

# The ichthyoneuston of Galway Bay (west of Ireland). II. Food of post-larval and juvenile neustonic and pseudoneustonic fish

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**ABSTRACT:** Stomach contents of 5 species of neustonic (*Ciliata septentrionalis*, *Ciliata mustela*, *Gaidropsaurus mediterraneus*, *Rhinonemus cimbricus*, *Scophthalmus maximus*) and 4 species of pseudoneustonic (*Pollachius pollachius*, *Pollachius virens*, *Merlangius merlangus*, *Cyclopterus lumpus*) post-larval and juvenile fish, caught in the neustal and the immediate sub-surface layer, were examined to compare diets and food consumption. Fish length ranged from 5 to 39 mm. The diets of *Ciliata* spp. were dominated by fish eggs and calanoid copepods. *G. mediterraneus* and *R. cimbricus* ate mainly copepods and Cladocera. *Oikopleura* spp., copepods and *Podon* spp. dominated in *S. maximus*. In the pseudoneustonic *Pollachius* spp., *Acartia* spp. and *Calanus* spp. were most important while *M. merlangus* preyed almost totally on copepods. *C. lumpus*, which associated with driftweed, specialised on harpacticoid copepods and crab megalopae. Dietary differences among species 5 mm length groups were investigated by step-wise discriminant analysis. The analysis isolated 17 diet categories which were significant in discriminating the diets of 5 mm length groups of 5 species (*C. septentrionalis*, *C. mustela*, *P. pollachius*, *P. virens*, *M. merlangus*) caught mainly during May and June. *Ciliata* groups were distinct from those of other species and their diets changed gradually as fish increased in length. Fish eggs were less important in larger fish which preyed more on fish larvae, crab megalopae and harpacticoid copepods. Five diet categories were significant in discriminating the diets of 5 mm length groups of species caught mainly during autumn (*G. mediterraneus*, *R. cimbricus*, *S. maximus*, *C. lumpus*). The diets of *S. maximus* and *C. lumpus* changed abruptly when fish reached 20 mm in length. *C. lumpus* switched from harpacticoid copepods to crab megalopae and *S. maximus* switched from *Podon* spp. to fish larvae and *Oikopleura* spp. *Podon* spp. were important in larger size groups of *G. mediterraneus* and *R. cimbricus*. Discriminant analysis did not find significant differences between the diets of smaller length groups of these 2 species. Diel variation in stomach fullness of *C. mustela* and *G. mediterraneus* showed that feeding occurred only during daylight. In all species except *G. mediterraneus* and *S. maximus* larger fish ate a greater number of prey than smaller fish. *C. mustela* over 25 mm, *P. pollachius* and *M. merlangus* over 15 mm and *C. lumpus* and *S. maximus* over 20 mm also had fuller stomachs than smaller fish. Stomach fullness was higher in neustonic than in pseudoneustonic species. Because of this, it is suggested that feeding conditions at the surface are unique and that neustonic species have adaptations that enable them to feed more successfully in this environment.

## INTRODUCTION

Conditions at the sea surface and the amount of food available there to predatory fish varies with geographic location. Zaitsev (1970) observed that the neustal of the Black Sea was important in the early ontogeny of many species of fish. Hartman (1970) and John (1973) found a scarcity of food by day in the neustal of the subtropical North East Atlantic where only areas of upwelling

supported high densities of neustonic fish such as *Belone belone* (L.). In coastal temperate regions neustonic communities are less well developed, the number of neustonic species is lower than in tropical waters and the plankton communities in the neustal by day are largely similar to those of subsurface layers (Hempel & Weikert 1972). The diets, food availability to and food consumption of neustonic fish species in the such areas may therefore be largely similar to those of species of similar size and morphology which occur at the surface but live predominantly in deeper water (pseudoneustonic species; Hempel & Weikert 1972). On the other

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hand if they are different it may infer that feeding conditions at the surface are unique and that neustonic species have adaptations that enable them to feed more successfully in the neustal than pseudoneustonic species. Even in areas where neustonic communities are poorly developed feeding conditions for fish at the sea/air contact zone may differ from those in deeper water due to a number of factors. Organic matter in the form of eolian and terrigenous material and also 'anti-rain' of dead plankters, moulted casts and exometabolites from the water column (Zaitsev 1970) and flotsam and its associated fauna (Tully & Ó Céidigh 1986a) accumulate at the surface. Migration of planktonic and benthic invertebrates to the surface at night leads to considerable changes in the density and species composition of possible prey items in the neustal at this time (Champalbert & Macquart-Moulin 1970, Champalbert 1971a, b, Macquart-Moulin 1984, Tully & Ó Céidigh 1986b, 1987). Light intensity at the surface is higher for longer periods than in deeper water. This may extend the time during which visual predators can feed, and such predators may also be able to feed by moonlight. Also, since neustonic species live essentially in a 2-dimensional environment (ignoring depth), escape options for prey species are reduced (Zaitsev 1970).

The present work describes the diets and feeding intensity of 5 neustonic and 4 pseudoneustonic species of post-larval and juvenile fish captured in the neustal and in immediate subsurface water of Galway Bay, a coastal temperate region of high primary productivity. Interspecific differences in diet and food consumption and differences among species 5 mm size classes are compared and related to individual species morphology and behaviour.

## STUDY AREA AND METHODS

**Galway Bay.** All fish were sorted from neuston samples taken in Galway Bay (Fig. 1) during daylight hours from June 1983 to September 1984, during the night from May to September 1984 and over two 24 h periods during September 1984 and August 1985. A 2-stage neuston net sampling the 0 to 100 mm and 120 to 480 mm surface microlayers was employed at all stations. Sample volume was ca 100 and 360 m<sup>3</sup> for the upper and lower nets respectively.

The hydrographic characteristics of Galway Bay were described by Berthois et al. (1971) and Booth (1975). Briefly, the inner bay (Stns 1 to 3; Fig. 1) is largely estuarine and salinities were reduced to 16‰ at Stn 1 during February. Salinities in the outer bay remained above 34‰ throughout the sampling period. Surface temperatures varied from 6°C in January to

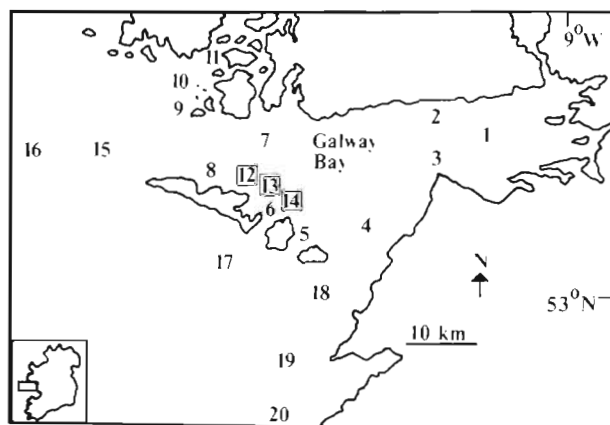


Fig. 1. Galway Bay showing day and night (□) locations where neuston samples were taken

18.3°C in August. Intrusions of oceanic water into the bay are known to occur frequently (Booth 1975).

**Fish distribution and behaviour.** Diverse larval and juvenile fish species assemblages, comprising 82 species, were recorded in the surface 0.5 m of water (Tully & Ó Céidigh 1988). Only 8 of these species, however, were neustonic at any stage of their life cycle. The diets of 5 of these are given here (Table 1). Four pseudoneustonic species caught in the surface 0.5 m of water, which were common and of comparable size range to the neustonic species, were also selected for dietary analysis (Table 1). The 9 species of fish are separable into 2 groups based on their temporal distribution. One group of 5 species (Table 1) occurred during May and June (spring group) while the remaining 4 species occurred predominantly during August and September (autumn group).

*Ciliata septentrionalis*, *Ciliata mustela* and *Ciliata* spp. (unidentified fish 10 to 14 mm in length) were the only abundant neustonic fish species in daylight samples. They occurred, as juveniles, predominantly during May (93 ind. 100 m<sup>-3</sup>) and June (21 ind. 100 m<sup>-3</sup>). Individuals longer than 14 mm were largely confined to the upper 100 mm of water. *Ciliata* spp. occurred at a density of 11.5 ind. 100 m<sup>-3</sup> in the surface layer in May. The pseudoneustonic species *Pollachius pollachius* (11.5 ind. 100 m<sup>-3</sup> in May), *Pollachius virens* (0.3 ind. 100 m<sup>-3</sup> in May) and *Merlangius merlangus* (2.3 ind. 100 m<sup>-3</sup> in May) were evenly distributed in the 2 layers sampled. *Gaidropsaurus mediterraneus* and *Rhinonemus cimbricus* were neustonic and occurred mainly during September 1984 (5.7 and 1.4 ind. 100 m<sup>-3</sup> respectively in the surface layer). *Scophthalmus maximus* occurred mainly during July and August 1983 in the surface layer (0.8 ind. 100 m<sup>-3</sup>). *Cyclopterus lumpus* was recorded in association with driftweed mainly during May (2.2 ind. 100 m<sup>-3</sup>) and June (4.0 ind. 100 m<sup>-3</sup>).

Table 1. Fish species whose diets were studied, the numbers and length range of individuals examined and the months during which they were most abundant in the neustal. Spring (species 1 to 5) and autumn (species 6 to 9) groups are distinguished.  
\* Neustonic species

Species	Abbrev.	No. of fish	Length range (mm)	Months of highest density
* <i>Ciliata septentrionalis</i> Collett	<i>C. s.</i>	465	14–39	May, Jun
* <i>Ciliata mustela</i> (L.)	<i>C. m.</i>	328	14–34	May, Jun
* <i>Ciliata</i> spp.	<i>C. spp.</i>	234	10–14	May
<i>Pollachius pollachius</i> (L.)	<i>P. p.</i>	241	5–25	May, Jun
<i>Pollachius virens</i> (L.)	<i>P. v.</i>	39	15–25	May, Jun
<i>Merlangius merlangus</i> (L.)	<i>M. m.</i>	77	5–20	May, Jun
* <i>Gaidropsaurus mediterraneus</i> (L.)	<i>G. m.</i>	119	5–35	Jul, Aug
* <i>Rhinonemus cimbricus</i> (L.)	<i>R. c.</i>	27	10–25	Sep, Nov
* <i>Scophthalmus maximus</i> (L.)	<i>S. m.</i>	25	5–25	Jul, Aug
<i>Cyclopterus lumpus</i> L.	<i>Cy. l.</i>	31	10–35	May–Aug

1984 but predominantly during August 1985 (1.0 ind. 100 m<sup>-3</sup>).

**Species assemblages in the neustal.** The species assemblages in the neustal during May and June and therefore the potential prey species available to the spring group of fish were distinct from those available to the autumn group (August and September). The diets of species within but not between groups can therefore be compared. The main species groups in the neustal during daylight hours were largely similar to those in the plankton of the area reported on by Ó Céidigh (1962) and Fives (1969, 1970, 1971) and few neustonic species were encountered. Fish eggs, larvae of Ammodytidae and low numbers of the neustonic copepod *Anomalocera patersoni* Templeman predominated in February and March. During April cyprids of *Balanus* spp. and fish eggs were very abundant and these were succeeded by blooms of *Calanus* spp., *Temora longicornis* Müller and *Acartia* spp. In July and August the zoeae and megalopae of portunid and porcellan crabs were abundant. Dense patches of *A. patersoni* were encountered during August 1983 but not during 1984 and *Centropages* spp. were also common at this time. Benthic peracarideans migrating to the neustal at night were the predominant species at the surface at night during July and August 1984 and were also common in May and September 1984 (Tully & Ó Céidigh 1987).

**Stomach content analysis.** The number of fish of each species examined and their size ranges are given in Table 1. For the abundant species the stomach contents of up to 10 fish in each 5 mm length group were identified and counted for each station sampled. This gives a good indication of the diet of individual species or length groups of fish for the whole sampling area. Any between-station variation in diet, which contributes to the overall variation in the diet of length groups of fish, is taken into account when comparing

the diets of different length groups of fish by the discriminant analysis used. In less abundant species all available fish were examined. Length groups with less than 5 fish were omitted from all analysis. Prey items were identified to the lowest possible taxonomic level. Unidentified copepods, euphausiids and fish were measured and grouped by size. Copepods that could not be measured or identified were counted and copepods that could not be counted were recorded as being present. The numerical importance of each of 57 prey categories is expressed as the percentage composition (the number of items of a particular prey category as a percentage of the total number of prey items) and the spread or distribution of each prey category in the fish population is given by the percentage occurrence or the percentage of fish containing the prey category. Before dissecting the stomach its state of distension or fullness was subjectively assessed. Points on a scale of 0 to 5 were given for a stomach which was empty (0), that had food present (1), that was 1/3 full (2), 2/3 full (3), full (4) and distended (5).

Comparison of the diets of 5 mm length groups of fish and the prey categories contributing most to group difference was assessed by step-wise discriminant analysis (Jennrich & Sampson 1981). Only fish with non-empty stomachs were used. The data, counts of individual prey types, was transformed to log (data value +1) to comply with conditions of normality before analysis and 54 quantitatively assessed prey categories were used (Table 2). In step-wise discriminant analysis prey categories for which group (5 mm length groups of fish) means differ most are entered into the analysis first so that group differences rather than quantitatively important dietary components per se are emphasised. However, because maximum among-group differences are sought by the analysis single discriminating prey categories are likely to be quantitatively important dietary components in at least some groups. The subset

Table 2. The % composition (% N) and % occurrence (% O) of 57 prey categories in 9 species of fish. *Ciliata* spp. are either *C. mustela* or *C. septentrionalis* 10 to 14 mm in length. See Table 1 for explanation of species abbreviations. \* < 0.5

Prey categories	<i>C. s.</i>		<i>C. m.</i>		<i>C. spp.</i>		<i>P. p.</i>		<i>P. v.</i>		<i>M. m.</i>		<i>G. m.</i>		<i>R. c.</i>		<i>S. m.</i>		<i>Cy. l.</i>		
	% N	% O	% N	% O	% N	% O	% N	% O	% N	% O	% N	% O	% N	% O	% N	% O	% N	% O	% N	% O	
Crustacea	•	3	•	3	•	3	-	-	-	-	-	-	•	1	-	-	-	-	•	3	
<i>Porcellana</i> zoea	2	3	•	2	-	-	-	-	-	-	•	1	-	-	-	-	-	-	-	1	5
Natantia, Decapoda	•	3	•	6	•	•	-	-	-	-	-	-	•	3	-	-	-	-	-	-	
<i>Crangon</i> zoea	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	1	8
<i>Macropipus</i> zoea 5	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
zoea 4	•	•	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
zoea 3	-	-	•	•	-	-	-	-	-	-	5	4	-	-	-	-	-	-	-	•	5
zoea 2	•	•	•	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
zoea 1	2	6	•	3	•	•	•	•	-	-	1	2	•	1	-	-	-	-	-	•	5
megalopa	•	3	1	8	-	-	•	•	-	-	1	2	•	2	-	-	1	13	35	50	
Copepod nauplii	2	1	-	-	7	3	-	•	-	-	-	-	-	-	-	-	-	-	-	-	
Copepods	2	9	6	15	3	12	1	2	4	9	2	3	2	3	7	11	4	7	4	8	
Copepods 1.4-1.6 mm	•	1	•	1	•	1	•	1	2	4	-	-	•	1	1	3	-	-	-	-	
1.2-1.4 mm	1	3	1	2	1	2	•	1	-	-	-	-	-	-	-	-	-	-	-	-	
1.0-1.2 mm	1	4	3	2	2	4	1	4	-	-	7	4	1	3	-	-	-	-	-	-	
0.8-1.0 mm	7	6	4	7	6	9	2	9	3	8	14	9	3	4	54	17	-	-	-	-	
0.6-0.8 mm	4	3	9	8	11	18	6	14	6	6	13	10	47	17	17	14	18	14	-	-	
0.4-0.6 mm	4	4	3	4	36	21	3	7	3	4	1	1	11	17	3	25	3	20	•	3	
0.2-0.4 mm	4	2	2	1	3	3	1	1	-	-	-	-	4	7	1	3	1	7	•	3	
<i>Corycaeus</i> spp.	-	-	-	-	-	-	2	11	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Isias</i> spp.	-	-	2	4	-	-	-	-	-	-	-	-	2	4	•	3	3	13	3	5	
<i>Calanus</i> 1.0-1.5 mm	•	1	•	1	•	2	1	2	7	13	1	2	•	1	-	-	-	-	-	-	
1.5-2.0 mm	2	9	3	10	1	5	5	19	22	32	1	14	•	2	-	-	-	-	5	8	
2.0-2.5 mm	12	36	9	35	•	5	8	30	23	43	24	24	1	3	2	8	-	-	3	13	
<i>Centrophages</i> spp.	2	7	1	9	1	3	5	2	-	-	1	1	14	23	6	25	5	13	3	16	
<i>Temora longicornis</i>	9	5	1	8	2	12	8	6	2	6	3	4	-	-	•	3	3	17	•	3	
<i>Acartia</i> spp.	8	6	1	2	1	3	43	37	9	13	8	10	1	2	2	8	6	13	•	3	
<i>A. patersoni</i>	•	1	•	3	-	-	-	-	-	-	-	-	•	3	-	-	-	-	-	-	
<i>Metridia</i> spp.	•	1	•	3	•	1	•	•	•	2	-	-	-	-	-	-	-	-	•	3	
<i>Pseudocalanus</i> spp.	•	•	-	-	•	1	•	•	-	-	-	-	-	-	-	-	-	-	-	-	
Polychaetes	•	1	•	2	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	
Harpacticoidea	12	5	11	15	•	2	•	3	-	-	4	3	-	-	-	-	3	10	34	60	
<i>Idotea</i> spp.	-	•	•	•	-	-	-	-	1	2	-	-	-	-	-	-	-	-	4	24	
<i>Hyperia</i> spp.	•	•	•	1	-	-	-	-	-	-	-	-	•	1	-	-	-	-	-	-	
<i>Parathemisto</i> spp.	•	4	•	2	•	•	-	-	-	-	-	-	•	1	•	3	-	-	-	-	
Gammaridea	•	•	•	1	-	-	-	-	-	-	-	-	•	2	-	-	•	3	4	21	
<i>Oikopleura</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	20	-	-	
Alga	•	•	•	•	•	•	•	•	-	-	1	-	-	-	-	-	3	-	3	-	
Invertebrate embryos	3	1	1	2	-	-	2	9	5	8	-	-	-	2	3	7	7	-	-	-	
Invertebrate eggs	•	17	•	19	•	47	•	5	•	2	-	-	1	-	-	-	-	-	-	-	
<i>Evadne</i> spp.	•	•	•	1	-	-	•	•	-	-	-	-	1	5	-	-	1	13	1	3	
<i>Podon</i> spp.	•	•	4	8	•	1	-	-	-	-	-	-	7	13	2	3	23	43	-	-	
Cladocera	2	4	5	7	6	6	•	1	-	-	•	1	1	5	2	14	-	-	•	3	
Insects	1	3	•	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Balanus</i> cyprids	•	•	•	1	-	-	•	2	-	-	-	-	-	-	-	-	•	7	-	-	
Fish 20-25 mm	•	2	•	1	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	
15-20 mm	•	2	•	2	-	-	•	•	-	-	-	-	-	-	-	-	-	-	•	3	
10-15 mm	•	3	•	1	-	-	-	-	-	-	-	-	•	1	-	-	1	10	-	-	
5-10 mm	•	4	•	5	•	•	•	2	1	2	-	-	-	-	-	-	1	7	-	-	
Fish eggs	32	50	28	47	17	48	4	20	9	17	-	-	•	2	1	3	-	-	-	-	
Adult euphausiids	•	1	•	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Furcilia 4.5-5.0 mm	•	2	•	2	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	
4.0-4.5 mm	•	2	•	1	•	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
3.5-4.0 mm	•	2	•	1	•	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
3.0-3.5 mm	1	8	1	9	1	5	1	•	1	4	-	-	-	-	-	-	-	-	-	-	
Calyptopids	-	•	•	•	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Copepods present		14		13		7		•		-		3		17		6		3		-	

of prey categories isolated by the analysis will be the categories that best describe quantitative dietary differences among all groups. Differences in stomach fullness (the amount of food consumed in proportion to fish length) and the log of the number of prey eaten among 5 mm length groups of individual species were assessed by analysing variance among groups (*F*-tests) and by pair-wise comparison of groups (*t*-tests). Only fish caught between 10:00 and 22:00 h were used in this analysis to control for observed diel differences in stomach fullness. Diel differences in stomach fullness was assessed in *Ciliata mustela* and *Gaidropsaurus mediterraneus* which were caught in adequate numbers over 24 h during August 1985.

## RESULTS

Fifty-seven prey types were distinguished among stomachs of the 9 species of fish studied. Copepod eggs contributed 70% of the total number of prey items taken by *Ciliata septentrionalis* (17% of fish), 63% by *Ciliata mustela* (19% of fish), 68% by *Ciliata* spp. (47% of fish) and 14% by *Pollachius pollachius* (5.3% of fish). Up to 600 copepod eggs were counted in fish caught during May at Stns 15 and 16 (Fig. 1). These eggs were intact in the intestine and were not digested. They have been omitted from calculations of % composition and % occurrence data and when assessing the average number of prey eaten by groups of fish as they occurred in few fish and their inclusion in percentage composition data obscures the importance of other prey types (Table 2). *C. septentrionalis* and *C. mustela* preyed extensively on fish eggs, calanoid copepods, harpacticoid copepods and adult *Calanus* spp. *Gaidropsaurus mediterraneus* and *Rhinonemus cimbricus* fed mainly on copepods and cladocera. Crab megalopae, harpacticoid copepods, *Calanus* spp., *Idotea* spp. and Gammaridea (predominantly *Gammarus locusta* L.) were the dominant prey categories taken by *Cyclopterus lumpus*. *Scophthalmus maximus* specialised on *Podon* spp., *Oikopleura* spp. copepods and fish larvae. *Pollachius virens* ate mainly *Calanus* spp., *Acartia* spp. and fish eggs. The important prey categories of *Pollachius pollachius* were *Acartia* spp. and *Calanus* spp. while *Merlangius merlangus* preyed almost totally on copepods.

Prey categories contributing most to differences among 5 mm length groups of fish, isolated by step-wise discriminant analysis, are given in Table 3 for the spring group of fish and in Table 4 for the autumn group. Overall only 18.2% and 25.6% of autumn and spring groups respectively were correctly classified in the analysis, reflecting considerable dietary overlap among 5 mm length groups. Percentage occurrence

Table 3. Coefficients on canonical variables 1 to 4, derived from step-wise discriminant analysis, of 17 prey categories, arranged in order of discriminating power, that best describe significant differences between the diets of 5 mm length groups of *Ciliata septentrionalis*, *C. mustela*, *Pollachius pollachius* and *Merlangius merlangus*

Prey category	Canonical variable			
	1	2	3	4
<i>Acartia</i> spp.	-1.02	2.21	-0.05	1.11
Fish eggs	0.93	-1.04	1.00	0.94
<i>Calanus</i> spp. 1-1.5 mm	2.01	0.86	0.82	1.22
Copepod eggs	0.20	-0.76	-0.08	0.31
<i>Podon</i> spp.	3.83	0.19	-4.10	0.47
Crab megalopa	5.83	1.68	-3.15	-2.44
Fish 20-25 mm	9.79	6.19	7.24	-20.13
Harpacticoidea	1.65	0.71	-1.85	0.73
<i>Porcellana</i> zoea	2.84	1.42	1.98	-0.89
<i>Corycaeus</i> spp.	-2.39	3.74	-2.56	2.13
Cladocera	1.76	-0.45	-1.36	0.07
<i>A. patersoni</i>	5.72	-0.74	-5.88	-3.50
Copepods 0.4-0.6mm	-0.57	-1.01	-0.49	-0.81
Fish 10-15 mm	6.56	1.67	8.58	1.71
5-10 mm	4.89	1.52	2.77	-2.79
<i>Centropages</i> spp.	0.56	-0.51	-0.81	2.09
Insects	3.16	0.24	4.60	3.08
Variance explained	39.7	22.7	12.9	7.8
Eigenvalue	0.87	0.49	0.28	0.17
Canonical correlation	0.68	0.57	0.47	0.38

Table 4. Coefficients on canonical variables 1 to 3, derived from step-wise discriminant analysis, of 5 prey categories, arranged in order of discriminating power, that best describe significant differences between the diets of 5 mm length groups of *Gaidropsaurus mediterraneus*, *Rhinonemus cimbricus*, *Scophthalmus maximus* and *Cyclopterus lumpus*

Prey category	Canonical variable		
	1	2	3
Crab megalopa	-9.34	0.62	3.07
<i>Idotea</i> spp.	-11.87	1.01	-0.55
Fish 10-15 mm	-3.14	-15.63	2.61
Harpacticoidea	-1.04	-2.01	-3.25
<i>Podon</i> spp.	0.23	-1.85	1.64
Variance explained	82.4	7.7	5.3
Eigenvalue	11.3	1.1	0.7
Canonical correlation	0.96	0.72	0.65

and composition data for these groups can be found in Tully (1986). The main features were the greater intra-specific differences in diet among 5 mm length groups of *Ciliata* spp. than between species as their diets gradually changed with increasing size, and the separation of all *Ciliata* groups from other species (Fig. 2). The high level of predation on fish eggs by *Ciliata* spp. and on *Acartia* spp. by *Pollachius* spp. were quantitatively important differences in the diets of these 2 main groups and these 2 prey categories were the most

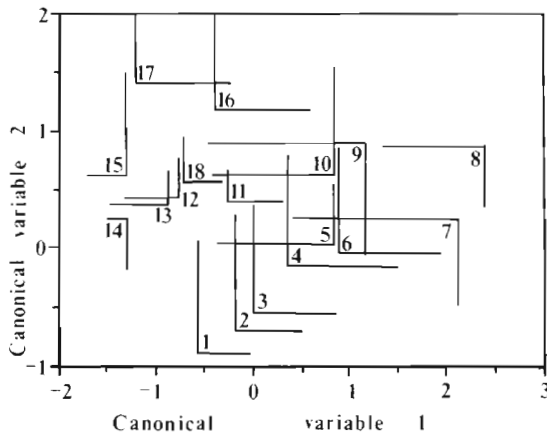


Fig. 2. Plot derived from step-wise discriminant analysis of the diets of 18 5 mm length groups of fish showing mean positions  $\pm$  standard deviation (horizontal and vertical lines) on canonical variables 1 and 2. Key: *Ciliata* spp. 10–14 mm (1), *C. septentrionalis* 14–19 mm (2), 19–24 mm (4), 24–29 mm (6), 29–34 mm (10), 34–39 mm (9), *C. mustela* 14–19 mm (3), 19–24 mm (5), 24–29 mm (7), 29–34 mm (8), *Pollachius pollachius* 5–10 mm (14), 10–15 mm (15), 15–20 mm (17), 20–25 mm (16), *P. virens* 20–25 mm (11), 25–29 mm (13), *Merlangius merlangus* 15–20 (12), 20–25 mm (18)

significant discriminating prey categories (Table 3). Discriminating variables with positive loadings on the first 2 canonical variables, mainly fish larvae *Anomalocera patersoni*, crab megalopae and insects (Table 3) are associated with *Ciliata* spp. over 25 mm length (Groups 7 to 10, Fig. 2) which also have positive loadings on both canonical variables. These prey were taken in greater numbers by these fish whereas fish eggs, small copepods and other negatively loaded prey categories on canonical variables 1 and 2 decreased in importance with increasing size. *Pollachius pollachius*, *Pollachius virens* and *Merlangius merlangus* groups are associated with variables, such as *Acartia* spp. and *Corycaeus* spp., which have negative loadings on canonical variable 1 and positive loadings on canonical variable 2 (Table 3, Fig. 2).

Five prey categories were significant in discriminating the diets of the autumn group of fish, compared with 17 for the spring group (Table 4). Although this may in part be due to the lower number of autumn fish examined it also reflects a specialisation by certain groups of *Cyclopterus lumpus* and *Scophthalmus maximus* on a few prey categories. Crab megalopae and *Idotea* spp. have high negative loadings on the first canonical variable (Table 4) and are associated with *C. lumpus* greater than 20 mm in length (Fig. 3). These 2 prey categories dominated the diet of these fish. *C. lumpus* less than 20 mm in length and harpacticoid copepods have low negative loadings on the first 2 canonical variables reflecting the greater importance of these copepods in small fish which took few megalopae

or *Idotea* spp. The third discriminating variable, fish larvae and *S. maximus* (20 to 25 mm) have high negative loadings on the second canonical variable (Table 4, Fig. 3). This was the only group of autumn fish which preyed on fish larvae. *Podon* spp. the fifth discriminating variable, was dominant in the diet of smaller individuals of *S. maximus* and was also important in discriminating larger size groups of *Gaidropsaurus mediterraneus* and *Rhinonemus cimbricus*. Copepods dominated the diet of smaller fish of these 2 species. No significant differences in the levels of individual prey categories among length groups of these fish were found by discriminant analysis (Fig. 3).

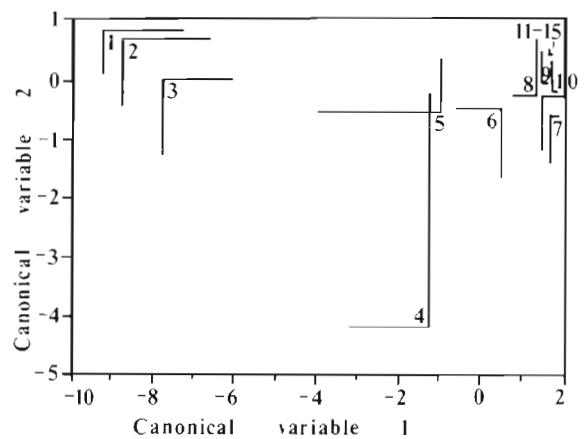


Fig. 3. Plot derived from step-wise discriminant analysis of the diets of 15 5 mm length groups of fish showing the mean positions  $\pm$  standard deviation (horizontal and vertical lines) on canonical variables 1 and 2. Key: *Cyclopterus lumpus* 10–15 mm (6), 15–20 mm (5), 20–25 mm (3), 25–30 mm (2), 30–35 mm (1), *Scophthalmus maximus* 10–15 mm (7), 20–25 mm (4), *Gaidropsaurus mediterraneus* 5–10 mm (14), 10–15 mm (11), 15–20 mm (15), 25–30 mm (9), 30–35 mm (8), *Rhinonemus cimbricus* 10–15 mm (13), 15–20 mm (12), 20–25 mm (10)

#### Diel variation in food consumption

*Ciliata mustela* and *Gaidropsaurus mediterraneus* caught over 24 h periods in September 1984 and August 1985 fed only during daylight hours. Stomach fullness increased throughout the day rising to a peak of over 4 (full) at 18:00 h. After sunset (ca 21:00 h) the index fell and was less than 1 at sunrise (06:00 h) (Fig. 4). Other indicators that feeding stopped after sunset were the partially digested state of stomach contents in fish caught after this time and the absence of vertically migrating benthic peracaridea in fish stomachs. These were the dominant species in neuston samples taken after sunset during August (Tully & Ó Céidigh 1987) and were within the size range of prey taken by these fish.

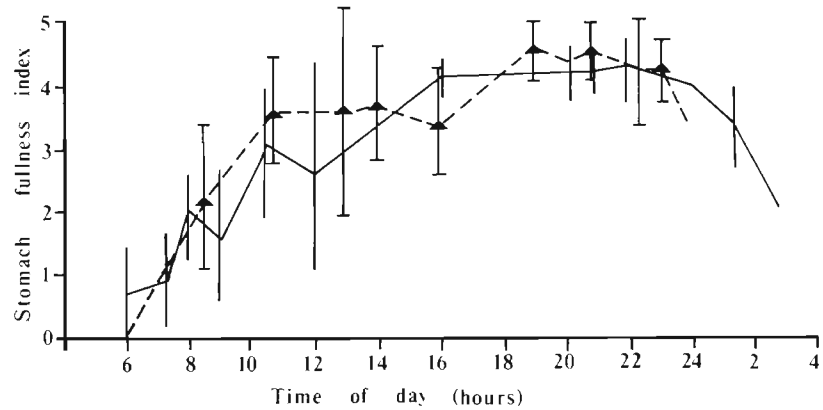


Fig. 4. Diel feeding pattern of *Ciliata mustela* (▲-----▲) and *Gaidropsaurus mediterraneus* (—) during September 1985 and August 1985 combined. Vertical lines indicate standard deviations

**Effects of fish species and fish length on food consumption**

In all species except *Scophthalmus maximus* and *Gaidropsaurus mediterraneus* the number of prey per fish was significantly different among 5 mm length groups, usually increasing with fish size (Table 5, Figs. 5 and 7). Among group differences in stomach fullness were insignificant in 5 species and significant in 4 species (Table 5, Figs. 6 and 8). In *Pollachius pollachius*

stomach fullness and the number of prey eaten increased significantly between all except two 5 mm length groups in fish up to 25 mm. In *Ciliata mustela* fish over 24 mm had fuller stomachs than *Ciliata* spp. 10 to 14 mm in length and there was also significant increases in the number of prey eaten by larger fish (Table 5). *Merlangius merlangus* over 15 mm and *Cyclopterus lumpus* and *Scophthalmus maximus* over 20 mm also had fuller stomachs than smaller fish (Table 5) although these increases were not always

Table 5. Variation in the number of prey per fish and stomach fullness among all and between individual pairs of 5 mm length groups of 9 species of fish. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

Species	Variation among groups (F-statistic)		Pair-wise comparison of groups		(t-statistic)	
	No. prey	Fullness	No. prey	Fullness	No. prey	Fullness
<i>C. septentrionalis</i>	5.19***	1.31	(10-14, 24-29) (10-14, 29-34) (14-19, 24-29)		-4.57*** -3.09* -3.34*	
<i>C. mustela</i>	16.12***	8.79***	(10-14, 14-19) (10-14, 19-24) (10-14, 19-24) (10-14, 24-29) (10-14, 29-34) (10-14, 29-34) (14-19, 24-29) (19-24, 24-29)		-3.36** -3.04* -7.21*** -4.11** -4.19*** -3.51**	-4.17*** -3.46*
<i>P. pollachius</i>	25.96***	19.99***	( 5-10, 10-15) ( 5-10, 15-20) ( 5-10, 20-25) (10-15, 15-20) (10-15, 20-25) (15-20, 20-25)	( 5-10, 15-20) ( 5-10, 20-25) (10-15, 15-20) (10-15, 20-25) (15-20, 20-25)	-3.29** -7.73*** -8.45*** -4.68*** -6.20*** -2.76*	-3.90** -5.56*** -4.66*** -6.46*** -2.95*
<i>P. virens</i>			(15-20, 20-25)		-5.40***	
<i>M. merlangus</i>	5.19**	4.61**	(10-15, 15-20)	( 5-10, 15-20)	-2.99*	-3.38*
<i>G. mediterraneus</i>	1.92	0.78	( 5-10, 15-20)		-3.65*	
<i>R. cimbricus</i>	5.79*	0.56	(10-15, 15-20)		-3.13*	
<i>S. maximus</i>	1.99	3.23		(10-20, 20-25)	-3.85*	
<i>C. lumpus</i>	4.44**	15.71***	(10-15, 20-25) (10-15, 30-35)	(10-15, 20-25) (10-15, 25-30) (10-15, 30-35)	-3.52* -3.52* -3.35*	-5.09*** -5.53*** -7.18***

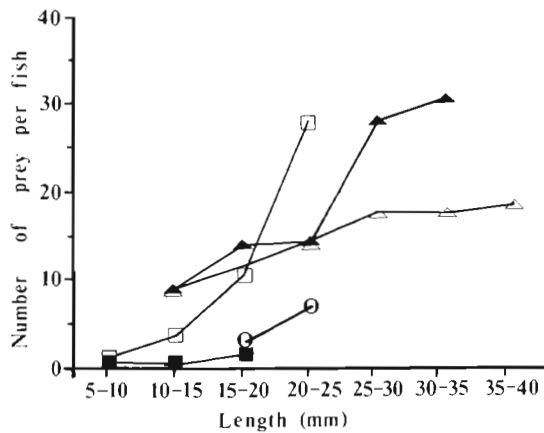


Fig. 5. Mean number of prey per fish for 5 mm length groups of *Ciliata septentrionalis* (△), *C. mustela* (▲), *Pollachius pollachius* (□), *P. virens* (○) and *Merlangius merlangus* (■)

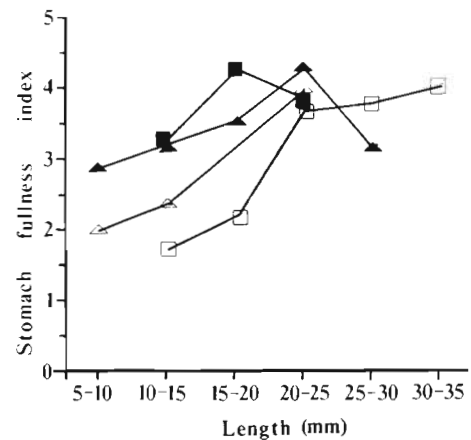


Fig. 8. Mean stomach fullness for 5 mm length groups of 4 species of fish. Key as in Fig. 7

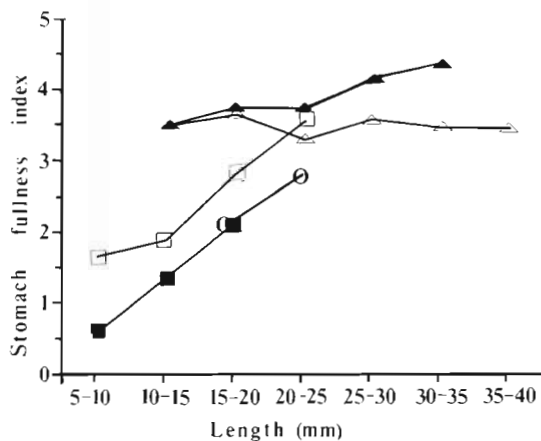


Fig. 6. Mean stomach fullness for 5 mm length groups of 5 species of fish. Key as in Fig. 5

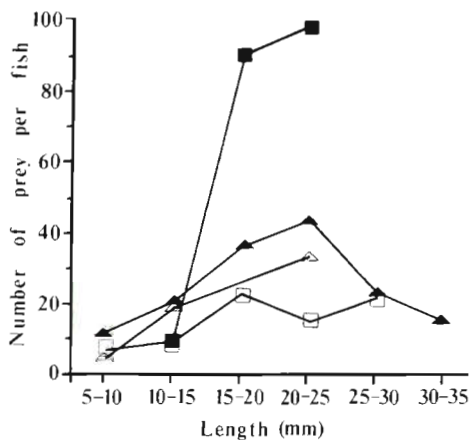


Fig. 7. Mean number of prey per fish for 5 mm length groups of *Gaidropsaurus mediterraneus* (▲), *Rhinonemus cimbricus* (■), *Cyclopterus lumpus* (□) and *Scophthalmus maximus* (△)

accompanied by increases in the number of prey eaten. This is evidence of a switch to larger prey in bigger fish and occurred in *C. lumpus* and *S. maximus* (Table 5).

Mean stomach fullness in neustonic species was consistently over 3.5 in *Ciliata septentrionalis* and *Ciliata mustela* (Fig. 6) and over 3 in *Gaidropsaurus mediterraneus* and *Rhinonemus cimbricus* in all sizes of fish analysed (Fig. 8). The pseudoneustonic species *Merlangius merlangus* and *Pollachius virens* ate very low numbers of prey and never had stomachs that were over 1/3 full (Figs. 5 and 6). Small individuals of *Pollachius pollachius*, *Cyclopterus lumpus* and *Scophthalmus maximus* also had comparatively low values on the fullness index (Figs. 6 and 8).

## DISCUSSION

The number of prey options available to post-larval and juvenile fish is limited both by the size-frequency distribution of the potential prey population and by the number of potential prey species present since individual prey species are likely to have species-specific behaviours and distributions. The inability to identify certain prey items beyond a broad taxonomic level and the creation of arbitrary prey size classes of unidentified prey items that may not really represent different prey options for predators are limiting factors in the interindividual comparison of diets by multivariate statistical analysis. The number of variables (prey categories) used in such an analysis depends both on the prey size classes created and the level to which prey were identified.

Within these constraints the food of some species in the spring and autumn species groups were shown to be different as were the diets of smaller and larger fish of individual species. Features of the diets of *Ciliata*



spp. were the numbers of fish eggs and copepod eggs eaten. Other post-larval and 0-group gadoids and neustonic rockling species recorded during autumn in the present work (*Gaidropsaurus mediterraneus* and *Rhinonemus cimbricus*) do not prey extensively on fish eggs (Last 1978, Conway 1980, Robb & Hislop 1980, Robb 1981, present data). Copepod eggs, which were eaten in large numbers by *Ciliata* spp. are unlikely to be optimal prey items for these fish because of their size (150 µm) and because they are resistant to digestion. Undigested copepod eggs were also recorded in *Mugil* spp. by Zismann et al. (1975) and in *Micromesistius poutassou* (Risso) by Conway (1980). The diet of *Scophthalmus maximus* in Galway Bay and that described for the species in the North Sea by Last (1978) were broadly similar. Differences included the absence of fish larvae and the presence of fish eggs in North Sea specimens and the predation on *Oikopleura* spp. by larvae under 11 mm in the North Sea but mainly by fish over 15 mm in Galway Bay. The diet of *S. maximus*, which was the only flatfish (family Bothidae) species studied, was very different to that of others. The food of *Cyclopterus lumpus* was also distinct and was made up mostly of crustaceans which, like *C. lumpus*, associate with driftweed, i.e. *Idotea* spp., *Gammarus locusta* L. (Tully & Ó Céidigh 1986) and harpacticoid copepods. The high degree of prey selectivity shown by *C. lumpus* and *S. maximus*, the different size, quality and quantity of food eaten by different sized fish, the high level of food consumption by neustonic species and the high density of juvenile fish in the neustal during daylight hours all indicate that an adequate food supply was available to the size range of fish studied. The degree to which copepod eggs were taken at stations outside of Galway Bay however, may indicate that in some instances food was scarce.

Two trends in dietary shift as fish increased in size were obvious. The diets of *Cyclopterus lumpus* and *Scophthalmus maximus* changed abruptly as fish length increased. These abrupt changes in the diets of these 2 species, which were accompanied by significant increases in stomach fullness but insignificant increases in the number of prey eaten by larger fish (i.e. a switch to larger and different species of prey), are evidence of different feeding stanzas (Paloheimo & Dickie 1965) or trophic groups within the length range of fish examined for these species. Using such changes in prey categories and sizes eaten as criteria for determining the existence of feeding stanzas only one trophic group was recognisable in other species as their diets changed only gradually with fish size. This gradual change in diet was also reported by Robb & Hislop (1980) for 0-group gadoids in the North Sea. However, larger individuals of *Ciliata mustela*, *Pollachius pollachius* and *Merlangius merlangus* ate

significantly higher numbers of prey and had significantly fuller stomachs. This increase in the number of prey eaten by larger fish is an alternative strategy to switching to larger prey. When accompanied by a significant increase in stomach fullness it is evidence of an increase in food consumption by larger fish above that expected simply from the increase in fish size (i.e. a greater amount of food consumed per unit size of fish). Shifts in the prey categories taken by these species as fish increased in length did occur simultaneously with this increase in stomach fullness. Tropho-dynamically speaking these groups of larger fish can be seen as belonging to a different trophic group also because, in proportion to fish size, their impact on the prey population is greater than that of smaller fish.

A comparison of the average stomach fullness of neustonic rockling species *Ciliata septentrionalis*, *Ciliata mustela*, *Rhinonemus cimbricus* and *Gaidropsaurus mediterraneus* between 10 and 25 mm in length with other gadoid species of similar length which were pseudoneustonic, i.e. *Pollachius pollachius*, *Pollachius virens* and *Merlangius merlangus*, showed that the neustonic species and *P. pollachius* over 20 mm had fuller stomachs than pseudoneustonic species. Rockling had consistently high values on the index regardless of fish length. Significant increases with length were evident only between 3 groups of *C. mustela*. Neustonic species, therefore, seemingly fed more successfully in the neustal than pseudoneustonic individuals. This may infer that feeding conditions at the sea surface are different to those of deeper water and that neustonic species have adaptations that enable them to cope with this environment more successfully than other species. Whether *M. merlangus* and *P. virens* feed more intensively in deeper water was not assessed. However, *M. merlangus* caught in a pelagic trawl in the North Sea by Robb & Hislop (1980) consumed a far greater number of prey than specimens caught in the neustal of Galway Bay.

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