

Hiding and feeding in floating seaweed: Floating seaweed clumps as possible refuges or feeding grounds for fishes

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Abstract

Floating seaweed is considered to be an important habitat for juvenile fishes due to the provision of food, shelter, a visual orientation point and passive transport. The importance of the presence of the highly dynamical seaweed clumps from the North Sea to juvenile neustonic fishes was investigated by analysing both neuston samples (without seaweed) and seaweed samples concerning fish community structure, and length-frequency distributions and feeding habits of five associated fish species. While the neustonic fish community was mainly seasonally structured, the seaweed-associated fish community was more complex: the response of the associated fish species to environmental variables was species specific and probably influenced by species interactions, resulting in a large multivariate distance between the samples dominated by *Chelon labrosus* and the samples dominated by *Cyclopterus lumpus*, *Trachurus trachurus* and *Ciliata mustela*. The results of the stomach analysis confirmed that *C. lumpus* is a weedpatch specialist that has a close spatial affinity with the seaweed and feeds intensively on the seaweed-associated invertebrate fauna. Similarly, *C. mustela* juveniles also fed on the seaweed fauna, but in a more opportunistic way. The shape of the size-frequency distribution suggested enhanced growth when associated with floating seaweed. *Chelon labrosus* and *T. trachurus* juveniles were generally large in seaweed samples, but large individuals were also encountered in the neuston. The proportion of associated invertebrate fauna in their diet was of minor importance, compared to the proportions in *C. lumpus*. Individuals of *Syngnathus rostellatus* mainly fed on planktonic invertebrates but had a discontinuous size-frequency distribution, suggesting that some of the syngnathids were carried with the seaweed upon detachment and stayed associated. Floating seaweeds can therefore be regarded as ephemeral habitats shared between several fish species (mainly juveniles) that use them for different reasons and with varying intensity.

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1. Introduction

A wide variety of fish taxa throughout the world’s oceans have a natural tendency to aggregate beneath or associate with floating structures such as plastic debris, floating seaweeds, pieces of wood, jellyfish, fish aggregation devices (FADs) and animal remains (e.g. Safran and Omori, 1990; Davenport and Rees, 1993; Moser et al., 1998; Masuda and Tsukamoto, 2000; Castro et al., 2001; Thiel and Gutow, 2005a,b). Generally, the fish community is found to be more

diverse below floating seaweeds than below other floating items (Fedoryako, 1989). According to Kingsford (1995), the increased diversity in the presence of floating seaweeds compared to the surrounding water column can be attributed to the substantial increase in habitat complexity of the pelagic environment.

Many authors have already attempted to classify fish based on the spatial and temporal relation between the fishes and the floating object. Castro et al. (2001) distinguished ‘associated’ fishes (circulate around the structure and do not show any dependence) and ‘aggregating’ fishes (live close to the floating object and depend on it). Dooley (1972) separated coincidentally associated fishes with rare occurrence, moderately associated fishes, seasonally occurring fishes, and closely

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associated fishes. Hirosaki (1960 – in Thiel and Gutow, 2005b), proposed a classification in: (1) fishes that stay within the branches of the algae; (2) fishes that remain underneath the floating patch; and (3) fishes that swim around the patch with close association; and Gooding and Magnuson (1967) discerned transients (no response to and no contact with the floating object), visitors (response but no contact) and residents (response and contact). Although different classifications have been used in literature, they all distinguish groups based on the dependency of the fishes to the floating object and are therefore relatively comparable and applicable in new studies.

Floating seaweed is considered to be an important habitat for juvenile fish. Masuda and Tsukamoto (2000) found that the onset of the association behaviour already starts at an early stage in some fish species (at 12 mm TL for *Pseudocaranx dentex*) and is probably triggered by visual and mechanical stimuli. The advantages of associating with floating seaweeds are numerous (reviewed in Castro et al., 2001): (1) the benefits of living in the shade in relation to predators and detection of prey (Kingsford, 1992); (2) the presence of abundant food sources like smaller fish, associated macrofauna or the seaweed itself (Wright, 1989; Safran and Omori, 1990; Davenport and Rees, 1993); (3) the shelter from piscivorous fish and birds (Wright, 1989; Kokita and Omori, 1998); (4) the potential for passive transport (Dooley, 1972); (5) the meeting point function for the formation and maintenance of schools or for spawning (Masuda and Tsukamoto, 2000); (6) the substitution of the seabed for non-pelagic fish; and (7) the function of floating objects as cleaning stations (Gooding and Magnuson, 1967). Accordingly, aggregative and associative behaviour of juvenile fish can be the expression of convergent behaviours resulting from different motivations (Castro et al., 2001).

Different studies indicate that the association between most fish species and floating seaweeds is of a temporary nature, particularly in the juvenile stages (e.g. Davenport and Rees, 1993; Castro et al., 2001; Ingólfsson and Kristjánsson, 2002). Furthermore, Shaffer et al. (1995) described that the function of floating seaweed with regard to juvenile fish may change seasonally. Juvenile *Sebastes diploproa*, for example, finds refuge from predators in spring and summer, whereas in autumn, the seaweed increasingly serves as a prey habitat. Several studies reported higher fish densities in summer months, probably due to the increased availability of floating seaweed in that period (Kingsford, 1992; Thiel and Gutow, 2005b). Next to temporal variation, variations in the size of floating seaweed patches strongly influence the densities and species composition of the associated ichthyofauna (Hunter and Mitchell, 1967; Dooley, 1972; Moser et al., 1998; Nelson, 2003). Because effects of seaweed species composition, distance to shore and raft age (increased epibiont load) have already been reported for rafting invertebrates (Fine, 1970; Ingólfsson, 2000; Castro et al., 2001; Ólafsson et al., 2001; Thiel and Gutow, 2005b; Vandendriessche et al., 2006b), these factors are also likely to apply to rafting fish.

Although research about the importance of association behaviour is very important from the perspective of fisheries ecology, very little information is available concerning the

relation between fishes and the highly dynamical floating seaweed clumps found in the North Sea. Therefore, the present study aims to investigate the species composition and association behaviour of fishes associated with floating seaweeds. To this end, we identified neustonic fishes with a tendency to associate with floating objects, and investigated the variability within the fish community. For each of the associated fish species, the underlying motivation for association behaviour (food, shelter or other) was investigated.

2. Material and methods

2.1. Sampling

Based on literature (e.g. Dooley, 1972; Ingólfsson, 1995; Cho et al., 2001) and personal experience, a neuston net and a dip net were found to be the most effective net types for sampling neustonic (not associated with floating objects) and seaweed-associated juvenile fish communities, respectively. This approach, however, was expected to result in variations concerning net efficiency, and therefore in differences concerning the fish species and sizes caught. In the present study, we took into account the variation in net efficiency by analysing the quantitative data from the two sampling methods separately.

2.1.1. Neuston net samplings

A year-round survey of the neuston (monthly samplings) was carried out in the Belgian part of the North Sea (BPNS) (6 sampling stations, Fig. 1) in the period July 2003–June 2004. Samples were taken with a rectangular net (2 m × 1 m, 1 mm mesh), of which only the lower half was immersed, thereby sampling the upper 0.5 m of the water column. After a tow of 15 min (average filtered volume: 2623 m³, average speed: 1.5 knots), the net was emptied and rinsed, while the contents were preserved in formalin solution. All fishes were first anaesthetised in a benzocaine (Ethyl amino-4-benzoate)-water solution to prevent regurgitation of the stomach contents.

2.1.2. Dip net samplings

Seaweed samplings were conducted from October 2002 to September 2004 in the BPNS. The RV 'Zeeleeuw' was used to collect patches of floating seaweed using a 40 cm diameter dip net with 300 µm mesh, ensuring that the captured fish had a spatial affinity with the seaweed. During the sampling period, 249 seaweed samples from 60 sampling sites (Fig. 1) were collected along with their associated macro-invertebrates and fish fauna. Three control samples (i.e. surface water samples without seaweeds) were taken at each sampling site. The size of the seaweed samples was dictated by the diameter of the sampling net used. In the field, all fishes were anaesthetised in a benzocaine – water solution and preserved in formalin solution together with the rest of the associated fauna.

Sampling intensity was not equal over the seasons because bad weather often prevented the search for floating seaweeds (especially in the period October–January). For successful samplings, the mean number of sampling points (and hence

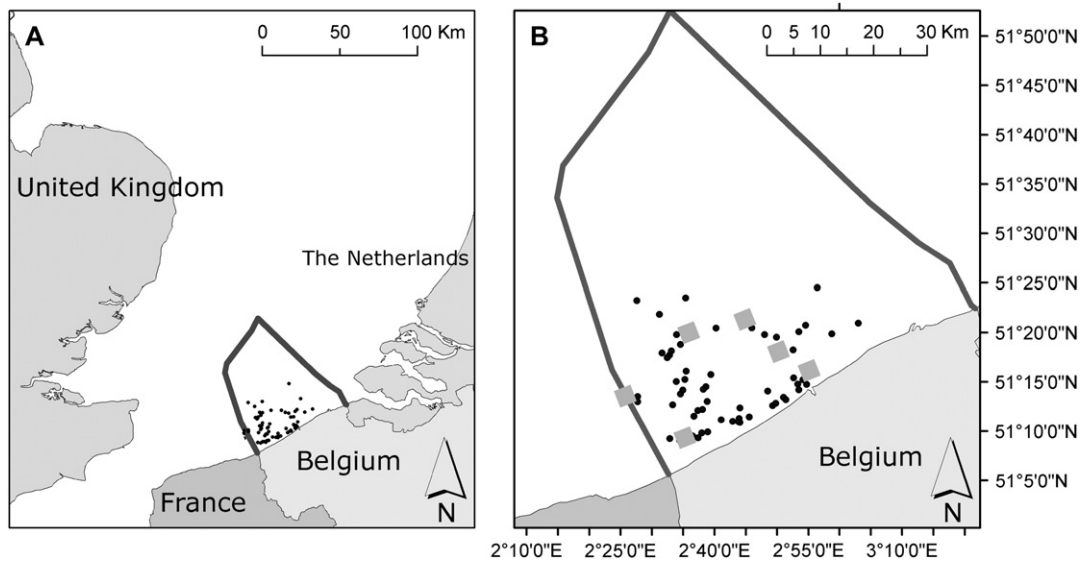


Fig. 1. Map of the southern part of the North Sea (A) and the Belgian continental shelf (B; delimited by black line), with indication of neustonic sampling stations (grey squares) and seaweed sampling sites (black dots).

the amount of encountered seaweed clumps) was highest in the periods February–April and June–September. Clumps of floating seaweed consisted of one or more seaweed species like *Fucus vesiculosus* (Fv, mean 30% of total clump volume), *Ascophyllum nodosum* (An, mean 10%), *Halidrys siliquosa* (Hs, mean <1%), *Fucus spiralis* (Fs, mean 29%), *Himantalia elongata* (He, mean 20%), *Cystoseira* sp. (Csp, mean <1%), Filamentous green algae (Fil. Gr. Algae, mean <1%), *Chorda filum* (Cf, mean <1%) and *Sargassum muticum* (Sm, mean 8%), and small amounts of other floating debris (mean 3%) like reed, feathers, plastic, nylon, wood and cardboard. Most clumps (85%) were composed of more than one seaweed species.

2.2. Laboratory treatment

Neuston- and seaweed samples were rinsed over a 1 mm sieve and the associated fishes and macro-invertebrates were removed. The volume of the seaweed constituents (and other debris) was recorded to the nearest millilitre, using a graduated cylinder. All fishes were counted and identified, and the total length (± 1 mm) of each individual was recorded. The macro-invertebrates found in seaweed samples were counted and identified.

2.3. Analysis of seaweed-associated macro-invertebrate data

Prior to the analyses, the dataset was reduced to the species: (1) accounting for >3% of the total abundance in any one sample; and (2) found significantly more in seaweed samples compared to control samples. Univariate two-way analysis of variance (ANOVA, 41 sampling occasions, 2 sample types) was used to test for differences in abundance between seaweed samples and control samples. If necessary, a $\log(x + 1)$ transformation was performed to meet the required assumptions. Of

all invertebrate species that were found significantly more in seaweed samples, the added value was calculated by subtracting background neustonic values from seaweed sample values per sampling occasion (see Vandendriessche et al., 2006a). These values were further used in the analysis of the fish data.

2.4. Stomach content analysis of seaweed-associated and neustonic fish

Diverse larval and juvenile fish species were recorded in the surface 0.5 m of water, and were either neustonic or associated with floating seaweed patches. The species *Trachurus trachurus*, *Chelon labrosus*, *Ciliata mustela*, and *Syngnathus rostellatus* were frequently and abundantly found in both sample types and were selected for stomach analysis. *Cyclopterus lumpus* was only found in association with floating seaweeds and was also included. For each of the selected fish species, the stomach contents of neustonic and seaweed-associated individuals were examined per 5 mm length class (for individuals >1.5 cm in *C. lumpus*, >2 cm in *C. labrosus*, *C. mustela* and *T. trachurus*, >6 cm in *S. rostellatus*). Length classes with fewer than 5 fish were omitted from all analyses. The intact stomachs were removed under a stereoscopic microscope, by cutting above the oesophagus and below the large intestine (for Syngnathidae, the entire gut was examined). An incision was made along the longitudinal axis and the contents emptied onto a Petri dish with a few drops of deionised water. All prey items encountered in the stomachs were counted, identified (if possible to species level), and measured. The biomass (mg Ash Free Dry Weight/m³) of each prey item was computed with length-AFDW regressions established formerly in the laboratory. Both fish and stomach contents were placed into separate vials for potential further investigation and subsequent drying. After identification and measuring, the stomach contents were placed in pre-weighed aluminium foil cups, dried at 110 °C for 5 h, incinerated in ceramic cups at

550 °C for 15 min, and cooled to room temperature in a desiccator for 2 h before weighing in order to obtain AFDW.

For the quantitative analysis of the stomach contents, the fullness index (FI) was used:

$$FI = \frac{S_i}{W_i} \times 100$$

where S_i is the AFDW of the stomach content in milligram (mg) and W_i is the AFDW of the fish (mg).

As a qualitative measure, the Shannon-Wiener index (H') of the stomach contents of the common fish species was calculated as

$$H' = - \sum p_i \ln p_i$$

where p_i is the proportion of the individuals found in the ' i 'th species.

Furthermore, frequencies of occurrence and numerical and gravimetric percentages were calculated to characterise the stomach contents (Hyslop, 1980). The frequency of occurrence (FO%) calculates the percentage of the total number of stomachs in which the specific prey species occur. The numerical percentage (N%) reflects the proportion (percentage) of the total individuals in all food categories, whereas the gravimetric percentage (G%) reflects the proportion of the total weight (expressed as AFDW).

The degree of dietary overlap was calculated using the Schoener index (1970):

$$\alpha = 1 - 0.5 \left(\sum_{i=1}^n |p_{xi} - p_{yi}| \right)$$

where p_{xi} and p_{yi} are the proportions of the ' i 'th prey category for the species pair x and y , and n the number of prey categories. The index ranges from 0 for no diet overlap to 1 for complete diet similarity.

2.5. Data treatment

Differences in fish species compositions between neustonic samples and seaweed samples were examined using non-metric MultiDimensional Scaling ordination (MDS) using the Bray-Curtis similarity measure. ANalysis Of SIMilarities (ANOSIM) was used to test for significant differences ($p < 0.05$) between groups (defined *a priori*), while the species contributing to dissimilarities between groups were investigated using a SIMilarity-PERcentages procedure (SIMPER). The relationship between seaweed-associated fish densities (individuals per litre of seaweed) and variables (seaweed volume, relative abundances of the seaweed constituents per sample, surface water temperature and salinity, distance to shore, atmospheric pressure and humidity) was analysed using the Spearman rank correlation and the significance was determined using a permutation procedure (RELATE, Clarke and Warwick, 1994). The BIO-ENV procedure was used to define suites of variables that best determine the macrofaunal assemblages. Empty

samples were excluded from the analyses and a square root transformation was performed on the abundance data prior to the analyses. All multivariate community analyses were done using the Primer v5.2.9 software package (Clarke and Gorley, 2001).

The univariate non-parametric Mann–Whitney U -test (MWU) was used to test for differences in stomach content parameters of fish found in neustonic samples and seaweed samples.

3. Results

3.1. Neustonic fish

ANOSIM revealed significant seasonal differences between samples (Global R: 0.206; significance level $p = 0.001$, Fig. 2); and pairwise tests showed that all seasons differed significantly, except summer samples and autumn samples. The MDS plot and the SIMPER analysis both indicated a large variability in the summer samples (average similarity: 34%), compared to the other seasons (average similarity autumn: 64%, winter: 54%, spring: 60%). Postlarvae and juveniles of *Ammodytes tobianus*/*Hyperoplus lanceolatus* and *Clupea harengus*/*Sprattus sprattus*/*Engraulis encrassicolus* were abundant throughout the year, but there were considerable differences in the seasonal occurrences of other fish species (Table 1). Effects of sampling station (spatial variability) and effects of the presence of small amounts of floating seaweed and debris were not significant.

3.2. Macro-invertebrates and fish associated with floating seaweed

Several macrofaunal invertebrates were found significantly more in dip net seaweed samples than in dip net control samples. Harpacticoid copepods, crab megalopae, gammarid amphipods, idoteid isopods and postlarval prawns constituted 95% of the added value (Fig. 3). Of all analysed seaweed

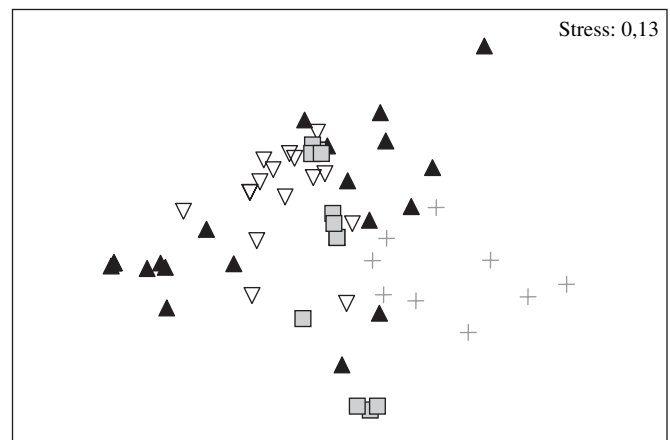


Fig. 2. MDS of neustonic fish data (sqrt transformation, Bray-Curtis similarity): black triangles = summer samples, white triangles = autumn samples, crosses = spring samples, squares = winter samples.

Table 1

List of fish species encountered in neuston samples, with indication of seasonal occurrence, length range (cm) and numbers caught

	Seasonal occurrence				Length range (cm)	# caught
	Spring	Summer	Autumn	Winter		
<i>Ammodytes tobianus</i> / <i>Hyperoplus lanceolatus</i>	■	■	■	■	0.3–12.2	884
<i>Arnoglossus laterna</i>		■			0.5	1
<i>Belone Belone</i>		■			0.9–3.7	69
<i>Chelon labrosus</i>		■	■	■	0.3–3.8	1591
<i>Ciliata mustela</i>	■	■			0.4–3.6	405
<i>Clupea harengus</i> / <i>Sprattus sprattus</i> / <i>Engraulis encrassicolus</i>	■	■	■	■	0.4–9.3	2257
Cottidae sp.		■	■	■	0.2–1.2	290
<i>Echiichthys vipera</i>		■			0.4–1.6	45
<i>Hippocampus guttulatus</i>			■		2.9–3.5	2
<i>Labrus bergylta</i>		■			0.6–1.1	2
<i>Merlangius merlangus</i>	■				0.6–4.1	10
Pleuronectidae sp.	■	■			0.7–1.3	3
<i>Pollachius pollachius</i>	■				3.2	1
<i>Pollachius virens</i>		■			2.5	1
<i>Scophthalmus maximus</i>	■	■			1.6–2.1	4
<i>Solea solea</i>	■	■	■	■	0.3–0.8	14
<i>Syngnathus acus</i>		■	■	■	2.9–5.5	7
<i>Syngnathus rostellatus</i>	■	■	■	■	1.0–5.7	28
<i>Trachurus trachurus</i>		■		■	0.3–4.2	258

samples, 41% contained fishes (590 specimens in total, Table 2), while control dip net samples only yielded two *Platichthys flesus* larvae.

MDS based on seaweed-associated fish data (Fig. 4) revealed four groups (ANOSIM R: 0.8, $p = 0.001$): a group of seaweed samples that exclusively contained *Chelon labrosus* (average similarity: 69%), and three other groups that were dominated (highest densities) by *Ciliata mustela* (average similarity: 48%), *Cyclopterus lumpus* (average similarity: 62%), or *Trachurus trachurus* (average similarity: 56%). These last three groups were more closely related and frequently contained other fish species. The multivariate pattern of the fish data were compared to the environmental data (seaweed volume, relative abundances of the seaweed constituents per sample, surface water temperature and salinity, distance to shore, atmospheric pressure and humidity, added values of associated

macro-invertebrates). RELATE indicated a significant correlation between the standardised Euclidian distance matrix of the variables and the similarity matrix of macrofaunal data ($p = 0.001$). The draftsman plot and the associated correlation matrix showed no evidence of collinearity, so all variables were used in the BIO-ENV analysis. Within the analysed seaweed samples, a combination of all variables best explained the macrofaunal assemblages, but the matching coefficient was very low ($\sigma = 0.23$). This implies that only a part of the biotic structure is explained by the measured variables, and that there are other factors that strongly structure the fish assemblages.

Correlation analyses between density data of abundantly and frequently occurring fish species and variables (Table 3) indicated different responses of the fish species: *Cyclopterus lumpus* was strongly associated with the occurrence of large

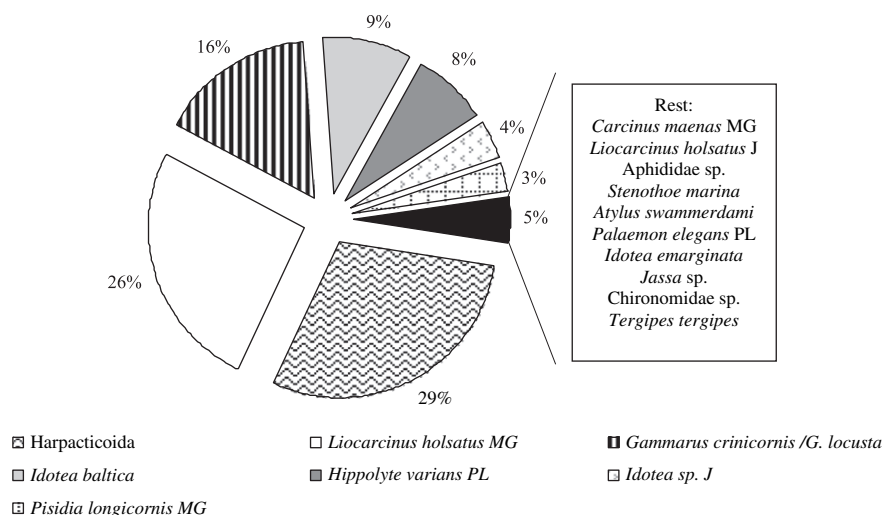


Fig. 3. Pie chart representing relative abundances of seaweed-associated macro-invertebrates (MG: megalopa; J: juvenile; PL: postlarva).

Table 2
List of all fish species encountered in dip net seaweed samples, with indication of seasonal occurrence, length range (cm) and numbers caught

	Seasonal occurrence				Length range (cm)	# caught
	Spring	Summer	Autumn	Winter		
<i>Belone belone</i>		■			4.0	1
Blennidae sp.		■			1–1.2	2
<i>Callionymus lyra</i>	■				–	1
<i>Chelon labrosus</i>		■	■		0.7–2.8	202
<i>Ciliata mustela</i>	■	■			1.0–4.0	147
Cottidae sp.		■			0.8–1.7	13
<i>Cyclopterus lumpus</i>	■	■	■	■	0.6–4.9	97
<i>Entelurus aequorius</i>	■	■		■	13.6–15	6
Gobiidae sp.		■			1.1–1.2	2
<i>Merlangius merlangus</i>		■			3.4	1
<i>Nerophis lumbriciformis</i>	■				5	1
<i>Pollachius pollachius</i>	■				2.3–2.6	11
<i>Pollachius virens</i>	■				2.3	1
<i>Syngnathus acus</i>		■			7.4–14.4	2
<i>Syngnathus rostellatus</i>		■			3.7–12.2	7
<i>Trachurus trachurus</i>		■			0.7–4.3	147

clumps of *Ascophyllum nodosum* and *Himanthalia elongata* and was most abundantly found in winter. *Trachurus trachurus* was associated with *Fucus spiralis*, *A. nodosum* and *H. elongata*, but showed a negative correlation with clump volume. This species was usually found off-shore in summer. *Chelon labrosus*, on the other hand, was abundantly found in near-shore stations in summer, but also showed a negative correlation with clump volume. *Syngnathus rostellatus* was found frequently, but in low abundance, in summer samples and showed a slight affinity for a *F. spiralis*. Finally, *Ciliata mustela* showed a strong positive correlation with the seaweed *Sargassum muticum*, and was abundantly found in spring samples close to the shore. For all fish species, there seemed to be no straightforward links between the added values of potential invertebrate prey items and fish densities, especially in the light of the stomach analyses results (see below).

3.3. Stomach analyses

3.3.1. *Cyclopterus lumpus*

Large numbers of young lumpfishes (up to 13 per clump) were frequently encountered in floating seaweed clumps (in

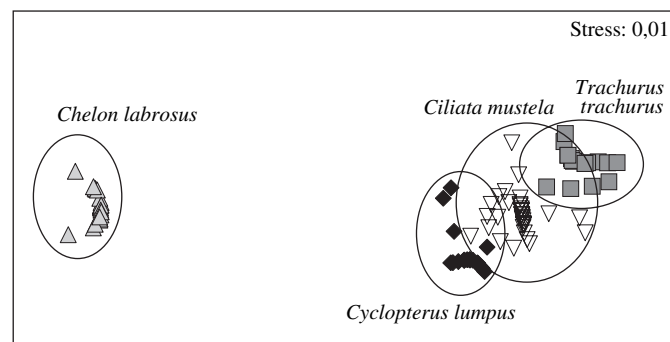


Fig. 4. MDS plot (Bray-Curtis similarities) of samples based on fish densities in seaweed samples, with indication of dominant fish species.

10% of all seaweed samples, 16% of total number of fish). Most lumpfishes were juveniles in their first (0.6–3 cm) or second (ca. 3.5 cm) year according to the estimates of Davenport and Rees (1993) and Ingólfsson and Kristjánsson (2002). The largest individuals were found in winter (mean length 3.5 cm); the smallest in spring (mean length 1.9 cm). Although 18 different prey items (mainly amphipods, isopods, decapod larvae, copepods and fish eggs) were found in the stomachs, the average Shannon-Wiener index was generally low (range 0.12–0.34; Table 4). Most fish had a full stomach (only two stomachs were empty), but only 1 to 4 different prey species could be distinguished per stomach. The average fullness index was positively correlated with the total length of the juvenile fish (Spearman R: 0.26; $p = 0.01$) and ranged between 0 and 18.3.

The qualitative stomach analysis (Fig. 5, only gravimetric percentage represented; frequency of occurrence and numerical percentage showed the same trends) showed a shift in dominant prey with increasing length of the juveniles, from a dominance of *Liocarcinus holtsatus* megalopae, calanoid and harpacticoid copepods and small gammarid amphipods (mainly *Gammarus* sp. juveniles) in the smallest length class to *Idotea baltica*, fish eggs, calanoids and large gammarid amphipods (*Gammarus locusta* and *Gammarus crinicornis*) in the larger length classes (rest: *Palaemon* postlarvae, small fish, *Sagitta* sp., *Idotea emarginata*, *Idotea linearis*, *Jassa* sp. and *Carcinus maenas* megalopae).

3.3.2. *Ciliata mustela*

Fivebeard rocklings were encountered in both neustonic and seaweed samples. However, the size distributions of both sample groups showed substantial differences: rocklings from seaweed samples were generally larger (2.5–4 cm) than specimens from neustonic samples (0.5–3 cm) without seaweed (Fig. 6). The food consumption of individuals in size classes found in both sample types (2.6–3 cm, 3.1–3.5 cm) will be further discussed. The Shannon-Wiener

Table 3
Results of Spearman rank correlations between fish densities and environmental variables and prey densities. Results indicate positive (+) or negative (–) correlations and the significance level (* significant $p < 0.05$, ** highly significant $p < 0.01$, *** very highly significant $p < 0.001$). Abbreviations: *Fucus vesiculosus* (Fv), *Ascophyllum nodosum* (An), *Halidrys siliquosa* (Hs), *Fucus spiralis* (Fs), *Himantalia elongata* (He), *Cystoseira* sp. (Csp), Filamentous green algae (Fil. Gr. Algae), *Chorda filum* (Cf) and *Sargassum muticum* (Sm)

	% Fv	% An	% He	% Fs	% Hs	% Csp.	% Cf	% Sm	% Fil. Gr. Algae	% Debris	Total vol. (ml)
<i>Cyclopterus lumpus</i>	/	+***	+***	/	+	+	/	/	+	/	+***
<i>Trachurus trachurus</i>	–*	–**	–**	+***	/	/	/	/	/	–*	–*
<i>Chelon labrosus</i>	/	/	/	/	/	/	+***	–*	/	/	–*
<i>Syngnathus rostellatus</i>	/	–*	/	+	/	/	/	/	/	/	–*
<i>Ciliata mustela</i>	/	/	–*	/	/	/	–*	+***	/	/	/
	Distance to shore (km)	Atm. Pres. (Pa)	Humidity (%)	Water temp. (°C)	Sal. (PSU)	<i>Gammarus locusta</i> /G. <i>crinicornis</i>	<i>Atylus swammerdami</i>	<i>Jassa</i> sp.	<i>Stenothoe marina</i>	<i>Idotea</i> sp. J	<i>Idotea baltica</i>
<i>Cyclopterus lumpus</i>	/	/	/	–***	+***	–***	–**	/	/	/	/
<i>Trachurus trachurus</i>	+**	–**	/	+***	+***	/	/	/	–*	/	/
<i>Chelon labrosus</i>	–**	/	–***	+***	–***	+***	/	/	–*	+	/
<i>Syngnathus rostellatus</i>	/	–**	/	+**	+	/	/	/	/	/	/
<i>Ciliata mustela</i>	–**	+**	+***	–***	–**	/	/	/	+***	/	/
	<i>Idotea emarginata</i>	<i>Liocarcinus holsatus</i> MG	<i>Liocarcinus holsatus</i> J	<i>Pisidia longicornis</i> MG	<i>Carcinus maenas</i> MG	<i>Hippolyte varians</i> PL	<i>Palaemon elegans</i> PL	<i>Tergipes tergipes</i>	Chironomidae sp.	Aphididae sp.	Harpacticoida sp.
<i>Cyclopterus lumpus</i>	+	/	–*	–**	/	–*	–*	/	/	/	/
<i>Trachurus trachurus</i>	/	+**	+	+***	/	+***	+***	/	–*	–**	–*
<i>Chelon labrosus</i>	–*	–**	–*	–**	/	/	/	+	–*	–**	–**
<i>Syngnathus rostellatus</i>	/	+	+	+**	/	+**	+***	/	/	/	/
<i>Ciliata mustela</i>	/	/	/	/	+**	/	–*	/	/	+***	+***

Table 4
Shannon-Wiener diversity index and Fullness index based on stomach content data per length group of fish species, for each of the sample groups (mean and standard deviation)

	Length classes (cm)	Shannon-Wiener diversity index		Fullness index	
		Neuston	Seaweed	Neuston	Seaweed
<i>Cyclopterus lumpus</i>	1.6–2	/	0.29 ± 0.44	/	5.86 ± 2.39
	2.1–2.5	/	0.13 ± 0.18	/	5.70 ± 2.87
	2.6–3	/	0.18 ± 0.27	/	6.46 ± 3.72
	3.1–3.5	/	0.34 ± 0.43	/	9.75 ± 5.01
	3.6–4	/	0.22 ± 0.28	/	8.30 ± 4.39
<i>Ciliata mustela</i>	2.1–2.5	0.32 ± 0.31	/	1.51 ± 1.14	/
	2.6–3	0.23 ± 0.3	0.16 ± 0.28	1.47 ± 0.91	1.28 ± 1.07
	3.1–3.5	0.41 ± 0.32	0.21 ± 0.32	0.91 ± 0.64	1.38 ± 1.17
	3.6–4	/	0.46 ± 0.31	/	1.81 ± 1.24
<i>Chelon labrosus</i>	2.1–2.5	/	0.17 ± 0.16	/	3.80 ± 1.52
	3.1–3.5	0.02 ± 0.02	/	4.17 ± 2.74	/
<i>Trachurus trachurus</i>	2.1–2.5	0.25 ± 0.34	0.12 ± 0.24	0.29 ± 0.01	2.57 ± 1.53
	2.6–3	0.72 ± 0.4	0.21 ± 0.3	1.34 ± 1.25	1.46 ± 0.56
	3.1–3.5	0.81 ± 0.08	0.11 ± 0.28	0.46 ± 0.46	0.59 ± 0.54
	3.6–4	0.65 ± 0.39	/	0.30 ± 0.31	/
<i>Syngnathus rostellatus</i>	<8.1	0.0	0.0	0.0	3.32 ± 3.16
	>8.1	/	0.13 ± 0.08	/	2.04 ± 1.53

indices and fullness indices of both size classes did not differ significantly between seaweed fish and neustonic fish (MWU, $p > 0.4$ in all cases). In both size classes of neustonic and seaweed-associated fish, calanoid copepods were the dominant prey item (Fig. 7). Neustonic fish also fed intensively on fish eggs and, as they grew, they started feeding on larger prey items like crab megalopae. The diet of the seaweed-associated fish was more variable and also comprised considerable amounts of harpacticoid copepods, small gammarid amphipods and invertebrate eggs (probably from isopods and amphipods).

3.3.3. *Chelon labrosus*

Chelon labrosus was found abundantly in seaweed samples (summer and autumn) and neuston samples (summer, autumn and winter), with the dominant size class being 0.5 cm larger in seaweed samples (1.6–2 cm), compared to neuston samples (1.1–1.5 cm) (Fig. 6). As only few individuals (17) larger than

2 cm were found, the results of the stomach content analysis will only be briefly discussed. Mulletts from seaweed samples (2.1–2.5 cm, mean FI: 3.8) most frequently fed on calanoid (all stomachs, N%: 95, G%: 99%) and harpacticoid copepods (54% of all stomachs, N%: 3.9, G%: <0.1), and on dipteran insects (27% of all stomachs, N%: 0.6, G%: <0.1). Calanoid copepods were also the main prey (found in all stomachs, N% and G% >99) for mulletts from neuston samples in the 3.1–3.5 cm length class (mean FI: 4.17). Dipteran insects and cypris larvae were rarely found; harpacticoid copepods were absent in stomachs of neustonic fish.

3.3.4. *Trachurus trachurus*

High numbers of juvenile horse mackerels were found in the neustonic environment in summer (only few individuals in winter). The individuals caught in association with floating seaweed clumps were generally larger (dominant size classes 1.6–2.5 cm) than the ones found in seaweed free areas (dominant size class 0.6–1 cm). The size classes between 2 and 3.5 cm were found in both sample types. The Shannon-Wiener index per size class was generally higher in neuston samples compared to seaweed samples (Table 4); these differences were significant in the 2.6–3 cm and 3.1–3.5 cm length classes (MWU $p = 0.05$ and 0.002, respectively). Although the mean fullness index in seaweed samples was higher than in neuston samples, the difference was only significant in the 2.1–2.5 cm size class (MWU $p = 0.003$). Fig. 8 shows that the diet from neustonic individuals was more varied than from seaweed-associated individuals: neustonic fish fed on 9 different planktonic prey species, mostly copepods, cladocerans and pelagic larvae of barnacles, crabs, prawns and bivalves. Seaweed-associated fish, on the other hand, predominantly fed on harpacticoid and calanoid copepods, but occasionally ingested larger prey items like postlarval prawns and gammarid amphipods.

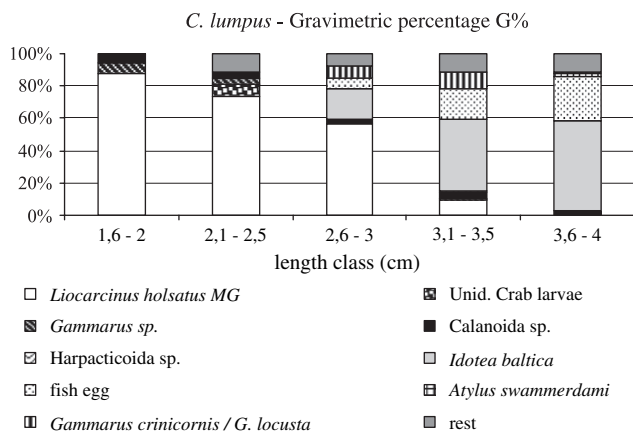


Fig. 5. Bar chart of the mean gravimetric percentages of the different prey items of *Cyclopterus lumpus* per length class in seaweed samples.

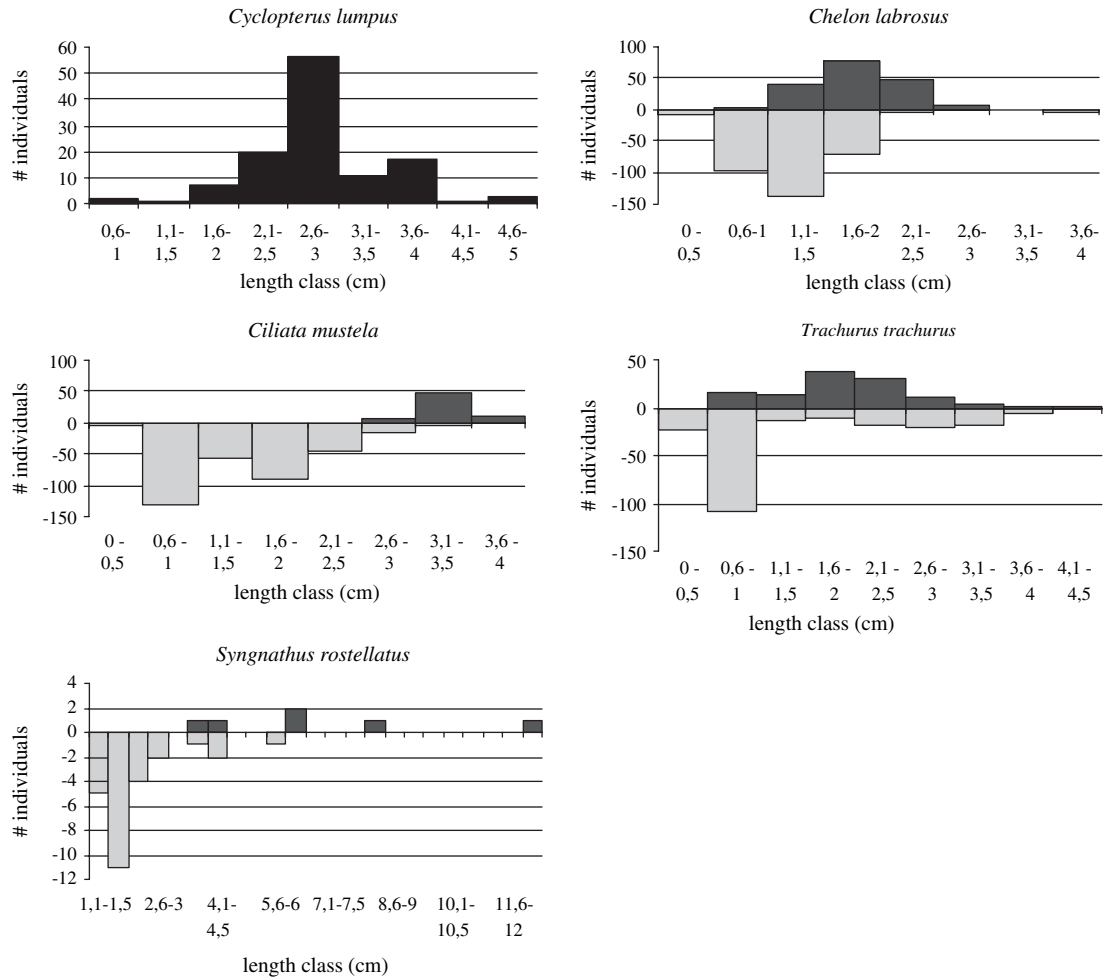


Fig. 6. Length-frequency distributions of the discussed fish species per length class of 0.5 cm. Black positive bars represent seaweed-associated individuals, grey negative bars represent neustonic individuals.

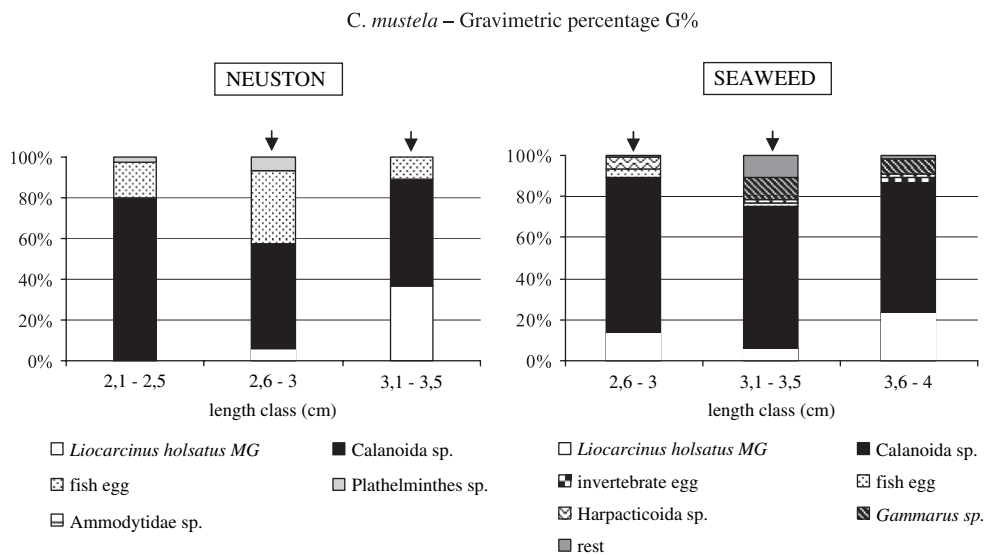


Fig. 7. Bar charts of the mean gravimetric percentages of the different prey items of *Ciliata mustela* per length class in neustonic samples and seaweed samples.

and abundantly encountered in and near floating seaweed patches are known residents or visitors in the neustonic layer. Juveniles of *Ciliata mustela*, for example, were found abundantly during a neuston survey in Galway Bay, Ireland (Tully and O'Ceidigh, 1989), while *Cyclopterus lumpus* has been recorded in association with floating seaweed on many occasions (Tully and O'Ceidigh, 1989; Davenport and Rees, 1993; Ingólfsson, 1995, 1998, 2000). Juvenile mullets (*Chelon labrosus* in the present study) are known to have protective coloration adapted to a neustonic life and to develop an air sac near the dorsal fins to enable them to remain near the surface (Zaitsev, 1970). Together with horse mackerels (*Trachurus trachurus* in the present study), mullets have frequently been reported as being associated with floating structures like fish farms (Dempster et al., 2005), FADs and drift algae (Dooley, 1972; Lenanton et al., 1982; Kingsford and Choat, 1985; Kingsford, 1992; Castro et al., 2001). Young pipefish (Syngnathidae) have been recorded in association with both permanently floating *Sargassum* (Fine, 1970; Kingsford, 1992; Cho et al., 2001; Ohta and Tachihara, 2004; Wells and Rooker, 2004a,b) and ephemeral seaweed patches (e.g. Kulczycki et al., 1981).

The observed temporal variation in the presence and abundance of neustonic fish is in accordance with the findings of Hempel and Weikert (1972), who found that temperature, wave action and solar radiation are the most important structuring factors. Similarly, the seasonal variation plays a major role in seaweed associated fish, as can be derived from Table 2 and the significant correlations with surface water temperatures in Table 3. However, there are other factors structuring the species composition, such as the floating seaweed presence and species composition, clump volume, distance to shore and the densities of the seaweed-associated invertebrate fauna (Safraan and Omori, 1990; Ingólfsson, 1995, 2000; Vandendriessche et al., 2006b). The low matching coefficient between fish data and environmental data indicates that only a part of the biotic structure is explained by the measured variables. These results do not agree with previous studies about fishes associated with floating objects, in which generally clear patterns of spatial and temporal variation could be observed (e.g. Dempster and Kingsford, 2004; Wells and Rooker, 2004a,b). The lack of spatial patterns in the present study may be due to the limited spatial scale of the samplings, which was also reflected in the community analysis of the neustonic assemblages; and the sampling area can therefore be considered as a single geographical entity. The large multivariate distance between the samples dominated by *Chelon labrosus* and samples dominated by *Cyclopterus lumpus*, *Trachurus trachurus* and *Ciliata mustela* could be caused by species interactions (e.g. territorialism (Ingólfsson, 2000) or predation (Dempster, 2005)), although the results of the stomach content analysis and diet overlap do not support the presence of such interactions between the investigated species. The data rather suggest that fish species associated with floating seaweeds have somewhat different nutritional requirements and feeding strategies. There may have been (large) predatory fish that were not sampled with the used net, but did have an influence on the species

composition of the associated fish fauna. However, Nelson (2003) hypothesises that there may be insufficient time or stability for factors as competition and predation to influence size and diversity of the fish fauna associated with floating objects.

The community analyses of neustonic and seaweed-associated fish show that the presence of floating seaweeds in the neuston influences the species composition of the fish fauna. One striking feature is the abundant presence of juvenile *Cyclopterus lumpus* and its total absence in the neuston samples. These functionally benthic juveniles (floating seaweed provides a substitute for the seabed in the pelagic zone – Davenport and Bradshaw, 1995) show adaptations of appropriate form and colour to the habitat: they have a ventral sucker which is suitable for adhering to the seaweed surface, and they are cryptically coloured (Davenport and Bradshaw, 1995). Similar adaptations are found in the *Sargassum* fish *Histrio histrio* displaying weed-like coloration and appendages. Some of these adaptations have also been reported for facultative rafters, which may enhance their survival in an environment with high predation pressure (Thiel and Gutow, 2005b). The impact of the presence and constitution of floating seaweed clumps, however, varies with the fish species (Dempster and Kingsford, 2004). Some species, like *C. lumpus*, are influenced by the volume and seaweed species composition of the clumps, while poor relationships were observed in the case of schooling fish like *Trachurus trachurus* (similar observations in Druce and Kingsford, 1995). There were no straightforward correlations between fish densities and densities of available prey species in any of the fishes.

4.2. Feeding habits and length-frequency distributions

Generally, dietary shifts were observed during the growth of the different fish species. Especially the diet of *Cyclopterus lumpus* changed markedly with increasing length of the fish, which was also observed in Ingólfsson and Kristjánsson (2002), where larger individuals switched from crustacean larvae and halacarid mites to harpacticoids, isopods, amphipods and smaller conspecifics. To a lesser extent, gradual changes were also observed in *Ciliata mustela*, *Trachurus trachurus* and *Syngnathus rostellatus*. These fish species tend to switch from smaller prey like copepods to larger prey items like crab megalopae, prawns and amphipods. According to Tully and O'Ceidigh (1989), larger individuals of *C. mustela* ate higher numbers of prey, rather than switching to other prey items.

Next to dietary changes with fish size, there were also clear differences between the diets of fish feeding in the neuston and in floating seaweed patches. Juvenile rocklings (*Ciliata mustela*) from seaweed samples, for example, had a more variable diet compared to conspecifics feeding in the neuston. Seaweed-associated fauna like harpacticoid copepods, idoteid isopods and gammarid amphipods (*Gammarus* sp.) were obviously suitable prey items for the associating fish species. The advantage of ingesting these prey items is reflected in the length-frequency distributions: juvenile fish from seaweed samples were generally larger than specimens from neustonic

samples, which was also reported in Kingsford (1992). This may be due to: (1) the fact that seaweed samples are colonised by older fish that can ingest larger (seaweed-associated) prey and can withstand possible harsh hydrodynamic conditions in order to stay associated with floating seaweed clumps; or (2) the fact that juvenile fish grow faster when associated with floating seaweeds due to the provision of shelter (i.e. lower energy expenditure) and high densities of potential prey items (i.e. ideal feeding conditions). Based on the absence of 3–3.5 cm individuals in the neuston, it can be hypothesised that the latter may be true for the species *C. mustela*. However, a detailed analysis of growth parameters is needed to confirm this hypothesis. The larger size classes of *Trachurus trachurus* and *Chelon labrosus* were found in both the neuston samples and seaweed samples (although in varying numbers), suggesting a turn-over of seaweed-associated fish (Safran and Omori, 1990). The discontinuous length distribution in *Syngnathus rostellatus* suggests that most of the seaweed associated specimens were caught in the seaweed upon detachment, instead of having colonised the seaweed from the surrounding neuston. As a result of their vulnerability in the surface water, they probably stay associated with the floating seaweed to avoid predators. From the presence of adult syngnathids, Kingsford and Choat (1985) concluded that floating seaweeds may provide a dispersal mechanism for this less mobile group.

4.3. Association behaviour

The absence of juvenile lumpfishes (*Cyclopterus lumpus*) outside floating seaweed patches and the composition of their diet (mainly seaweed-associated macro-invertebrates, especially in the larger size classes) confirm the findings of Davenport and Rees (1993) and Ingólfsson and Kristjánsson (2002): postlarval and juvenile lumpfishes are opportunistic predators specialised on floating seaweed patches in the North-East Atlantic, attaching themselves to seaweed fronds with their ventral sucker (personal observation) and feeding on prey concentrated beneath the weed cover. Therefore, they can be regarded as aggregated, closely associated residents that stay within the branches of the seaweeds (Hirosaki, 1960; Gooding and Magnuson, 1967; Dooley, 1972; Castro et al., 2001). *Ciliata mustela*, *Trachurus trachurus*, *Chelon labrosus* and *Syngnathus rostellatus* were found in both seaweed samples and neuston samples, so their association with floating seaweeds is of a more opportunistic nature and they can be regarded as being associated (Castro et al., 2001). *Ciliata mustela* seems to have most benefit of association with floating seaweeds: the juveniles clearly feed on the buffet of associated macro-invertebrates and length distribution data suggest that their growth is enhanced compared to neustonic conspecifics. The advantages for *T. trachurus* (transient visitors according to Langtry and Jacoby, 1996) and *C. labrosus* do not seem to be of similar importance: these species predominantly feed on planktonic prey, presumably in deeper layers (Hempel and Weikert, 1972) and there is no evidence of enhanced growth. Still, these species may benefit from

association with floating objects for reasons other than prey availability: both species are schooling and may use floating objects as shelters, meeting points or transports to enriched convergence zones, surface slicks or near shore habitats (Shanks, 1983; Kingsford and Choat, 1985; Kingsford, 1992; Castro et al., 2001; Thiel and Gutow, 2005b). *Chelon labrosus* commonly enters brackish lagoons and freshwater, but spawns offshore. Consequently, floating seaweeds may serve as a means of transport, thereby enhancing the survivorship of larval and juvenile species as they move from offshore waters into bays and estuaries (Wells and Rooker, 2004a). Postlarval *S. rostellatus* largely depend on floating seaweeds for their survival in the neustonic layer. Young individuals and adults of this demersal species are probably carried with the seaweed after detachment from the substrate, and stay within the seaweed branches to ensure protection from predators. For this particular species, floating seaweeds serve as substitutes of the seabed (Hunter and Mitchell, 1967 in Castro et al., 2001), thereby increasing chances of survival.

4.4. Conclusions

The neustonic fish community at the BPNS is mainly seasonally structured, but is also strongly influenced by the patchy occurrence of floating objects. Floating seaweeds can be regarded as temporary and unpredictable habitats shared between several fish species (mainly juveniles) that use them for different reasons and with varying intensity. Accumulations of floating seaweeds can increase the survival of young fish through avoidance of predators (larger predatory fish and diving birds), and the associated macrofauna can serve as a food source for fish, as was the case for *Cyclopterus lumpus*. This may result in an enhancement of survival and growth of juveniles. For some fish species, like *Trachurus trachurus*, *Syngnathus rostellatus* and *Chelon labrosus*, raft associated food items appear to represent opportunistic prey items. The association of these fish with floating seaweeds may result from other motivations like the formation of schools, transport to a more suitable habitat or survival in a habitat resembling the sea bed.

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