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Variations in the fish community of the Øra Estuary, SE Norway, with emphasis on the freshwater fishes[1]

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The fish fauna in a part of the River Glomma estuary, the Øra estuary, in SE Norway was studied from April to September in 1973 and 1976, and until October in 1975. Analysis of the variations in the fish community by diversity indices showed significant correlation between species diversity H and salinity. A seasonal cycle in the fish community occurred, i.e. a shift from a marine to a freshwater community in spring and the reverse in autumn. Salinity, which in the study area is dependent on river discharge and northern winds, is the main factor acting on the occurrence of the freshwater fishes. The maximum salinity tolerance of the six common freshwater species was 10—12 ‰. Growth features suggest that *Leuciscus idus* (L.) and *Perca fluviatilis* L. are semidiadromous. The migration pattern of other freshwater species is briefly discussed.

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INTRODUCTION

A number of European freshwater fishes are known to occur in estuarine and brackish waters (Redeke 1922, Duncker 1960, Berg 1964, Wheeler 1969, Curry-Lindahl 1975). In the brackish Baltic Sea about 20 freshwater species are regularly present off southern Finland (Segerstråle 1957) and even in mixo-mesohaline areas off the Polish coast the abundance of several species allows commercial fishing (Romanski 1965). According to Henking (1923), Berg (1964) and Cala (1970) freshwater fishes in some localities are also known to have established populations migrating into brackish areas to feed during the summer and returning upstreams in the autumn, i.e. semidiadromous populations (sensu Shubnikov 1976). In southern Norway, where the greatest diversity in freshwater fishes is confined to the extreme southeastern part, the occurrence of 13 species in the estuaries of the rivers Glomma and Tista was noted by Collett (1902—1905). Information concerning population structure, salinity tolerance, abundance and seasonal variations in occurrence is scarce from Norwegian estuarine areas. However, during the period June 1972 to Oct. 1976 a concervation survey which included the fish fauna was undertaken in the Øra area, which forms part of the Glomma estuary.

[1] Contribution No. 152 from the Zoological Museum, University of Oslo.

This paper considers the survey results concerning variations in fish community structure with regard to the occurrence, salinity dependence and migration pattern of the freshwater fishes in the Øra area.

Reports on the life cycle and growth of the common goby *Pomatoschistus microps* (Kröyer) and on the growth and migration pattern of the roach *Rutilus rutilus* in the Øra area were given by Pethon (1975) and Hansen and Pethon (1977).

THE LOCALITY

The Øra area is situated at the eastern outlet of the river Glomma within the city borders of Fredrikstad (Fig. 1). The central shallow area with depths from 0.25—1.5 m is about 7 km^2 and is on the western side bordered by the deep navigable river channel and on the eastern side by the Tammern channel with depths of 12—24 m. Along the Øra promontory and southwards the wetland is at present reclaimed with mud from river dredgings undertaken in 1970—71 and serves as a large rubbish dump for the local communities. On the southern side of this area a small channel, 1.8 m deep, was constructed in 1975 in an attempt to partly restore the original river water dispersal current along the Øra promontory.

The yearly variations of discharge in the Glomma River and the salinity and water tem-

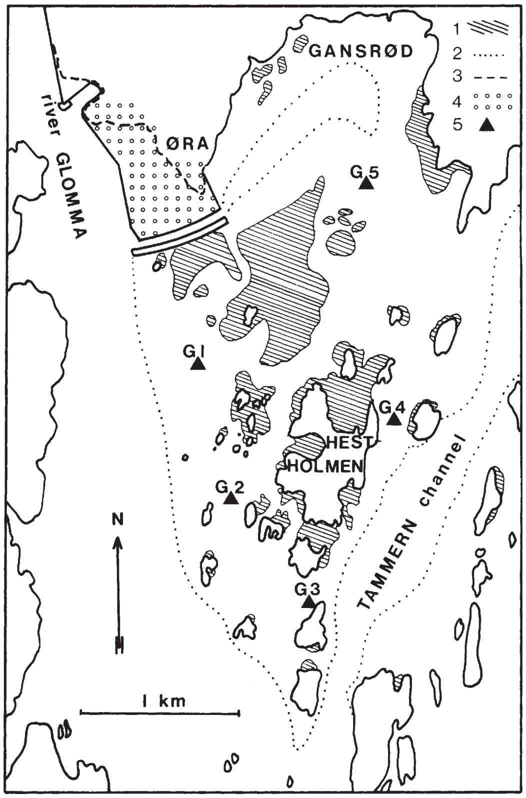


Fig. 1. The Øra estuary. 1: emergent vegetation, 2: 1.5 m depth contour, 3: the former shore line, 4: reclaimed area serving as rubbish dump, 5: fishing stations.

perature at Øra are given in Fig. 2. During calm weather conditions and a discharge of 500 m^3/s or more, a sharp halocline is present at 1.5—2 m depth. The seasonal change in salinity from ß-mesohaline conditions in summer to polyhaline in winter is mainly due to discharge variations, while short time, rapid increases in salinity are due to northern winds, causing upwelling of saline water from the Tammern channel. In contradiction to most other estuaries variations in salinity caused by the tide are negligible; summer tide averages only about 20 cm. Prior to the building of the artificial channel, the salinity of the surface water layer in the northern part was correlated with the river discharge and the strength and direction of the wind (Fig. 3). The eastwards current of river water through the artificial channel, averaging 13.8 m^3/s, has however been shown to reduce to some extent the wind induced increase in salinity in this northern part of the shallows (P. Pethon, Øra Survey Rep. 1976, unpubl.).

The distribution pattern of the emergent vegetation, *Phragmites communis* Trinius, *Scirpus maritimus* L. and *Scirpus tabernaemontani* Gmelin, is given in Fig. 1. The submerged vegetation of the shallows is dominated by *Ruppia* spp. Patches of *Fucus vesiculosus* L. are present in the eastern part close to the Tammern channel and patches of *Potamogeton perfoliatus* L. in the western part close to the river and the artifi-

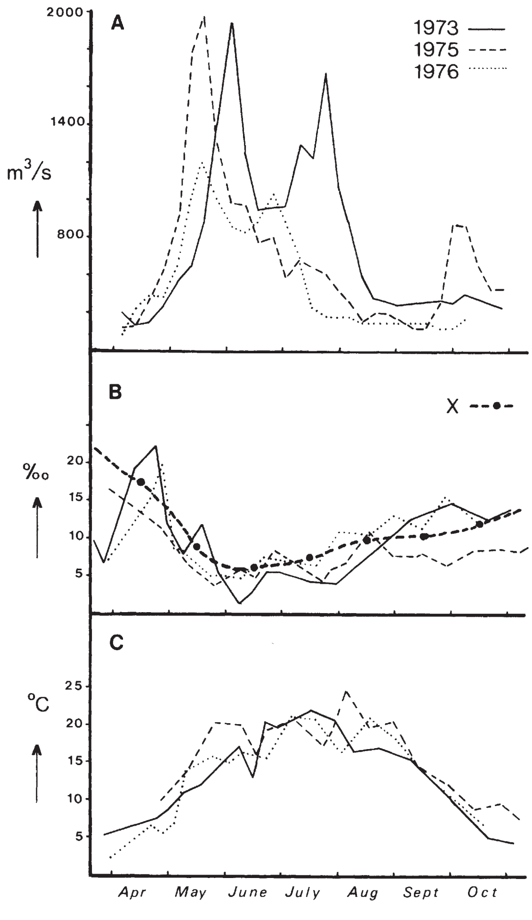


Fig. 2. River discharge (A), salinity (B) and water temperature (C) at Øra in 1973, 1975 and 1976. Salinity and temperature are given as averages of data from 27 hydrological stations. The teoretically calculated variations in salinity (x) based on long term data according to Fig. 3 are also given.

cial channel. Prior to the encroachments started in 1970, the shallows were densely populated by *Potamogeton perfoliatus,* which gradually disappeared due to the increasing and unstable salinity conditions after 1971.

The bottom substrate consists of firm clay with small amounts of fine gravel and organic debris. The diversity of the benthic fauna agrees closely to the «species minimum» discussed by Remane (1958), and only about 50 species have been recorded. The average density of macrofauna (1972—1976) retained on 0.5 mm sieve was 6 195 indiv./m^2, but the seasonal maximum in late autumn averages close to 20 000/m^2. *Nereis diversicolor* O.F. Müller, *Corophium volutator* (Pallas), *Neomysis integer* (Leach), *Hydrobia* spp. and *Potamopyrgus jenkinsii* (Smith) were the dominant species. The total benthic biomass was estimated to be 170 g wet weight/m^2.

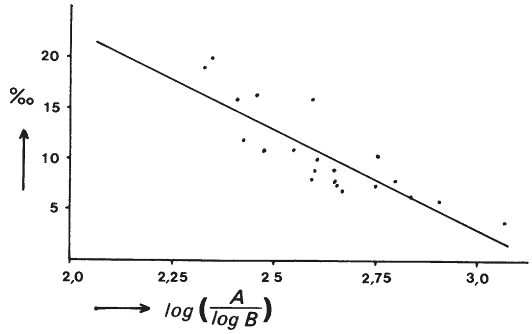


Fig. 3. Salinity (‰) in relation to river discharge (A) and northern winds (B). Line fits the equation $Y = 63.94 - 20.33\ X\ (P < 0.01)$. A: m^3/s, B: product of monthly no. of wind registrations and average force (Beaufort) in sector $270° < N \leqslant 90°$ relative to total sector (Data from H.R. Hovde, Øra Survey Rep. 1974, unpubl.)

Tab. 1. List of species recorded from gill net catches at Øra in 1973, 1975 and 1976. Salinity notes the maximum recorded for freshwater species and minimum for marine species.

Freshwater species	Total no. of specimens	Salinity (‰)
Trout *Salmo trutta* L.	10	Diadromous
Whitefish *Coregonus lavaretus* (L.)	97	Diadromous
Pike *Esox lucius* L.	2	10.5
Roach *Rutilus rutilus* (L.)	1455	11.5
Dace *Leuciscus leuciscus* (L.)	1008	10.9
Chub *Leuciscus cephalus* (L.)	1	8.3
Ide *Leuciscus idus* (L.)	2645	11.5
Rudd *Scardinius erythrophthalmus* (L.)	2	6.4
Bream *Abramis brama* (L.)	805	10.1
Perch *Perca fluviatilis* L.	1122	11.65
Pikeperch *Stizostedion lucioperca* (L.)	3	8.0
Ruffe *Acerina cernua* (L.)	628	11.5
Marine species		
Spur-dog *Squalus acanthias* L.	1	10.9
Herring *Clupea harengus* L.	41	4.5
Sprat *Sprattus sprattus* (L.)	140	4.25
Eel *Anguilla anguilla* (L.)	6	Diadromous
Garfish *Belone belone* (L.)	1	10.5
Hake *Merluccius merluccius* (L.)	3	8.5
Cod *Gadus morhua* L.	881	4.5
Haddock *Melanogrammus aeglefinus* (L.)	2	5.2
Whiting *Merlangius merlangus* (L.)	529	4.9
Blue Whiting *Micromesistius poutassou* (Risso)	1	4.5
Pollack *Pollachius pollachius* (L.)	1	7.2
Saithe *Pollachius virens* (L.)	3	16.0
Eelpout *Zoarces viviparus* (L.)	19	6.5
Grey Gurnard *Eutrigla gurnardus* (L.)	1	4.9
Brill *Scophthalmus rhombus* (L.)	1	7.65
Plaice *Pleuronectes platessa* L.	38	2.7
Flounder*Platichthys flesus* (L.)	1940	Diadromous
Sole *Solea solea* (L.)	5	4.35

MATERIAL AND METHODS

The material consists of 11 391 specimens of 30 species (Tab. 1). The fish were sampled with gill nets, and netting was carried out at five stations (Fig. 1) about every two weeks from late April to late September in 1973 and 1976, and until late October in 1975. Four nets of 39, 35, 32 and 22 mm mesh size, and 1.5 x 25 m overall size were used at each station. The station G1 was not sampled in 1973 and G4 not in 1976.

The extreme shallow water of the investigated area prevented using trawling gear, which is more suitable than gill nets due to its independence of fish activity. Abundance bias due to the catch size dependence of fish activity may thus be present. McErlean et al. (1973) stressed, however, that serial comparisons are perfectly justifiable as long as based on samples taken using one type of equipment.

The use of diversity indices was discussed by Pielou (1966), Wihlm (1967), Sanders (1968), McErlean et al. (1973) and others. In the present paper three indices are calculated; species richness $S = (s-1)/\ln N$ (Margalef 1951), species diversity $H = -\sum_{i=1}^{s} \frac{ni}{N} \log \frac{ni}{N}$ and eveness $J = H/\log s$ (Pielou 1966), where s is the number of species, n is the number of specimens of species i, and N is the total number of specimens. Since these indices are more strongly dependent on the number of species than the number of individuals errors due to abundance bias are assumed to be of minor importance.

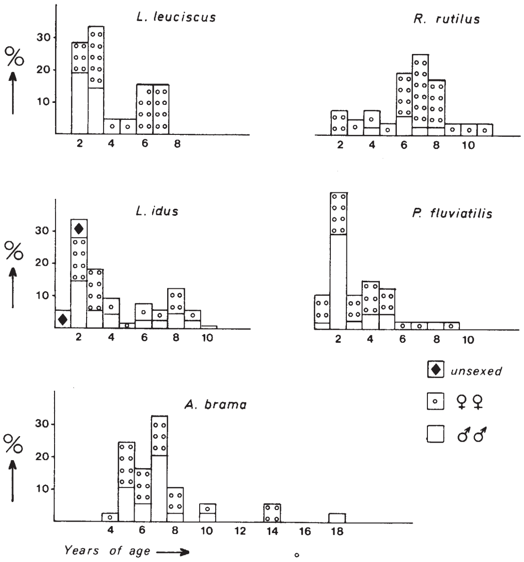


Fig. 4. Age- and sex distribution (%) of five freshwater species from Øra. Roach *Rutilus rutilus* data from Hansen & Pethon (1977).

In accordance with Hansen and Pethon (1977) an Hansen (1977) opercula were used for age determinations and back-calculations of growth. A linear correlation ($P < 0.01$) between fish length and operculum size was present in all three species investigated, viz. ide *Leuciscus idus*, bream *Abramis brama* and perch *Perca fluviatilis*. The calculated regression equations were: ide, $L = 17.31\,Op + 23.38$; bream, $L = 17.56\,Op + 2.78$; perch ♀♀, $L = 16.11\,Op + 22.55$; perch ♂♂, $L = 7.90\,Op + 29.66$; where L = total length in mm and Op = radius of operculum in mm.

Tab. 2. Yearly frequency distribution (%) of average catch of specimens per net night at Øra, and yearly indices of species richness S, species diversity H and eveness J.

Species	1973	1975	1976
Rutilus rutilus	5.7	12.2	20.8
Leuciscus leuciscus	3.9	12.2	9.9
Leuciscus idus	24.3	20.9	24.9
Abramis brama	10.4	4.9	6.1
Perca fluviatilis	7.4	9.9	12.3
Acerina cernua	4.9	7.0	4.3
Other freshwater spp.	0.1	0.1	0.1
Platichthys flesus	17.1	19.3	14.2
Other diadromous spp.	1.2	0.9	0.8
Gadus morhua	15.9	4.9	2.7
Merlangius merlangus	7.1	4.6	2.2
Other marine spp.	2.0	3.1	1.6
S	2.45	2.44	2.76
H	0.94	0.96	0.90
J	0.71	0.69	0.68

RESULTS

Twelve freshwater and 18 marine fish species were recorded from gill net catches in 1973, 1975 and 1976 (Tab. 1). However, only six freshwater and three marine species were commonly encountered.

The summarized catch statistics (Tab. 2) show that some yearly variation in relative abundance was present. Ide was the most stable and abundant species during the three years, while roach showed the most notable increase and cod

Tab. 3. Monthly variations in average catch of specimens per station night at Øra. Oct. data review 1975 only.

Species	April	May	June	July	Aug.	Sept.	Oct.
Rutilus rutilus	0.7	4.3	4.3	19.1	12.4	8.9	0
Leuciscus leuciscus	0.3	11.1	12.1	8.2	6.6	0.9	0.6
Leuciscus idus	3.0	20.4	19.8	27.2	19.2	8.7	2.0
Abramis brama	0	1.6	12.3	12.2	3.0	0.9	0
Perca fluviatilis	0	5.1	6.0	10.4	15.3	3.7	0
Acerina cernua	0.3	3.3	7.1	9.6	3.7	0	0
Other freshwater spp.	0.4	1.5	1.0	0.1	0.2	0.7	0.7
Gadus morhua	10.8	14.7	1.6	0.2	1.1	5.5	16.6
Merlangius merlangus	3.6	2.3	0.6	0.2	2.5	9.8	3.9
Platichthys flesus	13.6	8.4	14.7	15.5	11.6	10.3	10.4
Other marine spp.	5.8	0.7	0.2	0.7	2.4	3.7	0.4

Gadus morhua L. the most notable decrease in catch abundance. However, the small variations found in diversity indices calculated for years suggest that community structure and species richness were similar among the three investigation periods.

With exception of the youngest age groups, the freshwater species did not seem restricted to particular age or sex groups (Fig. 4). The lack of young dace *Leuciscus leuciscus* and roach was obviously due to their small size making them uncatchable. Young ide were rare and young bream were not recorded at all. A notable predominance of female roach in an upstream population (Hansen 1977) suggested female predominance, as is normal in this species.

Most mature individuals spawn up river, but spawning was recorded at Øra for smaller numbers of all six freshwater species regularly encountered. Fry of the freshwater species were not, however, caught in pushnet or fry traps (see Pethon 1975), nor were schools of fry observed during the investigation. This suggests that recruitment to the populations does not occur within the estuarine area.

The catches showed montly variations with an increase in relative abundance of the common freshwater species in spring and decrease in autumn, and the reverse in the marine species (Tab. 3). However, there were some differences among the freshwater species as dace was mainly taken during spring, bream during high summer and perch during late summer. The seasonal variations are reflected in the diversity indices calculated for months (Tab. 4) which show a recoursing pattern for the investigation periods. The species diversity index H, reflecting community structure, showed a spring increase and an autumnal decrease which compare to the abundance pattern of the freshwater species and appear to reveal their impact on the community. The species richness index S showed a peak in spring and a slight increase through the summer ending with a decline in late autumn. The spring peak coincides to the mixed species association in May when a shift from dominance of marine species to dominance of freshwater species took place. The gradual increase in the index throughout the summer reflects the increasing rate of accidental occurence of marine species and the notable decline in late autumn the disappearance of the freshwater species.

Most likely the seasonal variations in the occurrence of freshwater fishes and in diversity indices might be related to the variations of salinity or water temperature (Fig. 2), i.e. lowered salinity offers a tolerable habitat, or increase in temperature increases fish activity. On yearly

Tab. 4. Monthly variations in diversity indices. H: species diversity index, S: species richness index.

	Year	April	May	June	July	Aug.	Sept.	Oct.
H	1973	0.393	0.636	0.795	0.777	0.886	0.594	—
	1975	0.665	0.904	0.821	0.823	0.871	0.669	0.677
	1976	—	0.813	0.848	0.762	0.787	0.555	—
S	1973	0.59	1.74	1.51	1.53	2.45	1.97	—
	1975	1.72	2.32	1.39	1.57	1.66	2.52	1.54
	1976	—	1.77	1.60	1.59	2.20	1.07	—

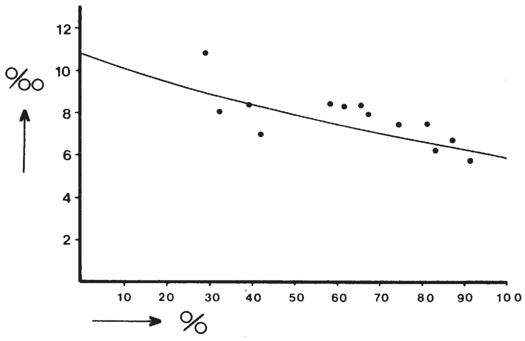


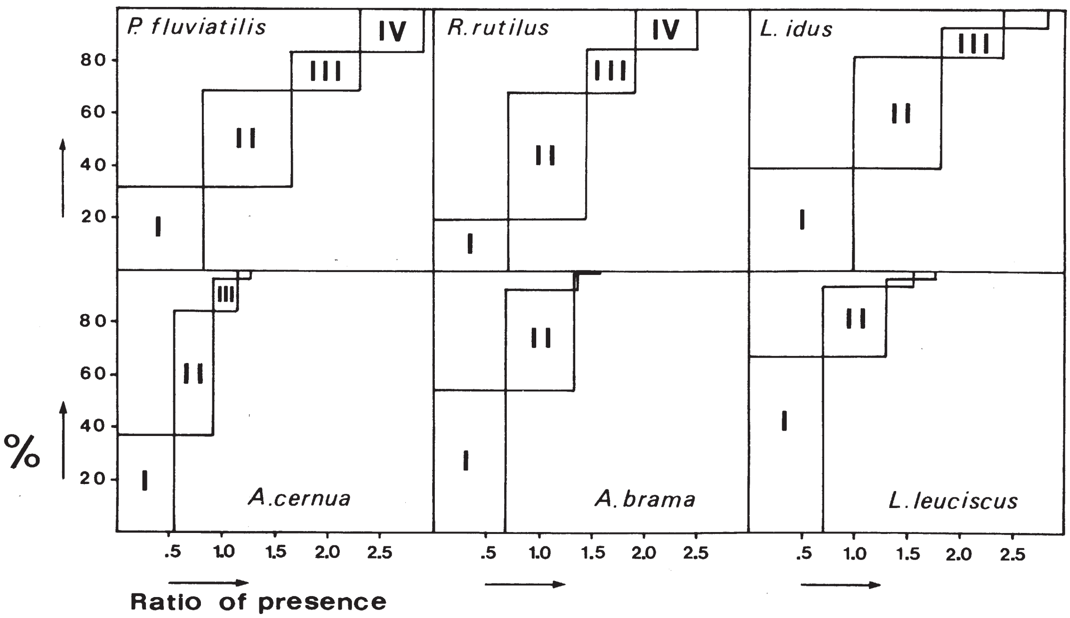
Fig. 5. The correlation between average salinity (‰) and the percentage of freshwater fishes in total catch, per station and year. Line fits the equation $Y = 10.81e^{-0.006x}$ ($P < 0.01$).

basis, however, regression analysis showed correlation ($P < 0.01$) between the percentage of freshwater fishes in the catch and average salinity (Fig. 5), but no correlation with temperature. This indicates that salinity is more important than temperature for the freshwater fishes of the Øra estuary. The frequency distribution of relative abundance and ratio of species occurrence in pooled salinity groups (Fig. 6) show the increased effect of higher salinities. Perch, roach and ide seem to be more tolerant to salinities in the 8—12 ‰ level than ruffe *Acerina cernua,* dace and bream. No freshwater species were caught in salinities above 12 ‰. The maximum salinities recorded for the freshwater species during this study are given in Table 1.

Fig. 6. The distribution of the common freshwater species in pooled salinity groupes (I: < 6 ‰, II: 6—8 ‰, III: 8—10 ‰, IV: 10—12 ‰).
Y-axis: cumulative frequency distribution (%) of average catch per net night,
X-axis: cumulative ratio of presence in the catch to total no. of catches.

The variations in diversity indices (Tab. 4) could not be correlated with water temperature. The species diversity index H was, however, correlated ($P < 0.01$) to salinity (Fig. 7) which suggests that the structure of the fish community at Øra is dependent on this parameter. An overall correlation between the species richness index S and salinity was not present, but these two parameters were correlated ($P < 0.01$) when confined to salinities above 7 ‰ (i.e. Y (= S) = —0.125 X(=‰) + 3.20). When these results are viewed together with those in Figs 2B and 6, and Tabs 1, 3 and 4, salinities of about 7 ‰ may be considered as the transition zone of freshwater and marine species maximizing species richness.

The back-calculated growth data of ide, bream and perch are given in Tab. 5. Consistent with Cala (1970) and Hansen (1977) no diffe-



Tab. 5. Average length (in mm) according to age of three freshwater species based on back-calculations of growth.

	Age in years													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Leuciscus idus (♂♂ + ♀♀)	87	123	178	226	260	288	308	328	348	357	364			
Abramis brama ♂♂ + ♀♀)	80	115	150	195	237	280	309	333	351	368	382	396	406	418
Perca fluviatilis ♂♂	62	131	200	232	249	263	281	299	320	329				
— « — ♀♀	60	118	174	234	282	299	310							

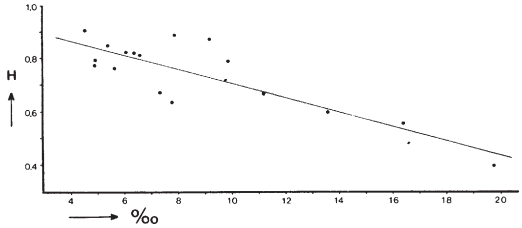


Fig. 7. The correlation between species diversity index H and salinity (‰). Pooled monthly data are used. Line fits the equation $Y = 0.973 - 0.027X$ ($P < 0.01$).

rence in growth of the sexes was found in ide and bream. Lee's phenomenon (see Ricker 1975, p. 215) was not detectable in either of the three species. The growth of ide and perch was more rapid than elsewhere in Norway, while that of bream closely resembled that of an upstream bream population (Hansen 1977). Comparison of the relative pattern of single growth zones showed close similarities both within and between the specimens examined of ide and perch, while bream showed 16% of growth zones irregularly dispersed and notably different (i.e. larger) from the «normal» pattern. The special growth pattern with a distinguished large growth zone during the last summer before capture, previously recorded for roach from the Øra area (Hansen and Pethon 1977) was not found in either of the three species.

DISCUSSION

The fish fauna in the Øra estuary resembles that of the coastal areas of the brackish Baltic Sea (Henking 1923, Romanski 1965, Gasowska 1962, Neumann 1974, Curry-Lindahl 1975). It also largely agrees with that previously described from Øra by Collett (1902—05), who stated that perch, roach, dace and ide were numerous. However, Collett (1902—05) also noted pike *Esox lucius,* pikeperch *Stizostedion lucioperca,* bream, smelt *Osmerus eperlanus,* bleak *Alburnus alburnus* and chub *Leuciscus cephalus* as common, but now only bream was encountered in any numbers.

In river estuaries the species composition is dependent not only on the environmental conditions within the estuary, but also on the species composition of the adjacent marine and lacustrine habitats. The lacustrine fauna about 15 km upsteam Øra is dominated by roach, bream, white bream *Blicca bjoerkna* and perch, while ide, dace and ruffe are rare (Halvorsen 1968, Borgstrøm et al. 1974). Some of the species as pike, white bream and smelt are common in brackish water elsewhere. The structural difference between the lacustrine fish fauna upstream and that at Øra, however, indicates that the exchange of freshwater fishes between far upstream areas and Øra is small.

Within the Øra area recruitment to the freshwater fish populations does not take place in spite of limited spawning in all the six common species. Experimental results on the impact of salinity on the development of eggs, embryos, larvae and young fish of salmonids, bream and pikeperch (Oliphan 1940, Conte 1969, Nesterenko 1976) have revealed that even low salinities (i.e. 3—4‰) have a toxic effect on larval stages causing 100% mortality in few days. Developing eggs and embryos are, however, more tolerant (up to 10‰) and influence of salinity on young fish is size dependent, i.e. survival rate increases rapidly with age/growth. The sensitivity of larvae to salinity is therefore suggested as the cause of lack of recruitment among the freshwater species from the Øra area.

The monthly variations present in the fish community at Øra are interpreted as a seasonal cyclicity. A regular cyclic pattern of variation in estuarine fish communities has been reported from U.S.A. (Dahlberg and Odum 1970, McErlean et al. 1973). In these North American estuaries, however, freshwater species were rare, and the cyclicity was caused by the migration pattern of various marine species. At Øra this cyclicity was time variable and salinity dependent. A shift took place in spring from a «marine» community dominated by three species, cod, whiting *Merlangius merlangus* and flounder *Platichthys flesus,* to a «freshwater» community dominanted by seven species, bream, ide, roach, dace, ruffe, perch and flounder. Throughout the summer this community characterized the area, although with a slight increase of accidentally occuring marine species until the autumn when the reverse shift took place. During the time of shift in spring and autumn species richness is maximized.

Salinity as a limiting factor for animal populations and species diversity has been discussed by Remane (1958) and Gunther (1961), while statements regarding salinity as a negligible factor were given by Allee et al. (1949) and Hela and Laevastu (1961). As far as freshwater fish are concerned, however, it is obvious from reviews by Kinne (1956), Black (1957), Conte (1969) and Halliday (1971) that the salinity level has a great impact on the fishes' salt and ion balance and on their oxygen uptake. Salinities below 8 ‰ did not seem to have a critical impact on the freshwater fishes at Øra, but at 8—12 ‰ an increasing effect was evident. Salinities above 12 ‰ seemed to exceed the natural tolerance level for these species. This result agrees with the overall salinity tolerance of 8 ‰ given by Remane (1958), experimental results on roach and perch showing exponential decrease in hours of survival with increasing salinity (Herbert and Mann 1958), and the 8.7 ‰ level stated by Schmitz (1956) to be harmless to cyprinids. Schmitz' balance disturbance experiments suggest, however, higher and species specific short time salinity tolerance, which the presented results substantiate.

The difference in salinity level may also explain the apparent contradiction between the results of Neumann (1974) and the present paper, since the salinity in Neumann's study area was stable and below 8 ‰ and thus most probably of minor importance.

During autumn the salinity at Øra increases and averages in winter close to 20‰, which is considered osmoregulatory fatal to the freshwater species in question. Thus only those migrating back to the river proper will survive. The regular occurrence of six freshwater species in the Øra estuary during summer suggests that these species populations are semidiadromous. Populations of semidiadromous, non-salmonid freshwater species have been reported by Henking (1923), Berg (1964), Cala (1970) and Shubnikov (1976), but are previously unknown from Norway. Hansen and Pethon (1977), however, concluded on the basis of the yearly growth pattern that the roach population at Øra was not semidiadromous, and that almost the entire summer population perished in the autumn.

The ide and perch at Øra showed an overall growth increase which was far better than reported from lacustrine and brackish habitats elsewhere (Huitfeldt-Kaas 1927, Segerstråle 1933, 1950, Jensen 1968, Wheeler 1969). Their yearly growth patterns were of normal type and different from the roach pattern, i.e. a noteably large last summer zone was absent in all individuals of the two species. The rapid growth suggests that ide and perch are regular migrants to the estuary where the food supply is plentiful, i.e. they may be considered as semidiadromous. However, the overall growth increase of ide was less than that of the semidiadromous ide population studied by Cala (1970). The bream on the other hand showed an overall growth rate closely resembling that of the upstream population reported by Hansen (1977), but individuals exhibit fairly large and irregular variations in summer growth pattern. One, rarely two, irregularly age dispersed large summer zones were present, and this pattern differs both from the even pattern of ide and perch and from the constantly large last summer zone pattern of roach. This indicates that the summer population of bream in the estuary consists of accidental migrants from the river. Growth features suggest that some return up river, but occasional findings of dead bream by local fishermen in the autumn show that not all individuals do.

The growth patterns of dace and ruffe were not examined. However, large sized specimens regularly occur at Øra. Some of these have been age determined and found to be rapidly growing, which may indicate that these species are also semidiadromous rather than accidental guests from the river population.

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