = 0.01$). The Student-Newman-Keuls test revealed that the difference lay between the two size-classes during day experiments ($p < 0.05$), and between day and night experiments for the small fish ($p < 0.05$). Although not significant for the large fish, there was a trend showing a different response by the two sizes during day and night: the large cod preferred *Zostera* during day, while the smaller exhibited no habitat preference. Neither of the size-classes made a choice during the night experiments (Fig. 3f).

The only significant difference in activity revealed in the three-factor ANOVA was between the two size-classes ($F = 17.40$, df = 4, $p = 0.0001$), which is a result of the lower activity expressed by the small juveniles during daytime (Fig. 4). There was also a tendency (although not significant) among the small fishes to increase activity, at least two fold, in the combinations with sand during night. The large fishes were equally active during day and night for all habitat combinations.

DISCUSSION

The results from this study showed that juvenile cod had a preference for vegetated habitats providing shelter during daytime, but not at night. There was also a difference in habitat utilization depending on the size of the juveniles, in that small juveniles seemed to be able to utilize all vegetation types provided, while the larger were restricted to *Fucus*.

Association of a species with a particular habitat might be a result of an active choice for this habitat; alternatively, initial distribution could be random and subsequent patterns of distribution would depend on differential mortality in the different habitats. Even if random association with habitats might influence distribution at early recruitment, many studies have shown that fish do distinguish between habitats and choose the most
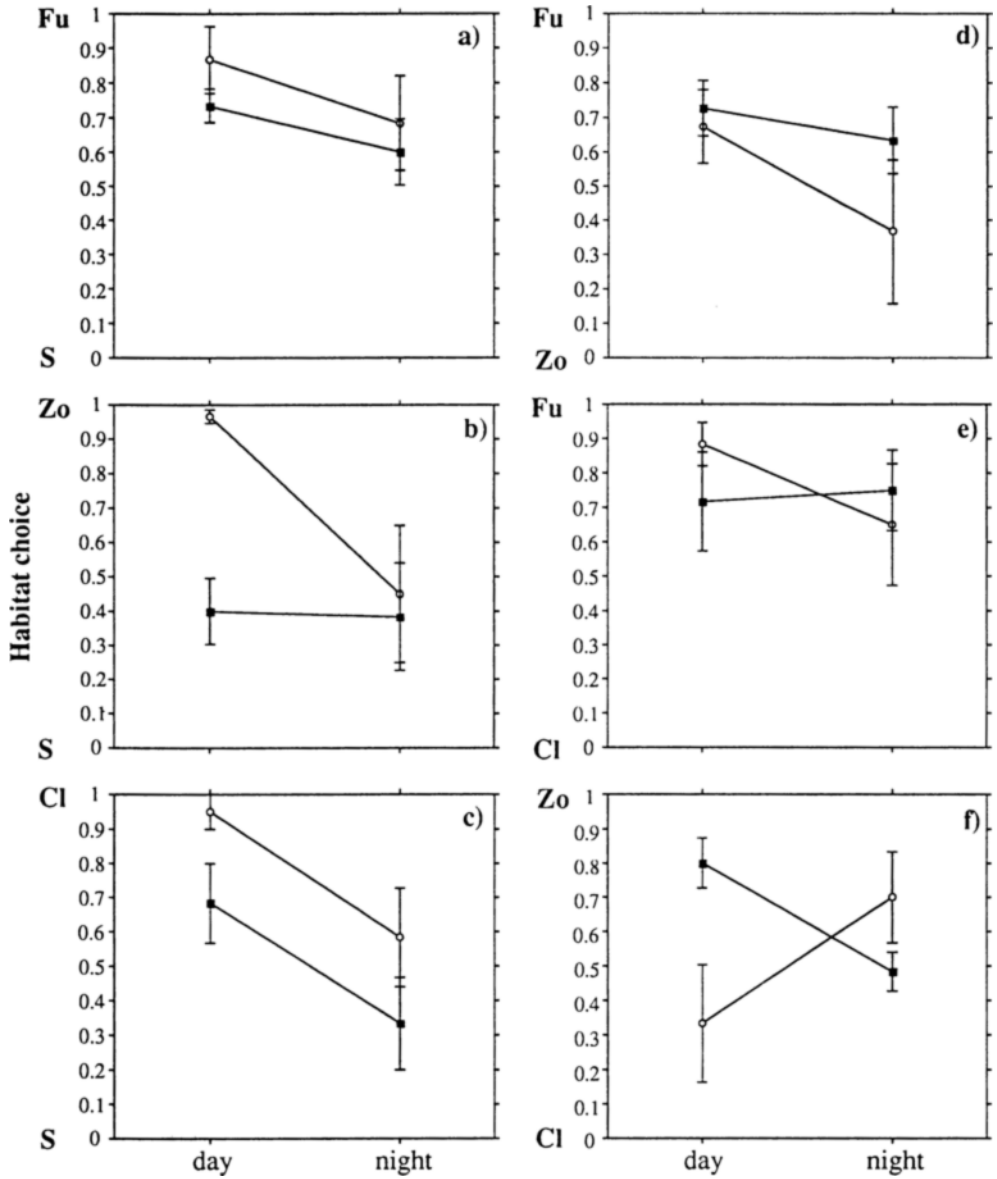
Fig. 3a–f. Habitat choice during day and night experiments for small (7–13 cm, circle) and large (17–28 cm, square) juvenile cod. Value on the Y-axis is the calculated ratio between time spent on habitat 1 and 0; 1 = preference for the habitat shown in the upper corner, 0 = preference for the habitat shown in the lower corner and 0.5 = random association with habitats. Fu = *Fucus vesiculosus*, Zo = *Zostera marina*, Cl = *Cladophora* sp. and S = bare sand. Each point is a mean of 5 replicates; vertical bars represent standard error
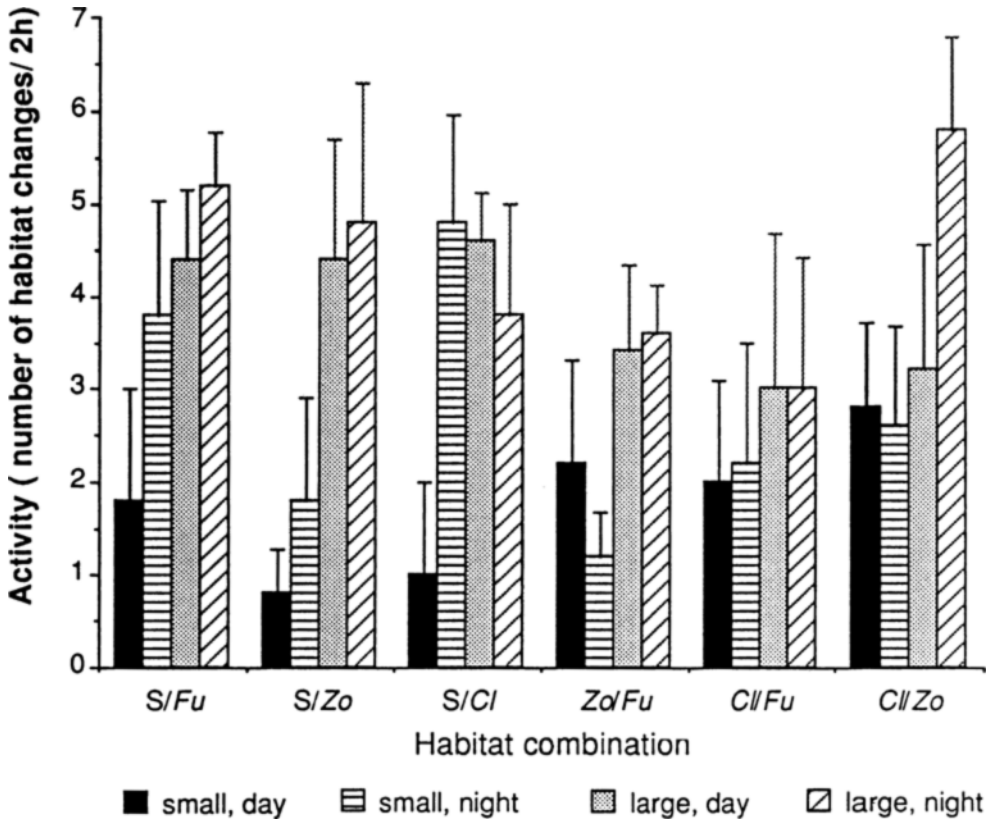
Fig. 4. Activity during day and night for small (7–13 cm) and large (17–28 cm) juvenile cod in the different habitat combinations, calculated as the number of habitat changes over the 2 h observational period. The means represent 5 replicates with standard error shown as vertical bars. The different habitats used are *Fucus vesiculosus* (Fu), *Zostera marina* (Zo), *Cladophora* sp. (Cl) and bare sand (S)

favourable one. In a study by Carr (1991), fish recruits were found to exhibit a strong and distinct habitat selection, the habitat chosen depending on the species. Carr concluded that the structural composition of the habitat strongly influences the magnitude and species composition of local fish recruitment. Gotceitas et al. (1995) found that juvenile cod shift their use of habitat in the presence of a foraging predator, from an open habitat to one providing shelter. Anti-predator behaviour, through hiding in cobble or kelp, reduced the risk of predation, and it was suggested that juvenile cod are able to evaluate the refuge potential of available habitats, choosing the safest when faced with an active predator. In a study by Gjøsæter (1987 b) small fish either avoided habitats occupied by a predator or stayed were they could hide, e.g. among stones and algae. Therefore, predator avoidance through habitat selection could be an important factor influencing the distribution of organisms vulnerable to predation (Gotceitas & Brown, 1993).

However, seeking shelter from predation may incur associated disadvantages for the prey as well, such as a decrease in foraging opportunities. Increasing habitat complexity

has a similar effect on the foraging success of both prey and predators (Gotceitas & Colgan, 1989). Hence, organisms might be faced with a trade-off situation between habitat complexity suitable for protection and for foraging (Gotceitas & Colgan, 1989; Gotceitas, 1990)

One way to minimize predation risk while maximizing foraging is to utilize heterogeneous habitats, e.g. sand and vegetation in a mosaic pattern. This enables the animal to forage in unvegetated habitats while at the same time remaining in close proximity to protective vegetated habitats (Orth et al., 1984). Another way to avoid the dilemma is to hide in protecting vegetation during daytime and migrate onto open bottoms to forage when night falls, since predation risk from visual predators is reduced during night (Adams, 1976; Pihl, 1982; Clark & Green, 1990). This seems to be the adopted strategy of the studied cod population in our investigation, where the fish were found to be associated with vegetation during day and more active over the open sandy habitat at night.

Irrespective of the lack of predators in our study, juvenile cod still chose habitats providing a refuge from predation during daytime, although the results differed for the two size-classes. Small cod appeared not to distinguish between the three different vegetation types, choosing vegetation and not sand on all occasions. Thus, it seems that all vegetation types used in this experiment were perceived as sufficient cover for fish of the smaller size-class. The only time a choice was documented between two vegetation types was in the combination with filamentous algae and *Fucus*, where *Fucus* was chosen, which indicates that this alga is a more suitable refuge for these fishes than is *Cladophora*. Large juveniles, on the other hand, preferred *Fucus* to all the other habitat types, and did not choose any other vegetation instead of sand. Thus, *Fucus* seems to be the only vegetation type used that suffices as cover for this size-class. *Zostera* appeared to be preferred to *Cladophora*, which might be due to the compact structure formed by the algae, in which larger fish may have difficulties in hiding and manoeuvering. As a probable consequence of size influence between size-classes, the small juveniles did not seem to have the same problem in entering the *Cladophora* and used this habitat for protection. Another explanation for the absence of preference in habitat for the large juveniles is that this size-class is not as susceptible to predation as the smaller size and therefore not so dependent on vegetation for protection. Keats et al. (1987) found that large juvenile cod (2-group) are less strongly associated with macrophytes than smaller juveniles, which is in accordance with our results.

Habitat choice was the same for both size-classes in the combinations with *Fucus* and independent of time of day, although not significant for all treatments. In Newfoundland, juvenile Atlantic cod moving into shallow waters in spring, have been found to be more abundant in areas with fleshy macroalgae than in areas with only crustose coralline algae (Keats et al., 1987). This association was suggested to be mainly for cover and to a lesser degree for food. *Fucus* is a very complex habitat, which provides shelter from aquatic as well as avian and terrestrial predators, due to its branched morphology. The crevices among the fronds of *Fucus* plants are of varying size, making it an ideal refuge for both small and large fish. Together with an adaptation in colour or body form which produces a resemblance to the surrounding vegetation, the shadows from the fronds make it difficult for a predator to detect structures such as prey in this vegetation, thus providing a good visual protection (Wheeler, 1980). Lough et al. (1989) found a resemblance in coloration of juvenile cod to the appearance of the habitat used as cover. In their study, the

preferred habitat was a pebble-gravel deposit at depths of 70–100 m, in contrast to macro-algae in shallow waters as found by Keats et al. (1987). Gotceitas et al. (1995) also found a preference for cobble in juvenile cod in the laboratory, although kelp was used for protection as well. In our study no cobble was available and the juvenile cod preferred vegetation, especially *Fucus,* for cover. Thus, it seems likely that the juveniles use whatever suitable habitat is available as a predation refuge.

Both size-classes were also well disguised in *Zostera* (pers. obs.), although only the small fish were found there to any extent. The density of *Zostera* used in our experiment might not have been high enough to be perceived as a predation refuge by the large juveniles. For example, Gotceitas & Colgan (1989) in laboratory showed that a threshold level of complexity is required before largemouth bass *(Micropterus salmonoides)* foraging on bluegill sunfish *(Lepomis macrochirus)* was significantly reduced. There was also a threshold density required before bluegill sunfish used the vegetation as protection, a density considerably higher than that needed to reduce predation risk. Hence, association with vegetation might increase survival, but it could also reduce foraging efficiency for the organism seeking shelter (Gotceitas, 1990). One might expect that the bigger the fish the denser the vegetation needs to be to provide sufficient cover. The threshold level should also be dependent on predator and prey species, as well as vegetation type.

In the combination with *Zostera* and *Cladophora* the habitat choices of the two size-classes were almost the opposite; the larger fishes choosing *Zostera* during day and no habitat during night, while the smaller fishes made no significant choice either in daytime or at nighttime. This difference in behaviour was probably caused by the difference in suitability of the habitats for the two size-classes. The small fishes seemed to be able to use both habitats as cover, while the larger size-class might be forced to use the *Zostera,* due to the insufficiency of the *Cladophora* as habitat. This indicates that *Zostera* might not be a habitat actually preferred by the larger fishes, which is in agreement with the results from the sand/*Zostera* combination. Since large cod is a major predator on smaller cod (Keats et al., 1987), the ability of the smaller juveniles to utilize different habitats than the larger ones do should be advantageous, enabling them to escape predation from larger conspecifics.

According to Pihl & Ulmerstrand (1993), 1-group cod on the Swedish west coast are relatively stationary during summer and autumn, starting an off-shore migration during winter at an age of two years. While remaining in-shore the cod move into shallower areas during night to feed (Pihl, 1982). Clark & Green (1990) found a similar migration pattern in juvenile cod in Conception bay, Newfoundland, with nocturnal feeding in shallow areas during summer. When the thermocline disappeared in the autumn, however, the juveniles remained within shallow-water home ranges, active diurnally over sand and inactive over a rocky substratum nocturnally.

In our experiment, juvenile cod appeared to utilize the habitats differently during day and night, since no preference was found during the night. This could be due to the fishes primarily seeking shelter from predation during the day, and emerging to forage on open habitats during night. The fact that no preference for sand was found might result from the absence of food. The fishes, therefore, retreated to cover sooner than expected if prey had been encountered. The lack of habitat choice in the combinations with two vegetation types might reflect a search for an open habitat to forage in. The non-significant tendency to spend more time on open habitats as well as the weaker preference

for *Fucus* during night also reflects the difference in habitat utilization between day and night.

Activity, i. e. the number of recorded changes in habitat made by a fish, differed between the two size-classes. This was due to the low activity in small juveniles during day, while large juveniles were more active at any time of day. Again, this difference probably reflects the dependence of the small juveniles on a predation refuge, which makes them relatively inactive during the day. During night, however, activity increases due to foraging, indicated by the non-significant tendency for small cod to spend more time on sand during night compared to daytime. In the combinations lacking an open habitat no such tendencies were seen, which further supports this hypothesis. The absence of differences in activity between day and night for the large juveniles was probably a result of the overall higher activity shown by these fishes, since they do not depend on vegetation for shelter to the same extent as the smaller juveniles.

Availability of habitats for juvenile cod on shallow soft bottoms differ spatially and temporally. Bare sand and *Zostera* beds cover vast areas, unless filamentous algae have formed mats and covered the sediment. *Fucus*, on the other hand, is sparser and is associated with rock outcrops, stones and musselbeds interspersed within the *Zostera* or the sand beds. Distribution and species composition of filamentous algae are variable, on both spatial and temporal scales (Pihl et al., 1995), making it a highly unpredictable habitat, and therefore not suitable as a settlement habitat for juvenile fish. Since fish are mobile they do not need to enter an unsuitable habitat, and can choose to continue searching for a more favourable area.

Food availability is also of importance for distribution and survival of the juveniles. In Swedish waters, juvenile cod seem to feed mainly on benthic crustaceans, such as *Carcinus maenas* and *Crangon crangon* (Pihl, 1982), which are most abundant on sandy soft bottoms. Along with the changes of habitat structure caused by nutrient enrichment, there follows a change in quantity and structure of associated fauna (Isaksson & Pihl, 1992), among which are important prey species for fish such as cod, therefore resulting in possible and probable alterations in trophic interactions in these habitats (Pihl et al., 1995). Foraging efficiency of young cod on their preferred prey was shown to be greatest in unvegetated areas, with a 30% cover of filamentous algae increasing the survival of prey species (Isaksson et al., 1994), thereby decreasing foraging efficiency of cod significantly. Increased cover of filamentous algae might therefore influence distribution and ultimately the survival of juvenile cod by reducing their food intake, resulting in a lower recruitment to the adult population.

CONCLUSIONS

Fucus seemed to provide sufficient cover for both size-classes of juvenile cod investigated in this study, while *Zostera* and *Cladophora* was sufficient for the smaller fishes only. The preference for *Zostera* over *Cladophora* by the larger juveniles was probably a result of avoidance of the algae structure or of algae-associated prey. Juvenile cod also utilized the habitats differently during day and night, moving out to open habitats at night.

The difference in habitat choice between the two size-classes of juvenile cod during day might be a result of two factors: Firstly, smaller juveniles can easily move and hide in

all three vegetation types, while larger juveniles might be restricted in their movements and find difficulties in hiding amongst the *Cladophora*, due to the structure of this type of vegetation. Secondly, shelter from predation is important for small juvenile cod; therefore choosing vegetation rather than open habitats during daytime is in their case advantageous. The dependence on vegetation is not so strong in larger juveniles, since their main predators are avian or come from deeper waters. In their case, due to its morphology, *Fucus* should prove to be a better shelter.

Availability of vegetation at daytime, as a predation refuge, as well as open sandy areas for feeding during night thus seems to be important for juvenile cod. This indicates that eutrophication-induced changes in habitat structure, such as increased dominance by filamentous algae, might have negative effects on juvenile cod by changing availability of predation refuges and foraging habitats. Although *Cladophora* might give shelter from predation (at least for the smaller juveniles), it changes foraging efficiency and does not provide the same prey organisms as sand and may therefore be a suboptimal habitat for juvenile cod.

LITERATURE CITED

Adams, S. M., 1976. The ecology of eelgrass, *Zostera marina* (L), fish communities. I. Structural analysis. – J. exp. mar. Biol. Ecol. *22*, 269–291.

Baden, S. P., Loo, L-O., Pihl, L. & Rosenberg, R., 1990. Effects of eutrophication on benthic communities including fish: Swedish west coast. – Ambio *19*, 113–122.

Baden, S. P. & Pihl, L., 1984. Abundance, biomass and production of mobile epibenthic fauna in *Zostera marina* (L) meadows, western Sweden. – Ophelia *23*, 65–90.

Bonsdorff, E., 1992. Drifting algae and zoobenthos – effects on settling and community structure. – Neth. J. Sea Res. *30*, 57–62.

Bonsdorff, E., Norkko, A. & Boström, C., 1995. Recruitment and population maintenance of the bivalve *Macoma baltica* (L.) – Factors effecting settling success and early survival on shallow sandy bottoms. In: Biology and ecology of shallow coastal waters. Ed. by A. Eleftheriou, A. D. Ansell & C. J. Smith. Olsen & Olsen, Fredensborg, 253–260.

Breuer, G. & Schramm, W., 1988. Changes in macrovegetation of Kiel Bight (Western Baltic Sea) during the past 20 years. – Kieler Meeresforsch. (Sdrh) *6*, 241–255.

Carr, M. H., 1989. Effects of macroalgae assemblages on the recruitment of temperate zone reef fishes. – J. exp. mar. Biol. Ecol. *126*, 59–76.

Carr, M. H., 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. – J. exp. mar. Biol. Ecol. *146*, 113–137.

Carr, M. H., 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. – Ecology *75*, 1320–1333.

Clark, D. S. & Green, J. M., 1990. Activity patterns of juvenile Atlantic cod, *Gadus morhua*, in Conception Bay, Newfoundland, as determined by sonic telemetry. – Can. J. Zool. *68*, 1434–1442.

Dionne, M. & Folt, C. L., 1991. An experimental analysis of macrophyte growth forms as fish foraging habitat. – Can. J. Fish aquat. Sci. *48*, 123–131.

Elliott, M., O'Reilly, M. G. & Taylor, C. J. L., 1990. The Forth estuary: a nursery and overwintering area for North Sea fishes. – Hydrobiologia *195*, 89–103.

Gibson, R. N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfish. – Neth. J. Sea Res. *32*, 191–206.

Gibson, R. N., Ansell, A. D. & Robb, L., 1993. Seasonal and annual variations in abundance and species composition of fish and marocrustacean communities on a Scottish sandy beach. – Mar. Ecol. Prog. Ser. *98*, 89–105.

Gjøsæter, J., 1987a. Habitat selection of juvenile cod *(Gadus morhua)*, whiting *(Merlangus merlangius)* and some littoral fish in an aquarium. – Flødevigen Rapp. Ser. *1*, 17–26.

Gjøsæter, J., 1987b. Habitat selection and inter year class interaction in young cod *(Gadus morhua)* in aquaria. – Flødevigen Rapp. Ser. *1*, 27–36.

Gotceitas, V., 1990. Variation in plant stem density and its effects on foraging success of juvenile bluegill sunfish. – Environ. Biol. Fish. *27*, 63–70.

Gotceitas, V. & Brown, J. A., 1993. Substrate selection by juvenile Atlantic cod *(Gadus morhua)*: effects of predation risk. – Oecologia *93*, 31–37.

Gotceitas, V. & Colgan, P., 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. – Oecologia *80*, 158–166.

Gotceitas, V., Fraser, S. & Brown, J. A., 1995. Habitat use by juvenile Atlantic cod *(Gadus morhua)* in the presence of an actively foraging and non-foraging predator. – Mar. Biol. *123*, 421–430.

Hull, S. C., 1987. Macroalgal mats and species abundance: a field experiment. – Estuar. coast. Shelf Sci. *25*, 519–532.

Isaksson, I. & Pihl, L., 1992. Structural changes in benthic macrovegetation and associated epibenthic faunal communities. – Neth. J. Sea Res. *30*, 131–140.

Isaksson, I., Pihl, L. & Montfrans, J. van, 1994. Eutrophication-related changes in macrovegetation and foraging of young cod *(Gadus morhua L)*: a mesocosm experiment. – J. exp. mar. Biol. Ecol. *177*, 203–217.

Jansson, B. O., Aneer, G. & Nellbring, S., 1985. Spatial and temporal distribution of the demersal fish fauna in a Baltic archipelago as estimated by SCUBA census. – Mar. Ecol. Prog. Ser. *23*, 31–43.

Keats, D. W., Steele, D. H. & South, G. R., 1987. The role of fleshy macroalgae in the ecology of juvenile cod *(Gadus morhua)* in inshore waters off eastern Newfoundland. – Can. J. Zool. *65*, 49–53.

Kingsford, M. J., 1992. Drift algae and small fish in coastal waters of northeastern New Zealand. – Mar. Ecol. Prog. Ser. *80*, 41–55.

Lough, R. G., Valentine, P. C., Potter, D. C., Auditore, P. J., Bolz, G. R., Neilson, J. D. & Perry, R. I., 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. – Mar. Ecol. Prog. Ser. *56*, 1–12.

Menge, B. A. & Sutherland, J. P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. – Am. Nat. *130*, 730–757.

Nixon, S. W., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. – Ophelia *41*, 199–219.

Norkko, A. & Bonsdorff, E., 1996. Rapid zoobenthic community responses to accumulations of drifting algae. – Mar. Ecol. Prog. Ser. *131*, 143–157.

Orth, R. J., Heck, K. L. & Montfrans, J. van, 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. – Estuaries *7*, 339–350.

Pihl, L., 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast. – Neth. J. Sea Res. *15*, 419–432.

Pihl, L. & Rosenberg, R., 1982. Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, western Sweden. – J. exp. mar. Biol. Ecol. *57*, 273–301.

Pihl, L. & Ulmestrand, M., 1993. Migration pattern of juvenile cod *(Gadus morhua)* on the Swedish west coast. – ICES J. mar. Sci. *50*, 63–70.

Pihl, L., Wennhage, H. & Nilsson, S., 1994. Fish assemblage structure in relation to macrophytes and filamentous epiphytes in shallow non-tidal rocky- and soft-bottom habitats. – Environ. Biol. Fish., *39*, 271–288.

Pihl, L., Isaksson, I., Wennhage, H. & Moksnes, P.-O., 1995. Recent increase of filamentous algae in shallow Swedish bays: effects on the community structure of epibenthic fauna and fish. – Neth. J. aquat. Ecol. *29*, 1–10.

Raffaelli, D., Hull, S. & Milne, H., 1989. Long-term changes in nutrients, weed mats and shorebirds in an estuarine system. – Cah. Biol. mar. *30*, 259–270.

Raffaelli, D., Lima, D., Hull, S. & Pont, S., 1991. Interactions between the amphipod *Corophium volutator* and macroalgal mats on estuarine mudflats. – J. mar. biol. Ass. U. K. *71*, 899–908.

Reise, K., 1983. Sewage, green algal mats anchored by lugworms, and the effects on Turbellaria and small polychaeta. – Helgoländer Meeresunters. *36*, 151–162.

Reise, K. & Siebert, I., 1994. Mass occurrence of green algae in the German Wadden Sea. – Dt. hydrogr. Z. (Suppl.) *1*, 171–180.

Reise, K., Herre, E. & Sturm, M., 1989. Historical changes in the benthos of the Wadden Sea around the island of Sylt in the North Sea. – Helgoländer Meeresunters. *43*, 417–433.

Rosenberg, R., 1985. Eutrophication – the future marine coastal nuisance? – Mar. Pollut. Bull. *16*, 227–231.

Rosenberg, R., Elmgren, R., Fleischer, S., Jonsson, P., Persson, G. & Dahlin, H., 1990. Marine eutrophication case studies in Sweden. – Ambio *19*, 102–108.

Sogard, S. M., 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. – Mar. Ecol. Prog. Ser. *85*, 35–53.

Sogard, S. M. & Able, K. W., 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. – Estuar. coast. Shelf Sci. *33*, 501–519.

Wheeler, A., 1980. Fish-algal relations in temperate waters. In: The shore environment. Ed. by J. H. Price, D. E. G. Irvine & W. F. Farnham. Acad. Press, London, 677–698.

Zijlstra, J. J., 1972. On the importance of the Wadden Sea as a nursery area in relation to the conservation of the southern North Sea fishery resources. – Symp. zool. Soc. Lond. *29*, 233–258.