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Diet of the squid *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae) in Irish waters

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Stomach contents of *Loligo forbesi* obtained from commercial landings and research cruises in Irish waters and the Irish Sea were examined. A total of 62.3% of stomachs were empty. Fish remains occurred in 73.7% of all full or partially full stomachs, with crustaceans and cephalopods occurring in 26.4% and 7.5%, respectively. *L. forbesi* was found to consume a wide range of fish and crustacean prey. Sagittal otoliths were used to identify fish species, and vertebrae to identify families. The most frequent species by per cent occurrence were sprat (*Sprattus sprattus*), poor cod (*Trisopterus minutus*), Norway pout (*T. esmarkii*), and transparent goby (*Aphia minuta*). Crustaceans were the main prey item in squid of less than 100 mm mantle length, together with small clupeids and gobies. The predominant prey of medium-sized squid (100–220 mm) was found to be gadoid and clupeid fish, while gadoids and other cephalopods were the main prey of larger squid (>220 mm). Seasonal differences in the diet were apparent but were shown to be influenced by seasonal changes in squid size.

Key words: diet, squid, *Loligo forbesi*.

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Introduction

Cephalopods, and particularly squid, are important members of marine food chains (Amarantunga, 1983). They are active carnivores, feeding mostly on crustaceans, cephalopods, and fish (Boucher-Rodoni *et al.*, 1987; Nixon, 1987), and, in turn, are important in the diets of fish, marine mammals, and seabirds (Summers, 1983). In particular, loliginid squid are primarily piscivorous (Fields, 1965; Vovk, 1983; Worms, 1983).

Loligo forbesi Steenstrup is distributed from the Azores to Norway (Roper *et al.*, 1984) and is the most common squid species in British waters (Holme, 1974). It is found all round the Irish coast (Massy, 1928), where it is a valuable by-catch in commercial bottom trawls.

The diet of *L. forbesi* has been investigated in the Azores (Martins, 1982), Spanish waters (Rocha *et al.*, 1993), Scottish waters (Ngoile, 1987), and in the north-east Atlantic generally (Pierce *et al.*, 1993). Fish are the main prey item, with crustaceans and other cephalopods also consumed. These studies have, however, concentrated on commercial catches and hence the diet of small squid may not have been well represented.

Variability of feeding patterns of loliginid squids has been investigated in few species (Nixon, 1987). For example, dietary composition has been shown to vary with squid size in some loliginid species (Fields, 1965; Vovk, 1983), while Sauer and Lipinski (1991) found seasonal and diurnal differences in feeding patterns of *L. vulgaris reynaudii* on their spawning grounds.

This paper provides the first extensive description of the species and size composition of prey consumed by *L. forbesi* around the Irish coast and assesses variation in the diet with respect to predator size and season.

Methods

From August 1991 until September 1993 monthly samples of approximately 200 individuals of *Loligo forbesi* were obtained from commercial landings in the Irish ports of Kilmore Quay, Dunmore East, Youghal, and Dingle. All samples were trawled but precise details of location of capture and gear type were not known. In some months, particularly March–June of each year, only very small numbers of animals were obtained. Additional samples were obtained from research cruises

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Table 1. Numbers of stomachs of *Loligo forbesi* sampled in each size category each quarter of the year.

L. forbesi ML (mm)	1st quarter	2nd quarter	3rd quarter	4th quarter	Total
21–60	0	1	12	151	164
61–100	0	26	29	127	182
101–140	1	19	75	26	121
141–180	16	10	96	143	265
181–220	46	8	60	167	281
221–260	37	8	20	78	143
261–300	23	3	7	39	72
301–340	15	0	1	18	34
>340	14	3	1	13	31
Total	152	78	301	762	1293

in the Irish Sea (March, July, and September 1992 and 1993), the Celtic Sea (June 1992, July 1993), and off the west coast of Ireland (November 1991, October 1993) undertaken by the Department of Agriculture Northern Ireland and the Irish Department of the Marine. The samples from the Irish Sea and west of Ireland were caught with a standard commercial rockhopper trawl, fitted with a 20-mm lining bag. Samples from the Celtic Sea were caught with a courlene three-bridle butterfly trawl with 10-mm cod-end liner.

Dorsal mantle length (ML) of squid was measured to the nearest mm. Squid were then weighed, dissected, and sexed. Stomach fullness was visually assessed and recorded on a scale of zero to four; zero being empty and four fully distended. Full and partially full stomachs were dissected from freshly-caught squid and frozen for later analysis. If the rectum contained food remains it was also retained. All full or partially full stomachs were examined from commercial samples, whereas a sub-sample of stomachs was taken across the size range from research cruise samples.

Stomachs were initially sorted under a dissecting microscope, then washed and sieved (250 μm) to separate hard parts from soft tissue. Contents were first sorted into major taxa, i.e. crustaceans, fish, polychaetes, cephalopods, or other. These were then further identified to family, genus, and species where possible. Fish remains were identified to the species level from sagittal otoliths, when present, using Harkonen's (1986) guide and from a reference collection. When no otoliths were present vertebrae were used to identify the family. Possible otolith pairs were identified to estimate the minimum number of fish consumed. The lengths of fish prey were estimated using relationships between otolith lengths or widths and fish length in Harkonen (1986) and from personal otolith collections. Cephalopods were identified from statoliths, beaks (Clark, 1986), and soft tissue. Crustaceans were identified from diagnostic exoskeleton fragments. The main characters employed were mandible morphology and telson and rostrum spination (Lagardère, 1971; Smaldon, 1979).

Detrended correspondence analysis (DCA) (Hill and Gauch, 1980) was used to investigate the influence of predator size and season on the dietary composition of *L. forbesi*. Subsequently, axis scores of prey classes were correlated with squid size and season (quarter of the year) using Spearman's rank order correlation co-efficient.

Results

General diet composition

Table 1 shows the numbers of stomachs examined in each size class in each quarter of the year. The majority of stomachs were obtained from the third and fourth quarters, which reflects the abundance of squid at this time. No significant difference ($\chi^2=4.904$; d.f.$=6$; $0.5<p<0.75$) was found between the diet of male and female squid, so the data were pooled. Small squid (<100-mm ML) were only obtained from research cruises in June, July, September, and October, since they would be too small to be retained by commercial trawl nets.

Of a total of 4552 stomachs examined, 2837 (62.3%) were found to be empty, whilst only 53 (1.2%) were fully distended. The remainder of the stomachs contained partially-digested remains. Some stomachs visually classified as empty may have contained small traces of food, such as fish scales. The contents of 1293 stomachs were examined microscopically. All results are expressed in per cent occurrence, i.e. as a percentage of all full or partially full stomachs that were microscopically examined. Multiple prey items were found in 19.5% of stomachs, hence the sum of the per cent occurrences exceeds 100%. Crustacean and cephalopod remains often occurred in the same stomach as fish. Gobies and sprat (*Sprattus sprattus*) remains were often present in large numbers and one stomach contained 26 sprat sagittal otoliths.

Fish remains were present in 73.4% of stomachs and sagittal otoliths occurred in 57% of these. Most otoliths

Table 2. Fish prey and their per cent occurrence in the diet of *Loligo forbesi*.

Prey item	Per cent occurrence
Family Clupeidea	
Sprattus sprattus	10.98
Clupea harengus	0.38
Unidentified Clupeidae	8.35
Family Argentinidae	
Argentina sphyraena	1.01
Unidentified Argentinidae	0.23
Family Gonostomatidae	
Maurolicus muelleri	0.77
Family Gadidae	
Trisopterus minutus	6.88
Trisopterus esmarkii	2.94
Trisopterus spp.	4.48
Merlangius merlangus	1.16
Gadiculus argenteus	2.32
Enchelyopus cimbrius	0.46
Unidentified Gadidae	12.14
Family Gobidae	
Lesuerigobius friesii	0.93
Aphia minuta	4.10
Gobius niger	0.07
Pomatoschistus minutus	1.24
Unidentified Gobidae	4.48
Family Callionymidae	
Callionymus lyra	2.01
Callionymus maculatus	0.15
Unidentified Callionymidae	0.31
Family Carangidae	
Trachurus trachurus	1.24
Family Ammodytidae	
Ammodytes spp.	0.46
Unidentified Ammodytidae	0.15
Family Cepolidae	
Cepola rubescens	0.07
Family Triglidae	
Eutrigla gurnardus	0.15
Unidentified Triglidae	0.07
Family Agonidae	
Agonus cataphractus	0.07
Family Pleuronectidae	
Pleuronectes platessa	0.07
Unidentified Pleuronectidae	0.15
Unidentified fish	10.83
Total fish	73.70

were identified, but a few, particularly in the diet of small squid, could not be classified. Table 2 lists the percentage occurrence of identified fish species and unidentified fish in the diet of *L. forbesi*. The most common fish species identified in the diet were sprat, small gadoids, such as poor cod (*Trisopterus minutus*) and Norway pout (*T. esmarkii*), and gobies. Many goby otoliths were found, but only those of transparent gobies (*Aphia minuta*), Fries goby (*Lesuerigobius friesii*), sand goby (*Pomatoschistus minutus*), and black goby (*Gobius niger*) were identified. Unidentifiable fish remains were found in 10.8% of stomachs and usually consisted of a few scales and bones.

Table 3. Crustacean prey and percentage occurrence in the diet of *Loligo forbesi*.

Prey item	Per cent occurrence
Order Euphausiacea	
Meganyctiphanes norvegica	14.77
Order Decapoda	
Dichelopandalus bonnieri	3.09
Pasiphaea sivado	0.31
Nephrops norvegicus	0.31
Oplophoridae	0.15
Crangonidae	0.07
Palaemonidae	0.07
Paguridea	0.15
Order Isopoda	
Gnathia sp. (larvae)	0.15
Unidentified Crustacea	9.27
Total Crustacea	26.40

Table 4. Cephalopod prey and per cent occurrence in the diet of *Loligo forbesi*.

Prey	Per cent occurrence
Loliginidae	3.02
Loliginidae (arms and tentacles only)	1.93
Octopodidae	0.23
Sepiolidae	0.07
Unidentified Cephalopoda	2.24
Total Cephalopoda	7.49

Crustaceans were found in 26.4% of stomachs. Table 3 lists the identified crustacean and their percentage occurrence. The most important items were the euphausiid, *Meganyctiphanes norvegica*, and the caridean shrimp, *Dichelopandalus bonnieri*.

Table 4 lists the cephalopods, which were found in 7.5% of stomachs. Loliginids comprised the majority of identifiable cephalopods, with octopodids also present. Loliginid prey were likely to be either *Alloteuthis subulata* or small *L. forbesi*, since these are the only loliginid species caught in the area. In all cases where loliginid beaks were found the prey was considerably smaller than the predator. Pieces of loliginid arms and tentacles were found in 1.9% of stomachs. Remains of a sepiolid were found in a single stomach.

Polychaete remains were found in 0.4% of stomachs; all were *Nereis pelagica* from the September 1993 sample and may have been the free-swimming epitoke stage. Benthic molluscs were found in 0.7% of stomachs and belonged to the scallop (*Chlamys* spp.) and a topshell (*Calliostoma zizyphinum*), which were found together with dragonet (*Callionymus* spp.) remains and are likely to have been secondarily ingested. The radulae of unidentified gastropods were found in the stomachs of two small squid. Algae were found in 0.4% of stomachs.

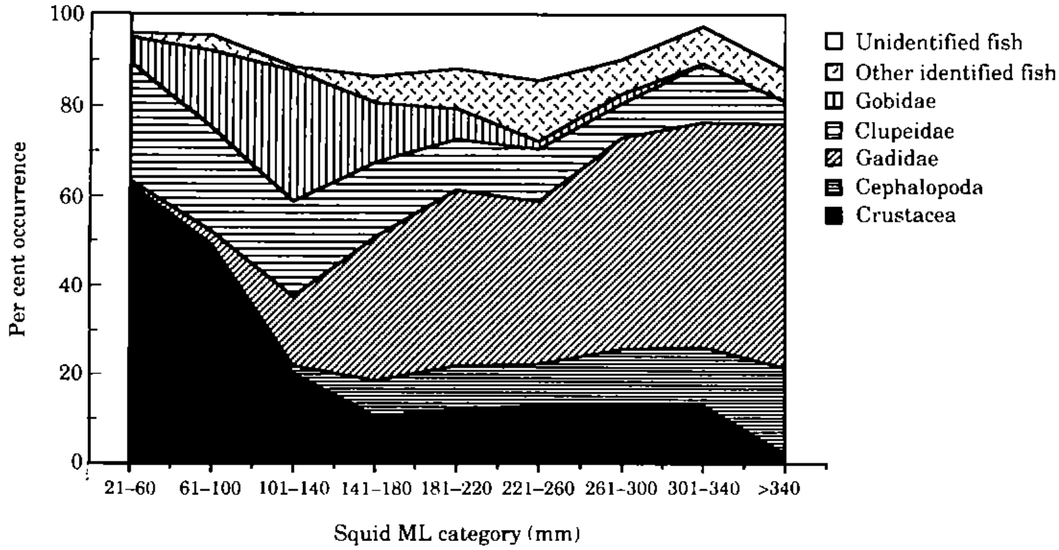

Figure 1. Variation in the diet of *Loligo forbesi* with predator size.

Variability of the diet

Two of the samples were obtained from commercial catches in depths of approximately 400 m. The stomachs of these squid (ML 150–300 mm) contained fish and cephalopod remains. The main fish prey species differed from squid caught in inshore areas, the most important being silvery pout (*Gadiculus argenteus*), argentines (*Argentina sphyraena*), and pearlsides (*Maurolicus müelleri*).

The diet of *L. forbesi* was found to vary with predator size (Fig. 1). At the smaller sizes sampled (ML 21–100 mm) crustaceans were the main component of the diet. With increasing predator size fish prey became more important. In medium-sized squid (101–140 mm) clupeids, gadoids, and gobies were found to be the dominant prey. The importance of gadoid fish increased with predator size and they were the most important prey of the larger squid (>140 mm). Cephalopods were taken only by the larger squid (>100 mm) and their importance increased with predator size. The crustacean component of the diet also changed with increased predator size. Euphausiids (mostly *M. norvegica*) were eaten by the smaller (21–100 mm) animals whilst larger squid also preyed on decapods, such as *D. bonnieri*.

Figure 2 shows the seasonal variation of the diet of *L. forbesi* of ML greater than 100 mm. Gadoids were common prey throughout the year, but crustaceans, cephalopods, clupeids, and, particularly, gobies showed seasonal variation. Figure 3 shows seasonal variation in the diet of small (<100 mm) *L. forbesi*. Crustaceans were clearly more important in the diet of the small squid later in the year.

It is apparent from Figures 1–3 that time of year and squid predator size have an effect on the variability of the diet. DCA was used to determine whether predator size or time of year was the main influence on diet variability. Figure 4 presents the ordination results of the prey groups, only axes 1 and 2 are presented as they cumulatively account for 65.2% of the total variance. Squid size was positively correlated with axis 1 ($r=0.75$; $p<0.001$) and axis 2 ($r=0.52$; $p<0.01$). Yearly quarter was negatively correlated with axis 1 ($r=-0.35$; $p>0.01$) and only weakly correlated with axis 2 ($r=0.18$; $p>0.01$). Hence, it can be seen that larger squid predominantly consumed gadoids and cephalopods, whilst smaller squid eat mostly crustaceans, clupeids, and gobies.

Predator–prey relations

The relationship between squid mantle length and estimated length of teleost prey is illustrated in Figure 5. Only when otoliths were found could prey size estimations be accuractely made and no estimations could be made of transparent goby sizes because of lack of data. Figure 5 also shows the predator size to prey size relationships for the gadoid, clupeid, and callionymid families. A straight-line regression has been fitted to all data sets. In all cases prey size is positively correlated ($p=0.05$), with predator size, indicating that larger squid consumed larger fish prey items. There is also an increase in the range of prey sizes taken with increase in squid size. The slope of the regression is much lower for the clupeid prey than for gadoids and callionymids, indicating that there is a comparatively small increase in clupeid prey size with predator size. Many stomachs

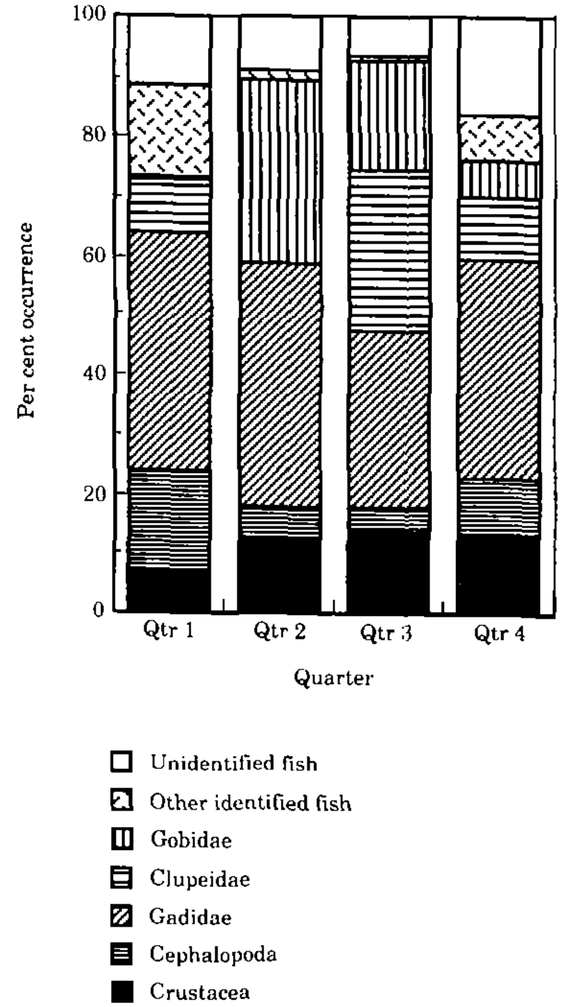

Figure 2. Quarterly variation in the diet of large (ML>100 mm) *Loligo forbesi*.

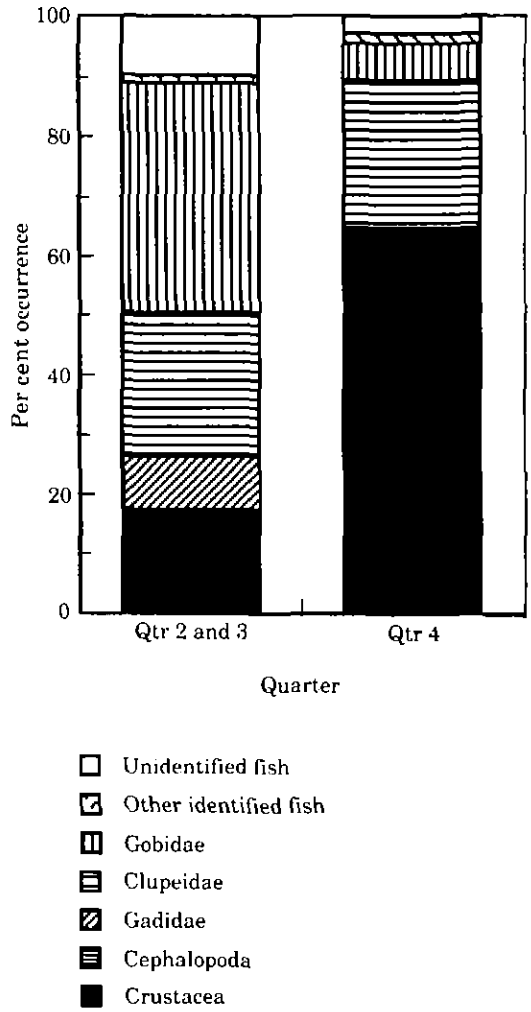

Figure 3. Quarterly variation in the diet of small (ML<100 mm) *Loligo forbesi*.

contained multiple sprat prey items, which may explain why the relationship is weaker.

Discussion

Stomach contents analysis using percentage occurrence methods provides a quick but crude assessment of diet (Hyslop, 1980). However, there are a number of problems associated with accurately assessing cephalopod diets (Nixon, 1987; Dawe, 1992). Squid macerate prey during ingestion, making identification of stomach contents difficult. Rapid digestion rates of perhaps as little as 4–6 h (Bidder, 1966) mean that stomach contents analysis tends to rely on the presence of identifiable hard structures such as otoliths from fish, beaks from cephalopods, and diagnostic exoskeletal fragments of crustaceans. Prey items lacking hard parts are likely to be underestimated (Nixon, 1987). To confound the problem of fish prey assessment further it is unclear to what extent otoliths are ingested and retained (Dawe, 1992). Otoliths when ingested remain well preserved in the mildly acidic environment of the squid stomach (Jobling and Brieby, 1986), but when eating relatively large fish prey *L. forbesi* may reject the head and consume only the body and flesh (Bidder, 1950; Porteiro *et al.*, 1990). Secondary ingestion may also influence the results. Some of these problems may be overcome using serological methods, but because of time constraints these methods are best suited to answering specific questions rather than routine diet analysis (Grisley and Boyle, 1985).

Martins (1982) and Pierce *et al.* (1993) found fish to be the major component of the diet of commercially caught *L. forbesi* from the Azores and Scottish waters, respectively, with crustaceans and cephalopods also consumed,

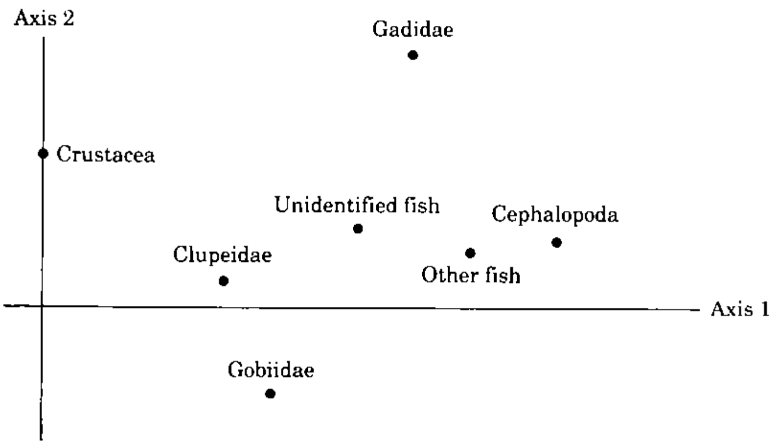

Figure 4. Detrended correspondence analysis plot of prey items.

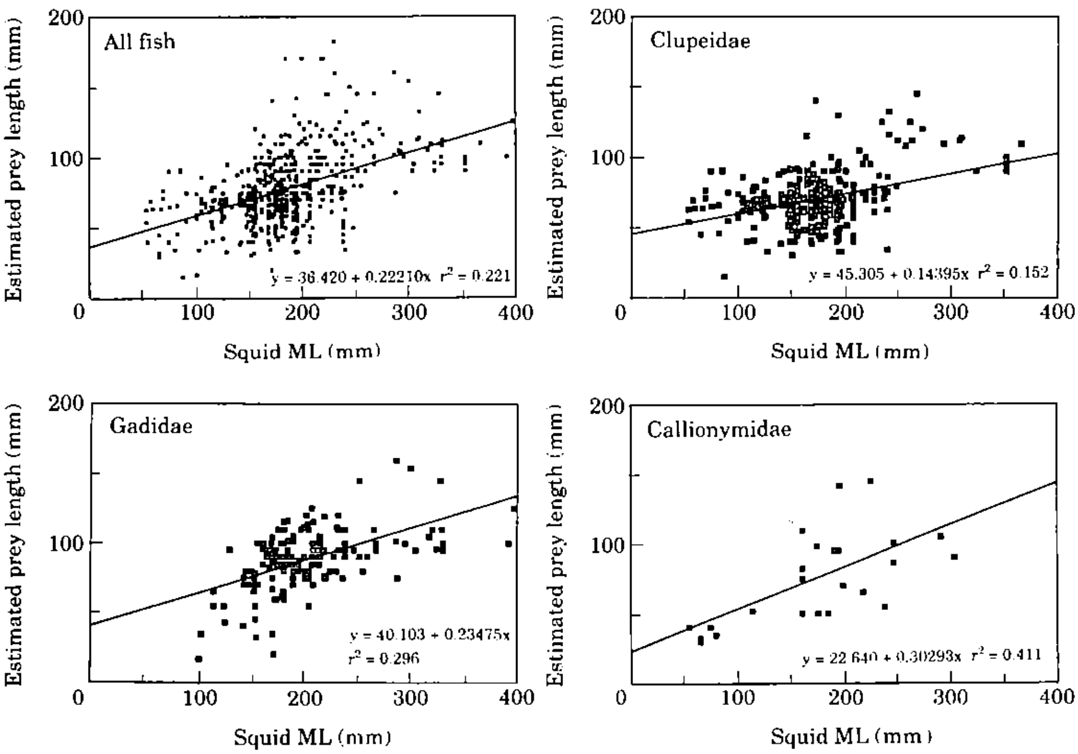

Figure 5. Relationship between squid mantle length (mm) and estimated fish prey length (mm) for all teleost prey and separately for prey of families Clupeidae, Gadidae, and Callionymidae.

but less frequently. Most other loliginid species are predominantly piscivorous (Fields, 1965; Macy, 1982), *L. gahi*, however, feeds predominantly on crustaceans (Guerra *et al.*, 1991).

In some of the larger squid crustacean and gobiid remains were found in association with the remains of larger fish and may have been secondarily ingested. Polychaetes have previously been reported in the diet of *L. forbesi* (Ngoile, 1987), and in this study *N. pelagica* appears to be a primary prey item since in some cases no other remains were found with them.

The fish prey composition of the squid stomachs in inshore Irish waters was dominated by sprat and poor cod, and offshore by silvery pout, argentines, and pearlsides, whereas in adjacent inshore Scottish waters the most frequently identified otoliths were from whiting (*Merlangius merlangus*), Norway pout, and *Ammodytes* spp. (Pierce *et al.*, 1993). In Galicean waters, Rocha *et* *al.* (1993) found a similar range of teleost families to those detected in the present study. Geographic differences in the specific teleost component of the diet probably reflect local abundances of fish rather than different dietary preferences. Given the importance of small gadoid fish in the diet of *L. forbesi* it is possible that *L. forbesi* is an important predator on the nursery grounds of the commercially important gadoids such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), which may not have been sampled in the present study.

Few previous studies of the diet of *L. forbesi* have included specific identifications of the crustacean prey, although Ngoile (1987) raised antisera to *Pandalus* and *Crangon* to confirm the presence of decapod remains in the caecal contents of *L. forbesi*. Martins (1982) found euphausiid remains in a single stomach of *L. forbesi* from the Azores, whilst Pierce *et al.* (1993) found decapod or euphausiid remains in the stomachs of *L. forbesi* from Scottish waters. The comparative abundance of euphausiids in the present study was due in part to the large number of small squid sampled. Most of the decapod remains belong to pelagic species such as *D. bonnieri*.

The variety of fish prey taken by *L. forbesi*, which included pelagic species such as sprat, semi-pelagic species such as poor cod, and demersal species such as dragonets, suggests that it is an opportunistic predator, taking whatever prey of a suitable size that are abundant in the area. Opportunistic predation tends to be typical of cephalopods in general (Boucher-Rodoni *et al.*, 1987). *L. vulgaris* has been described as nektobenthic (Worms, 1983), showing pelagic behaviour during hunting. *L. vulgaris reynaudii*, however, is reported to feed on the bottom (Sauer and Lipinski, 1991). In offshore areas *L. pealei* is thought to remain on or near the bottom in the day, dispersing in the water column to feed at night (Macy, 1982). There is no evidence of night-time dispersion in *L. forbesi*.

Ontogenetic changes in the diet have been shown in other loliginid squid (Macy, 1982; Vovk, 1983; Sauer and Lipinski, 1991) and in *L. forbesi* (Pierce *et al.*, 1993). Typically, as in the present study of *L. forbesi*, smaller squid consumed primarily crustaceans, with fish increasing in importance with predator size. Fields (1965) found that the ratio of crustacea to fish changed from 3:1 in small *L. opalescens*, to 1:3 in the spawning population. The diet of *L. pealei* was also found to change with size (Vovk, 1983), changing from crustaceans to fish and squid. In the present study of *L. forbesi* the ratio was found to be 3:2 crustaceans to fish in the small (21–60 mm), changing to 1:4 in the large animals.

Vovk (1983) also found changes in the crustacean component of the diet with *L. pealei* size. Very small squid (10–40 mm) took copepods, those of 41–60 mm took euphausiids, whilst at 61–100 mm decapods were taken. In this study the crustacean component of the diet of *L. forbesi* shifted from euphausiids at the smallest sizes sampled (21–60 mm) to decapods in larger squid.

Pierce *et al.* (1993) suggested that fish may be the preferred prey of all sizes of *L. forbesi*, providing greater energetic profitability than crustaceans. Small squid may only take crustaceans when suitably-sized fish are unavailable. Most of the small squid sampled in this study were caught in the autumn but it appears that in summer more small fish are taken and the amount of crustacea consumed is less, perhaps reflecting the seasonal availability of small gadoids and gobies such as transparent gobies.

The change in the diet with squid size represents a shift from smaller to gradually larger prey items. Few studies have related squid predator size to estimated prey size. Vovk (1983) found an increase in the range of prey sizes with an increase in the size of *L. pealei*. Rodhouse *et al.* (1992) found no evidence that prey size is related to predator size, over a small size range of the ommastrephid squid *Martialia hyadesi*. In the present study there was a trend of increased prey size with predator size (see Fig. 5), with *L. forbesi* taking prey of roughly one half to two thirds its own size. An increase in the range of prey sizes taken was also apparent. However, it is possible that larger fish than those identified are consumed by *L. forbesi*, but that the head is rejected (Porteiro *et al.*, 1990). Bidder (1966) reported that *L. forbesi* will prey on fish of equal size to itself. In predatory fish increase in food size reduces the energy expenditure of foraging (Weatherley and Gill, 1987), and the same presumably applies to squid.

Cannibalism and predation on other cephalopods are typically restricted to squid of size greater than 100 mm, and have previously been reported in *L. forbesi* (Martins, 1982; Pierce *et al.*, 1993; Rocha *et al.*, 1993) and other loliginids (Fields, 1965; Macy, 1982; Sauer and Lipinski, 1992).

Since *L. forbesi* appears to be an annual species (Holme, 1974; Collins *et al.*, 1993), certain sizes of squid are only available at particular times of year and so seasonal variation in the diet of *L. forbesi* is inextricably linked with squid size. Variability in the diet of *L. forbesi* was shown here to be primarily influenced by squid size, which means that squid of different sizes are feeding at different trophic levels and hence not competing with each other. *L. forbesi* thus represents an important link in energy transfer between trophic levels, as was suggested by Vovk (1983) for *L. pealei*.

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