DOMINATING SUBLITTORAL FISH SPECIES IN A WEST NORWEGIAN FJORD AND THEIR TROPHIC LINKS TO COD (*GADUS MORHUA* L.)

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The fish fauna in the sublittoral habitat of Masfjorden, western Norway, has been studied in order to reveal survival and growth prospects of released juvenile cod in a large-scale stock enhancement experiment. Seasonal changes in abundance of dominating fish species and in the diet of potential competitors and predators to juvenile cod were emphasized. A total of 44 species from 17 families of Teleostei and 4 families of Chondrichthyes were recorded at 5–20 m depth of the sublittoral of Masfjorden. Gadids were dominating (50.2 % by numbers, 10 species) and saithe (*Pollachius virens*), pollack (*P. pollachius*), poor-cod (*Trisopterus minutus*) and cod (*Gadus morhua*) were most numerous. Labrids form a second dominating family (44.7 % by numbers, 5 species) of which *Centrolabrus exoletus*, *Ctenolabrus rupestris*, *Labrus bimaculatus* and *L. bergylta* were the most abundant. Pollack and saithe had highest abundance during summer and autumn. The labrids and poor-cod had maximum abundance in summer. All labrids, pollack and saithe showed minimum abundance in winter while poor-cod had lowest abundance in spring and highest in summer. Dietary studies showed that gobies were one of the major preys for small individuals of cod, pollack, saithe and poor-cod in the summer and autumn. Gadids and labrids were important prey for large cod and pollack.

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INTRODUCTION

Most investigations on fish in Norwegian fjords have been faunistic (TAMBS-LYCHE 1954, 1987), or have focused on a few species, mostly of commercial significance, (e.g. LØVERSEN 1946; DANNEVIG 1959; RUUD 1968; DENSTADLID 1972; LOPEZ 1979; GJØSÆTER 1973, 1981; GODØ & al. 1989). However, some ecosystem-oriented studies have also been conducted (RUUD 1968; DAHL & al. 1973; PEARCY & al. 1979; FALK-PETERSEN & HOPKINS 1981; HOP & al. 1992). A comprehensive ecosystem study including investigations of pelagic and sublittoral habitats has been going on in a west Norwegian fjord (Masfjorden) since 1985 (SALVANES 1986a, b; KAARTVEDT & al. 1988; AKSNES & al. 1989; GISKE & al. 1990; FOSSÅ 1991; GISKE & al. 1991; MARTINUSSEN 1991; NORDEIDE & SALVANES 1991; NORDEIDE & FOSSÅ 1992; SALVANES & ULLTANG 1992; SALVANES & al. 1992; BALIÑO & AKSNES 1993). The principal aim of this study is to investigate the potential for increasing cod production through large-scale juvenile releases. Basic information about the fish fauna in the sublittoral and their trophic links to cod is therefore required. In this paper we 1) identify the dominating fish species in the sublittoral habitat of Masfjorden, 2) investigate seasonal changes in the fish fauna and 3) study seasonal changes in the diet of potential competitors and predators to juvenile cod in order to reveal survival and growth prospects of released juvenile cod.

MATERIAL AND METHODS

Study site

Masfjorden is separated from Fensfjorden by a 75 m deep sill at the mouth (Fig. 1) through which it is connected with the Norwegian coastal current (AKSNES & al. 1989). The fjord is approximately 22 km long and 0.3–1.5 km wide with a maximum depth of about 500 m. The 70 km long shoreline alternates between rocky and steep sections and shallow bays. The macrovegetation consists of relatively continuous distributions of *Fucus* spp. and patchy distributions of *Laminaria* spp. (FJELDSTAD 1990).

Masfjorden is a typical northern temperate fjord, and temperatures at 0 and 5 m depths are low during the winter (about 4 °C), but higher in the summer (14–16 °C) (FOSSÅ & al. 1993). The watermasses are stratified into brackish water (0–3 m), intermediate layer (3–75 m depth) and deep water (below sill depth: > 75 m) (AKSNES & al. 1989). The hydrographical conditions in the intermediate layer (3–75 m depth) are dynamic, and changes in the Norwegian coastal current rapidly propagate through Fensfjorden into Masfjorden.

Sampling

The fish fauna was sampled by experimental net groups set on the bottom of the sublittoral during four nights each month at depths 5–20 m from October 1985 through September 1987, a period before any large-scale juvenile
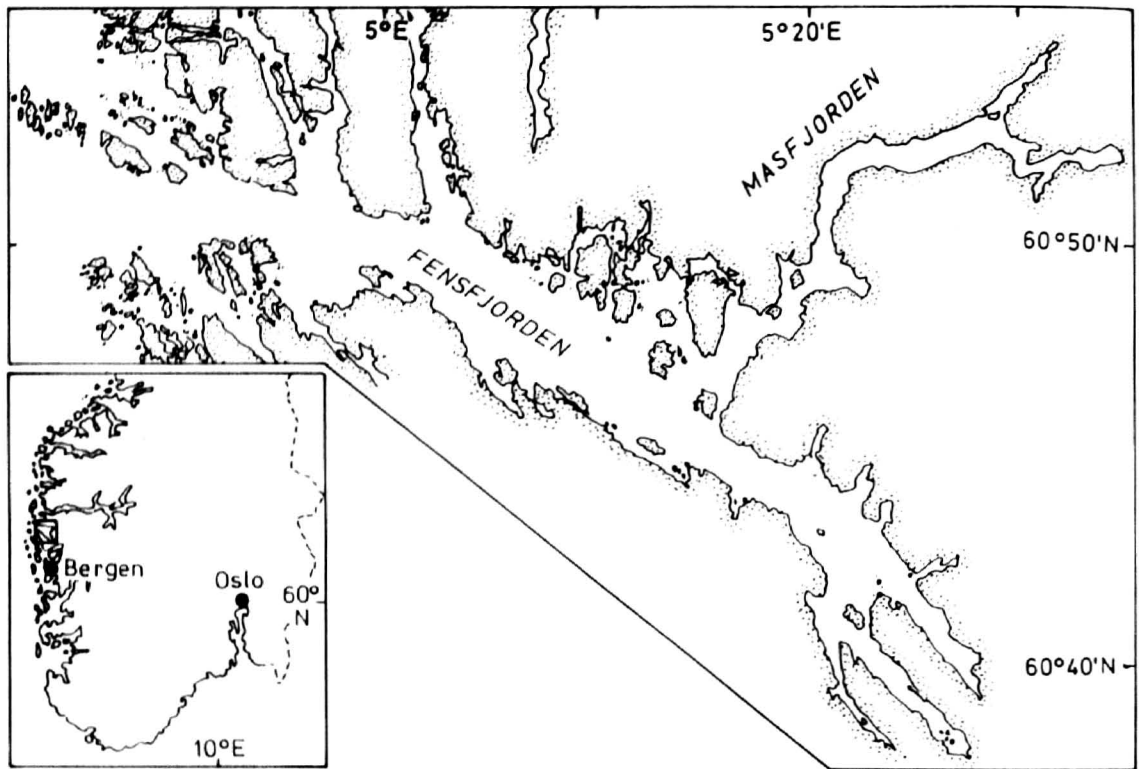
Fig. 1. Map of Masfjorden.

cod releases were made. The net groups consisted of one type of gillnet (25 × 1.5 m, 39 mm stretched mesh) and two types of trammel-nets (SALVANES 1991). The trammel-nets were 21 × 2 m and 28 × 2 m, and had 45 and 70 mm stretched meshes in the inside net, respectively. Both nets had 261 mm stretched mesh in the outside nets. Each net group was set on the bottom and fished about 15 hours before hauling, always including the night.

The experimental net-groups sampled 1-group and older cod approximately nonselectively from winter and onwards (SALVANES 1991a, b). The selectivity of the net groups towards other species sampled have unfortunately not been investigated, although we may expect selective sampling particularly for smaller individuals of each species, but also species with a slim body-shape as well as those remaining small the entire life span (e.g., gobies, FOSSÅ 1991). These fish sizes would be underrepresented or absent from our experimental net group samples. Hence, the obtained abundance indices should be considered as minimum estimates for species which were represented in the net group samples.

The net groups were randomly distributed in the fjord after locations topographically unfavorable for net sampling were excluded. The obtained data were pooled and stratified by season (winter: January–March, 110 settings; spring: April–June, 108 settings; summer: July–September, 120 settings and autumn: October–December, 107 settings). The captured fish were preserved on ice just after hauling until further processing within the same day. Catch in numbers of all species was recorded, and total length (cm) and weight (g) of individuals were measured.

The stomachs from cod, pollack, saithe and poor-cod were preserved in 6 % neutralized formaldehyde. The stomach contents were identified to lowest possible taxon. For each group wet weight and number of individuals were recorded. Weighing was done to nearest mg after blotting with paper tissue. Emphasis was put on comparing weight % of various prey groups (pooled prey sizes) of predator length groups 15–25 cm (I), 26–45 cm (II) and > 45 cm (III). The numbers of analyzed stomachs are given in Fig. 3. Consumption of fish is often underestimated because they are generally digested at higher rates than e.g. crustaceans (HYSLOP 1980). We have not adjusted for digestibility of different prey, and the importance of fish in the diet should therefore be considered as minimum estimates.

Similarities in diet

The diets of the dominating gadids were studied for similarities. Detrended Correspondence Analysis (DCA) (JONGMAN & al. 1987; TER BRAAK 1988) was applied on data sets pooled over seasons. Weight % of various prey groups (pooled prey sizes) of predator length groups 15–25 cm (I), 26–45 cm (II) and > 45 cm (III), were input to DCA. Prey groups with weight % < 0.01 were considered incidental and excluded from DCA.

The DCA technique organizes information into points in a multidimensional space by second-order polynomial 'detrending' (JONGMAN & al. 1987; TER BRAAK 1988). The use of DCA is founded on the assumption that species are distributed normally with a range of about 4 standard

deviations (SD) along eigenvectors (axes) in a multidimensional space (JONGMAN & al. 1987). Points in space refer to scores on the eigenvectors in multiples of the SD's. In our study closely located points correspond to similar diets while points far apart represent dissimilar diet. Maximum dispersion of species scores along each eigenvector is represented by the eigenvalue (λ_i). The most important axis has the highest eigenvalue. If the eigenvalue exceeds 0.5, the corresponding axis is often interpreted as an ecological gradient (JONGMAN & al. 1987). As diet similarity values would depend strictly on the level of aggregation of prey, absolute values may not be used to compare diet similarities unless the comparisons are made between indices originating from the same type of grouping. The same type of prey grouping were used for all predator groups in our analysis.

As abundance indices of the prey were not available for our analysis, we have chosen the widely used symmetrically modified MACARTHUR & LEVINS (1967) competition index proposed by PIANKA (1974) to calculate the degree of intra- and interspecific niche overlap between predator groups each season:

$$\alpha_{jk} = \alpha_{kj} = \frac{\sum\limits_{i=1}^{n} p_{ij} \cdot p_{ik}}{\sqrt{\sum\limits_{i=1}^{n} p_{ij}^2 \cdot \sum\limits_{i=1}^{n} p_{ik}^2}}$$

where p_{ij} and p_{ik} are the weight percentages of the i'th prey group in the stomach content of predator groups j and k and $\alpha_{jk} = \alpha_{kj}$ is the dietary overlap between predator groups j and k. We apply the index as a measure of overlap in resource use, not as a measure of competition. The overlap indices ranges from 0 (no overlap) to 1 (all prey groups are found in equal proportions in the diet of both predator j and k). The degree of pooling the prey data before the calculations are done, influences both the absolute values of the index and the significance value of statistical tests when predator groups are compared. High degree of pooling gives a high index and p-value. Since the outcome of the test is determined by how the data sets are pooled, we do not present results from statistical tests. We distributed the results according to three levels of overlap [low overlap: $\alpha_{jk} \leq 0.3$; moderate overlap: $0.3 < \alpha_{jk} \leq 0.6$; high overlap: $\alpha_{jk} > 0.6$].

RESULTS

Fish fauna composition

A total of 44 species from 17 families of Teleostei and 4 families of Chondrichthyes were recorded (Table 1). The gadid family was dominating (50.2 % by numbers, 10 species). In this family saithe, pollack, poor-cod and cod were most numerous. Labrids was a second dominating family (44.7 % by numbers, 5 species) of which Centrolabrus exoletus, Ctenolabrus rupestris, Labrus bimaculatus and L. bergylta were the most abundant.

Seasonal changes in the fish fauna

Seasonal changes in species composition are indicated in Table 1. The total number of individuals and the total number of species were highest during summer (38 species, 8103 individuals per 100 net group settings) and lowest during winter (29 species, 1498 individuals per 100 net group settings). The pollack and saithe had highest abundance during summer and autumn. The four dominating labrids and the poor-cod had maximum abundance in the summer. All labrids, pollack and saithe showed minimum abundance in winter, while poor-cod had lowest abundance in spring. The cod had higher abundance in autumn and winter than in summer and spring.

General diet of dominating gadids

A total of 115 prey taxa were distinguished in the diet of the four dominating gadids. Cod consumed 88 taxa, pollack 71 taxa, saithe 34 taxa and poor-cod 60 taxa (Appendix 1). Typical prey consumed by cod were those associated to the benthic of the sublittoral habitat (in the following referred to as benthic prey). The most important cod prey were gobies, labrids and gadids, large benthic crustaceans such as Galathea spp., Carcinus maenas (L.), Hyas spp. and Polychaeta. Poor-cod also consumed mostly benthic prey such as gobies, polychaets and benthic crustaceans. Pollack, however, included both the typical benthic prey and prey normally inhabiting the pelagic habitat: Maurolicus muelleri (GMELIN), Sprattus sprattus (L.), Micromesistius poutassou, Calanus finmarchicus (GUNNERUS) and Euphausiacea. The saithe was even a more pronounced pelagic feeder as the pelagic crustaceans Calanus finmarchicus and Euphausiacea, and the pelagic fishes Maurolicus muelleri and Sprattus sprattus were eaten in even larger proportions, whereas the benthic prey such as Polychaeta and gobies were eaten less frequently.

Diet similarities between size groups

The DCA technique applied to the 54 most common taxa (all seasons pooled) stratified by predator length groups, indicates diet similarities between some predator groups and differences between others. For stomach content analysis it is not routinely possible to identify all prey to the same taxonomic level because of differences in stage of digestion. If all prey types were equal digestible, one could redistribute prey identified to higher taxa according to the fractions of the identifiable prey, and thus remove some potential bias from the results. As we have no information on the digestibility of the various prey for the gadids studied, we have not in this analysis redistributed aggregated prey taxa. We presume that this does not severely bias the output from DCA because the number of aggregated prey taxons are few compared with total number of taxa included in DCA.

Table 1. Catch in numbers per 100 experimental net group settings (U) and average individual weight (w) stratified by season for fish species caught in Masfjorden from October 1985 through September 1987. Nomenclature according to WHITEHEAD & al. (1986). Weight range refors to pooled seasons. *means not available.

Taxonomic group	Winter U	w (g)	Spring U	w (g)	Summer U	w (g)	Autumn U	w (g)	Weight range (g)
SCYLIORHINIDAE									
Galeus melastomus RAFINESQUE	0		0		1	470	11	474	275–640
Scyliorhinus sp.	0		0		0		8	478	234–830
SQUALIDAE									
Squalus achantias L.	2	2200	3	4148	12	2372	25	2454	860–6800
RAJIDAE									
Raje clavata L.	0		0		6	2900	1	2450	630–4900
Raja radiata DONOVAN	0		0		0		1	1360	*
CHIMAERIDAE									
Chimaera monstrosa L.	0		1	1610	0		0		*
CLUPEIDAE									
Clupea harengus L.	0		4	158	1	55	1	*	55–175
SALMONIDAE									
Salmo spp.	23		5		19		11		
ANGUILLIDAE									
Anguilla anguilla (L.)	0		0		3	*	1	*	*
MERLUCIIDAE									
Merluccius merluccius (L.)	0		0		2	635	6	422	210–770
GADIDAE									
Brosme brosme (ASCANIUS)	1	1290	0		2	1045	2	1720	960–2200
Ciliata mustela (L.)	1		0		0		0		*
Gadus morhua L.	259	621	197	601	201	574	332	641	15–10100
Merlangius merlangus (L.)	5	294	6	302	22	355	33	448	42–1160
Melanogrammus aeglefinus (L.)	18	910	10	697	10	641	17	692	74–2980
Molva molva (L.)	12	1012	3	1105	8	583	12	880	115–3474
Pollachius pollachius (L.)	195	371	377	224	529	326	521	344	15–2955
Pollachius virens (L.)	390	244	531	348	843	223	1523	357	25–2220
Raniceps raninus (L.)	1	230	5	128	3	185	3	218	96–305
Trisopterus minutus (L.)	325	70	271	64	1057	62	827	76	9–290
CARANGIDAE									
Trachurus trachurus (L.)	0		0		1		5	397	345–495
LABRIDAE									
Centrolabrus exoletus (L.)	6	44	248	40	1481	43	99	41	20–140
Ctenolabrus rupestris (L.)	14	43	125	39	723	42	234	40	10–111
Labrus bergylta ASCANIUS	67	537	208	343	1087	308	395	426	25–1880
Labrus bimaculatus L.	45	127	496	91	1463	89	401	116	21–500
Symphodus melops (L.)	4	66	43	55	408	72	61	66	20–210
SCOMBRIDAE									
Scomber scombrus L.	0		0		2	585	7	308	130–610
CALLIONYMIDAE									
Callionymus lyra L.	0		2	81	1	75	2	*	60–102
ANARHICHADIDAE									
Anarhichas lupus L.	4	*	5	4250	3	3258	0		1015–5500
SCORPAENIDAE									
Sebastes viviparus KRØYER	6	164	0		8	185	0		70–265
TRIGLIDAE									
Eutrigla gurnardus (L.)	0		25	264	25	237	2	345	115–350
COTTIDAE									
Myoxocephalus scorpius (L.)	13	90	10	121	13	81	20	114	20–465
Taurulus bubalis (EUPHRASEN)	6	49	1	30	8	60	14	46	18–125
Taurulus liljeborgi COLLETT	0		1	56	1	390	0		56–390
CYCLOPTERIDAE									
Cyclopterus lumpus L.	5	1976	6	*	3	1361	0		555–3625
SCOPHTHALMIDAE									
Lepidorhombus whiffiagonis (WALBAUM)	12	173	6	157	13	263	7	263	16–440
Phrynorhombus norvegicus (GÜNTER)	1	*	0		1	40	3	17	1–40
Zeugopterus punctatus (BLOCH)	0		2	108	4	79	1	63	20–195
PLEURONECTIDAE									
Hippoglossoides platessoides (FABRICIUS)	5	112	4	235	3	257	0		15–580

Taxonomic group	Winter U	w (g)	Spring U	w (g)	Summer U	w (g)	Autumn U	w (g)	Weight range (g)
Limanda limanda (L.)	11	416	1	210	0		1	*	180–640
Microstomus kitt (WALBAUM)	43	305	173	321	109	253	34	326	28–1135
Platichthys flesus (L.)	14	451	10	470	20	441	10	503	65–870
Pleuronectes platessa L.	13	774	18	991	12	1126	7	1580	40–2942
LOPHIIDAE									
Lophius piscatorius L.	1	*	0		0		3	*	11500–18150
Total number individuals	1498		2796		8103		4638		
Total number species	29		31		38		37		

Ordination axes 1 and 2 explain about 78 % of the variation in the diet. Estimated eigenvalues are: $\lambda_1 = 0.580$, $\lambda_2 = 0.345$ and $\lambda_3 = 0.261$, of which axis 1 indicates some kind of gradient as $\lambda_1 > 0.5$. Cod I and pollack I have scores to the left on axis 1, cod II and pollack II in the middle and cod III and pollack III to the right (Fig. 2A). This result suggests that axis 1 reflects a size gradient for cod and pollack. Whether the apparent gradient strictly reflects a prey size gradient is, however, uncertain as prey size groups were not explicitly expressed in the DCA analysis. Nevertheless, we can distinguish

prey types having the possibility of growing large to the right on Fig. 2B (e.g., labrids, gadids and large crustaceans), whereas many, although not all, prey remaining small during their entire life span (e.g., copepods, polychaets, gobies) have scores to the left on Fig. 2B.

Highest similarities in diet are shown among the different saithe size groups, which all have scores to the left on Fig. 2A. The scores for pollack I, poor-cod I and cod I are also close to scores for the saithe groups, most probably reflecting consumption of small prey. The diets of cod I and II and
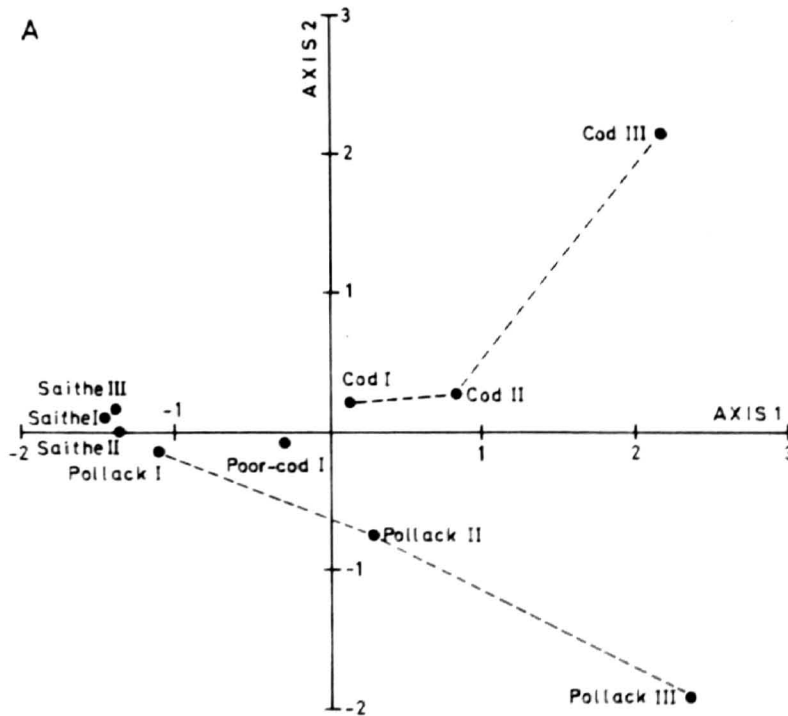

Fig. 2. Predator (A) and prey (B) (see next page) scores (in units of SD) along the two first ordination axes resulting from Detrended Correspondence Analysis of stomach content data of three predator length groups (I:15–25 cm, II: 26–45 cm, III: > 45 cm) of cod, pollack and saithe, and one length group (I: 15–25 cm) of poor-cod. Stomach data sets are pooled from October 1985 through September 1987. Prey size groups are pooled. Note that *G. flavescens* refers to *Gobiusculus flavescens*.
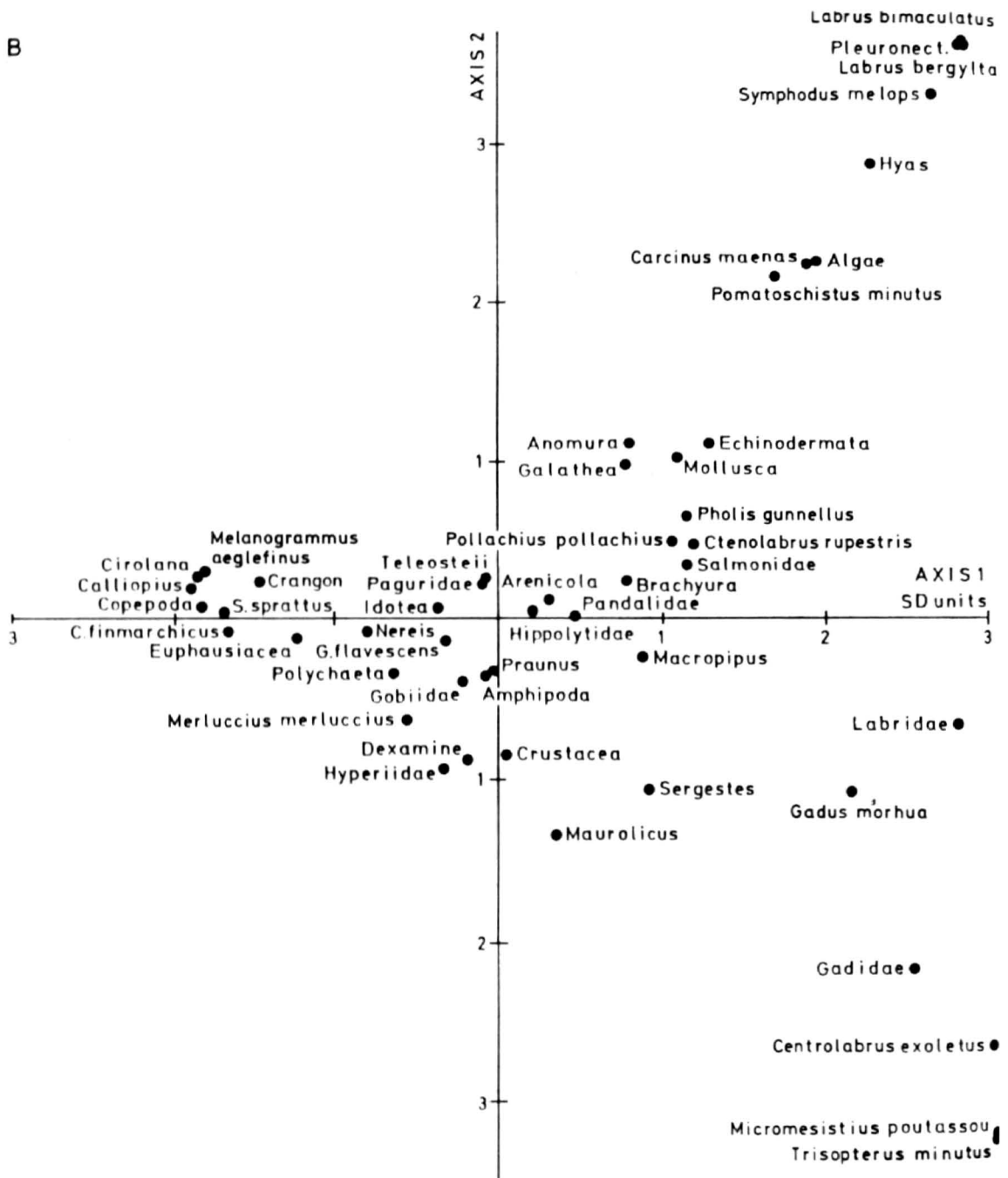
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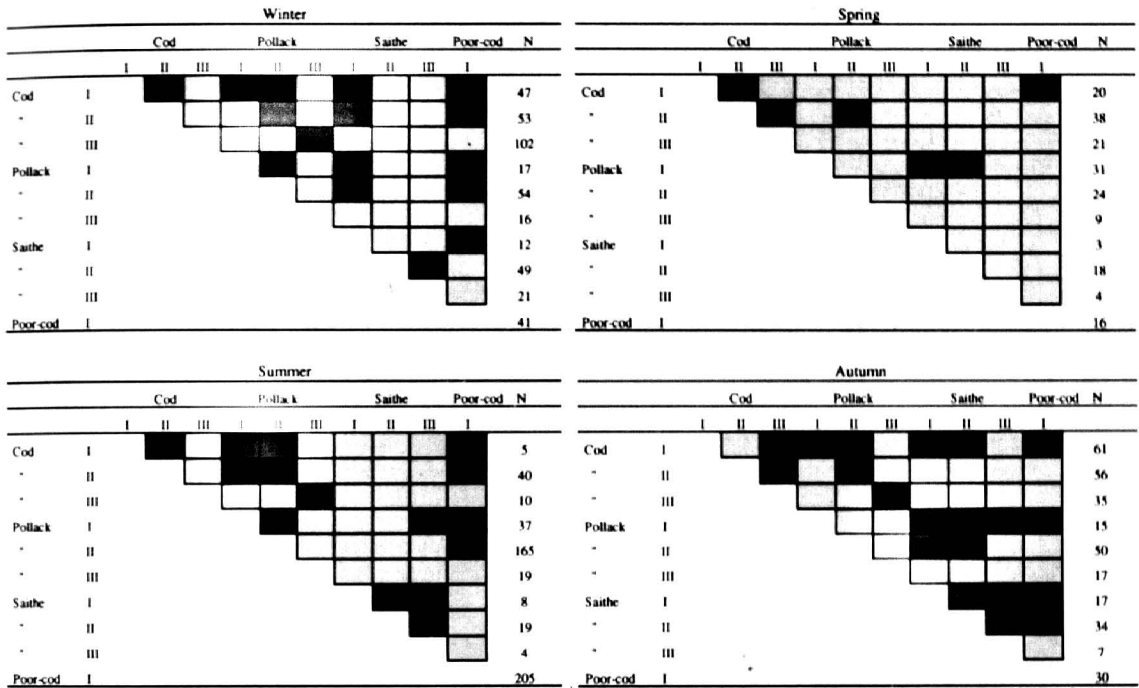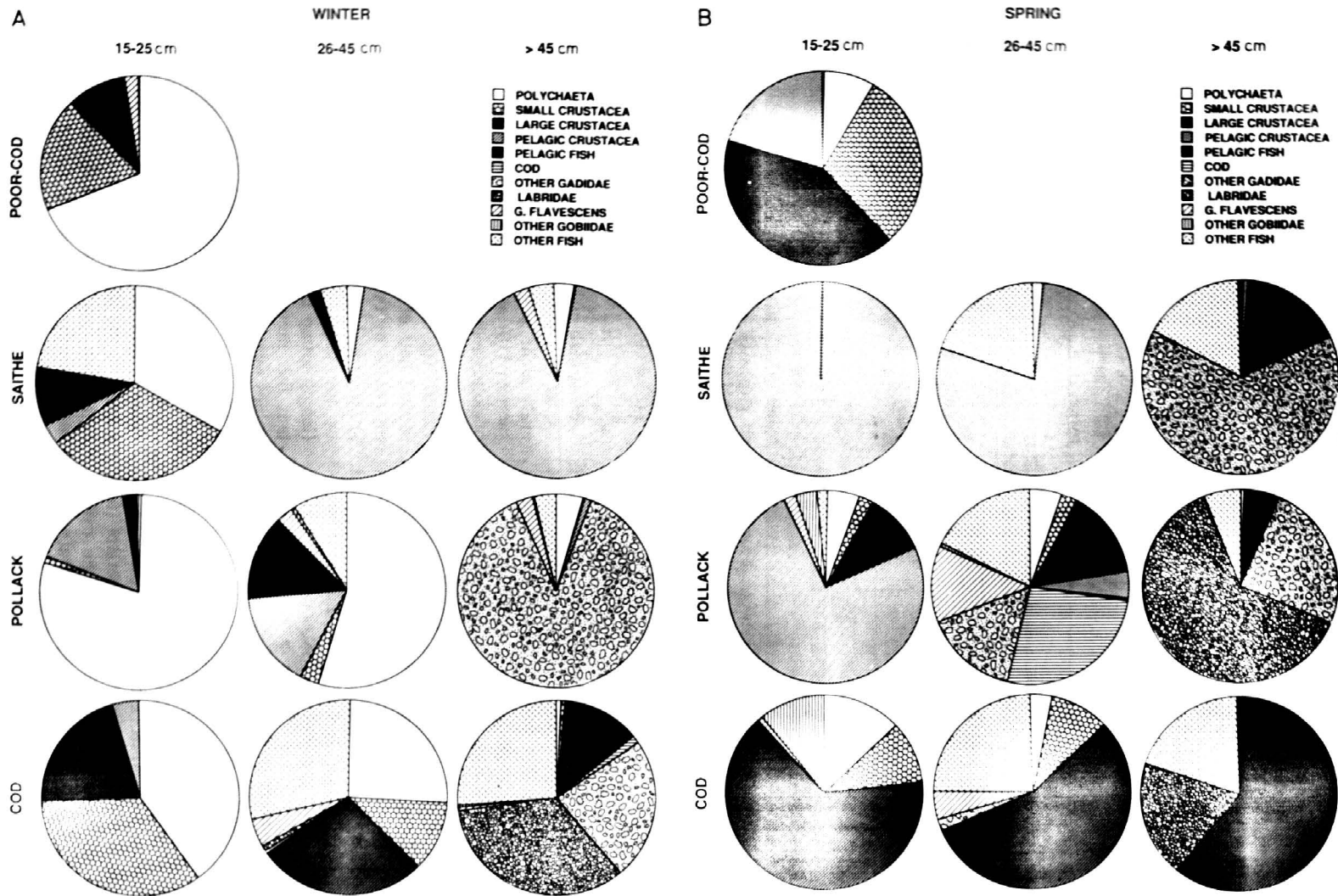
Fig. 3. Niche overlap indices (α_{jk}) between the predator length groups 15–25 cm (I), 26–45 cm (II) and > 45 cm (III) of cod, pollack, saithe and poor-cod for the winter, spring, summer and autumn computed using weight % of various prey groups in the stomach contents. N refers to the number of stomachs examined. The overlap indices ranges from 0 (no overlap) to 1 (all prey groups are found in equal proportions in the diet of both predator j and k). Light shaded squares means low overlap ($\alpha_{jk} \leq 0.3$), medium shaded squares refer to moderate overlap ($0.3 < \alpha_{jk} \leq 0.6$), and black squares refer to high niche overlap ($\alpha_{jk} > 0.6$).

pollack I and II are more similar than the diets of cod II and III and pollack II and III. This result indicates higher diet overlap between the smaller cod and pollack length groups than between the two larger groups. Large differences in diet are indicated between the three saithe groups (I, II and III) and cod III, between saite (I, II and III) and pollack III (as the scores on axis 1 exceed 4 SD's). Cod III and pollack III have similar scores on axis 1, but have significantly different scores on axis 2 (Fig. 2A). Because $\lambda_2 < 0.5$, axis 2 cannot be interpreted as any gradient (cf. JONGMAN & al. 1987).

Seasonal changes in diet

Seasonal changes in diet similarities of the various predator size groups are indicated from the overlap indices calculated pairwise between the predator groups (Fig. 3). In addition, Fig. 4 illustrates the dominating prey types causing similarities and differences. Of all the calculated niche overlaps (total of 180, all seasons included), low niche overlap occurs in 123 occasions (68 %), moderate niche overlap in 34 occasions (19 %) and high niche overlap in 23 occasions (13 %).

Most high niche overlaps (Fig. 3) occurred in the winter (10) and fewest in the spring (2), while moderate niche overlaps occurred most frequently in summer (10) and autumn (13). The high fractions of polychaets in the stomach content of many predator groups may explain the high overlap in the winter. The frequent moderate niche overlaps in the second half of the year may be due to predation on gobies by the smallest predator groups (length group I) and by predation on cod and other gadids by the large pollack and cod predator groups (length group III) (cf. Fig. 4). Of the most important fish preys (gobies, labrids and gadids), the gobies were eaten primarily during the summer and autumn, and in largest proportions by length group I (summer: cod 70 %, pollack 45 %, poor-cod 30 %, saithe 3 %; autumn: cod 50 %, pollack 30 %, poor-cod 30 % and saithe 35 %). With increasing size of cod and pollack, the fraction of gobies in the diet decreased and the fraction of larger fish (gadids and labrids) increased. Gadids (pooled) were consumed by cod and pollack III in most seasons, with maximum in autumn (by cod) and in winter (by pollack) (Fig. 4). Cod was distin-
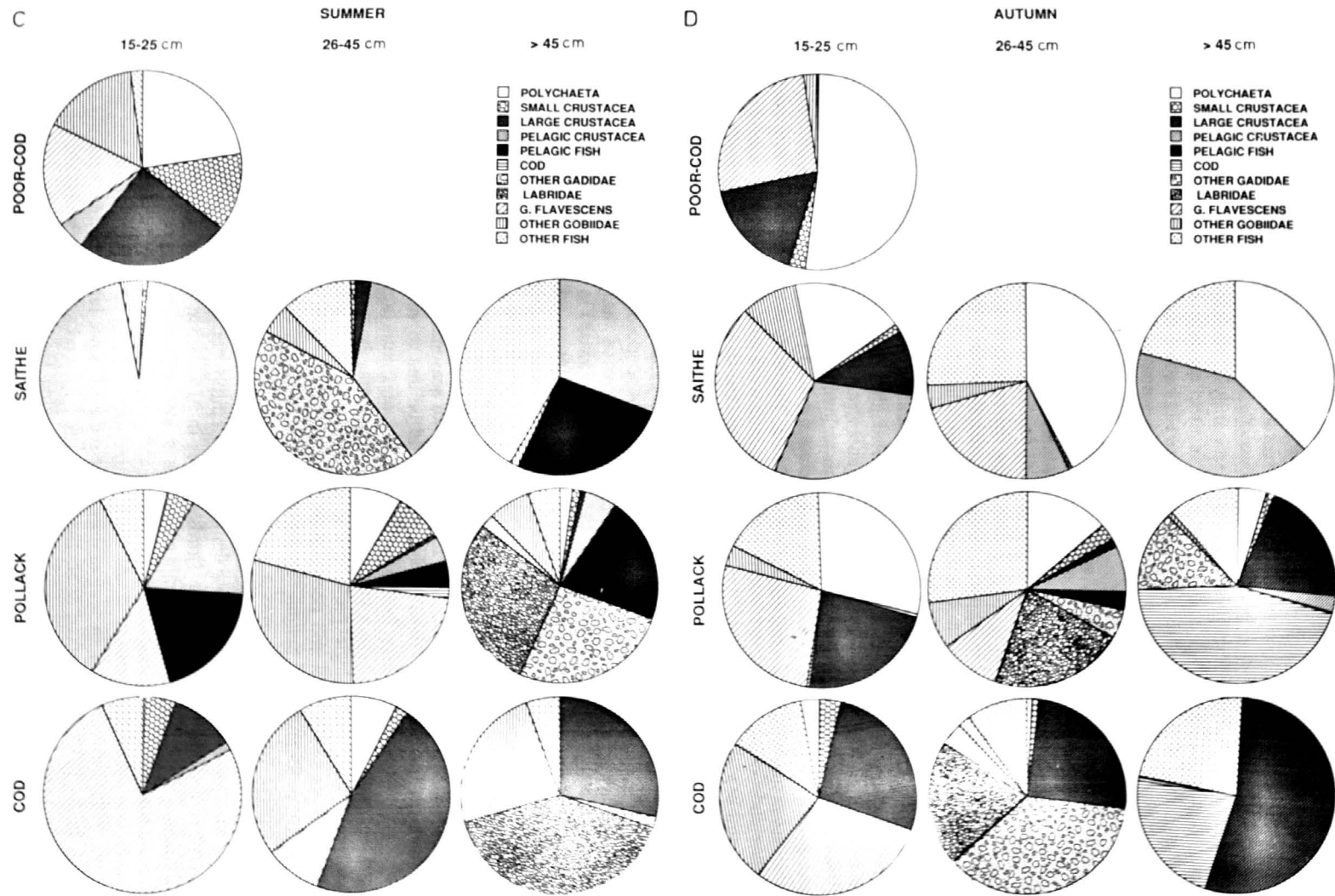
A — WINTER

15-25 cm · 26-45 cm · > 45 cm

POOR-COD · SAITHE · POLLACK · COD

B — SPRING

15-25 cm · 26-45 cm · > 45 cm

POOR-COD · SAITHE · POLLACK · COD

Legend:
- POLYCHAETA
- SMALL CRUSTACEA
- LARGE CRUSTACEA
- PELAGIC CRUSTACEA
- PELAGIC FISH
- COD
- OTHER GADIDAE
- LABRIDAE
- G. FLAVESCENS
- OTHER GOBIIDAE
- OTHER FISH

Fig. 4. Weight percent of principal prey groups in the diet of predator length groups I (15–25 cm), II (26–45 cm) and III (> 45 cm) of cod, pollack and saithe, and one length group (I: 15–25 cm) of poor-cod in A) winter; B) spring; C) summer and D) autumn. Note that *G. flavescens* refers to *Gobiusculus flavescens*.

guished explicitly in the stomach content of pollack III (> 40 weight %) and of cod III (20 weight %) in the autumn. This maximum predation on cod coincided with high abundance of cod as judged by the abundance indices (Table 1), and with absence of labrid predation. Labrid predation occurred all other seasons for cod III (20–30 %), and in spring (> 60 %) and summer (30 %) for pollack III (Fig. 4).

DISCUSSION

Few species dominate the sublittoral fish fauna in Masfjorden. In the net group samples four gadids and four labrids dominated (Table 1), and three gobids are even more numerically abundant (Fosså 1991), although not recorded in the experimental net groups due to their small size. The dominance of few species is consistent with the general trend of inshore ecosystems (e.g., Hoff & Ibara 1977; Wrigth 1988; Henderson 1989). The habitat type used by the gadids cod, pollack, saithe, poor-cod and the labrids *Labrus bergylta, L. mixtus, Centrolabrus exoletus,* and *Ctenolabrus rupestris* contained gravel, rocks and sea-weeds, which are typical for these species in near coastal waters in Europe (Nagabushanam 1965; Whitehead & al. 1986). The type of habitats present in Masfjorden may thus to some extent explain why these species dominated in the fjord.

The prey types eaten by the four dominating gadids in Masfjorden were in general in accordance with studies from other coastal areas and fjords (Powles 1958; Nagabushanam 1965; Denstadlid 1972; Tyler 1972; Gordon & Da Silva 1980; Langton & Bowman 1980; Hacunda 1981; Hawkins & al. 1985; Kristiansen 1987; Nedreaas 1987; Hop & al. 1992). However, the feeding pattern for cod in Masfjorden deviated to some degree from that for cod in north Norwegian fjords where a larger fraction of the food consists of pelagic preys (Falk-Petersen & Hopkins 1981). Cod and poor-cod in Masfjorden were predominantly benthic feeders, saithe was a pelagic while pollack was a mixed feeder consuming both benthic and pelagic prey. The pollack in Masfjorden seemed to have a similar feeding pattern to cod in north Norwegian fjords.

Seasonal changes in fish faunas in temperate coastal areas have been explained by migrations related to the reproduction cycle (Macdonald & al. 1984; Jansson & al. 1985), to variations in temperature (e.g., Hoff & Ibara 1977; Macdonald & al. 1984; Rainer 1984; Nellbring 1985; Murawski & Finn 1988; Henderson 1989) and to food availability

(Macdonald & al. 1984; Claridge & al. 1986; Potter & al. 1988). We could expect that the higher cod abundance in autumn and winter revealed the reproduction cycle as we do know that 0-group cod (spawned in the fjord), settled in the sublittoral habitat by June–July (Fosså & al. 1993). However, this effect seems to have been removed by the combined effect of the numerous 1984 year-class and poor recruitment of 0-group in 1985 and 1986 (cf. Salvanes & Ulltang 1992; Nordeide & al. in press). Immigration of mature cod may explain part of the high abundance during the winter. It is common that two units – one local fraction remaining in the area the entire year, and another consisting of immigrating individuals from contiguous fjords or more distant areas – mix at spawning grounds in Norwegian fjords (Godø 1984; Jakobsen 1987; Jørstad & Nævdal 1989). The maximum abundances of pollack and saithe in the autumn reveal the reproduction cycle. As these species generally spawn offshore during the winter, and since juveniles migrates into nursery areas of near coastal areas of Europe during the autumn (Wheeler 1969), the high abundances in Masfjorden in the autumn were due to immigrations of juveniles as judged by inspection of size distributions (own obs.). Moreover, as they do not spawn to any large extent in Masfjorden (own obs.), their minimum abundances in the winter (cf. Table 1) may reflect migration to deeper habitats where temperature is higher than in the sublittoral. The higher abundance of poor-cod in the summer and autumn compared to winter and spring (Table 1, Fosså & al. 1993, fig. 8) does not reflect recruitment of 0-group poor-cod as otolith readings (own obs.) have shown that most individuals belong to 2-group or older, but may rather indicate seasonal vertical migrations, or seasonal changes in activity, features which could be due to variations in temperature.

The maximum abundance of labrids during the summer may be a result of migration from deeper waters due to a rise in temperature at shallower depths (e.g., Wheeler 1969). Increasing activity connected to rising temperature, as observed for *Tautogolabrus adspersus* (Green & Farewell 1971), offers an alternative explanation. The latter would imply that the abundance indices for the labrids in Masfjorden (Table 1) were underestimated as a low activity is expected to result in a lower catch rate by passive gears. On the other hand, predation on less active fish would not necessarily be reduced. Since labrids were frequently consumed by the large cod and pollack also during the winter and spring (Fig. 4) despite the fact that the experimental catches were low during these seasons,

a temperature dependent activity level seems likely for labrids in Masfjorden.

The settlement of 0-group cod and other gadids in the sublittoral habitat of Masfjorden by the autumn might result in an increased availability of suitable preys to the large predators of cod and pollack. Significant amounts of cod were recorded in the diet of large cod and pollack during the autumn, but gadids in general were important preys also in winter. Hence, the dietary analysis suggests a high mortality rate for juvenile cod and other gadids in autumn and winter. These results are consistent with the conclusion of NORDEIDE & al. (in press) who report a high mortality rate on 0-group and 1-group cod as judged by the development of three year classes of cod (1988–1990) in Masfjorden.

Although the mortality risk seemed high for juvenile cod in the autumn, its growth prospects in the benthic habitat seemed also good during the same period. The maximum abundance of gobies [principal preys to juvenile gadids (Fig. 4; SALVANES 1986 a)] occurred in the summer and autumn when small gadids had maximum predation on gobies (FOSSÅ 1991). For stock enhancement purposes good growth prospects in the autumn may be an argument for conducting large-scale releases in this season, whereas the high mortality risk is an argument against it. An evaluation of the trade off between mortality and growth conditions is therefore required. Perhaps a release of cod in large-scale when the mortality rate per growth rate is at minimum in the shallow habitat may be a useful strategy as suggested in SALVANES & al. (in press). If so, this would require monitoring of growth and mortality prospects at the release sites used for stock enhancement.

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