Spatial and temporal distribution of the demersal fish fauna in a Baltic archipelago as estimated by SCUBA census

B.-O. Jansson, G. Aneer & S. Nellbring

Askö Laboratory, Institute of Marine Ecology, University of Stockholm, S-106 91 Stockholm, Sweden

ABSTRACT: A quantitative investigation of the demersal fish fauna of a 160 km² archipelago area in the northern Baltic proper was carried out by SCUBA census technique. Thirty-four stations covering seaweed areas, shallow soft bottoms with seagrass and pond weeds, and deeper, naked soft bottoms down to a depth of 21 m were visited at all seasons. The results are compared with those obtained by traditional gill-net fishing. The dominating species are the gobiids (particularly *Pomatoschistus minutus*) which make up 75 % of the total fish fauna but only 8.4 % of the total biomass. *Zoarces viviparus*, *Cottus gobio* and *Platichthys flesus* are common elements, with *P. flesus* constituting more than half of the biomass. Low abundance of all species except *Z. viviparus* is found in March–April, gobies having a maximum in September–October and *P. flesus* in November. Spatially, *P. minutus* shows the widest vertical range being about equally distributed between surface and 20 m depth. *C. gobio* aggregates in the upper 10 m. The *Mytilus* bottoms and the deeper soft bottoms are the most populated areas. The former is characterized by *Gobius niger*, *Z. viviparus* and *Pholis gunnellus* which use the shelter offered by the numerous boulders and stones. The latter is totally dominated by *P. minutus*. Annual mean values for the total demersal fish fauna are 2.1 ind m⁻² and 4.3 g m⁻² fresh weight. The maximum biomass value, 17 g m⁻² fresh weight, was measured on very exposed *Mytilus* bottoms. Comparisons with other geographical areas such as shallow soft bottoms in the North Sea, seagrass beds in the northeastern USA and Texas and *Spartina* marsh ponds in North Carolina show these figures to be surprisingly high.

INTRODUCTION

Proportional to its size the Baltic Sea is undoubtedly one of the most intensively investigated marine areas of the world. At the ecosystem level, several large-scale investigations have been made. Stratified random sampling has yielded values for the main marine biological variables both for hard bottoms (Hällfors et al. 1981, Jansson & Kautsky 1977, Kautsky et al. 1981) and soft bottoms (Ankar & Elmgren 1976, Elmgren et al. 1984).

In very shallow areas with soft and more or less vegetation-free bottoms, drop-traps, drop-nets or other enclosure methods give reliable estimations (cf. Kjelson et al. 1973, Aneer & Nellbring 1977, Evans & Tallmark 1979, Pihl & Rosenberg 1982) but for deeper bottoms, especially with mixed substrates (stones, boulders, algae), none of these methods are really reliable.

With the exception of Aneer & Nellbring (1977) and Thorman & Wiederholm (1983), who worked in very shallow waters (0 to 1.2 m), truly quantitative data on fish abundance in the Baltic are almost totally lacking (for a review of Baltic fishes and fisheries see Ojaveer et al. 1981). Even the most ambitious studies in the past (e.g. Neuman 1977, 1982) are difficult to interpret in relation to actual abundance as they are based on gill-net fishing. As other approaches were less successful, we decided to use visual transect census. SCUBA census of fish was first described by Brock (1954) and has been used especially on coral reefs (for a review see Russell et al. 1978). It has also been used in the Baltic Sea, where Bagge et al. (1975) counted resting fish at night at 3 localities in a Finnish archipelago. The results presented here describe the quantitative distribution in space and time of the different species, while their food ecology and trophic relations will be treated in a future paper.

Fig. 1. Primary investigation area of the Askö Laboratory (160 km²) with the stratified random sampling stations (adopted from Jansson & Kautsky 1977). Stippled areas are shallower than 6 m; filled stars: sampling sites; open star: position of laboratory. Circle: position of permanent hydrographic-biological monitoring station of the Askö Laboratory

STUDY AREA

The area of investigation coincides with the primary research area of the Askö project 'Dynamics and energy flow in the Baltic ecosystem' (Jansson 1972). The total area covers 160 km² of open archipelago with rocky islands (Fig. 1). The areal distributions of main bottom substrate and depth of the investigated area are presented in Fig. 2. As can be seen, the mean depth of the research area is roughly 25 m, and rock and coarse sand dominate down to 15 m depth. We have intentionally restricted the study to the vegetation zone. The sites of the 34 studied localities are shown in Fig. 1. All except 2, close to the laboratory, were randomly chosen as described by Jansson & Kautsky (1977). The distribution of different bottom communities is to a large extent governed by water turbulence. Based mainly on the amount of fine material and type of

Fig. 2. Left: areal distribution of bottom substrate of the 160 km² primary investigation area (based on Jansson & Kautsky 1977); right: hypsographic curve of the area (A. M. Jansson 1973)

Fig. 3. Examples of the localities, classified into 4 groups according to degree of exposure, from sheltered (1) to very exposed (4). (A) Grade 1: soft bottom at 1 m depth showing patchy vegetation of the phanerogams *Myriophyllum spicatum* and *Ruppia spiralis*. Typical locality for sand goby. September 1982. (B) Grade 2: *Fucus vesiculosus* belt at 2 m depth with the red alga *Ceramium tenuicorne* growing both on rocks and *Fucus*. Typical species: bullhead, black goby, eelpout, gunnel. September 1982. (C) Grade 3: stony shallow sublittoral at 1 m depth with autumnal vegetation of *Ceramium tenuicorne*. Bullhead is very common here. September 1982. (D) Grade 4: 8 m depth; amount of accumulated detritus still very small due to high wave action. Filter feeders such as barnacle *Balanus improvisus*, bryozoan *Electra crustulenta* and mussel *Mytilus edulis* cover the rocks. Sparse fish fauna consists of sand goby, black goby and eelpout. November 1981

Table 1. Mean length, mean maximum depth and ranges for transects studied in the SCUBA census. The different grades of exposure are: 1 sheltered; 2 moderately sheltered; 3 moderately exposed; 4 very exposed. Number of transects = n

Degree of exposure	Mean length (m) $\pm$ SD	Range	Mean maximum depth (m) $\pm$ SD	Range	n
1	51.3 $\pm$ 42.9	20 - 133	4.5 $\pm$ 1.1	3.0 - 5.7	6
2	62.1 $\pm$ 25.1	25 - 100	7.4 $\pm$ 3.0	2.9 - 13.0	11
3	60.6 $\pm$ 20.1	45 - 100	10.0 $\pm$ 3.3	4.4 - 15.0	9
4	37.8 $\pm$ 38.1	30 - 120	10.7 $\pm$ 5.6	4.5 - 21.0	8
Total	59.9 $\pm$ 28.3	20 - 133	8.4 $\pm$ 4.2	2.9 - 21.0	34

vegetation the localities were divided into 4 groups representing different grades of exposure (Table 1). As shown in this table, the mean depth of the transects is roughly 8 m and few transects are deeper than 15 m. Underwater photographs of the 4 community types and their major elements are shown in Fig. 3.

The salinity in the area varies from 6 to 7 ‰ S. The temperature shows a strong annual pulse from slightly below zero to ca 20°C, and an ice cover is generally present from January through March. Tidal range is restricted to a few cm only.

METHODS

The localities were visited in September-October 1980, and March-April, July-August and November 1981. The census periods had a maximum duration of 4 wk. A meter line was laid perpendicular to the shore or from the shallowest part of the transect and down to a depth where the vegetation ended, if possible. Two divers followed the line, one counting the fish within a strip 0.5 m broad beside the line and within a 1 m high water column above, noting depth, type of vegetation and bottom substrate and drawing a rough profile of the transect. Pilot studies had shown that an inspection field wider than 0.5 m largely increased the probability of counting the same fish twice or of failing to identify fast moving species. Cryptic fish species were traced by carefully parting the vegetation and turning stones. By moving gently, most specimens could be measured against a stick marked in cm. Notes were made with a lead pencil on a white plastic sheet. All counting and measuring was undertaken by the same diver (Jansson) throughout the investigation. The second diver (Nellbring) followed the first, collecting qualitative information on the area and also fish for stomach analysis. Scientific names of fish are presented in Table 2.

The nocturnal dives in September-October 1982 were made at 4 localities starting after 2100 h, after at least 2 h of darkness. The localities had been visited the same day during daylight starting at 0930 h. The procedure at night was the same as for daytime except for the use of an ordinary underwater torch.

The duration of the dives varied between some 20 min to well over 1 h due to the care taken not to scare fish away. Species such as perch, pike, three-spined stickleback and cod, were visibly disturbed by the sound and sight of the divers. We therefore restrict the presentation of estimates of numbers and biomasses to figures for the total observed material and to some 10 species for which we feel reasonably confident of having adequate data.

The abundance and biomass figures presented in Fig. 6 to 8 are averages for the total material on a seasonal basis (6), on an annual basis (7), or with regard to degree of exposure and vegetation type only for the period September-October 1980 (8). For fish whose length could not be adequately measured in the field, weight was calculated from data on seasonal size distributions using length/weight relationships obtained during this and/or earlier studies in the area. Consequently the smallest average size for each species and season was chosen. In cases where the species could not be recorded, the weight of an unknown fish was obtained from size-distribution data and length/weight relationships for all species. The length of the smallest individual recorded for that period, regardless of species, was used for this calculation. Therefore, we emphasize that numbers and biomass figures should be regarded as minimum values, as recommended by Brock (1982) in his critical study of the visual census method.

In the Baltic proper, *Pomatoschistus* spp. consists of 2 species, sand goby and common goby. It is difficult to separate these during diving but on the basis of previous studies, we are convinced that the sand goby makes up the major part (probably more than 95 %) which is why the name 'sand goby' will be used hereafter, except in the tables.

No efforts were made to test the accuracy of the method using parallel transects within the same small area. Firstly, to our knowledge, no method exists for recording the true number of fish in a large open body of water. Secondly, even parallel transects very close to each other would offer rather different bottom structure to small fish due to the heterogeneous distribution of stones, vegetation, patches of soft material, etc. We

Table 2. Composition of total material of gill-net catches and diving census work. Number of specimens: n; biomass in wet weight: B; + values above 0.0 too small to be shown within the given scales of precision

Scientific name	Common name	Gill-net catches				Diving census			
		n	%	B (g)	%	n	%	B (g m ⁻²)	%
<i>Perca fluviatilis</i>	Perch	552	61.27	63957.4	41.31	8	0.10	0.006	0.14
<i>Rutilus rutilus</i>	Roach	72	7.99	3582.9	2.31	1	0.01	0.001	0.02
<i>Clupea harengus</i>	Baltic herring	71	7.88	3157.2	2.04	—	—	—	—
<i>Gadus morhua</i>	Cod	60	6.66	22861.2	14.77	2	0.03	0.131	3.13
<i>Sprattus sprattus</i>	Sprat	29	3.22	284.0	0.18	—	—	—	—
<i>Myoxocephalus scorpius</i>	Father-lasher	29	3.22	4095.2	2.65	12	0.15	0.118	2.80
<i>Platichthys flesus</i>	Flounder	19	2.11	4491.3	2.90	44	0.56	2.929	69.81
<i>Esox luxius</i>	Pike (northern)	15	1.66	29453.3	19.03	2	0.03	0.045	1.08
<i>Abramis brama</i>	Bream	9	1.00	6480.9	4.19	—	—	—	—
<i>Alburnus alburnus</i>	Bleak	9	1.00	101.1	0.07	10	0.13	0.016	0.37
<i>Stizostedion lucioperca</i>	Pike-perch	7	0.78	3372.9	2.18	—	—	—	—
<i>Leuciscus idus</i>	Ide	6	0.67	8210.0	5.30	—	—	—	—
<i>Scophthalmus maximus</i>	Turbot	4	0.44	3187.1	2.06	—	—	—	—
<i>Taurulus bubalis</i>	Sea scorpion (Longspined)	4	0.44	51.2	0.03	17	0.22	0.006	0.13
<i>Nerophis ophidion</i>	Straight-nosed pipefish	3	0.33	0.4	+	2	0.03	0.002	0.04
<i>Zoarces viviparus</i>	Eelpout	3	0.33	146.7	0.09	134	1.70	0.344	8.19
<i>Hyperoplus lanceolatus</i>	Sand eel (greater)	2	0.22	55.4	0.04	1	0.01	+	0.01
<i>Gymnocephalus cernua</i>	Ruffe	2	0.22	55.3	0.04	—	—	—	—
<i>Blicca bjoerkna</i>	White bream	1	0.11	58.4	0.04	—	—	—	—
<i>Coregonus lavaretus</i>	Whitefish	1	0.11	1080.0	0.70	—	—	—	—
<i>Cyclopterus lumpus</i>	Lumpfish	1	0.11	101.0	0.07	2	0.03	0.051	1.21
<i>Gobius niger</i>	Black goby	1	0.11	6.3	+	411	5.23	0.140	3.33
<i>Cottus gobio</i>	Bullhead	1	0.11	3.7	+	227	2.89	0.123	2.97
<i>Pomatoschistus minutus/microps</i>	Sand/Common goby	—	—	—	—	3733	47.48	0.194	4.63
<i>Gobiusculus flavescens</i>	Two spotted goby	—	—	—	—	1543	19.62	0.009	0.22
Gobiidae juveniles	Juvenile gobies	—	—	—	—	1534	19.51	0.007	0.17
<i>Pholis gunnellus</i>	Butterfish	—	—	—	—	30	0.38	0.065	1.55
<i>Pungitius pungitius</i>	Nine-spined stickleback	—	—	—	—	21	0.27	0.001	0.02
<i>Siphonostoma typhle</i>	Broad-nosed pipefish	—	—	—	—	4	0.05	0.002	0.04
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	—	—	—	—	3	0.04	+	+
<i>Spinachia spinachia</i>	Fifteen-spined stickleback	—	—	—	—	3	0.04	0.002	0.04
<i>Liparis liparis</i>	Sea snail	—	—	—	—	2	0.03	0.002	0.06
<i>Phoxinus phoxinus</i>	Minnow	—	—	—	—	2	0.03	0.001	0.02
	Undertermined	—	—	—	—	115	1.46	0.001	0.03
Total		901		154792.9		7863		4.196	

have attempted to compensate for this by visiting many localities and by pooling them into a few categories, representative of the Baltic coast and recognizable from sea charts and diving-sample tests.

For comparison, gill nets of the 'experimental' gang-type were used in all 4 seasons. The nets consisted of 12 segments, 2 m deep and 3 m long, with the following mesh sizes (knot to knot): 10, 13, 18, 22, 25, 32, 34, 38, 44, 50, 63 and 73 mm. The nets were put out at 1700 h and taken up at 0800 h the following day at 4 typical stations close to the laboratory.

RESULTS

Environmental conditions

Apart from bottom topography and bottom substrate, only water temperature was measured. Bi-weekly

temperature recordings for the whole water column down to 25 m at the permanent hydrographic-biological monitoring station in the middle of the area (Fig. 1) are shown in Fig. 4. In March-April and November homothermic conditions prevail throughout the water column with intermittent ice-cover in the former period. In July-August and September-October a thermocline is formed, weak at 5 m depth and more pronounced at 15 m. The strong annual pulse, with larger ranges during the summer maximum and practically constant temperature during winter, is evident.

Day and night observations

Sumari (1963, cited in Bagge et al. 1975) recommended SCUBA census work during hours of darkness since most pelagic fish are less disturbed by divers

Fig. 4. Temperature conditions at the permanent hydrographic-biological station in the middle of the investigation area (Fig. 1). Mean ($\bar{t}$) values and range (stippled lines) based on bi-weekly measurements

during that period. In order to observe probable differences in abundance over the 24 h cycle, day and night dives were undertaken during 2 periods. Table 3 shows the results of these dives. When abundances are compared, more specimens are found during the day,

Table 3. Comparison between day and night mean values obtained from diving census work on 4 transects. Day census work was carried out between ca 0930 and 1500 h, night studies started ca 2 h after onset of darkness and were carried out between 2100 and 0300 h

Species	Day n m ⁻²	Day n	Night n m ⁻²	Night n
1 Sand/Common goby	1.58	308	1.71	317
2 Two spotted goby	3.81	742	0.31	55
3 Black goby	0.09	17	0.05	10
4 Sea scorpion	0.02	4	0.01	2
5 Bullhead	0.02	4	0.02	3
6 Father-lasher	0.01	2	0.03	5
7 Eelpout	0.03	5	—	—
8 Butterfish	—	—	0.02	3
9 Three-spined stickleback	0.01	1	—	—
10 Nine-spined stickleback	0.03	6	—	—
11 Fifteen-spined stickleback	—	—	0.01	1
12 Perch	—	—	0.03	6
13 Flounder	0.01	2	0.01	2
14 Cod	—	—	0.01	1
15 Broad-nosed pipefish	—	—	0.01	1
16 Undetermined	0.03	5	0.02	3
Total inspected area (m ²)	194.5		185.0	
Total abundance	n m ⁻²		g m ⁻² (wwt)	
	Day	Night	Day	Night
September	5.31	2.43	5.99	11.95
October	3.78	1.72	3.88	5.79

with a mean of 4.5, compared to 2.1 ind m⁻² at night. Except for the two spotted goby there was no significant difference (Student's t-test) in the abundances during day and night. When biomasses are compared, however, there is a clear dominance in the dark hours. This is mostly due to the presence of large specimens of father-lasher, cod and flounder. The results give no substantial evidence that night census for demersal species is preferable to counting during daylight. Brock (1982) states that 'visual census data should be restricted to the diurnally exposed species'.

Total gill-net and diving-census material

Table 2 lists the total material from the gill netting and SCUBA census. It shows the typical species mixture of the brackish Baltic Sea, with common freshwater species like perch, pike, roach and bream mixed with saltwater species such as herring cod, sprat and flounder. Perch was by far the most common pelagic or semi-pelagic fish in the gill-net catches followed by roach, herring and cod. Of the species recorded by the diving technique, the sand goby, the two spotted goby,

Fig. 5. Example of type of information acquired from diving census work. Vertical bars: numbers and locations on transect of the different species

Table 4. Composition (%) of phytal fish community in the Askö-Landsort area as observed by SCUBA census. Numbers in normal typing: % of abundance; numbers in italics: % of biomass. Right hand column: total means of abundance ($n\ m^{-2}$) and biomass ($g\ m^{-2}$ wet weight) in absolute values (not in per cent). Areas investigated in different seasons and totally are shown in parentheses

	Sand/Common goby	Black goby	Two spotted goby	Juvenile gobiidae	Bullhead	Sea scorpion (longspined)	Father-lasher	Eelpout	Butterfish	Flounder	Undetermined	Others	$n\ m^{-2}$ $g\ m^{-2}\ wwt$
Sep-Oct 1980 (1027.5 m^2)	68.3 <i>15.4</i>	8.1 <i>6.8</i>	14.5 <i>0.3</i>	—	4.2 <i>5.6</i>	0.2 <i>0.2</i>	0.0 <i>1.9</i>	1.8 <i>12.7</i>	0.4 <i>3.3</i>	0.2 <i>47.5</i>	1.7 <i>0.0</i>	0.8 <i>6.1</i>	3.6 <i>4.2</i>
Mar-Apr 1981 (666.5 m^2)	14.0 <i>0.4</i>	10.3 <i>2.1</i>	20.1 <i>0.3</i>	—	12.2 <i>2.0</i>	—	1.8 <i>1.1</i>	28.6 <i>20.2</i>	3.0 <i>0.4</i>	4.9 <i>64.1</i>	5.5 <i>0.0</i>	4.9 <i>9.3</i>	0.2 <i>2.2</i>
Jul-Aug 1981 (1089 m^2)	17.9 <i>1.4</i>	2.4 <i>3.2</i>	11.7 <i>0.3</i>	63.2 <i>0.6</i>	0.8 <i>0.9</i>	0.2 <i>0.2</i>	0.0 <i>7.3</i>	0.8 <i>2.6</i>	0.1 <i>0.3</i>	0.8 <i>71.3</i>	1.3 <i>0.0</i>	0.6 <i>11.1</i>	2.2 <i>5.0</i>
Nov 1981 (520 m^2)	39.4 <i>1.0</i>	7.4 <i>1.2</i>	22.9 <i>0.1</i>	—	12.9 <i>3.2</i>	—	—	5.4 <i>4.9</i>	3.0 <i>1.6</i>	3.0 <i>87.7</i>	5.0 <i>0.0</i>	0.8 <i>0.2</i>	0.5 <i>5.4</i>
Annual average (3303 m^2)	34.9 <i>4.6</i>	7.1 <i>3.3</i>	17.3 <i>0.3</i>	15.8 <i>0.2</i>	7.5 <i>2.9</i>	0.1 <i>0.1</i>	0.5 <i>2.6</i>	9.2 <i>10.1</i>	1.6 <i>1.4</i>	2.2 <i>67.7</i>	3.4 <i>0.0</i>	1.8 <i>6.7</i>	2.1 <i>4.3</i>

Fig. 6 (A) and (B). Abundance ($n\ m^{-2}$, black bars) and biomass ($g\ m^{-2}\ wwt$, white bars) in space and time of main fish species. Note different scales of numbers and biomasses. Numbers (N) in vertical column to the right of each seasonal diagram: number of visited transects within each respective depth range. + recorded abundance but too small to appear in the scale of the diagram

juvenile gobies and the black goby constituted more than 90 % of all counted fish. Sander's similarity index (Sanders 1960) calculated for abundance (1.8 %) and biomass (10.2 %) shows the marked differences between the 2 methods.

Most of the type of information collected in the field work for each transect is illustrated in Fig. 5. The total diving census material with means of numbers and biomasses, weighted with respect to inspected bottom areas, is presented for species and seasons in Table 4.

Spatial distribution of the most common species

The vertical distribution of the most common species during the different seasons is shown in Fig. 6 A–B. The sand goby has the widest range: in September–October it was almost homogeneously distributed down to the maximum visited depth, 21 m. Of the other species, few were noted below 15 m depth. Biomass values were generally higher above 10 m than below.

The black goby is most abundant on either hard or partially soft bottoms but with shelter readily available under stones, in crevices, etc. (cf. Zander 1979). We often observed frequently used caves with their inhabitants, pointing to a certain territoriality of the species (cf. Bopp 1957).

The flounder was often noted to be patchily distributed. The distribution of the total fish assemblage over the different types of bottoms is illustrated for the period of maximum abundance, September–October, in Fig. 8.

Temporal distribution

The occurrence of the different fish species during the 4 seasons is also shown in Fig. 6 A–B. The most striking feature is the very low abundance of all species during March–April, except for eelpout. The sand goby, the black goby and the two spotted goby have their maxima in September–October. The large maximum of *Pomatoschistus* spp., nearly 10 times higher than in the other periods, was followed by a marked reduction in winter abundances with very low numbers in March–April (Fig. 6A). The result of the spawning in shallow water during May–July (Nellbring unpubl.) can be seen in the large percentage of juveniles in July–August (Table 4). A clear maximum of biomass in November is shown by flounder (Fig. 7B; Table 4).

The eelpout constituted nearly a third of the total fish assembly on the hard bottoms in March–April (Table 4). The size distribution of this species with regard to depth and season is shown in Table 5. In March–April small individuals, 4 to 5 cm long and

apparently newly released, reduced the mean length; only two 5 cm long specimens were found during the rest of the year. The mean length of the total material from the investigation area (0 to 21 m depth) was 10.4 cm. Aneer (1975), bottom trawling over soft bottoms at 30 to 50 m depth in the area over a 2 yr period, recorded a different size distribution. The mean size was 25 cm and no individuals smaller than 11 cm were found. The smallest mesh size of the trawls was 10 mm. The frequency of trawling and the well known compression of the meshes of the trawl sack should in theory have yielded smaller specimens had they been present in any substantial numbers.

Annual averages

As a basis for rough estimates of the amount of demersal fish in the neritic zone of the investigation area, annual averages of numbers and biomass have been calculated (Fig. 7A; Table 4). The dominance of the sand goby, the two spotted goby and their juveniles is apparent with respect to abundance as is also the effect of flounder on the biomass values.

The seasonal means of total numbers and biomasses are shown in Fig. 7B, where also the fractions of biomass represented by flounder is indicated. There is a clear abundance maximum in September–October. The biomass is high in July–November. If the fraction of flounder is excluded, the biomass of all others reaches its maximum in September–October.

The annual mean for the whole investigated area is

Table 5. Mean length $\pm$ standard deviation for eelpout in different depth intervals and seasons. The material used in depth interval 0 to 15 m is from the diving census; the material in the 30 to 50 m interval comes from bottom trawl hauls carried out 1970–72 (Aneer 1975). Values in parentheses: numbers of specimens

Depth (m)	Mar–Apr	Jul–Aug	Sep–Oct	Nov
0.0–2.5	6.3 $\pm$ 1.8 (6)	12.8 $\pm$ 4.6 (5)	11.1 $\pm$ 4.7 (21)	10.6 $\pm$ 4.0 (5)
2.5–5.0	9.9 $\pm$ 5.8 (14)	9.0 $\pm$ 2.2 (4)	9.8 $\pm$ 4.8 (25)	11.3 $\pm$ 5.9 (6)
5.0–7.5	9.1 $\pm$ 7.1 (8)	10.4 $\pm$ 3.7 (7)	12.6 $\pm$ 3.9 (7)	12.7 $\pm$ 8.3 (3)
7.5–10.0	8.0 $\pm$ 5.7 (2)	7 (1)	6.7 $\pm$ 0.6 (3)	–
10.0–12.5	20 (1)	11 (1)	20 (1)	–
12.5–15.0	–	–	20 (1)	–
$\bar{x}(0–15\text{ m})$	9.2 $\pm$ 5.8 (31)	10.6 $\pm$ 3.7 (18)	10.8 $\pm$ 4.9 (58)	11.4 $\pm$ 5.4 (14)
$\bar{x}(30–50\text{ m})$	28.3 $\pm$ 3.2 (43)	19.3 $\pm$ 3.9 (27)	23.1 $\pm$ 4.0 (7)	25.0 $\pm$ 4.5 (12)

Fig. 7. (A) Annual averages in numbers and biomasses of the most common species (cf. Table 4). (B) Seasonal distribution of abundance, expressed as number m^{-2} and biomass m^{-2} (wwt) of total fish assembly. Due to its relative importance in terms of biomass, flounder is represented separately

2.1 individuals m^{-2} and a biomass of 4.3 g (wwt) m^{-2} (Table 4). Maximum mean values attained for a selected time and depth interval were 5.7 ind m^{-2} at 0 to 2.5 m depth in July-August and 71 g m^{-2} at 15 to 17.5 m depth, in September-October (Fig. 6B).

DISCUSSION

Gill-net catches versus diving census

The large difference between net catches and diving-census values is partly caused by differences inherent in the methods, partly by biological features. Gill-net fishing results are based not only upon abundance and activity of the fish, but also on a much longer 'registration time', i.e. length of time the nets are exposed compared to diving results which are based upon the activity of the diver and time taken to complete the census. The latter gives a more instantaneous picture of fish abundance, instead of an integration over time as obtained by using gill nets.

The poor correlation of abundance with Sanders' similarity index (Sanders 1960) is partly a function of body form and body size. Fish with slender and soft bodies like eelpout are seldom caught in nets, neither are small-sized fish like gobies. Big fish are more scarce than small fish in both pelagic and benthic systems. They usually feed at higher trophic levels and their higher food requirements force them to forage over wider areas, their 'specific area of maintenance' is large. The higher similarity index for biomass is to a certain extent explained by the impact of individual big fish on the biomass of the transect study. The effect

of single large individuals for the total fish biomass is obvious, especially when comparing the numerous small *Pomatoschistus minutus* with the few large *Platichthys flesus* (Fig. 6A, B). A knowledge of the 'specific area of maintenance' of the flounder would translate the abundance and biomass values into functional information at the system level.

Seasonal habitat changes

The importance of the sand goby in the area is also reflected in their share of the total amount of larvae in the pelagic zone as estimated by Bongo-net trawling (Aneer unpubl.). Here gobiid larvae constitute 78 % of the total number of pelagic larvae caught in August and about 60 % on an annual basis. These findings agree well with our data. As stated earlier we are convinced that the sand goby makes up the major part of the observed *Pomatoschistus* spp. individuals. The only exceptions would be among larvae and fish observed in the shallowest areas (1 m or less) where the common goby might constitute a considerable but still unknown part (except for those areas investigated by drop traps).

The abundance maximum in September-October is certainly a result of the change to demersal life of these larvae. These findings contrast with the condition in the Dutch Wadden Sea where Fonds (1973) reported an immigration to shallow waters in March, an emigration to spawning areas at 10 to 25 m depth in April-May and emigration out of the estuary in winter. A main question concerning this important species in the Baltic is therefore whether the spawning is restricted to the shallowest areas and to those populations which

emigrate in June or whether spawning takes place also in deeper waters like in the Dutch Wadden Sea. From our frequent diving we have at present only one observation of nests from deeper areas, between 4 and 5 m depth at the beginning of July, which might support this latter assumption.

A clear increase in average bodylength of eelpouts from March–April through November can be seen in the mean lengths for the depth interval 0 to 15 m (Table 5). This corresponds well with the release and subsequent growth of the young. Our material also shows that younger fish of at least 2 year classes dominate in this interval. In the deeper interval, 30 to 50 m, a similar cycle with a minimum in July–August is noted. This could indicate that a downward migration with an addition of younger fish takes place in the middle of summer. This agrees well with the impression obtained from diving on the soft bottoms at 20 to 30 m depth where the largest eelpouts were always found. The suitability of the algal belts as nurseries for this species is apparent. Mating in late summer–autumn and release of young early in the year fits well with the numbers of old specimens in September–October and young ones in March–April. This is in good agreement with the conditions in Danish estuaries and lagoons as reported by Muus (1957). Kristoffersson and Oikari (1975), collecting eelpout in the Gulf of Finland, found only young specimens and adults over 4 yr. Their suggestion that the 2 to 4 yr olds (15 to 25 cm long) spend their time in shallower water is partly supported by our data (Table 5). Zander & Hartwig (1982) found single specimens of eelpout on the mud flats on Sylt Island, North Sea, only in January and April. This could be further evidence for the aggregation of members of the species at the surface nursery waters during the colder seasons (Fig. 6B).

The distribution of biomass does not intimately follow the distribution of numbers. This is especially apparent for species attaining a fairly large size when adult such as father-lasher, flounder and eelpout. Thus different age/size classes appear to have different habitat preferences.

Fish assemblages and bottom types

The distribution of fish with respect to the different grades of exposure shows higher numbers and biomasses for the intermediate and exposed localities. This can be explained by a 2-fold effect of water movement. In sheltered areas, sedimentation is high and several subsystems are missing or poorly developed due to lack of hard substrate (e.g. the red algal belt and the *Mytilus* bottoms). In very exposed areas, the mechanical stress in the surf zone is too high for large, vagile

species like fish, and *Ruppia-Potamogeton* bottoms are absent as no sediment settles in the turbulent, shallow areas.

In general, the most populated bottom types are those dominated by *Mytilus* and the 'deep' soft bottoms. The total high abundance values for these 2 bottom types are almost exclusively due to the abundance of sand goby. The *Mytilus* bottoms in the area are often rocky and offer good shelter for black goby, eelpout and gunnel. It should be kept in mind, however, that this investigation concerns demersal fish and that pelagic species have not been considered. The *Fucus* belt is certainly the most diversified habitat due to its structure with hard or stony bottoms and broad to filamentous algal trunks. The highly diverse invertebrate fauna (e.g. Haage & Jansson 1970) should offer numerous niches to the fish. But the counts amounted to only half the number of individuals recorded on *Mytilus* bottoms. The typical fish fauna – pike, perch, sticklebacks, pipe-fish and other more actively swimming species – have been recorded but since it is difficult not to disturb the fish when looking for them in the dense *Fucus* vegetation the numbers are certainly underestimates.

Total abundance and biomass of fish

Comparison of the calculated abundance and biomass values of fish (Table 6) with values from other areas is difficult for at least 2 reasons. Firstly the differences in methods call for caution, secondly the differences in bottom types must be considered. Our mean values are based upon densities on a variety of bottoms ranging from 'pure', naked mud to heterogeneous, vegetation-covered bottoms. Most other studies of demersal fish distribution deal with only 1 type of substrate, a sandy bottom, a *Zostera* bed, a mudflat. Abundance values of an isolated study of a seagrass bed will tend to be greater than if the same study was only a part of an estimation of a larger and more heterogeneous area. With the census technique, however, where each fish is recorded even to its exact location on the bottom, it is possible to compute the abundance of each subarea.

Table 6 summarizes some quantitative investigations from other areas. In the temperate regime, the shallowest systems – soft bottoms shallower than ca 1 m – showed the highest mean numbers, up to 20.4 ind m⁻². Dominating species were *Pomatoschistus* spp. and sticklebacks. In our study the highest abundance, 23 ind m⁻², was recorded on soft bottoms deeper than 6 m (Fig. 8). The totally dominating species here was the sand goby. The highest average biomass values were recorded on the Swedish west

Table 6. Abundance and biomass of fish in some coastal systems. Values in italics are annual ranges, others are means. Values in parenthesis: biomass (g m^{-2} dry weight). In cases where the original figures were presented in wet weight, dry weight was calculated assuming it to be 20% of the wet weight. A: study carried out in all seasons; P: study carried out only during a restricted period of the year

Area	Fish fauna	Abundance (n m^{-2})	Biomass (g m^{-2} , dwt)	Source
Baltic Sea: Southern Bothnian Sea. Mud-sand with macrophytes Depth range 0–1.2 m	14 species caught. Sand, common and black goby, sticklebacks and minnow dominant	<i>1.5–12.3</i> 6	–	Thorman & Wiederholm 1983 (A)
Northern Baltic proper. Mud-sand with macrophytes. Depth less than 1 m	16 species caught. Mainly gobies and sticklebacks	<i>0–89</i> 15.7	<i>0–25</i> 0.9	Aneer & Nellbring 1977 (A)
Northern Baltic proper. Mud-sand with macrophytes. Depth less than 1 m	12 species. Mainly sand and common goby and sticklebacks	<i>0–89</i> 17.6	<i>0–5.3</i> 0.6	Nellbring (unpubl.) (A)
Northern Baltic proper. Archipelago with all types of bottoms from rocky to soft Depth range 0–20 m	33 species. Sand/Common goby dominant by number, flounder by biomass	<i>0.05–13.8</i> 2.1	<i>0.001–7.3</i> 1.5	This study (A)
Swedish west coast (North Sea) Silty clay with <i>Zostera</i> and <i>Ruppia</i> . Depth range 0.1–0.3 m	16 species. Mainly common goby, sticklebacks and eel	<i>0.2–109.7</i> 20.4	<i>0.01–10.56</i> 1.2	Thorman & Fladvad 1981 (A)
Swedish west coast. Sandy silt inside eelgrass beds. Depth range 0–0.7 m	Sand/Common goby and plaice	<i>0–25.7</i>	<i>0–0.7</i>	Pihl & Rosenberg 1982 (A)
Lake Grevelingen, North Sea. Shallow water and deeper channels. Depth range 0–>15 m	Sand goby and three-spined stickleback dominant by number, plaice by biomass	2.6	1.2	Doornbos 1982 (A)
Mustang Island, Texas Sand beach, surf area	47 species. Striped mullet dominant	–	<i>0.6–2.3</i>	McFarland 1963 (A)
Laguna Madre, Texas Sea grass beds	31 species. Striped mullet dominant, spot and anchovy	–	<i>0–6.55</i>	Hellier 1960 (A)
Narraganset Bay, Rhode Island	Winter flounder dominant	<i>0.01–0.05</i>	<i>0.36–1.25</i>	Oviatt & Nixon 1973 (A)
Rhode Island. Eelgrass in coastal pond and tidal river	Silverside dominant	4 resp. 12	0.04 resp. 0.4	Nixon & Oviatt 1972 (P)
Narraganset Bay, Rhode Island. Salt marsh	Common mummichog	<i>–>40</i>	<i>0.3–14</i>	Nixon & Oviatt 1973 (A)
Beaufort, North Carolina. Eelgrass beds	39 species. Pinfish dominant	<i>0.08–6.6</i> 2.1	<i>0.08–2.9</i> 1.5	Adams 1976 (A)
North Carolina. <i>Spartina</i> marsh ponds and Newport river estuary	Menhaden, pinfish and striped mullet dominant	0.82	1.2 resp. 0.3	Kjelson et al. 1973 (?)
Puget Sound. Nearshore sandflat	4 species of flounder	0.09 summer	1.5	Walton & Bartoo 1975 (P)
Guam, Mariana Islands. Coral reef	276 species <i>Cromis</i> sp. dominant	0.1 and 1.7 (means of 2 transects)	<i>0.06–3.4</i>	Jones & Chase 1975 (P)

coast, 3.4 g m^{-2} (dwt) on shallow soft bottoms. In our study the maximum mean biomass for a certain bottom type was found on *Mytilus* bottoms below ca 5 m depth where 3.4 g m^{-2} (dwt) was also recorded (Fig. 8).

Seagrass beds feature values of 2 to 12 ind m^{-2} and

0.04 to 1.5 g m^{-2} (dwt). Flatfish studies concentrated specifically on sandy substrates. The highest abundance amounted to 3.5 ind m^{-2} ; only biomass value recorded was 1.5 g m^{-2} (dwt).

In our study the only flatfish, the flounder, made up

Fig. 8. Mean number and biomass of fish associated with different bottom types in the 4 different grades of exposure. Classification of bottom types (I to IV) based on extensive material from large-scale stratified sampling program described in detail by Jansson & Kautsky (1977). Types I to IV are hard bottoms with the annual belt at the surface, dominated by the green alga *Cladophora glomerata* during summer, replaced by the red alga *Ceramium tenuicorne* during autumn and winter. Type V comprises shallow soft bottoms, VI deeper ones without macrovegetation

only 2.2 % of the total abundance of fish with a mean number of 0.05 ind m⁻². The biomass, however, amounted to 67.7 % of the total value of the area, with a mean value of 0.6 g m⁻² (dwt) (2.9 g wwt). Aneer et al. (1978) found a mean biomass (wwt) of 0.17 g m⁻² on soft bottoms at about 30 to 50 m depth in January. This emphasizes the generally small size of the fish typical for Baltic Sea bottoms.

For comparison, 1 example of a tropical system has been included in Table 6. The coral reefs of Guam do not show remarkably high abundances for this type of system. The highest densities were recorded on the seaward slopes of the reef with ca. 1.7 ind m⁻². The biomass, however, showed a maximum 3.4 g m⁻² (dwt) in the channel walls of the reef. However, the greatest difference between this tropical system and the temperate examples lies in the number of species. While the Baltic studies are based on some 30 species, and

the north American subtropical samples comprise ca 30 to 50 species, the coral-reef study yielded 276 species.

These comparisons should all be considered as reasonably quantitative, despite the difficulties involved in catching fish. They are certainly all underestimates. Our own values represent only the fish restricted to the sea bottom; abundances of pelagic and other mobile species are only vaguely suggested by the gill-net catches (Table 3). All in all, the Baltic fish fauna is surprisingly rich compared to seas with higher salinities. The sand goby is by far the most common species in terms of numbers, while the flounder totally dominates the annual average in terms of biomass. Current analyses are designated to reveal how this is reflected in the food web and energy-flow network.

Acknowledgements. We thank R. Elmgren and M. W. Kemp for constructive criticism of the manuscript. B. Mayerhofer prepared the figures and M. Moir corrected the English. This study was supported by Swedish Natural Science Research Council grant B-BU 2969-120.

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
- Aneer, G. (1975). Composition of food of the Baltic herring (*Clupea harengus* v. *membras* L.), fourhorn sculpin (*Myoxocephalus quadricornis* L.) and eel-pout (*Zoarces viviparus* L.) from deep soft bottom trawling in the Askö-Landsort area during two consecutive years. Merentutkimuslait. Julk./Havsforskningsinst. Skr. 239: 146–154
- Aneer, G., Nellbring, S. (1977). A drop-trap investigation of the abundance of fish in very shallow water in the Askö area, northern Baltic proper. In: Keegan, B. F., Ceidigh, P. O., Boaden, P. J. S. (ed.) Biology of benthic organisms. Pergamon Press, New York, p. 21–30
- Aneer, G., Lindquist, A., Westin, L. (1978). Winter concentrations of Baltic herring (*Clupea harengus* var. *membras* L.). Contr. Askö Lab., Univ. Stockholm 21: 1–19
- Ankar, S., Elmgren, R. (1976). The benthic macro- and meiofauna of the Askö-Landsort area (northern Baltic proper). A stratified random sampling survey. Contr. Askö Lab. Univ. Stockholm 11: 1–115
- Bagge, P., Ilus, E., Motzkin, F. (1975). Line census of fish made by the SCUBA diving method in the archipelago of Loviisa (Gulf of Finland). Merentutkimuslait. Julk./Havsforskningsinst. Skr. 240: 57–70
- Bopp, P. (1957). Verhaltenstudien an Meergrundeln (Gobiidae) in Gefangenschaft. Physiologia comp. Oecol. 4: 247–269
- Brock, V. E. (1954). A preliminary report on method of estimating reef fish populations. J. Wildl. Mgmt 18: 297–308
- Brock, V. E. (1982). A critique of the visual census method for assessing coral reef fish populations. Bull. mar. Sci. 32: 269–276
- Doornbos, G. (1982). Changes in the fish fauna of the former Grevelingen estuary, before and after the closure in 1971. Hydrobiol. Bull. 16: 279–283

- Elmgren, R., Rosenberg, R., Andersin, A.-B., Evans, S., Kangas, P., Lassig, J., Leppäkoski, E., Varmo, R. (1984). Benthic macro- and meiofauna in the Gulf of Bothnia (northern Baltic). *Finn. mar. Res.* 250: 3–18
- Evans, S., Tallmark, B. (1979). A modified drop-net method for sampling mobile epifauna on marine shallow sandy bottoms. *Holarctic Ecology* 2: 58–64
- Fonds, M. (1973). Sand gobies in the Dutch Wadden Sea (*Pomatoschistus*, Gobiidae, Pisces). *Neth. J. Sea Res.* 6: 417–478
- Haage, P., Jansson, B.-O. (1970). Quantitative investigations of the Baltic *Fucus* belt macrofauna. 1. Quantitative methods. *Ophelia* 8: 187–195
- Hällfors, G., Niemi, Å., Ackefors, H., Lassig, J., Leppäkoski, E. (1981). Biological oceanography. In: Voipio, E. (ed.). *The Baltic Sea*. Elsevier Publ. Co., Amsterdam, p. 219–274
- Hellier, T. R. (1960). Fish production and biomass studies in relation to photosynthesis in the Laguna Madre of Texas. *Publ. Inst. mar. Sci. Univ. Tex.* 8: 1–22
- Jansson, A.-M. (1973). Depth distribution and bottom types in the primary research area of the Askö Laboratory. Mimeographed report, Askö Laboratory
- Jansson, A.-M., Kautsky, N. (1977). A quantitative survey of hard bottom communities in a Baltic archipelago. In: Keegan, B. S., Ceidigh, P. O., Boaden, P. J. S. (ed.) *Biology of benthic organisms*. Pergamon Press, New York, p. 259–266
- Jansson, B.-O. (1972). Ecosystem approach to the Baltic problem. *Ecol. Bull., Stockholm* 16: 1–82
- Jones, R. S., Chase, J. A. (1975). Community structure and distribution of fishes in an enclosed high island lagoon in Guam. *Micronesica* 11: 127–148
- Kautsky, H., Widbom, B., Wulff, F. (1981). Vegetation, macrofauna and benthic meiofauna in the phytal zone of the archipelago of Luleå – Bothnian Bay. *Ophelia* 28: 53–77
- Kjelson, M. A., Johnson, G. N., Garner, R. L., Watson, J. D. (1973). Biomass and densities of the fish and macrovertebrates of the Newport River Estuary, North Carolina. In: Rice, T. R. (ed.) *Annual report to the Atomic Energy Commission*. National Marine Fisheries Service, Beaufort, N.C., p. 169–182
- Kristoffersson, R., Oikari, A. (1975). Notes on the biology of the eel-pout, *Zoarces viviparus* (L.), in the brackish water of Tvärminne, Gulf of Finland. *Ann. Zool. Fennici* 12: 143–147
- McFarland, W. N. (1963). Seasonal change in the number and the biomass of fishes from the surf at Mustang Island, Texas. *Publ. Inst. mar. Sci., Univ. Tex.* 9: 91–112
- Muus, B. (1957). The fauna of Danish estuaries and lagoons. *Meddr Kommn. Danm. Fisk.-og Havunders. (N.S.)* 5: 3–316
- Neuman, E. (1977). Activity and distribution of benthic fish in some Baltic archipelagoes with special reference to temperature. *Ambio Spec. Rep.* 5: 47–55
- Neuman, E. (1982). Species composition and seasonal migrations of the coastal fish fauna in the southern Bothnian Sea. In: Müller, K. (ed.) *Coastal research in the Gulf of Bothnia*. Dr. W. Junk Publ., The Hague, p. 317–353
- Nixon, S. W., Oviatt, C. A. (1972). Preliminary measurements of midsummer metabolism in beds of eelgrass, *Zostera marina*. *Ecology* 53: 150–157
- Nixon, S. W., Oviatt, C. A. (1973). Ecology of a New England salt marsh. *Ecol. Monogr.* 43: 463–498
- Ojaveer, E., Lindroth, A., Bagge, O., Lehtonen, H., Toivonen, J. (1981). Fishes and fisheries. In: Voipio, E. (ed.) *The Baltic Sea*. Elsevier Publ. Co., Amsterdam, p. 275–350
- Oviatt, C. A., Nixon, S. W. (1973). The demersal fish of Narragansett Bay: An analysis of community structure, distribution and abundance. *Estuar. coast. mar. Sci.* 1: 361–378
- 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
- Russell, B. C., Talbot, F. N., Anderson, G. R., Goldman, B. (1978). Collection and sampling of reef fishes. In: Stoddard, D. R., Johannes, R. E. (ed.) *Coral reefs: research methods*. Monographs on Oceanographic Methodology 5 UNESCO: 329–345
- Sanders, H. L. (1960). Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. *Limnol. Oceanogr.* 5: 138–153
- Sumari, O. (1963). The line diving method in the evaluation of fish populations (Finnish). *Luonnon Tutkija* 67: 40–47
- Thorman, S., Fladvad, B. (1981). Growth and production of fish in River Broälven estuary on the Swedish west coast. *Rep. Nat. Swedish Environ. Prot. Board PM 1416*: 1–112
- Thorman, S., Wiederholm, A.-M. (1983). Seasonal occurrence and food resource use of an assemblage of nearshore fish species in the Bothnian Sea, Sweden. *Mar. Ecol. Prog. Ser.* 10: 223–229
- Walton, J. M., Bartoo, N. W. (1976). Flatfish densities determined with a diver-operated flounder sampler. *J. Fish. Res. Bd Can.* 33: 2834–2836
- Zander, C. D. (1979). On the biology and food of small-sized fish from the North and Baltic Sea areas. II. Investigation of a shallow stony ground off Møn, Denmark. *Ophelia* 18: 179–190
- Zander, C. D., Hartwig, E. (1982). On the biology and food of small-sized fish from North and Baltic Sea area. IV. Investigations on an eulittoral mud flat at Sylt Island. *Helgoländer Meeresunters.* 35: 47–63

This paper was submitted to the editor; it was accepted for printing on January 20, 1985