PREDATION BY COD (GADUS MORHUA) ON AMPHIPOD CRUSTACEANS IN THE NORTHWESTERN ATLANTIC

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PREDATION BY COD (*GADUS MORHUA*) ON AMPHIPOD CRUSTACEANS IN THE NORTHWESTERN ATLANTIC

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COD
PREDATION
AMPHIPODS
NORTHWESTERN ATLANTIC

ABSTRACT. – Cod of all sizes caught offshore in the northwest Atlantic fed on amphipods. Eighty two species were identified as prey. Many were collected only at restricted depths and locations. Cod on the Southeast Shoal of the Grand Bank preyed on shallow water species that have a relict distribution. The sizes of amphipods consumed increased rapidly up to 36 cm long cod, but there was little further increase to the size of amphipods consumed by larger cod. The preponderance of mature males amphipods and the occurrence of sympagic (under ice) species in the cod indicates that they forage extensively off the bottom and may at times rise to near the surface under the pack ice.

MORUE
AMPHIPODES
PREDATION
ATLANTIQUE NORD-OUEST

RÉSUMÉ. – Les Morues de toutes tailles recueillies au large, dans l'Atlantique du nord-ouest, se nourrissent d'Amphipodes. Quatre vingt deux espèces ont été identifiées comme proies. De nombreuses espèces ne peuvent être récoltées qu'à des profondeurs et des emplacements limités. Les Morues du haut-fond sud-est du Grand Banc capturent les espèces d'eau peu profonde qui ont une distribution relictuelle. La taille des Amphipodes consommés augmente rapidement jusqu'à ce que les Morues atteignent 36 cm, puis elle n'augmente que modérément pour les Morues de taille plus élevées. La prépondérance des mâles d'Amphipodes mûrs et l'occurrence d'espèces sympagiques (sous la glace) parmi les Morues indique qu'elles capturent bien leurs proies au fond et qu'il peut leur arriver de chasser aussi presque jusqu'à la surface.

INTRODUCTION

The cod stock complex known as 'Northern Cod' found in Northwest Atlantic Fisheries Organization (NAFO) Subareas 2J and 3KL and the Grand Bank cod, Subareas 3N and 3O were the largest stocks in the northwestern Atlantic. A collapse of these stocks resulted in a fishing moratorium being declared in 1992, but since then cod have not recovered to any significant degree in the offshore waters. The present study deals with fish caught offshore (Fig. 1) before the moratorium was invoked.

Adult offshore cod spawn primarily but not exclusively along the margin of the continental slope from Labrador to the northern margin of the Grand Bank, from February to May, depending upon the latitude. The eggs and larvae drift south with the Labrador Current. As juveniles, cod associate with pelagic cnidarians (Sars 1879, J.M. Green pers obs) and by August, they appear inshore (< 25 m) where they are attracted to algal beds and other types of cover (Keats *et al* 1986). However, even at this time they continue to feed primarily on pelagic copepods (Keats *et al* 1986). There is a gradual shift to benthic prey such as harpacticoid copepods, amphipods, annelids amd molluscs (Keats & Steele 1992). As they age (one and two years old) and grow in size, they occur in deeper water (Gregory *et al.* 1996), but migrate inshore at night (Keats 1990). With increasing size they become increasingly piscivorous. For 'Northern Cod' of 40-70 cm length, capelin and sand lance become the dominant foods (Lilly & Fleming 1981) because of their abundance and relatively small size. Thus 'Northern Cod' tend to become predominantly piscivorous at a younger age and smaller size than do cod in more southern areas where herring, a larger fish, is the dominant prey (Powles 1958).

Although predominantly piscivorous, even large cod (> 70 cm) continue to feed on crustaceans (Powles 1958, Lilly 1991) if they are abundant or when fish are scarce (Templeman 1965; see however Fahrig *et al.* (1993) for evidence of lack of switching). Cod are opportunistic predators and can always find some kind of food, but their behaviour is complex and variable.

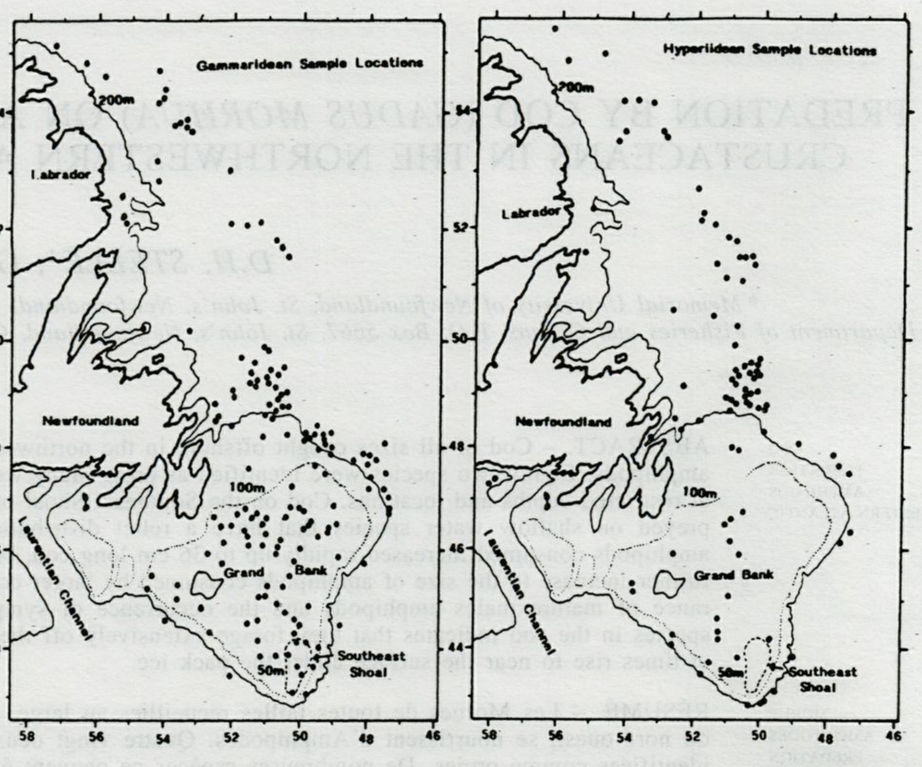

Fig. 1. – Gammaridean (left) and Hyperiidean (right) sample locations.

Following offshore spawning, spent 'Northern Cod' migrate inshore (Templeman 1965, Rose 1993) and in early summer feed intensely on the spawning shoals of capelin. At the time of their inshore migration they were the basis of the historic Newfoundland inshore fishery.

The inshore-offshore migrations of 'Northern Cod' became the subject of considerable speculation after the offshore spawning aggregations were discovered. They formed the basis of a massive offshore fishery in the 1960s and inshore catches declined. However, it was uncertain whether there was a causal relationship, or whether the cod were simply failing to come inshore. After spawning in the relatively warm water off the continental slope, the fish have to cross an intermediate layer of cold water (CIL) before they reach the warm coastal water near shore where the spawning capelin shoals are found in early summer. The CIL could therefore form a potential thermal barrier to the inshore migrations.

The interactions between 'Northern Cod' and capelin have been considered in detail because of the presumed influence on the concentrations and movements of 'Northern Cod' (Lilly 1984). Little or no attention has been given to other types of prey. The present study considers the predatory activities of cod on amphipod crustaceans and what this can indicate about cod behaviour. It also provides some information on the occurrences of amphipods from an area for which there is relatively little published information.

MATERIALS AND METHODS

297 of the cod caught on research cruises made between 1979 and 1992 contained amphipods. Most were obtained in the spring (March-May) (Table I). They were caught at depths between 40 and 450 m, between southern Labrador and the tail of the Grand Bank (Fig. 1), with peaks at 60-100, 180-220 and 300-400 m (Fig. 2 top). Cod with amphipods ranged in length from 20 to 126 cm, but most were 30 to 70 cm in length (Fig. 2 middle).

Since the size of prey consumed is constrained primarily by the mouth size of the fish, fish length has been converted to mouth size, estimated as the product of the length of the mandible x the distance between the right and left mandibles. The relationship between mouth size and body length is allometric (Fig. 2 bottom) so that large fish have proportionately larger mouths than do small.

Table I. – Seasonal distribution of samples.

Month	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
Number	16	100	23	46

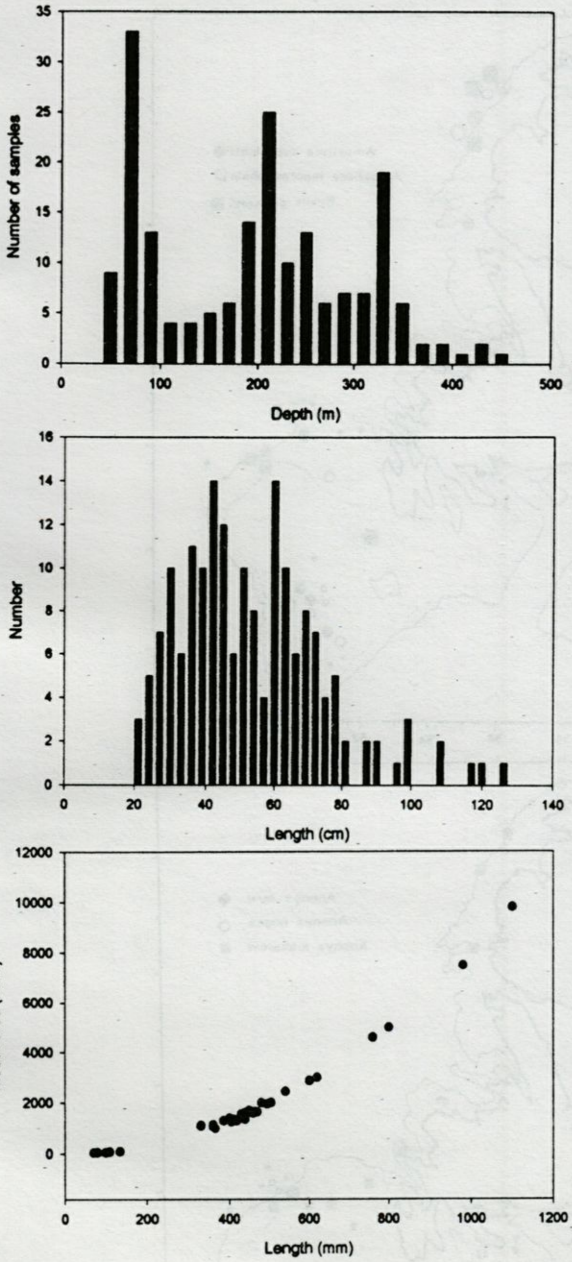

Fig. 2. – Top, deph distribution of cod samples. Middle, length frequency distribution of contaiing amphipods. Bottom, length-mouth area relationship of cod.

Table II. – Distributional patterns of Gammaridean and Caprellidean amphipods in cod stomachs.

Shallow (Southeast Shoal)	
Fine Sediments	Rocks and Algae
Anonyx sarsi	*Pontogeneia inermis*
Psammonyx terranovae	*Metopa alderi*
Hippomedon serratus	*schyrocerus anguipes*
Monoculodes edwardsi	*Corophium bonelli*
Monoculodes tuberculatus	*Paramphithoe hystrix*
Monoculodes intermedius	*Pardalisca cuspidatus*
Unciola irrorata	*Tiron acanthurus*
Amphiporeia lawrenciana	*Caprella septentrionalis*
Acathohaustorius spnosus	*Aeginina longicornis*
Sympagic (Ice associated)	
Pseudalibrotus nanseni	*Pseudalibrotus glacialis*
Gammarus wilkitzkii	*Gammaracanthus loricatus*
Grand Bank (except SE Shoal)	
Anonyx nugax	*Onisimus edwardsi*
Anonyx laticoxae	*Haploops tubicola*
Anonyx lilljeborgi	*Arrhis phylloyx*
Eusirus cuspidatus	*Paroediceros lynceus*
Rozinante fragilis	*Melita dentata*
Unciola leucopis	*Ischyrocerus commensalis*
Cold Intermediate Layer	
Anonyx makarovi	
Continental Slope	
Anonyx nugax	*Orchomene serratus*
Anonyx ochoticus	*Uristes umbonatus*
Anonyx compactus	*Aristias tumidus*
Tmetonyx 'cicada'	*Stegocephalus inflatus*
Haploops setosa	*Haliragoides inermis*
Stenopleustes latipes	*Eurysteus melanops*
Eusirus holmi	*Lilljeborgia fissicornis*
Maera loveni	*Protomedeia stephenseni*
Goesia depressa	*Neohela monstrosa*
Ischyrocerus megacheir	*Ischyrocerus latipes*
All Depths (except SE Shoal)	
Tmetonyx albidus	*Ampelisca macrocephala*
Ampelisca eschrichti	*Byblis gaimardi*
Syrrhoe crenulatus	*Rhachotropis aculeata*
Erichthonius hunteri	

RESULTS

82 species of amphipods (76 gammaridean, 2 caprellideans, 4 hyperiideans) were identified in the stomachs. A few species were found in cod at all depths but most occurred in depth-defined patterns (Table II). Representative distributions are shown in Fig. 3, 4, 5.

The Southeast Shoal of the Grand Bank has shallow depths and variable habitats. Thus it supports a diverse assemblage of shallow water species that either burrow into sandy sediments or that live on rocks and algae. Most of these shallow water species such as *Anonyx sarsi* (Fig. 3 bottom) also occur at shallow depths around Newfoundland (Frost 1936, Fenwick & Steele 1983, Kennedy 1985) but *Acanthohaustorius spinosus*, and *Hippomedon serratus* which are endemic to the northwestern Atlantic were not known previously east of coastal Nova Scotia. Their presence is probably due to the fact that the Shoal is shallow enough (< 50 m) that warm surface water reaches the bottom in the summer. Similar offshore shallow habitats with warm water in the summer occur on Banquereau Bank and at Sable Island.

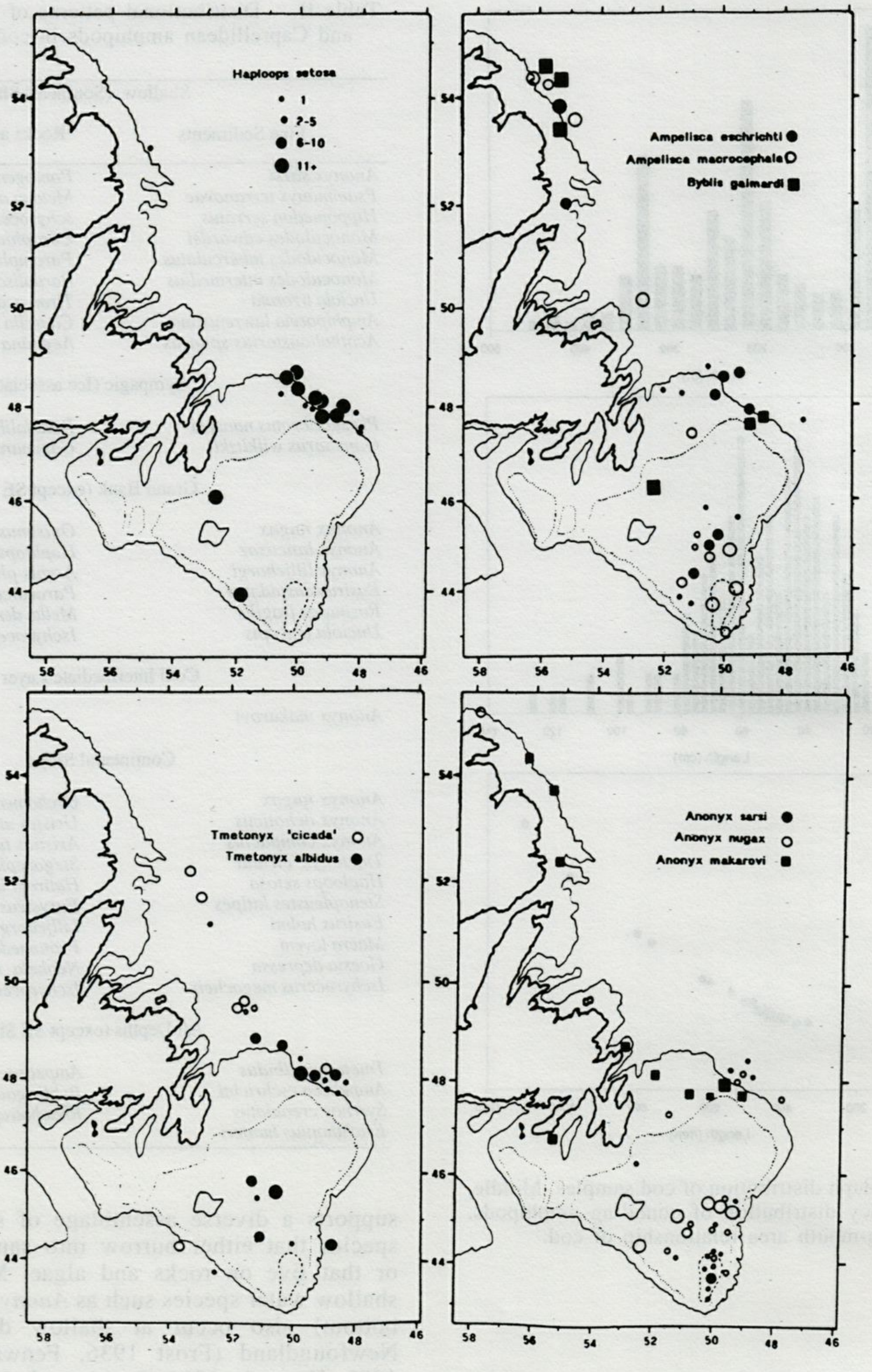

Fig. 3. – Top right, distribution of *Ampelisca* spp. and *Byblis gaimardi* top left distribution of *Haploops setosa*. Bottom right, distribution of *Anonyx* spp.Bottom left, distribution of *Tmetonyx* spp.

At the other extreme, a number of species (e.g. *Tmetonyx* spp, Fig. 3 bottom) were obtained only in relatively deep water off the edges of the banks (Table II), where the water is also relatively warm (slope water). *Anonyx nugax* was found here and on the top of the Grand Bank, but in the CIL on the northeast side of the bank it was replaced by *Anonyx makarovi*. This depth defined *Anonyx* distribution is similar to what is found in the Gulf of St. Lawrence (pers obs).

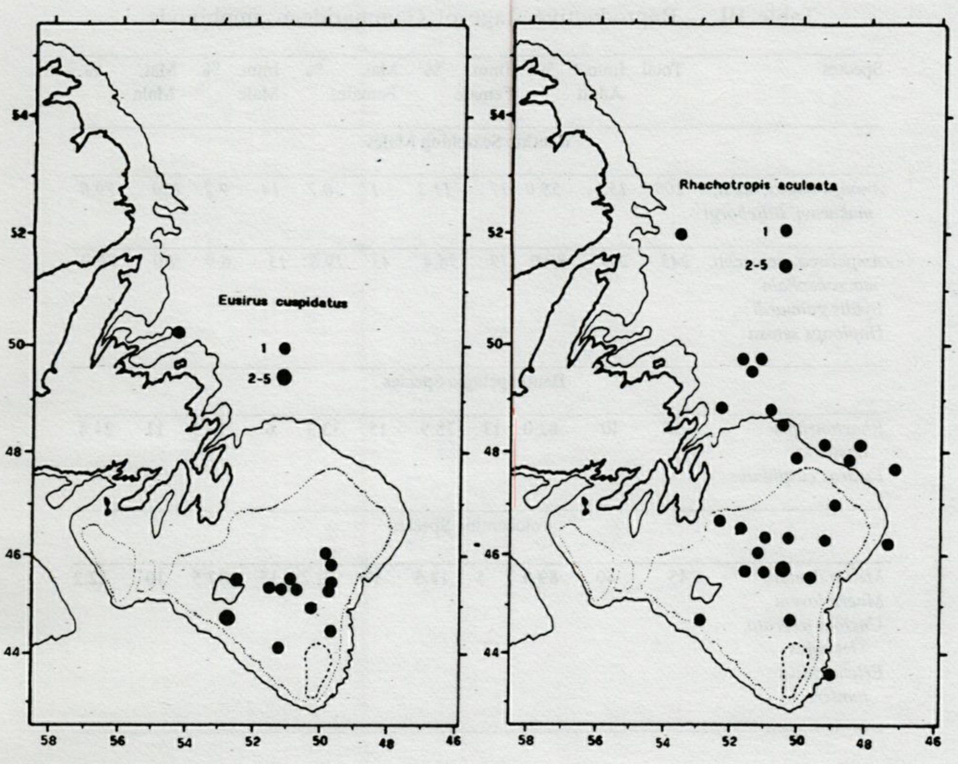

Fig. 4. – Left, distribution of *Eusirus cuspidatus.* Right, distribution of *Rhachotropis aculeata.*

The ampeliscid *Haploops setosa* (Fig. 3 top) was also found only in cod caught off the northeast slope of the bank. This is probably related to the substratum in this region since it is not restrained in its depth distribution. *Ampelisca* spp and *Byblis gaimardi* were found at all depths (Fig. 3 top).

The benthopelagic predaceous *Rhachotropis aculeata* and *Eusirus cuspidatus* were also found to be widely distributed, except on the Southeast Shoal (Fig. 4).

Pelagic hyperiidean amphipods occurred in many stomachs and in large numbers (Fig. 5). Hyperiideans occurred almost exclusively in cod caught on the slopes of the banks and consisted mainly of large adults.

Four species of pelagic gammaridean amphipods (*Gammaracanthus loricatus*, *Gammarus wilkitzkii*, *Pseudalibrotus glacialis*, *Pseudalibrotus nanseni*) were also found in cod stomachs (Fig. 5 left). These are Arctic sympagic species, normally associated with the undersurface of multiyear sea ice.

Prey Selection

Size of Amphipods

There is a rapid increase in the diameter of the amphipods consumed up to a mouth size of 1,000 mm^2 (Fig. 6, 7). The maximum diameter of the amphipod prey increases rapidly with an increase in mouth size, but the minimum size increases much more slowly. Large cod (up to 150 cm) continue to feed on amphipods although there is little further increase in the sizes of the amphipod prey since larger species do not exist in the cod habitat. The dominant prey of the larger cod are decapod crustaceans (shrimp and crabs) and fish.

A mouth size of 1,000 mm^2 corresponds to a cod body length of 36 cm and is approximately the size at which they cod begin to feed intensively on capelin (100 mm) and sand lance (150 mm) (Lilly & Fleming 1981). These fish prey have corresponding diameters of 13-33 and 13-22 mm respectively (Fig. 6 top). The sizes of the fish prey are not correlated with the sizes of the cod (Lilly & Fleming ibid).

Sex and maturity of the amphipods

The males of some benthic species become pelagic at maturity and search for females in the water column, at times as far up as the surface (pers obs). When they achieve maturity they develop a distinctive morphology (Steele 1995). Such sexually mature males with their distinctive morphology were more abundant in cod stomachs than the immatures which tend to remain close to the bottom. While this bias could be due to size selection for amphipods of larger size, the fact that the mature specimens were mostly males

Table III. – Reproductive stage of Gammaridean amphipods.

Species	Total	Imm.+ Adult	%	Imm. Female	%	Mat. Female	%	Imm. Male	%	Mat. Male	%
Benthic Searching Males											
Anonyx nugax, sarsi, makarovi, lilljeborgi	200	152	58.0	17	11.2	1	0.7	14	9.2	120	79.0
Ampelisca eschrichti, macrocephala *Byblis gaimardi* *Haploops setosa*	243	217	89.0	79	36.4	43	19.8	15	6.9	80	36.9
Benthopelagic Species											
Rhachotropis aculeata *Eusirus cuspidatus*	55	40	82.0	13	28.9	15	33.3	6	13.3	11	24.4
Holobenthic Species											
Melita dentata *Maera loveni* *Unciola irrorata, leucopis* *Erichthonius hunteri*	45	40	89.0	5	12.5	10	22.2	15	37.5	10	22.2

(Table III) indicates that the latter were more vulnerable to cod predation. Similar numbers of mature males and females of the benthopelagic and holobenthic species were found in the stomachs (Table II).

DISCUSSION

Although traditionally classed as a groundfish and caught commercially on the bottom when in excess of 45 mm in length, it is apparent from

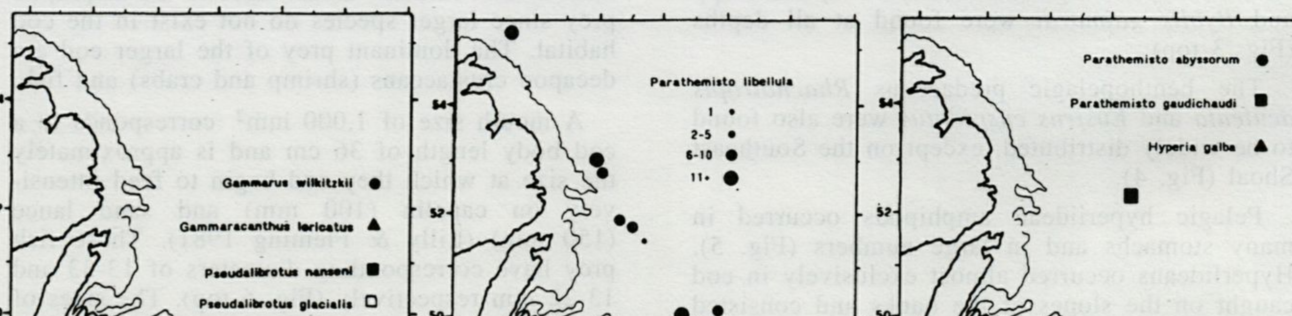

Fig. 5. – From left to right, distribution of sympagic species, of *Parathemisto libellula*, and of *Hyperia galba* and *Parathemisto* spp.

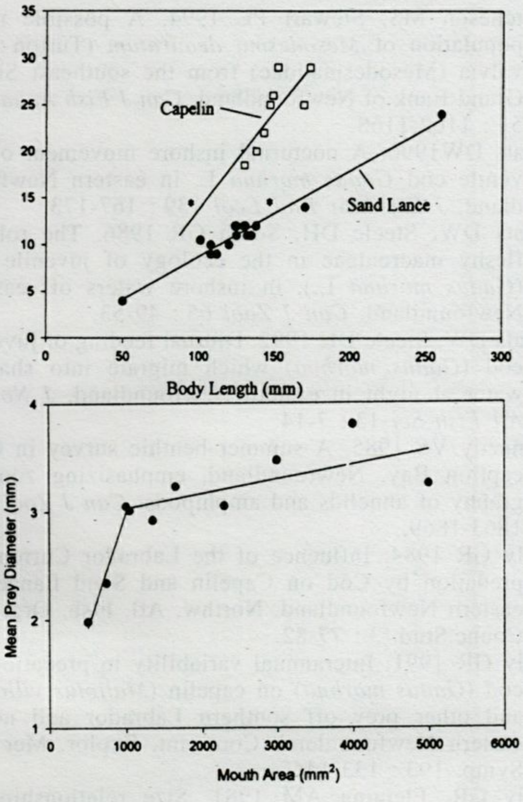

Fig. 6. – Top, diameter/body length relationships of capelin and sand lance. Asteriscs indicate the body lengths at which cod begin to feed intensively on these fish. Below, size frequencies (diameter) of amphipod prey in cod of varying mouth size categories.

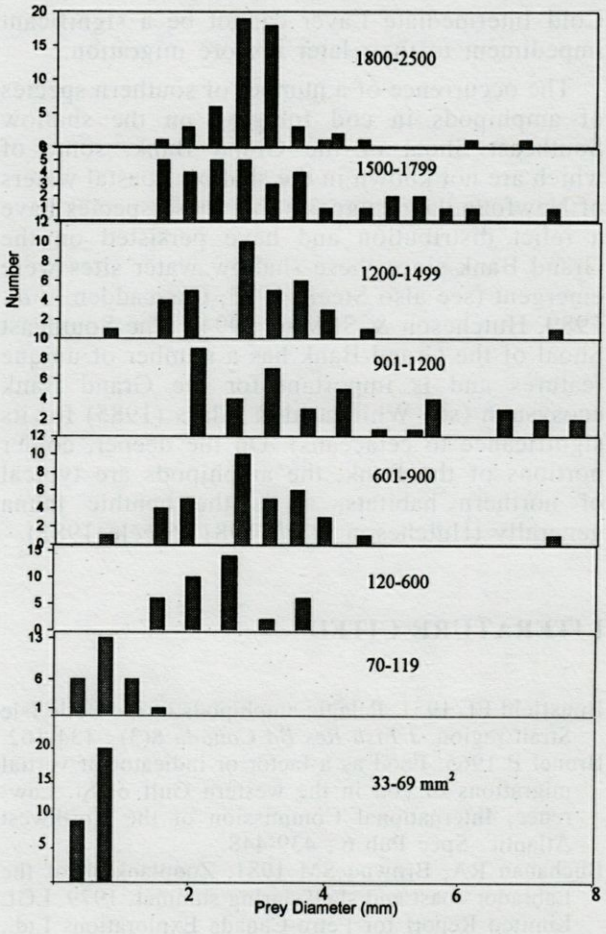

Fig. 7. – Mean diameter of amphipod prey related to cod mouth size.

their predation on capelin and sand lance (Lilly & Fleming 1981) as well as on the pelagic stages of bottom dwelling gammaridean and pelagic hyperiidean amphipods, that cod forage extensively above the bottom and probably undergo vertical feeding migrations above the bottom, as discussed by Brunel (1965). Their predation on sympagic species indicates the CIL is not a barrier to their movements. This behaviour has also been extensively documented by De Blois & Rose (1995) when cod were feeding intensively on benthopelagic shrimp.

The present study demonstrates that information on cod behaviour can be obtained from analysis of the sizes and reproductive states of the amphipod prey, as well as the species composition. The presence of adult hyperiid and the pelagic stages of bottom dwelling gammarideans provides further evidence in support of pelagic foraging.

Although planktonic hyperiidean amphipods are common in the region (Frost 1936, Bousfield 1951, Strong 1981, Buchanan & Browne 1981) and are an important food source of sea birds and marine mammals, their distribution has not been described in any detail, and the species and their reproductive stages have not usuually been differentiated. The cod in the present study fed preferentialy on the larger adults and those cod with many hyperiideans were obtained off the edges of the banks (Fig. 5). This is consistent with the observations of Strong (1981) who found adult hyperiideans only beyond the 200 m depth contour.

Many of the samples of 'Northern Cod' were obtained in deep water and when the surface of the oean was covered by pack ice (Table I, Fig. 1, 2). It is therefore of interest that some cod contained sympagic gammaridean species that live on the under surfaces of multiyear pack ice. They include *Gammarus wilkitzkii* which Gulliksen & Lonne (1989) consider to be autocthonous sympagic and not normally benthic or pelagic. Moreover Gulliksen & Lonne (1989) also consider the hyperiidean *Parathemisto libellula* to be associated with sea ice at times and consider it to be allocthonous sympagic. The occurrence of these ice associated gammarideans and hyperiideans suggests therefore that some cod forage, at times, almost up to the surface under the pack ice. To do so, they must tolerate cold water. Thus the

Cold Intermediate Layer cannot be a significant impediment to their later inshore migration.

The occurrence of a number of southern species of amphipods in cod foraging on the shallow Southeast Shoal of the Grand Bank, some of which are not known in the shallow coastal waters of Newfoundland suggests that these species have a relict distribution and have persisted on the Grand Bank since these shallow water sites were emergent (see also Steele 1983, Carscadden *et al.* 1989, Hutcheson & Stewart 1994). The Southeast Shoal of the Grand Bank has a number of unique features and is important for the Grand Bank ecosystem (see Whitehead & Glass (1985) for its significance to cetaceans). On the deeper, colder portions of the Bank, the amphipods are typical of northern habitats, as is the benthic fauna generally (Hutcheson *et al.* 1981, Steele 1983).

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