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Trophic ecology of deepwater fishes associated with the continental slope of the eastern Norwegian Sea

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ABSTRACT

In June 1995 and 1996 demersal fishes on the continental slope of the eastern Norwegian Sea were sampled to study distribution patterns and community structure. The diets of the more abundant slope species were characterised and linkages within the upper slope food-web identified.

Few cases of predator-prey relationships between the typical slope fishes were found. Most of the smaller fishes fed on epibenthic crustaceans such as amphipods and mysids, while pelagic crustaceans and fish dominated the diets of larger fishes. Herring (*Clupea harengus*) and blue whiting *(Micromesistius poutassou)* were important prey items of Greenland halibut (*Reinhardtius hippoglossoides*), and were also eaten by *Lycodes frigidus*, *Raja hyperborea* and roughhead grenadier (*Macrourus berglax*). At least for the latter three species this probably reflected scavenging.

Keywords: deep-water fish, demersal, diets, Norwegian Sea, scavenging, trophic ecology

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INTRODUCTION

As an element of the Norwegian "Mare Cognitum" programme, studies of the demersal fish communities along the upper slope of the eastern Norwegian Sea were initiated. Based on bottom trawl samlping in 1995 and 1996 in the depth range 400 – 2050 m off western Norway, Bergstad *et al.* (1998) identified four species assemblages with characteristic compositions and distributions. The deepest was the "Norwegian Sea Deepwater"-assemblage with only 3 species. The "Upper slope 1 (warm)" and "Upper slope 2 (cold)" assemblages had higher richness and diversity and inhabited the transition zone between the warm Atlantic Watermass and the cold Norwegian Sea Deepwater. Even shallower, i.e. on the shelf-break, a fourth species assemblage comprising 16 species occurred.

In this paper we focus primarily on the trophic ecology of fishes belonging to the first three (and deepest) assemblages. Based on our new data, Skjæraasen (1998), and previous reports on the diet of the different species, we constructed simple food-webs which outline the most important trophic relationships between the slope fishes and other members of the eastern Norwegian Sea communities.

MATERIAL AND METHODS

In June 1995 and 1996, samples of demersal fishes were collected by the RV *Håkon Mosby* in two areas on the continental slope off Norway, at approximately 62-63°N in 1995 and at 67-68°N in 1996 (Fig. 1). The depth range sampled was 430 to 2050 m using two different otter trawls, a semi-balloon otter trawl (OTSB) and the Campelen 1800 sampling trawl. Details concerning the gear and sampling were given by Bergstad *et al.* (1998).

Stomach samples were extracted for most fish species, but few useful samples were obtained for abundant species which unfortunately tend to have everted stomachs, e.g. *Sebastes* sp. and *Macrourus berglax.* Stomachs showing signs of regurgitation were excluded from further analyses. Most stomachs were labelled individually and preserved in 4% seawater solution of formaldehyde buffered with sodium tetraborate, but for Greenland halibut stomachs within 10 cm length groups were pooled. Some of the smaller species, and specimens that needed to be identified later, were preserved whole and brought to the laboratory for further examination.

The stomach contents were sorted and all identifiable prey were identified to the lowest possible taxon, preferably species. Dry weights of the different prey categories were

measured separately after being kept in a drying oven at 60-70°C for at least 48 h or until a constant weight was obtained. The composition of the stomach contents was described in terms of percentages by weight of the different prey, i.e. weight of an item as percentage of the pooled contents of all stomachs examined for a given predator. The frequency of occurrence of different food items, i.e. the proportion of non-empty stomach containing the item, was also calculated.

Total length (TL, to nearest unit below) and ungutted weight (g) was recorded for all species. For the macrourid *Macrourus berglax,* pre-anal fin length was measured because tails were often broken and/or regenerated.

RESULTS AND DISCUSSION

The "Norwegian Sea Deepwater" assemblage.

Lycodes frigidus Collett

This species was caught in two hauls at 1521 m at 63°N and 2015 m at 68°N, and the length distribution ranged from 5 to 65 cm TL (Fig. 2). Individuals smaller than 22 cm were only caught in the haul at 2015 and 22 of these were examined for food. Fish larger than 22 cm were caught at both stations and 41 of these were examined.

Most of the fish smaller than 22 cm had either empty stomachs or stomachs only containing unidentifiable soft tissue, while most of the larger fish had some identifiable stomach contents. Polychaetes dominated the contents of the smaller specimens whereas fish was the most important food of the larger (Table 1). Some of the smaller specimens also contained small crustaceans (copepods, ostracods, tanaids and amphipods), while cephalopods and large crustaceans like the shrimps *Pasiphaea* spp. and *Hymenodora glacialis* and the amphipod *Eurythenes gryllus* occurred in the stomachs of larger fish. The most striking observation was the occurrence and apparent dominance of pelagic fish, i.e. herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*), of total lengths 20 - 30 cm observed at both locations investigated. These species are confined to shallower depths, and it seems likely that their occurrence in stomachs of *L. frigidus* results from scavenging. In some cases only the head of the herring was found in the stomach. Among the fish prey also one of the other three species of the "Norwegian Sea Deepwater" assemblage, *Paraliparis bathybius,* occurred. The measureable specimens were 16 and 20 cm TL.

Collett (1880) recorded various deepwater crustaceans and remains of a cephalopod in the stomachs of five *L. frigidus* caught in the Norwegian Sea. Prey species found by

Collett (1880) also found in the present study include *Pasiphaea tarda*, *Hymenodora glacialis* and *Saduria megalura*, while fish was not reported as prey by him. Andriyashev (1964) states that fish remains are only rarely found in stomachs *of L. frigidus*, a statement which contrasts strongly with our findings.

Rhodichthys regina Collett

Three specimens of this species measuring 18.6, 27.8 and 28.4 cm TL were caught at 1521 m depth at approximately 63°N. The stomachs of the two largest individuals were examined (table 2) and in the largest specimen the remains of a large crustacean, probably a *Hymenodora glacialis*, were found. The stomach of the other specimen only contained sediment. These sediments were rich in foraminiferans of the genera *Cibicides*, *Cribostomoides* and the planktonic *Neogloboquadrina pachyderma*, but the nutritional value of these are questionable.

Collett (1880) reported that the type specimen's stomach contained two shrimps of the species *Bythocaris leucopis*, one *Pseudomysis abyssi* and a hyperid amphipod. Collett (1905) later examined two specimens from the same area as in our study, and found a *Calanus hyperboreus* in one of the stomachs and a *Hymenodora glacialis*. Johnsen (1921) examined one individual, but found only crustacean remains in the stomach.

Paraliparis bathybius Collett

This species was caught in the four deepest hauls ranging from 2051-1498 m. The hauls at 2051 and 1498 m yielded only one specimen each, while 17 and 15 specimens were caught in the two other hauls performed at 2015 and 1521 m respectively. The total length ranged from 13 to 26 cm. Stomachs of all individuals, except the specimen caught at 2051 m, were examined (Table 1).

Only 13 stomachs contained identifiable prey, while most of the others contained small quantities of soft tissue or were empty. The stomach contents were dominated by the same foraminiferan ooze as observed in the previous species, and again the nutritional value is probably limited. The presence of sediments in this species is strange since most identifiable remains were pelagic organisms. Crustaceans such as the shrimps *Pasiphaea sivado* and *Hymenodora glacialis* and the amphipods *Themisto abyssorum* and *Cyclocaris guilelmi,* which were all found in the diet, are listed by Murray and Hjort (1912) as members of the pelagic fauna in the cold layer below the Atlantic water.

Little is known about the diet of this species from previous studies, but Collett (1880) reported that hyperid amphipods, parts of a mysid and a small gastropod occurred in the type specimen. All individuals examined later by Collett (1905) contained hyperid amphipods of

the genus *Themisto*, and this was also found in one individual examined by Johnsen (1921). Lampitt *et al.* (1983) observed *P. bathybius* at baited traps placed at about 4000 m in the Porcupine Seabight in the north-eastern Atlantic (approximately 50°N). The fish gathered around the traps feeding on necrophagous amphipods like *Paralicella* spp., *Orchomene cavimanus* and *Eurythenes gryllus*.

The "Upper slope 1 (cold)" assemblage

Onogadus argentatus (Reinhardt)

In total 29 specimens in the size range 8-31 cm TL were caught, and they occurred in six of the hauls in the depth interval 482 – 1521 m. The stomach content of 18 individuals were examined, and 16 of these contained identifiable prey.

The diet consisted exclusively of crustaceans, and mysids seemed to be the most important prey as they occurred in most of the stomachs and comprised over 30% of the total weight of the stomach contents (Table 3). Three different species of *Pseudomma* were identified with *P. roseum* and *P. frigidum* being the dominating species in weight and smaller specimens of *P. truncatum* occurring in one third of the stomachs investigated. Two stomachs contained remains of carideans, and because of their large size these also contributed more than 30% to the total contents. Although these shrimp fragments were partly digested, their characteristic orange-red colour indicated that they originated from *Hymenodora glacialis*. Other important prey were the amphipod species *Eusirus holmi* and *Amathillopsis spinigera*, and fragments of euphausids were found in two stomachs.

Several different benthic, bentho- and bathypelagic crustaceans have been found in the stomachs of the few examined individuals of this species in previous studies, and it seems like it is rather euryphagous and has a wide depth distribution. Ponomarenko (1983) found a *Pandalus borealis* in the stomach of an individual collected in the north-eastern Norwegian Sea. Collett (1880) also found remains of carideans and a fish in the stomach of the first specimens he examined, while the second contained members of the amphipod genera *Themisto* and *Anonyx* (*Tmetonyx*?). These specimens were caught at 75°N, and a few years later Collett (1905) examined some specimens caught in the same area as the southern locality in our study. He reports to have found a large herring and a *Bythocaris leucopis* in the stomach of a 38.6 cm long fish caught at 1150 m depth, while a variety of crustacean prey species (e.g. *Pseudomma roseum*, *Meganyctiphanes norvegica* and some gammaridean amphipods species) were found in the smaller ones. It is likely that the occurrence of large

herring in the stomachs of this species could be explained as a case of scavenging, as it probably will not encounter living herring at these great depths.

Lycodes pallidus Collett

The eight specimens, which were caught in five different hauls between 650 - 1521 m depths, were 7.4-17.0 cm TL and all were examined for food. Three had empty stomachs, but the other five contained small amounts of identifiable food (Table 3).

The stomach contents consisted primarily of polychaetes and unidentifiable crustacean fragments, but one individual had consumed a 12 mm long *Harpinia abyssi*, a 8 mm *Caprella* sp. and a small bivalve, while another stomach contained a 10 mm long ampeliscid amphipod and a not yet identified amphipod measuring 7 mm.

Previous studies have shown that *L. pallidus* feeds on polychaetes, small bivalve mollusks and amphipods (Briskina 1939; Collett 1905), and in addition to prey also found in the present study, ophiuroids are mentioned as important food. All stomachs investigated by Dolgov (1994) from the Barents Sea were empty.

Lycodonus flagellicauda (Jensen)

The largest individual of this species was caught in the haul made at 1521 m at 63°N, while the two other specimens were caught at 900 and 1000 m at approximately 68°N. Table 2 shows the total lengths and stomach contents of these specimens.

The stomach of the largest fish was empty and the smallest contained a single partly digested gammaridean amphipod. In the stomach of the individual caught at 900 m two species of gammaridean amphipods (*Byblis minuticornis* and *Ischyroceirus megacheir*), a mysid (*Pseudomma truncatum*) and an isopod (*Munnopsis typica*) were identified.

The largest and the smallest of the individuals described by Collett (1880) as *Lycodes muraena* were in fact *Lycodonus flagellicauda*, and the stomach content of the largest individual was exclusively fragments of *Themisto libellula*. Collett (1905) adds two other small crustaceans to the diet of this species, *Podocerus assimilis* (amphipod) and *Hemilamprops uniplicata* (cumacean).

Raja hyperborea Collett

In total, 31 individuals were caught in six different hauls taken at approximately 63°N. The depth range was 482-1521 m, but most specimens (21) were caught in the two hauls at 530 and 585 m. The total lengths were 23-84 cm, with 26 of the specimens measuring more than 55 cm. In the haul taken at 1000 m in the northern locality (68°N) a single specimen measuring 73 cm was caught. All the individuals caught at the southern locality were

examined for food by Skjæraasen (1998) (see also Poster O:64 of this Council Meeting), and we were allowed to present some of the results (Table 3) in this paper. The specimen caught at the northern locality was not checked for stomach contents.

Five stomachs were empty, while the stomach contents of the other were dominated by fish remains. These were mostly partly digested and could not be identified, but one stomach contained blue whiting *Micromesistius poutassou* contributing 29.3% to the total weight of the stomach content. Two stomachs contained recognisable zoarcid remains comprising 15.3% of the total weight. Euphausids were found in many of the stomachs and *Meganyctiphanes norvegica* was identified in 11 stomachs and contributed 6.0% to the total. The total contribution of euphausids, including fragments and *Thysanoessa inermis* found in a single specimen, was 12.4%. The pelagic caridean *Pasiphaea* sp. occurred in one stomach.

Collett (1880 and 1905) reported that 3 of the 4 adult specimens examined by him had fish remains in their stomachs. Zoarcids occurred among the fish ingested by one of the specimens, the remainder could not be identified. Collett also found pelagic crustaceans in the stomachs, but these were hyperid amphipods (*Themisto*) and *Hymenodora glacialis*, i.e. items not found in this study. In addition he found a large cephalopod in one of the stomachs.

The "Upper slope 2 (warm)" assemblage

Reinhardtius hippoglossoides (Walbaum)

Eleven individuals of this species were caught in the hauls at about 68°N, while 275 were caught at the southern locality. The depth range of the seven hauls in which *R. hippoglossoides* was caught was 482 - 812 m, and the total lengths were 39 - 81 cm. Of the 128 examined for food, 54 were smaller and 74 larger than 50 cm.

Among the fish smaller and larger than 50 cm, 70 and 54 % of the stomachs were empty, respectively. The stomach contents consisted mostly of fish and fish remains (about 90% in weight) and did not differ much between the two length groups (Table 4). Some of the smaller fish had also been feeding on crustaceans, of which the amphipods *Eusirus holmi* and *Eurythenes gryllus* were the most common, while *Gonatus fabrici* (Cephalopoda) contributed about 5% to the weight in the diet of larger fish. Herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) of total lengths between 20 and 30 cm dominated the fish fraction. Only the heads of these were found in the stomach in some cases. Smaller mesopelagic species i.e. *Notoscopelus kroeyeri* and *Notolepis rissoi* occurred only once each.

Several studies of the diet of this species have been carried out in the western Barents Sea/north-eastern Norwegian Sea (Nizovtsev 1969; Haug and Gulliksen 1982; Shvagzhdis

1990; Michalsen and Nedreaas, in press), off West Greenland (Pedersen and Riget 1993; Jørgensen 1997), in Icelandic waters (Paschen 1968; Skúladottir and Jónsson 1991) and in the north-eastern Atlantic (Bowering and Lilly 1992), while information on diet in the eastern Norwegian Sea south of 71°N is scarce. The general impression from these studies is that Greenland halibut is piscivorous but also to some degree feeds on shrimps and cephalopods. The results of the present study thus fits well with studies in other areas of the north Atlantic. Also other studies have shown that fish species generally considered to be epipelagic sometimes occur in the diet. Skúladottir and Jónsson (1991) and Bowering and Lilly (1992) both report that capelin (*Mallotus villosus*) is the most important prey item, while studies from the western part of the Barents Sea showed that herring and blue whiting occur in the diet (Shvagzhdis 1990; Michalsen and Nedreaas in press). The occurrences of fish heads in some stomachs examined in this study suggests that scavenging may be important. The vertical distribution of *R. hippoglossoides* and herring rarely overlap in these areas, while blue whiting can be found at the same depths as the halibut. *R. hippoglossoides* is however known to perform extensive vertical feeding migrations in West Greenland waters (Christensen and Lear 1977; Jørgensen 1997), but this has not been reported from the eastern Norwegian Sea and the fish observed pelagically by Jørgensen (1997) were rarely more than one year old. Michalsen and Nedreaas (in press) conclude that adult *R. hippoglossoides* also leaves the bottom to feed on pelagic organisms such as herring in the water column in the western Barents Sea.

Macrourus berglax Lacepède

This species was caught in four of the hauls, at 530 and 585 m at 63°N and 596 and 638 m at 68°N, and the preanal length distribution ranged from 17 to 42 cm (Fig. 3). A total number of 69 individuals were caught and 67 of these were examined for food.

The percentage of everted stomachs were high for this species (78%), and the stomach contents of the 15 stomachs containing food are shown in Table 4. The results are difficult to interpret because of the occurrence of a herring head in one stomach at the southern locality and a large, partly digested herring in another stomach at the northern locality. These herring remains together with some unidentifiable fish fragments comprised 78.5% of the stomach content by weight, while the more frequently encountered, smaller prey such as the amphipods *Liljeborgia fissicornis* and *Apherusa* sp., euphausids and ophiuroids did not contribute very much in terms of weight. In one of the stomachs a relatively large cephalopod occurred which comprised 6% of the total food weight. This was most likely remains of the octopus *Bathypolypus arcticus*, but this could not be confirmed because of the degree of digestion.

High frequency of everted stomachs has also been reported for this species by Savvatimskyi (1984), and suggested by Eliassen *et al.* (1985). Some studies of the trophic ecology of this species have been carried out in the north-eastern Norwegian Sea (Eliassen *et al.* 1985; Savvatimskiy 1985), and they show that *M. berglax* is an euryphagous predator feeding primarily on epibenthic and benthopelagic crustaceans like shrimps and amphipods, but also having several other different prey categories in the diet (polychaetes, cephalopods, ophiuroids and others). Eliassen *et al.* (1985) also found fish in the stomachs of *M. berglax*, and this was primarily observed during the summer months. The fishes found by Eliassen *et al.* (1985) were all benthopelagic, and the presence of herring in stomachs examined in our study should probably be regarded as cases of scavenging. This might also be the explanation for the occurrence of capelin in the stomachs of a few individuals examined by Collett (1885) from fjords at the Barents Sea coast of Norway. Thus it might be added to the classification of *M. berglax* as being a non-specialist predator on prey of both benthic and pelagic origin by McLellan (1977), that this species may also act as a scavenger.

Cottunculus microps Collett

A total number of 15 specimens ranging between 8-21 cm in total length were caught, and they occurred in four of the hauls ranging in depth from 585 to 1000 m. The stomach content of 14 individuals were examined, and all of them contained identifiable prey.

The diet was dominated by benthic prey like pycnogonids of the genus *Nymphon* and polychaetes, which comprised 67 and 14% of the weight respectively. In addition 14 different, mostly epibenthic amphipod species were identified in the stomach content.

Collett (1905) reported polychaetes, pycnogonids and amphipods in the specimens collected by him from northern Norwegian waters, and our study confirmed the impression that this species feeds predominantly on benthic organisms. Studies from the Barents Sea support this conclusion (Briskina 1939; Dolgov 1994).

Lycodes esmarki Collett

The 17 specimens of this species, which were caught in four different hauls from 428 to 585 m, ranged from 9 to 53 cm. Only five of the 15 individuals examined had identifiable stomach contents, while the others were either empty or contained small amounts of unidentifiable food.

The smallest specimen caught (at 482 m) measured 98 mm and contained four *Pseudomma affine* and four *Munnopsis typica*, while in another small specimen (105 mm) caught at 428 m a large (27 mm) *Meganyctiphanes norvegica*, a bivalve and some peracarid fragments were found. Two larger individuals taken at 482 m, measuring 44 and 49 cm,

contained mostly echinodermata, both crinoids and ophiuroids (*Ophiura* sp.), but also some amphipods (*Epimeria loricata*). Only some polychaete fragments were found in the last individual with identifiable stomach contents. This specimen measured 34 cm, and was caught at 585 m.

Collett (1903) has examined the stomach contents of some specimens caught in the Barents Sea and the north-eastern Norwegian Sea. In the adult individuals he found mostly echinoderms, whereas the smaller fish (< 30 cm) examined by him a few years earlier (Collett 1880) actually belonged to a different species (*L. eudipleurostictus*) (Jensen 1904). It seems, however that *L. esmarki* changes its feeding habits with increasing size and age. Small individuals seem to feed on a variety of crustaceans and bivalves, but when the fish reaches lengths between 30 and 40 cm there is probably a gradual shift towards a diet composed almost exclusively of echinoderms.

Lycodes seminudus Reinhardt

Eight individuals ranging from 23 to 46 cm were caught in the haul taken at 812 m depth in the southern locality, but no stomachs were sampled.

The only specimen collected in the same area by Collett (1905) was unfortunately empty, while Andriyashev (1964) reports that various amphipods, decapods, isopods and polychaetes have been found in the stomachs without mentioning in what area these were sampled.

Lycodes eudipleurostictus Jensen

Three individuals of this species, measuring 10.6, 11.3 and 31 cm TL were caught at 650 m, while one 22.5 cm long specimen occurred in the 585 m haul in the southern locality (Table 2).

Only the smallest specimen from 650 m and the specimen from 585 m were examined for food, and both stomachs were empty.

Collett (1880) examined the stomachs of two specimens measuring 26.5 and 29.5 cm which he identified as *L. esmarki*. These were later identified as *L. eudipleurodtictus* by Jensen (1904), and their stomachs contained polychaete fragments and *Themisto libellula*. Collett (1905) later examined some more individuals, and reports that several different benthic and pelagic prey were found in the stomachs. Among the pelagic prey were the caridean *Pasiphaea tarda* and the euphausid *Thysanoessa inermis*, while the bottom living forms were *Ophiocten sericeum*, isopods, polychaetes and priapulids.

Lycenchelys muraena (Collett)

One individual of this species was caught at 1000 m, while three specimens occurred in the 650 m haul in the southern locality. The total lengths of the specimens ranged from 12.6 to 15.5 cm, and Table 2 gives the stomach contents.

Three of the stomachs contained food, and remains of small crustaceans were found. The gammaridean amphipod *Maera tenera* and the caprellidean *Caprella septentrionalis* were identified, but also fragmented isopods could be recognised.

The type specimen of Collett (1880) and two other individuals examined by him later (Collett 1905) also contained amphipods (*Themisto* and *Podocerus* (*Ischyrocerus*?) *assimilis*) and isopods (*Astacilla granulata* and *Nannoniscus bicuspis*).

Raja radiata Donovan

In total, 19 specimens of this species were caught at three stations at depths between 428 and 585 m in the southern locality. The six individuals caught in the deepest haul all measured between 11 and 27 cm TL, while nine of the ten specimens caught at 482 m measured between 45 and 61 cm TL (the tenth specimen measured 11 cm TL). These 16 individuals were all examined for food, while the three specimens caught in the shallowest haul (measuring 11, 23 and 41 cm) were not examined.

Only two of the larger individuals had empty stomachs, while the other 14 contained identifiable prey. The composition of the stomach contents is given in Table 5. The stomach contents were dominated by pelagic crustaceans such as hyperid amphipods and euphausids, but also some fish remains were found in the larger individuals. Among the fish remains a zoarcid could be identified in one stomach, and specifically a 45 mm long *Lycodes esmarki* was observed in another.

The diet of this species has been studied in several regions of the northern Atlantic previously (McEachran *et al* 1976; Templeman 1982; Daan *et al* 1993; Dolgov 1997), but these studies has been carried out in the north-western Atlantic, or in shallower areas of the north-eastern Atlantic (North Sea and Barents Sea). The general impression of these studies is that the smaller *R. radiata* feeds on a variety of crustaceans, and that a gradual shift towards a diet dominated by demersal fish occurs with increasing size. Information on stomach contents of *R. radiata* from the continental slope area of the Norwegian Sea is scarce, but Berestovskiy (1989) reports that the diet of fish caught at the slope in the north-eastern part consisted primarily of *Pandalus borealis*, but also some *Bathypolypus arcticus* (cephalopod) and fish.

Bathyraja spinicauda (Jensen)

The eleven specimens, which were caught in three different hauls at 482 - 585 m depth in the southern locality, measured 37-95 cm and all were examined for food. All stomachs contained identifiable food (Table 5).

The stomach contents consisted primarily of fish, but due to the degree of digestion it was not possible to determine what species these fragments originated from. Two of the fish eaten were however zoarcids. Pelagic crustaceans such as euphausids and *Pasiphaea* sp. also occurred in some stomachs, but these contributed less than 10% to the total weight of the stomach contents.

Information on the diet of this species is scarce, but Jensen (1948) reports that fishes (*Raja radiata* and capelin) and *Pandalus borealis* were found in the stomachs of large specimens from Greenland waters.

Trophic relationships of the species assemblages

Simplified food-webs were drawn for each of the three species assemblages of Bergstad *et al.* (1998) highlighting the most important trophic relationships between the fish species and between the fish species and other prey groups (Fig. 4-6). We utilised primarily the results of the present study, but also findings of other studies from the Norwegian Sea slope and adjacent waters. As noted above, no information is included for the redfishes *Sebastes* sp. which are particularly abundant characteristic members of the "Upper slope (warm)" assemblage. The redfishes are assumed to be planktivores, but very little documentation exists at present.

Demersal slope fishes basically have two alternative categories of food resources 1) benthos, plankton or fish produced locally, 2) food produced elsewhere but made available through advection, migration or sinking. Both alternatives were utilised by the fishes of the upper slope of the Norwegian Sea. Few fishes were true benthivores. Only two species, *Cottunculus microps* and *Lycodes esmarki* had a diet dominated by benthic prey, but the same may be the case for *Lycodes pallidus, Lycodonus flagellicauda, Lycenchelys muraena* and *Lycodes seminudus* for which little information was available.

Planktonic, nektonic or hyperbenthic crustaceans (euphausids, ampipods, carideans) were, however, prominent in the diets of many of the slope fishes, and even relatively large species such as *Raja radiata, Raja hyperborea* and *Bathyraja spinicauda* fed on relatively small pelagic prey. These prey items must either be produced locally or brought to the relevant depth through vertical migration or advection. Recent studies have shown deep

scattering layers of vertically migrating nekton along the shelf-break and off the shelf in the eastern Norwegian Sea (Torgersen *et al.* 1997). Hydroacoustic observations showed diurnal migrations between about 50 and 450 m. In addition to comparatively high local pelagic production, there is evidence of advective production of nekton and plankton in the northeasterly Atlantic current (Mauchline 1986). This may provide a steady food supply to demersal fish along the upper slope. A strange observation, however, is the scarcity of mesopelagic fishes in the diets of the slope fishes. Only Greenland halibut seems to a limited degree to feed on these abundant fishes.

For several of the larger fish species indications of scavenging were found. This may be particularly significant for the deep-living *Lycodes frigidus* which is only abundant in the cold Norwegian Sea Deepwater. Herring and blue whiting are at times very abundant in the surface and mid-depth waters above the slope, and it is not unlikely that carcasses of these provide a significant input of food to fishes on the middle and lower slope where other resources are probably limited. Carcasses of herring and blue whiting may also be significant to other large and shallower slope fishes, i.e. Greenland halibut and *Macrourus berglax,* but the relative importance of scavenging and feeding on live prey is uncertain.

The only predator-prey relationships *between* members of the fish assemblages were the ones between *Paraliparis bathybius* and *Lycodes frigidus* and between zoarcids and the rajids. It is noteworthy that a large species like Greenland halibut seems rather to feed on herring and blue whiting (living or dead) than on other slope fishes or even mesopelagic fishes.

We concluded previously (Bergstad *et al.* 1998) that the strong and permanent temperature front between the Norwegian Sea Deepwater and the overlaying Atlantic Water is a strong structuring force along the Norwegian Sea slope, both influencing the identity and distribution of species assemblages. We hypothesised that a second structuring factor might be the spatial distribution of prey to demersal fishes, probably primarily nekton like euphausids, amphipods and meso- and epipelagic fish. The diet studies showed that these prey groups, perhaps with the exception of mesopelagic fishes, were indeed important to many of the abundant slope fishes. In addition we suggest that carcasses of epipelagic fishes may be significant food resources, at least to the middle and lower slope fishes. Further and more comprehensive analyses of feeding patterns in relation to the spatial distribution of the different prey categories is, however, beyond the scope of this paper.

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Table 1. Stomach contents of fishes of the "Norwegian Sea Deepwater" species assemblage (Bergstad & al. 1998) in terms of percentage by weight (%W) and number of stomachs in which the given prey category was found (F).

	Lycodes frigidus				*Paraliparis bathybius*	
	> 22 cm		< 22 cm			
	%W	F	%W	F	%W	F
Unidentified remains	0.9	6	65.8	9	15.3	18
Foraminifera indet.	0.1	4			61.5	4
Polychaeta indet.			25.6	4		
Crustacea fragments			0.4	1		
Copepoda indet.			0.4	1		
Calanoida indet.					+	2
Harpacticoida indet.			0.2	1		
Ostracoda indet.			0.4	1		
Peracarida fragments					1.3	1
Tanaidacea						
Leptognathia sp.			0.4	1		
Sphyraphus anomalus			1.5	1		
Isopoda						
Saduria megalura	+	1				
Amphipoda fragments					0.3	1
Gammaridea fragments	+	2	1.9	1	0.6	2
Lysianassidae						
Uristes umbonatus					+	1
Cyclocaris guilelmi					0.2	1
Eurythenes gryllus	1.0	1				
Orchomene sp.	+	1				
Corophiidae						
Neohela monstrosa	+	1				
Oedicerotidae						
Monoculodes packardi			2.7	1		
Phoxocephalidae						
Harpinia abyssi	+	1				
Liljeborgidae fragments			0.8	1		
Liljeborgia fissicornis	+	1				
Hyperiidea						
Themisto abyssorum					1.4	2
Caridea fragments	+	1			5.6	3
Pasiphaea fragments	0.5	3				
P. sivado					10.0	1
P. tarda	0.4	1				
P. multidentata	0.9	1				
Hymenodora glacialis	0.3	2			3.1	1
Cephalopoda fragments	5.1	2				
Bathypolypus arcticus	0.4	1				
Ophiuroidea fragments	0.1	2				
Teleostei fragments	4.6	5				
Fish eggs	0.1	3			0.8	1
Clupea harengus	47.5	3				
Clupea harengus head	12.3	2				
Liparidae fragments	1.9	1				
Paraliparis bathybius	12.4	2				
Micromesistius poutassou	11.3	2				
No. of fish examined	41		22		33	
No. of fish with empty stomachs	11		4		4	
No. of fish with unrecognizable food	3		9		16	
No. of fish with recognizable food	27		9		13	
No. of stations	2		1		3	
Depth distribution	1521-2015 m		2015 m		1498-2015 m	

Table 2. Stomach contents and total lengths of rarely caught fishes from the continental slope of the eastern Norwegian Sea. The trawling depth is given and locality is indicated with letters (S for the southern, 62-63°N and N for the northern, 67-68°N).

Species	Total length (cm)	Depth (m)	Locality	Stomach contents
Liparidae				
Rhodichthys regina	27.8	1521	S	Ooze with foraminiferans
	28.4	1521	S	One digested crustacean, probably *Hymenodora glacialis* (Caridea)
	18.6	1521	S	Not examined for food
Zoarcidae				
Lycodonus flagellicauda	21.7	1521	S	Empty
	13.5	1000	N	One partly digested gammaridea
	15.0	900	N	One *Pseudomma truncatum* (Mysidacea), one *Munnopsis typica* (Isopoda), one *Ischyroceirus megacheir* and one *Byblis minuticornis* (Gammaridea)
Lycodes eudipleurostictus	10.6	650	S	Empty
	11.3	650	S	Not examined for food
	31.0	650	S	Not examined for food
	22.5	585	S	Empty
Lycenchelys muraena	15.5	1000	S	Empty
	13.7	650	S	One *Maera tenera* (Gammaridea), one *Caprella septentrionalis* (Caprellidea)
	12.6	650	S	One partly digested gammaridea
	12.8	650	S	Partly digested crustaceans (Isopoda and Gammaridea)

Table 3. Stomach contents of fishes of the "Upper slope 1 (cold)" species assemblage (Bergstad & al. 1998) in terms of percentage by weight (%W) and number of stomachs in which the given prey category was found (F).

	Onogadus argentatus		*Lycodes pallidus*		*Raja hyperborea*	
	%W	F	%W	F	%W	F
Unidentified remains	0.9	1			0.2	3
Polychaeta indet.			22.1	2	0.1	1
Crustacea fragments	8.8	2	55.2	1	0.5	3
Calanoida indet.	+	1				
Peracarida fragments	2.7	1				
Mysidacea fragments	7.4	2				
Pseudomma fragments	5.6	5				
P. frigidum	7.0	2				
P. roseum	10.4	7				
P. truncatum	1.1	6				
Parerythrops obesa	0.1	1				
Amphipoda fragments	3.9	1			0.2	2
Gammaridea fragments	0.2	3	3.1	1		
Eusiridae fragments	1.4	1				
Eusirus holmi	7.0	2				
Lysianassidae indet.	+	1				
Synopiidae						
Syrrhoe crenulata	0.1	1				
Amathillopsidae						
Amathillopsis spinigera	2.7	2				
Stenothoidae						
Metopa norvegica	+	1				
Ampeliscidae indet.			4.9	1		
Phoxocephalidae						
Harpinia abyssi			12.3	1		
Liljeborgidae						
Liljeborgia fissicornis	0.2	1				
Caprellidea						
Caprella sp.			1.7	1		
Caprella septentrionalis	0.1	1				
Eucarida fragments					+	1
Euphausiacea fragments	5.4	2			5.1	8
Meganyctiphanes norvegica					6.0	11
Thysanoessa inermis					1.3	1
Decapoda					1.1	1
Caridea fragments	34.9	2			0.6	1
Pasiphaea sp.					3.0	1
Calocaris macandreae					0.4	1
Brachyura					+	1
Bivalva			0.7	1		
Teleostei fragments					37.0	14
Micromesistius poutassou					29.3	1
Zoarcidae					15.3	2
No. of fish examined	18		8		31	
No. of fish with empty stomachs	1		3		5	
No. of fish with unrecognizable food	1		0		0	
No. of fish with recognizable food	16		5		26	
No. of stations	6		5		6	
Depth distribution	482-1521 m		650-1521 m		482-1521 m	

Table 4. Stomach contents of fishes of the "Upper slope 2 (warm)" species assemblage (Bergstad & al. 1998). Further details as in legend to Table 1 and 2.

	Reinhardtius hippoglossoides				*Macrourus berglax*		*Cottunculus microps*	
	< 50 cm		> 50 cm					
	%W	F	%W	F	%W	F	%W	F
Unidentified remains	6.7	2			13.0	9	2.0	1
Polychaeta fragments					0.1	1	14.1	4
Goniadidae indet.					0.1	1		
Crustacean fragments			+	2				
Malacostraca fragments	2.1	1					2.4	1
Mysidacea								
Pseudomma fragments							0.2	1
Pseudomma frigidum	+	1						
Boreomysis sp.							0.4	1
Amphipoda fragments	0.1	1			+	2	0.2	1
Gammaridea fragments	2.2	6	+	1			0.3	3
Eusiridae fragments			+	1				
Eusirus holmi	2.4	4	+	1				
Lysianassidae indet.	0.2	1						
Eurythenes gryllus	1.8	2					2.4	1
Centromedon productus					+	1	0.1	2
Cyclocaris guilelmi	+	1						
Onisimus brevicaudatus							2.9	2
Anonyx liljeborgi							1.9	1
Orchomene faeroensis							0.1	1
Acidostoma laticorne							0.1	1
Ischyroceridae								
Erichtonius (Ischyrocerus) megalops							+	1
Ischyrocerus megacheir							+	1
Amathillopsidae								
Amathillopsis spinigera							1.6	1
Stegocephalidae								
Stegocephalus inflatus							3.5	3
Melitidae								
Maera loveni							0.4	1
Stenothoidae								
Metopa spitsbergensis							+	1
Phoxocephalidae								
Harpinia abyssi							0.1	2
Calliopiidae								
Apherusa sp.					0.1	3		
Liljeborgidae								
Liljeborgia fissicornis					0.2	7		
Caprellidea								
Caprella septentrionalis							+	1
Euphausiacea fragments	0.1	1			0.1	3		
Meganyctiphanes norvegica	+	2	+	1	0.2	1		
Stylocheiron indet	+	1						
S. elongatum					+	1		
Decapoda fragments							0.1	1
Brachyura fragments					+	1		
Caridea fragments	0.1	1	0.1	3				
Pasiphaea tarda			0.2	1				
Pandalus montagui			0.2	1				
Hymenodora glacialis	0.1	1						
Bythocaris simplicirostris					0.1	1		
Pycnogonida fragments							0.4	1
Nymphon sp.							66.6	8
Cephalopoda fragments (beak or tissue)	+	1			6.1	1		
Gonatus fabrici			5.2	2				
Ophiuroidea					0.2	5		
Ophiactis balli			+	1				
Ophiactis abyssicola					1.3	1		
Teleostei remains	21.5	10	18.1	16	7.6	2		
Fish eggs	0.4	1						
Clupea harengus	16.7	1	54.8	5	36.4	1		
Clupea harengus head	27.7	1	2.2	2	34.5	1		
Notoscopelus kroeyeri			1.6	1				
Notolepis rissoi			1.9	1				
Micromesistius poutassou	17.8	1	14.4	7				
Micromesistius poutassou head			1.3	1				
No. of fish examined	54		74		67		14	
No. of fish with everted stomachs	0		1		52		0	
No. of fish with empty stomachs	38		40		0		0	
No. of fish with unrecognizable food	0		0		2		0	
No. of fish with recognizable food	16		33		13		14	
No. of stations	4		6		3		3	
Depth distribution	482-638 m		482-812 m		530-638 m		812-1000 m	

Table 5. Stomach contents of rajids of the "Upper slope 2 (warm)" species assemblage (Bergstad & al. 1998) in terms of percentage by weight (%W) and number of stomachs in which the given prey category was found (F).

	Raja radiata		*Bathyraja spinicauda*	
	%W	F	%W	F
Polychaeta	0.5	1		
Crustacea	1.0	1	1.2	3
Gammaridea			1.2	1
Hyperiidea	4.1	1		
Isopoda	0.3	1		
Eucarida	10.2	3		
Euphausiidae	35.7	5	0.5	1
Meganyctiphanes norvegica	35.4	3	3.6	3
Thysanoessa inermis			2.3	2
Caridea				
Pasiphaea sp.			1.0	2
Teleostei	5.2	2	71.6	6
Zoarcidae	6.0	1	14.7	1
Lycodes sp.			3.8	1
Lycodes esmarki	1.7	1		
No. of fish examined	16		11	
No. of fish with empty stomachs	2		0	
No. of fish with identifiable contents	14		11	
No. of stations	2		3	
Depth distribution	482-585 m		482-585 m	

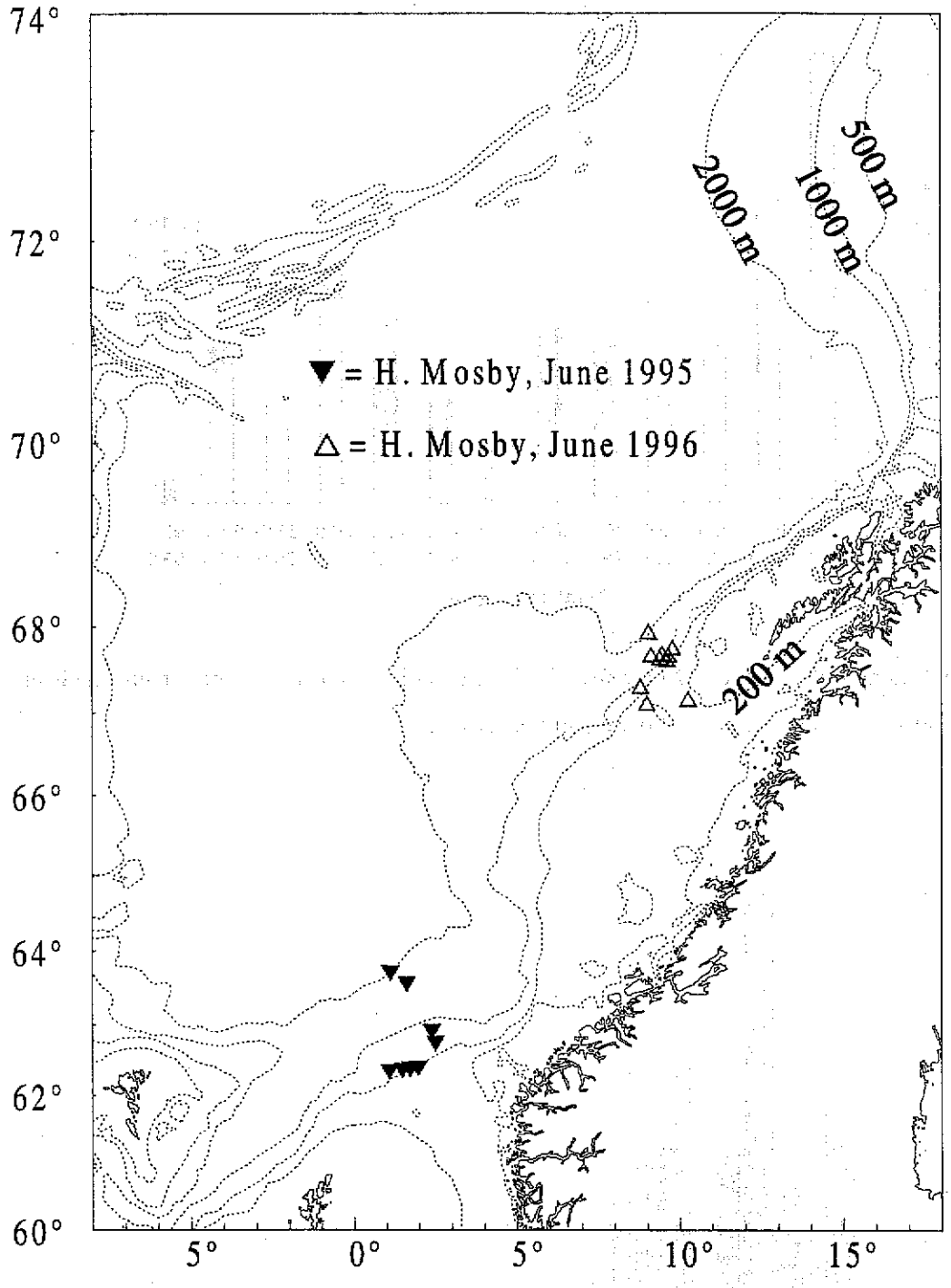

Figure 1. The study area and locations of demersal trawl stations along the continental slope of the eastern Norwegian Sea in June 1995 and 1996.

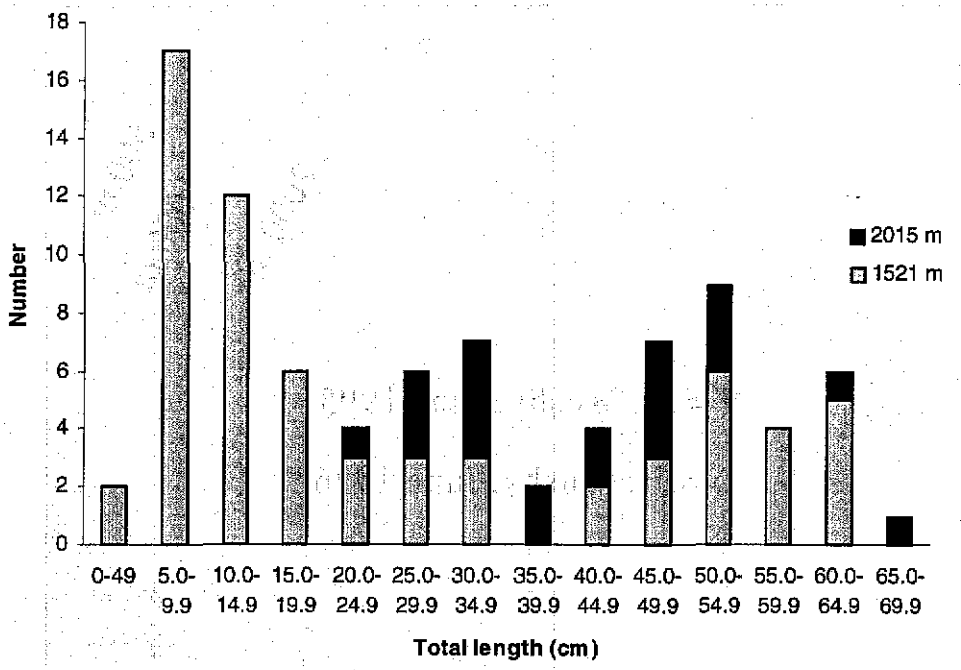

Figure 2. Length distribution of *Lycodes frigidus* caught in two demersal trawl hauls made at 2015 and 1521 m in the eastern Norwegian Sea. N=87.

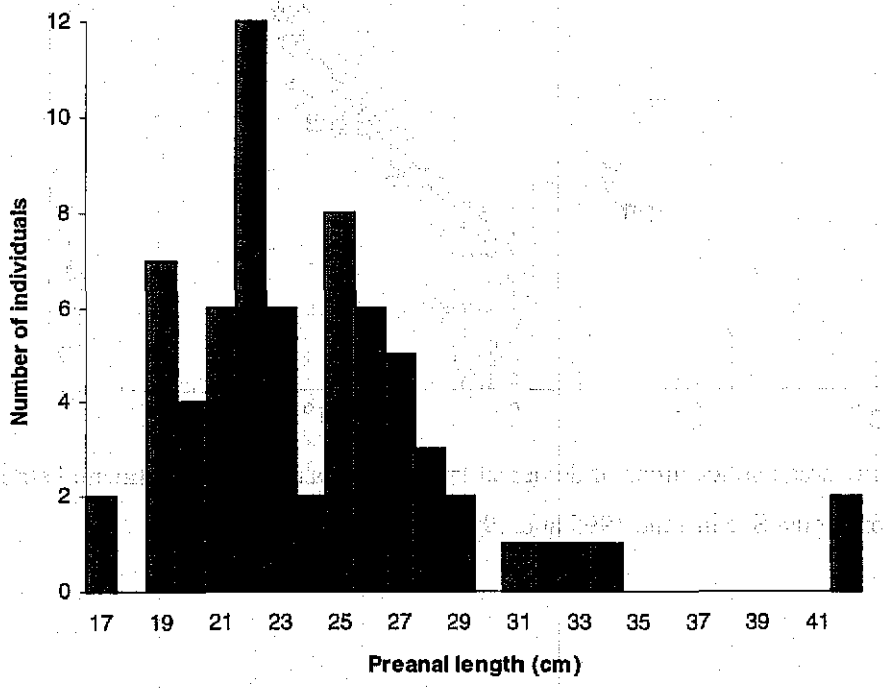

Figure 3. Length distribution (preanal length) of *Macrourus berglax* caught four demersal hauls (530 to 638 m) in the eastern Norwegian Sea 1995 and 1996. N=69.

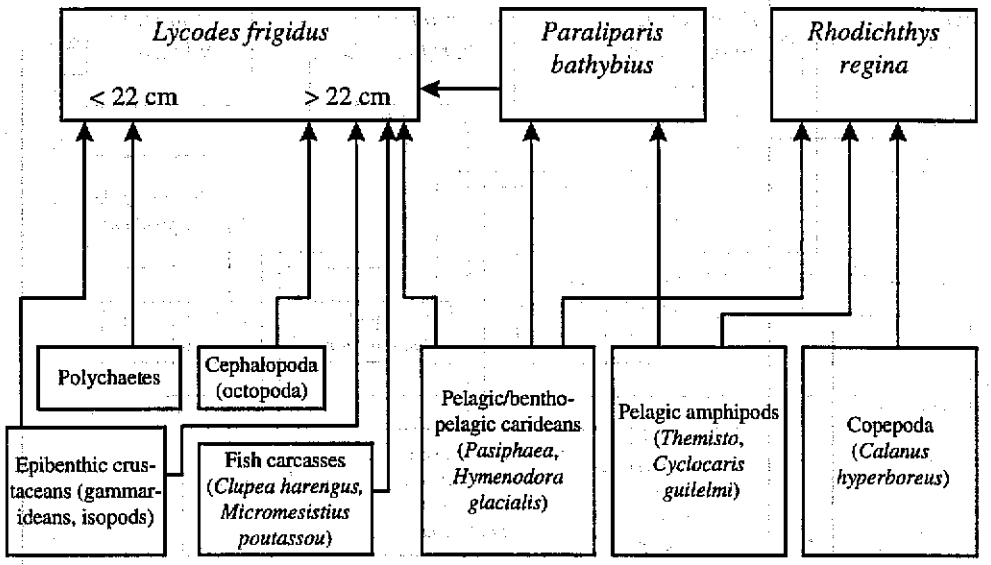

Figure 4. Simplified food-web for the fishes of the "Norwegian Sea Deepwater" species assemblage (Bergstad & al. 1998). Lines are drawn according to the results of the present study, supported by previous studies (Collett 1880 and 1905; Johnsen 1921).

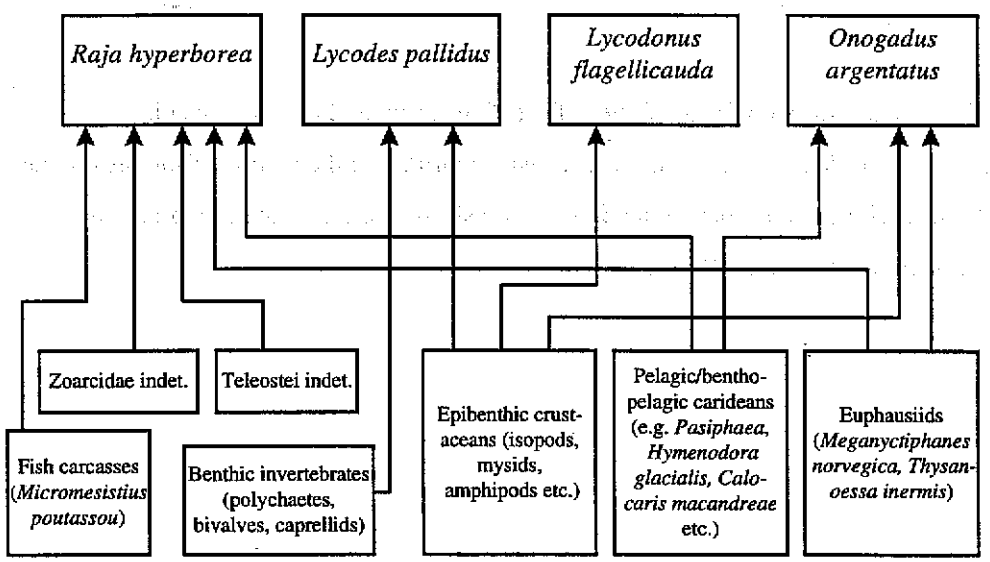

Figure 5. Simplified food-web for the fishes of the "Upper slope 1 (cold)" species assemblage (Bergstad & al. 1998). Lines are drawn according to the results of the present study, supported by previous studies (Collett 1880, 1905; Briskina 1939; Dolgov 1994).

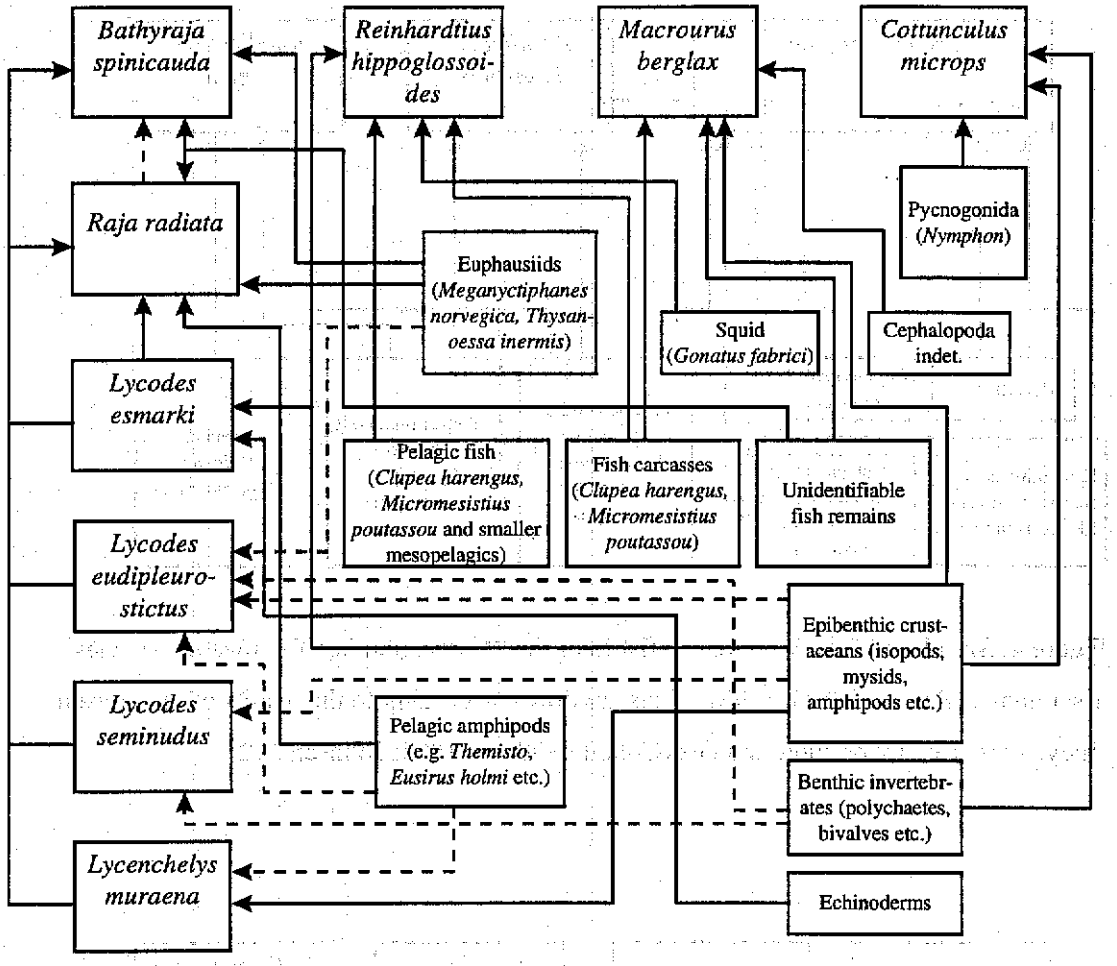

Figure 6. Simplified food-web for the fishes of the "Upper slope 2 (warm)" species assemblage (Bergstad & al. 1998). Lines are drawn according to the results of the present and previous studies, with broken lines indicating relationships found by others (Collett 1880, 1905; Andiyashev 1964; Jensen 1948).