Trophic ecology of deep-water fishes associated with the continental slope of the eastern Norwegian Sea

Otte Bjelland, Odd Aksel Bergstad, Jon Egil Skjæraasen & Kenneth Meland

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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.

Most of the smaller fishes fed on hyperbenthic 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. Few cases of predator-prey relationships between the typical slope fishes were found.

Otte Bjelland, Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway. – Odd Aksel Bergstad, Institute of Marine Research, Flødevigen Marine Research Station, N-4817 His, Norway. – Jon Egil Skjæraasen, Trondhjem Biological Station, Norwegian University of Science and Technology, Bynesveien 46, N-7018 Trondheim, Norway. – Kenneth Meland, University of Bergen, Department of Fisheries and Marine Biology, PO Box 7800, N-5020 Bergen, Norway.
E-mail: otte.bjelland@imr.no

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INTRODUCTION

The trophic ecology of continental slope fish communities has been studied extensively in different parts of the eastern North Atlantic (Clarke & Merrett 1972; Mauchline & Gordon 1983a, 1983b, 1984a, 1984b; Merrett & Domanski 1985; Mahaut & al. 1990). In the Norwegian Sea, however, only a few single species studies have been carried out (Eliassen & Jobling 1985; Savvatimskyi 1985; Berestovskyi 1989; Michalsen & Nedreaas 1998). These studies focused on the feeding of commercially interesting species like Greenland halibut (*Reinhardtius hippoglossoides*), roughhead grenadier (*Macrourus berglax*), and starry ray (*Raja radiata*) in the slope areas between 68°N and 76°N. Collett (1880, 1885, 1905) also reported on stomach contents of many of the fishes collected from the Norwegian Sea during the pioneer cruises on the research vessels *Vøringen* (1876-78) and *Michael Sars* (1900-04).

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 sampling in 1995 and 1996 in the depth range 400-2050 m off western Norway, Bergstad & al. (1999) identified four species-assemblages with characteristic compositions and distributions. The deepest was the 'Norwegian Sea Deepwater'- assemblage with only three 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. A fourth species assemblage (The 'Atlantic Water' assemblage), comprising 16 species, occurred even shallower, i.e. on the shelf-break.

In this paper we focus primarily on the trophic ecology of fishes belonging to the first three (and deepest) of these assemblages. Based on our new data 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 & al. (1999).

Stomach samples were extracted for most fish spe-

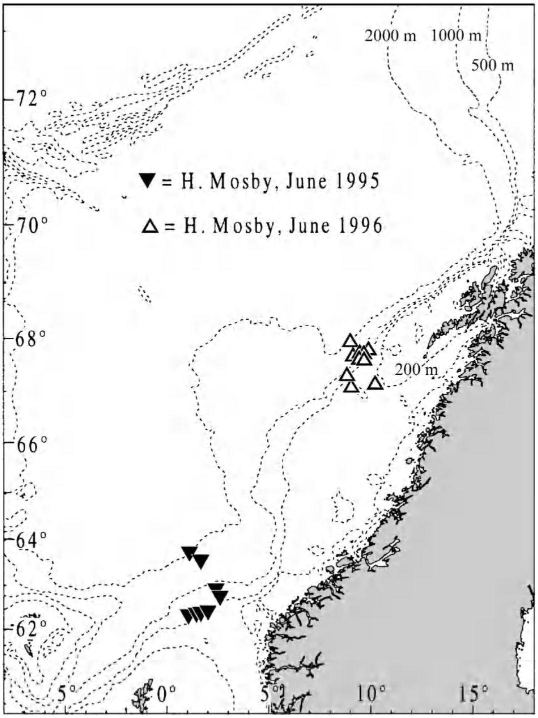

Fig. 1. The study area and locations of demersal trawl stations along the continental slope of the eastern Norwegian Sea in June 1995 and 1996.

cies. Stomachs showing signs of regurgitation were excluded from further analyses. Unfortunately, few useful samples were obtained for abundant species which tend to have everted stomachs, e.g. *Sebastes* spp. and *Macrourus berglax*. Stomachs with contents were labelled individually and preserved in 4 % seawater solution of formaldehyde buffered with sodium tetraborate. 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 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 hours or until a constant weight was obtained. For the rajids, wet weights were used (Skjæraasen 1998). 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). 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 heads of 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 measurable 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 were 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

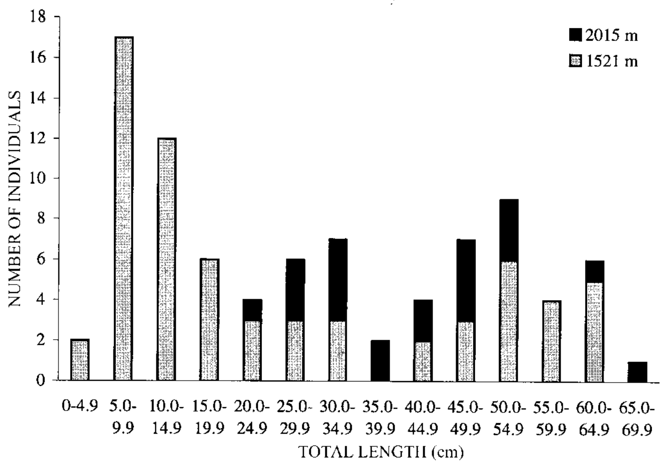

Fig. 2. Length distribution of *Lycodes frigidus* caught in two demersal trawl hauls made at 2015 and 1521 m in the eastern Norwegian Sea. N = 87.

sediments were rich in foraminiferans of the genera *Cibicides*, *Cribostomoides*, and the planktonic *Neogloboquadrina pachyderma*, but the nutritional values 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

Thirty-four specimens of this species were caught in the four deepest hauls at 2051-1498 m. Their total length ranged from 13 to 26 cm. Only 13 stomachs contained identifiable prey, while most of the others contained small quantities of soft tissue or were empty (Table 1). The stomach contents were dominated by the same foraminiferan ooze as observed in the previous. The presence of sediments in this species is strange since most identifiable remains were pelagic organisms. Possibly sediments were ingested during the tow. 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 & 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 & al. (1983) observed *P. bathybius* at baited traps placed at about 4000 m in the Porcupine Seabight in the northeastern 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 2 (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 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. Two stomachs contained remains of carideans, and because of their large size these also contributed more than 30 % to the total contents. The characteristic orange-red colour indicated that the fragments originated from *Hymenodora glacialis*. Other important prey were the amphipods *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 individuals examined in previous studies, and the species appears rather euryphagous and is distributed within

Table 1. Stomach contents of fishes of the "Norwegian Sea Deepwater" species assemblage (Bergstad & al. 1999) 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	

a wide depth range. 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, but a few years later Collett (1905) examined some specimens caught in the same area as our southern locality. He 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 crustaceans (e.g. *Pseudomma roseum*, *Meganyctiphanes norvegica*, and some gammaridean amphipods) occurred in the smaller ones. It is likely that the occurrence of herring in stomach contents of this species reflects scavenging, as the probability of encountering live herring at these great depths is low.

Lycodes pallidus Collett

Eight specimens were caught in five hauls at 650-1521 m depths, and they measured 7.4-17.0 cm TL. The stomach contents (Table 3) consisted primarily of polychaetes and unidentifiable crustacean fragments, but one individual had consumed a 12 mm long *Harpinia abyssi*, an 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 molluscs, and amphipods (Collett 1905; Briskina 1939), 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.

It should be noted that ongoing work on the phylogeny of the *Lycodes* genus has indicated that most of the specimens treated as *L. pallidus* in the present study probably belong to a not yet described species (P.R. Møller pers. commn, Zoological Museum of Copenhagen).

Lycodonus flagellicauda (Jensen)

Only three specimens occurred in the catches; one at 1521 m at 63°N, and two small specimens 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 third specimen, caught at 900 m, gammaridean amphipods (*Byblis minuticornis* and *Ischyroceirus megacheir*), a mysid (*Pseudomma truncatum*), and an isopod (*Munnopsis typica*) occurred.

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-

Table 2. Stomach contents and total lengths of rarely caught fishes on 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 2 (cold)" species assemblage (Bergstad & al. 1999) 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	

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 (Table 3). Five stomachs were empty, while the contents of the others were dominated by fish remains. Not all remains could be identified, but one stomach contained blue whiting *Micromesistius poutassou* contributing 29.3 % to the total weight of the stomach contents. 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 three of the four adult specimens examined by him had fish remains in their stomachs. Zoarcids occurred among the fish ingested by one of the specimens, the remainder being unidentifiable. 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 1 (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 was 482-812 m, and the length range of the Greenland halibut was 39-81 cm. Among the fish smaller and larger than 50 cm, 70 and 54 % of the stomachs were empty, respectively (Table 4). The stomach contents consisted mostly of fish and fish remains (about 90 % in weight) and did not differ much between the two arbitrarily selected length groups. 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 20 to 30 cm dominated the fish fraction. Only the heads of these were found in some cases. Smaller mesopelagic species i.e. *Notoscopelus kroeyeri* and *Arctozenus 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 & Gulliksen 1982; Michalsen & Nedreaas 1998), off West Greenland (Pedersen & Riget 1993; Jørgensen 1997), in Icelandic waters (Paschen 1968), and in the north-eastern Atlantic (Bowering & Lilly 1992), while information on diet in the eastern Norwegian Sea south of 71°N is scarce. The general impression from most studies is that Greenland halibut is piscivorous but also to some degree feeds on shrimps and cephalopods. Also other studies have shown that fish species generally considered to be epipelagic sometimes occur in the diet. Bowering & Lilly (1992) 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 (Michalsen & Nedreaas 1998). The occurrence 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 & 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 & Nedreaas (1998) concluded 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.

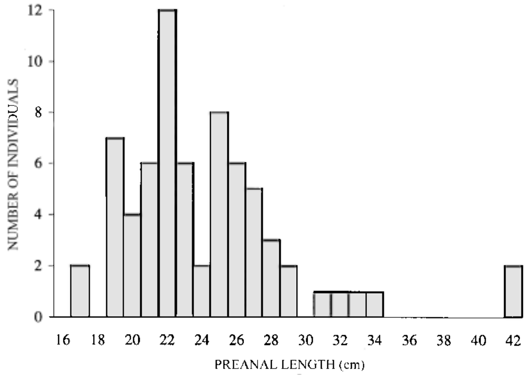

Fig. 3. Length distribution (preanal length) of *Macrourus berglax* caught in four demersal hauls (530 to 638 m) in the eastern Norwegian Sea 1995 and 1996. N = 69.

Macrourus berglax Lacepède

This species was caught in four of the hauls, at 530 and 585 m at 63°N, at 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 incidence of everted stomachs was 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 from 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 & Jobling (1985). Some studies of the trophic ecology of this species have been carried out in the north-eastern Norwegian Sea (Eliassen & Jobling 1985; Savvatimskiy 1985), and they show that *M. berglax* is an euryphagous predator feeding primarily on hyperbenthic and benthopelagic shrimps and amphipods, but polychaetes, cephalopods, and ophiuroids.

Table 4. Stomach contents of fishes of the "Upper slope 1 (warm)" species assemblage (Bergstad & al. 1999). 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		

Eliassen & Jobling (1985) also found fish in the stomachs of *M. berglax*, and this was primarily observed during the summer months. The fishes found by Eliassen & Jobling (1985) were all benthopelagic, and the presence of herring in stomachs examined in our study probably reflects 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 of 15 specimens of 8-21 cm TL were caught, all from the depth range 585-1000 m. The stomach content of 14 individuals were examined, and all 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 hyperbenthic amphipod species were identified in the stomach content.

Collett (1905) also reported polychaetes, pycnogonids, and amphipods in the specimens collected by him from northern Norwegian waters, and our study

Table 4. (continued)

	Reinhardtius hippoglossoides				*Macrourus berglax*		*Cottunculus microps*	
	< 50 cm		> 50 cm					
	%W	F	%W	F	%W	F	%W	F
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				
Arctozenus 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	

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. 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) 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 feeding habits with increasing size and age. Small individuals seem to feed on a variety of crustaceans and bivalves, but there is probably a gradual shift towards a diet composed almost exclusively of echinoderms starting when the fish reach lengths between 30 and 40 cm.

Lycodes seminudus Reinhardt
Eight individuals ranging from 23 to 46 cm were caught in the haul taken at 812 m 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 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 originally 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 occurred.

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 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 locations in the northern Atlantic previously (McEachran & al 1976; Templeman 1982; Pedersen 1995; Dolgov 1997; Skjæraasen 1998), but these studies were either from the north-western Atlantic, or shallower areas of the north-eastern Atlantic. The general impression from 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 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 various fishes have been reported from stomachs of specimens caught in the western Barents Sea (Koefoed 1956), and 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

Based on our own and previous findings we attempted to draw simplified food-webs for each of the three species assemblages of Bergstad & al. (1999) highlighting the most important trophic relationships between the fish species and between the fish species and other prey groups (Figs 4-6). Some connections shown by broken lines are based on very limited data or studies from other parts of the north-eastern Atlantic and are admittedly speculative. Also, no information is included for fishes of the 'Atlantic Water (shelf edge)' assemblage of which species like the redfishes (*Sebastes* spp.) and blue whiting (*Micromesistius poutassou*) are particularly abundant characteristic members. These species do to some extent co-exist with those included in Fig. 6. The redfishes are assumed to be planktivores (Pedersen & Riget 1993; Dolgov & Drevetnyak 1995), but very little documentation exists for the eastern Norwegian Sea at present. The trophic ecology of blue whiting has been studied earlier (Timokhina 1974; Plekhanova 1989), and the results show that the diet is dominated by pelagic crustaceans, i.e. euphausids (which is the most important prey), copepods, and hyperid amphipods.

Demersal slope fishes basically have two alternative categories of food resources 1) benthos, hyperbenthos

Table 5. Stomach contents of rajids of the "Upper slope 1 (warm)" species assemblage (Bergstad & al. 1999) 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		
Euphausidae	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	

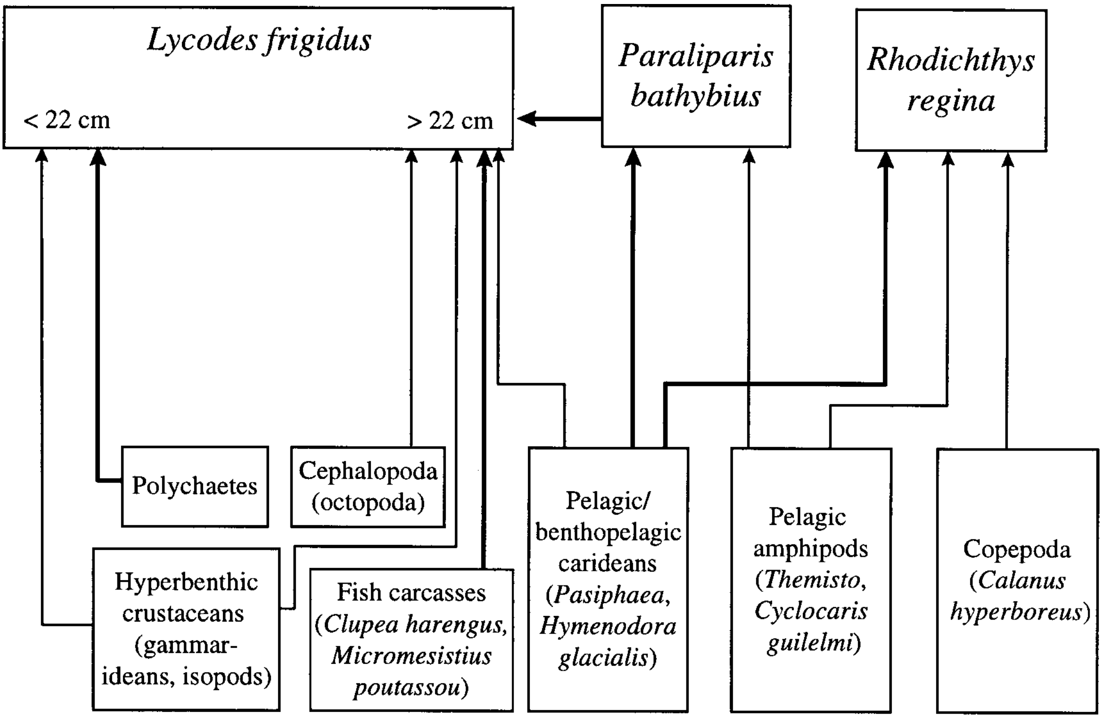

Fig. 4. Simplified food-web for the fishes of the 'Norwegian Sea Deepwater' species assemblage (Bergstad & al. 1999). Lines are drawn according to the results of the present study, supported by previous studies (Collett 1880, 1905; Johnsen 1921). Trophic relationships of special importance are outlined.

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 small *Lycodes frigidus*, *L. pallidus*, and *L. seminudus* for which little information was available. Little is known about the biomass of macrobenthos in the Norwegian Sea, but Zatsepin & Rittikh (1976) give some rough figures for the distribution of biomass of different trophic groups. The lack of detailed information in their study makes it difficult to relate their findings to the present study, but the benthos appears relatively poor at depths below 600 m in the Norwegian Sea.

Planktonic, nektonic or hyperbenthic crustaceans (euphausids, amphipods, mysids, carideans etc.) 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.

Different terms like 'hyperbenthos', 'suprabenthos', 'hypoplankton', 'demersal zooplankton', and 'benthopelagic plankton' have been used for the association of small animals living in the water layers close to the sea bed (mysids, copepods, amphipods, isopods, decapods etc.), and Mees & Jones (1997) recommend to use the term 'hyperbenthos' for this fauna. They further recommend to keep the subdivisions into 'tychobenthos' and 'hekobenthos' introduced by Beyer (1958) to describe two different components of the hyperbenthos. The terms are used to describe both basically pelagic species that are 'accidentally' (<Gk *tycho* accident) found close to the bottom (krill, copepods, hyperid amphipods, pelagic carideans etc.) and species which are in some way truly related (<Gk *hekon* voluntary) to the bottom (mysids, amphipods, cumaceans, isopods etc.). Members of both these components occur in the diets of various fish species, and although information is scarce for many of the species, the results of the present and previous studies indicate that both tycho- and hekobenthos are important food for most of the slope fishes. Hekobenthos seems to be particularly im-

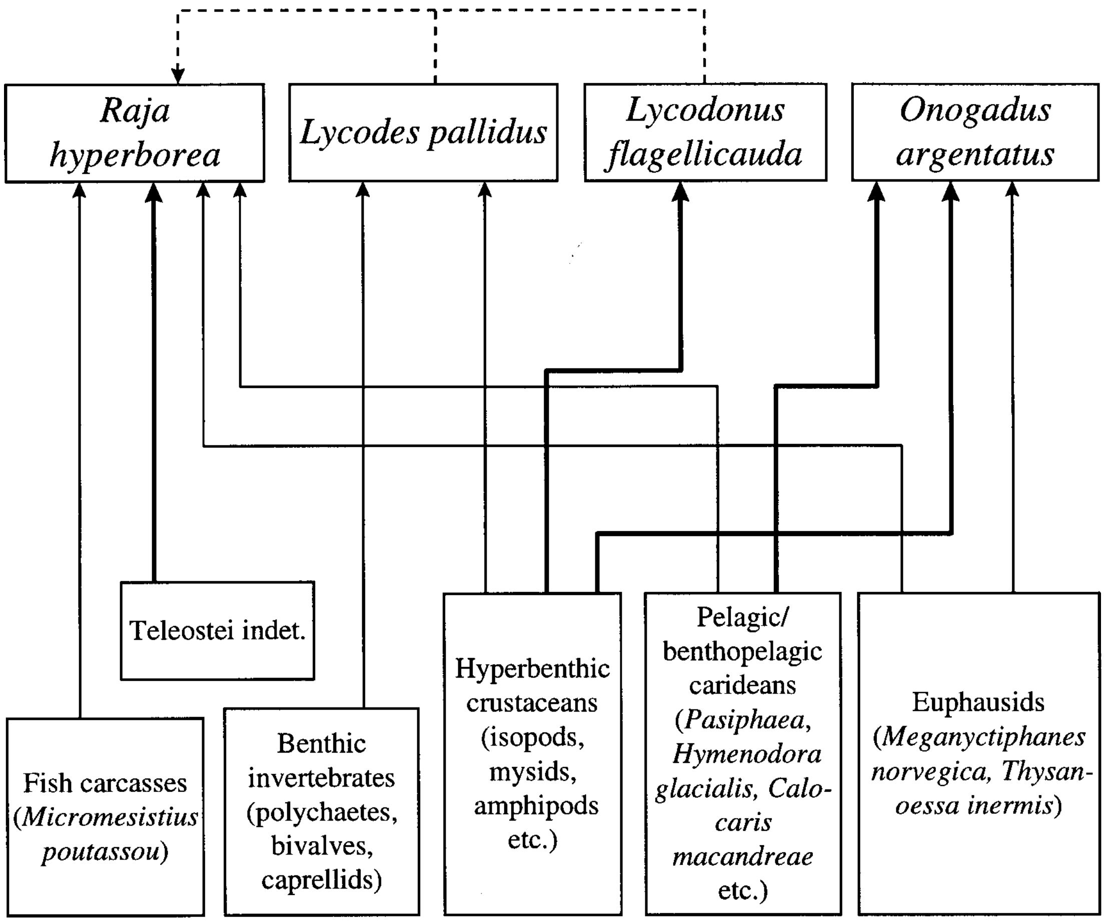

Fig. 5. Simplified food-web for the fishes of the 'Upper slope 2 (cold)' species assemblage (Bergstad & al. 1999). Lines are drawn according to the results of the present study, supported by previous studies (Collett 1880, 1905; Briskina 1939; Dolgov 1994). Broken lines are drawn between the zoarcids and *Raja hyperborea* because they could not be identified to species in the stomach contents. Trophic relationships of special importance are outlined.

portant to species like *Lycodonus flagellicauda* and *Onogadus argentatus*, but possibly also to *Lycodes eudipleurostictus* and *Lycenchelys muraena* for which information on diet is scarce. The knowledge of the hyperbenthic fauna in the transition zone between Atlantic Water and Norwegian Sea Deep-water is poor, but unpublished data (T. Brattegard pers. commn, University of Bergen; Skjoldal & al. 1993) indicate that this zone is remarkably rich, both in diversity and biomass. This part of the slope is an environment characterised by rapid changes in hydrography and current regime. The rapid shifts in hydrographical conditions, where the temperature at a given depth can change from below zero to 2-3 °C in a few days, are caused by internal waves between the water masses (Helland-Hansen & Nansen 1909). Another interesting aspect is the near-bottom currents at this part of the slope. Sælen (1959), working in the south-eastern Norwegian Sea, measured velocities of up to 30 cm/s at depths of 650 m, while little water movement was recorded below 900 m. Carrying out similar studies a couple of years later Sælen (1963) found that the currents along the bottom contours shifted in direction from N-E to S-W within 30 hours, and concluded that although the net transport of water is low in this transition zone, considerable velocities can be found. This physical scenario together with sedimentation/sinking of organic material from the productive epipelagic layers in these areas probably results in an environment rich in particulate organic matter (bottom currents favouring resuspension) with high local production of hyperbenthic organisms of both Atlantic and Arctic origin.

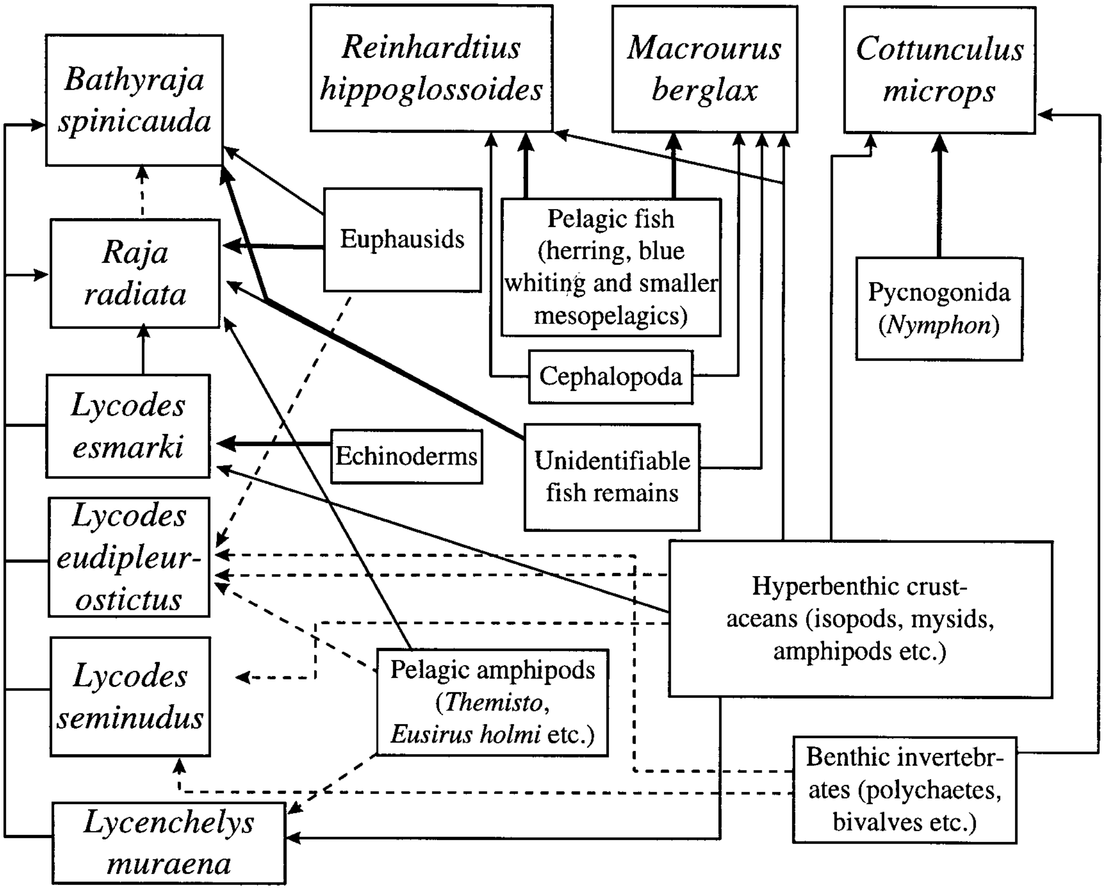

Fig. 6. Simplified food-web for the fishes of the 'Upper slope 1 (warm)' species assemblage (Bergstad & al. 1999). Lines are drawn according to the results of the present and previous studies, with broken lines indicating relationships found by others (Collett 1880, 1905; Andriyashev 1964; Jensen 1948). Trophic relationships of special importance are outlined.

Pelagic crustaceans seem to be particularly important prey for many of the slope fishes, and in most cases this probably reflects occurrences of these prey organisms in the vicinity of the sediments (i.e. as tychobenthos). Mauchline & Gordon (1991) examined the occurrence of planktonic and micronektonic species in the diets of benthopelagic fishes at the slopes of the Rockall Trough (northeastern Atlantic), and they discussed several different mechanisms making these pelagic organisms available to the fish assemblages at the slope. They concluded that the major factor involved is the impingement of organisms onto the slope through the truncation of the vertical distribution of the epi- and mesopelagic species in the water column. 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 & al. 1997). Hydroacoustic observations showed diurnal migrations between 50 and 450 m. These observations suggest that vertical impingement of pelagic fauna is also important in the food supply to the fish assemblages on the slope of the eastern Norwegian Sea. It has been shown in other areas of the north-eastern Atlantic that the vertical distribution of some of the crustaceans generally considered as pelagic organisms (e.g. *Meganyctiphanes norvegica*, *Hymenodora glacialis*, and *Sergestes arcticus*) can extend down to the layers close to the sediments, where they may also aggregate (Mauchline & Fisher 1969; Hargreaves 1984; Domanski 1986). A strange observation of the present study is the scarcity of mesopelagic fishes in the diets of the slope fishes. Only Greenland halibut is to a limited degree found to feed on these abundant fishes. Mesopelagic fishes are, on the other hand, probably more capable of actively avoiding the areas close to the slope than other nektonic organisms. The predation risk is probably much higher in these areas compared with the open waters of the Norwegian Sea.

In addition to the comparatively high local pelagic production, there is evidence of advective production of nekton and plankton in the northeasterly Atlantic current from the Rockall Trough (Mauchline 1986). This may provide a steady food supply to demersal fish along the upper slope, and Mauchline & Gordon (1991) suggested that this kind of horizontal impingement of pelagic fauna on the slope is important as the bottom depth shallows in the northern parts of the Rockall Trough. This might also play a significant role in parts of the slope area of the Norwegian Sea.

In some cases the presence of pelagic prey in the fish stomachs might be a result of vertical feeding migrations of the fishes into the water column. The two species of liparids and *Onogadus argentatus* all seem to have diets dominated by pelagic crustaceans. This fits well with reports of catches of these species more than 100 m off the sea bed in the eastern Norwegian Sea (Johnsen 1921). As mentioned earlier the blue whiting and the redfishes also feed pelagically, and the potential for vertical feeding migrations by Greenland halibut has also been discussed.

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. The occurrence of the widely distributed, scavenging amphipod *Eurythenes gryllus* in the diets of slope fishes further demonstrates the importance of this input. Carcasses of herring and blue whiting may also be significant to other large and shallower distributed slope fishes, i.e. Greenland halibut and *Macrourus berglax*, but the relative importance of scavenging and feeding on live prey is uncertain for these species. Evidence of scavenging among deep-sea demersal fishes is rare and results sometimes difficult to interpret (Clarke & Merrett 1972; Mauchline & Gordon 1984c; Merrett & Domanski 1985). Mauchline & Gordon (1984c) found that blue whiting was important as food for many different deep-sea demersal fishes of the Rockall Trough, and found evidence of scavenging, explaining this in at least four different species. In the Rockall Trough blue whiting occurred in stomach samples mainly during spring, and it was suggested that the spawning migration of this species into the area might provide significant contributions to the diets of scavengers. Similarly, the results of the present study indicate that many of the larger members of the fish assemblages at the slopes of the eastern Norwegian Sea may benefit from the feeding migrations of this species into the area during summer. The Norwegian Sea is currently utilised as a feeding area by several large stocks of pelagic fish, and it seems that food-falls originating from the pelagic zone are more important to the deep-water demersal fishes in this area than reported from other areas. This, however, contrasts somewhat with the review on this topic by Merrett & Haedrich (1997).

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 such as Greenland halibut seems rather to feed on herring and blue whiting (live or dead) than on other slope fishes or even mesopelagic fishes.

We concluded previously (Bergstad & al. 1999) 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.

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