THE DIET AND ECOLOGICAL IMPORTANCE OF ILLEX COINDETII AND TODAROPSIS EBLANAË (CEPHALOPODA: OMMASTREPHIDAE)
IN IRISH WATERS

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Between November 1993 and May 1997, the stomach contents of trawl-caught Illex coindetii and Todaropsis eblanae from the edge of the continental shelf west and south-west of Ireland were examined. When visually assessed, 82.1% of the I. coindetii stomachs and 73.4% of the T. eblanae stomachs had no food remains present. In both I. coindetii and T. eblanae stomachs with prey, crustaceans, particularly euphausiids, are relatively more important as prey in smaller squid. As the squid grow, fish and squid become increasingly important prey. The small mesopelagic fish Maurolicus muelleri is a particularly important prey item of both species, occurring in 48.3% of I. coindetii and 34.7% of T. eblanae stomachs with prey remains. M. muelleri otoliths were also often found in high numbers. In one I. coindetii stomach, 43 pairs of otoliths were found. However, this great abundance may be an over-representation of their importance in the diet as a result of the techniques used to identify prey remains in squid stomachs. Three other pelagic fish, Galiticus argenteus, Micromesistius poutassou, Argentia sp. and the euphausid Meganyctiphanes norvegica, are also important prey of both species. Data on possible trawl-net-associated feeding are also presented, although the importance of this as a source of error in diet studies is unclear. Using data from research vessel surveys, there seems to be a peak in feeding intensity in the early morning in I. coindetii.

The ecological importance of cephalopods in multispecies communities is often overlooked by fisheries biologists and fisheries managers. Captive Illex illecebrosus consume an estimated 3.6–6.7% of their body mass per day (O’Dor et al. 1980). Dawe’s (1988) results suggest that I. illecebrosus may be a cause of considerable fish mortality and could even affect recruitment of commercial fish species in years of abundance of squid. Cephalopods such as Illex coindetii (Verany, 1839) and Todaropsis eblanae (Ball, 1844) are voracious opportunistic predators. Understanding the ecological role of both species in the ecosystem is imperative if a proper multispecies fisheries management programme is to be implemented in Irish waters.

The edges of the continental shelf, from 100 to 800 m deep, west of Ireland and in the Celtic Sea (ICES Subareas VIIc, b, g, h, j, k) are among Europe’s most heavily exploited fishing grounds. In recent years, fish landings in the area have increased to almost 500 000 tons (ICES STATLANT 27A Database). Seasonally, both I. coindetii and T. eblanae are important bycatches of commercial demersal trawls in the area shaded in Figure 1. Until recently the bycatches of both species were discarded, but both are now becoming attributable to the nature of the multinational fleet fishing there and the fact that cephalopods are non-quota species within EU waters. Because of these two factors, fish and cephalopod catches from the area are landed in several different EU countries and cephalopod catches do not have to be recorded in EU fishing vessel logbooks.

The diet of I. coindetii and T. eblanae in several areas has been described previously. The studies showed that both species are primarily piscivorous. In Galician waters, the semi-pelagic gadoid, blue whiting Micromesistius poutassou, was the most important species in the diet of I. coindetii (Rasero et al. 1996). Blue whiting were also found in nearly 50% of T. eblanae stomachs examined (Rasero et al. 1996). In the Catalan Sea I. coindetii feeds primarily on pelagic and bathypelagic species, including Engraulis encrasicolus, Lampanyctus cocodrilus [crocodilus], Maurolicus muelleri, Myctophidae and Meganyctiphanes norvegica (Sánchez 1982). On the North-West African shelf, teleost fish are the most important prey taxa, constituting 56.9% of the diet of adult and 45.1% of juvenile I. coindetii (Castro and Hernández-García 1995). Prey species in that area include M. muelleri, Diaphus dumerilii, the euphausid Thysanoessa sp. and several cephalopod species (Castro and Hernández-García 1995). In South African waters, the diet of

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T. eblanae is dominated by the lanternfish Lampanyctodes hectoris (Lipiński 1992). Previous studies on the diets of both species show that feeding is mainly in mid-water, opportunistically on the most abundant mesopelagic prey of appropriate size. Changes in the diets of several squid species provide evidence that relative prey size is critical (Hanlon and Messenger 1996). The best evidence of this is in L. forbesi, for which the size of teleost prey increases with predator size (Collins and Pierce 1996). In Galician waters, the diet of T. eblanae changes significantly with both squid size and maturity, which are strongly interdependent (Rasero et al. 1996). In the same study, no evidence was found for changes in diet with maturity in I. coindetii. Differences in prey taxa in the diet of immature and mature I. coindetii were, however, found on the North-West African continental shelf by Castro and Hernández-García (1995). In the present study, ontogenic changes in the prey taxa found in the diets of both species are described.

Potential predators of the ommastrephids of the west coast of Ireland include several large teleosts, some elasmobranchs, marine mammals and possibly seabirds. The relative importance of these groups as predators of I. coindetii and T. eblanae is poorly recorded in the literature for the continental shelf west and south of Ireland and in other areas (Clarke 1996, Croxall and Prince 1996, Klages 1996, Smale 1996). This paper describes the diet, trophic position and aspects of the feeding ecology of mature and maturing post-recruit I. coindetii and T. eblanae in Irish waters.

MATERIAL AND METHODS

Source of samples

Between November 1993 and April 1997, samples of trawled I. coindetii and T. eblanae were obtained seasonally (November-May) from the area shaded in Figure 1. The samples came from 3 sources:

(i) landings of commercial demersal trawlers;
(ii) samples taken at sea on commercial demersal trawlers;
(iii) samples taken at sea on a research vessel.

Dates and the numbers of stomachs collected from commercial landings and at sea on both research and commercial vessels are presented in Table I. The commercial demersal trawlers catch ommastrephid squid as part of a mixed species fishery (from 250 to 600 m deep) targeting monkfish Lophius piscatorius and L. budegassa, hake Merluccius merluccius, megrim Lepidorhombus boscii and L. whiffiagonis, cod Gadus morhua and ling Molva molva. The fishing vessels are typically 28–36 m long and tows generally last 6–7 h.

The samples collected on the research vessels were taken during the CEFAS (U.K.) Celtic Sea groundfish surveys and the IFREMER (France) Biscay and Celtic Sea young fish survey aboard R.V. Cirolana and R.V. Thalassa respectively. On those surveys, precise trawled location, time shot and hauled, water depth, weather condition, gear type and number of squid caught in the trawl were recorded. In all, 965 I. coindetii were sampled in 72 tows on the March Cirolana surveys of 1994, 1995 and 1997. The number of squid sampled and the number with prey remains in their stomachs, for each hourly interval from 06:00 to 18:00, were pooled and the percentages feeding at each hour were calculated.

During the 1996 season (November 1995–May 1996), catch masses of both species were recorded for each tow (approximately 6–7 h each) on a 34-m 1 000 hp demersal fishing vessel, the M.F.V. Shannon (a typical demersal trawler in the area). These values were averaged to calculate daily catch per unit effort (cpue) for the vessel in the sampling area. During December 1996 and April 1997, a 35 kg subsample of both
species was examined after 12 individual trawls aboard M.F.V. Shannon. The numbers of squid with physical damage thought to be consistent with cephalopod attack in the subsample were recorded. The occurrence of cephalopod remains in the stomach contents of the squid sampled and the total combined masses (kg) of both ommastrephids were also recorded for these individual tows. All tows were of similar duration, 6.5–7 h, and the catches of other cephalopod species in these tows were negligible.

Macroscopic examination

Dorsal mantle length (DML) of the squid was measured to the nearest millimetre (mm) and most squid (except those examined at sea on commercial vessels) were weighed (wet mass) to the nearest 0.1 g. All squid were dissected by cutting along the ventral midline of the mantle, sexed and assigned a maturity stage using a maturity scale similar to that of González and Guerra (1996), where Stages I–III are immature and...
Stages IV and V are mature. Stomach and caecum contents were first assessed visually using a six-point scale, zero being empty and five being fully distended. The stomachs were also macroscopically assessed and assigned a prey type; teleosts, crustaceans, cephalopods or a combination of the three types. It was often necessary to open the stomach before deciding prey type to reduce error in identification of the remains.

Microscopic examination

A random subsample of stomachs with stomach fullness levels of 1–5 was examined microscopically (569 I. coindetii and 432 T. eblanae). A further 102 stomachs initially classified as being stomach fullness level 0 (i.e. empty stomachs), were also examined microscopically to see if they contained small quantities of prey remains initially not identified. These stomachs were dissected out, labelled and stored at -27°C for later analysis. Many of the stomachs which contained food remains also had remains in the spiral and saccular parts of the caecum or in the intestine, oesophagus or rectum. In those cases, all parts of the digestive system containing food remains were removed and frozen for more detailed analysis.

The frozen samples were later thawed, opened and washed in a shallow dark tray before the gut lining was removed, leaving only the stomach contents in the tray. Most of the fish otoliths and other prey fragments of use in elucidating prey species could be identified and removed by gently swirling the contents of the tray. The remaining stomach contents were sorted into the lowest possible prey taxon using a binocular dissecting microscope. Fish remains were identified by their otoliths, vertebrae and scales by comparing them to reference material in the National University of Ireland, Cork (NUIC), otolith and vertebrae guides (Härkönen 1986, Watt et al. 1997) and a computerized otolith database developed at NUIC. The cephalopod remains were identified from statoliths, beaks and gladii, using reference material in accordance with Clarke (1986) and Hess and Toll (1981). Crustacean remains were identified from fragments of the exoskeleton and comparisons with reference material (Allen 1967).

Lengths of teleost prey were calculated from published regressions (Härkönen 1986, Watt et al. 1997) and unpublished regressions calculated at NUIC. The occurrence of prey taxa is expressed according to the following equations:

\[
\text{Percentage occurrence of all taxa} = \frac{100}{1} \times \frac{\text{Number of stomachs containing the prey taxon}}{\text{Total number of stomachs containing prey}}
\]

\[
\text{Percentage occurrence of teleosts} = \frac{100}{1} \times \frac{\text{Number of individual teleosts}}{\text{Total number of teleosts}}
\]

The percentage occurrences of the individual taxa are added to give the percentage occurrence in the main prey groups, i.e. teleosts, crustaceans and molluscs. As some stomachs contained more than one prey taxon, the sum of the percentage occurrence exceeds 100%.

Statistical analysis of the results were performed with \( \chi^2 \) contingency tables (Zar 1984).

RESULTS

The mean daily catch mass of each of the two species here investigated caught by the Shannon from November 1995 to June 1996 are presented in Figure 2. The graph shows increasing catch masses of both ommastrephids from November to March, followed by decreases in April and May. During the remainder of the year catches are negligible (<100 kg day\(^{-1}\)). Similar patterns have been noted but not quantified since research began on ommastrephid squid in this area in 1993.

A total of 3,085 I. coindetii stomachs was assessed visually for the occurrence of prey remains. Of these,
2,532 had no remains or negligible remains present in their digestive tract. Another 2,870 *T. eblanae* stomachs were examined and, of these, 2,107 had no remains or negligible remains in their stomachs. The remaining 553 (17.9%) *I. coindetii* and 763 (26.6%) *T. eblanae* had some prey remains present in their digestive tract.

The stomach fullness levels of male and female *I. coindetii* were significantly different ($\chi^2 = 13.04$, $df = 5$, $p < 0.025$). Female *I. coindetii* had more distended stomachs (Level 5) than males. There were also significant differences between the diets of immature (Stages I, II and III) and mature (Stages IV and V) female *I. coindetii*. Mature females had higher levels of stomach fullness than expected ($\chi^2 = 6.45$, $df = 11$, $p < 0.025$). There was no significant difference between the stomach fullness levels of male and female *T. eblanae* ($\chi^2 = 6.43$, $df = 5$), between those of mature

<table>
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<td><strong>Taxon</strong></td>
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<td><strong>TELEOSTS</strong></td>
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<tr>
<td>Chupeforms</td>
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<td>Sprat <em>Sprattus sprattus</em></td>
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<td>Herring <em>Clupea harengus</em></td>
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<td>Family Argentinidae</td>
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<td>Argentine <em>Argentinia</em> sp.</td>
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<td>Family Sternoptychidae</td>
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<td>Pearside <em>Maerolitus muelleri</em></td>
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<td>Family Myctophidae</td>
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<td><em>Diaphus</em> sp.</td>
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<td>Family Gadidae</td>
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<tr>
<td>Blue whiting <em>Micromesistius poutassou</em></td>
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<td>Silvery pout <em>Gadiculus argenticus</em></td>
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<tr>
<td>Pouting <em>Trisopterus</em> sp.</td>
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<td>Family Gobiidae</td>
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<tr>
<td>Transparent goby <em>Aphia minuta</em> 0.5</td>
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<td>Unidentified goby <em>Gobiodae</em> sp.</td>
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<td>Family Carangidae</td>
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<td>Sead <em>Trachurus trachurus</em></td>
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<td>Family Scopridae</td>
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<td>Mackerel <em>Scomber scombrus</em></td>
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<td>Unidentified teleosts</td>
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<td><strong>CRUSTACEANS</strong></td>
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<td>Order Euphausiacea</td>
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<tr>
<td>Meganyctiphanes <em>norvegica</em></td>
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<td>Unidentified euphausids</td>
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<td>Order Decapoda</td>
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<td><em>Dichelopandalus bonnieri</em></td>
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<td><em>Pasiphoea</em> sp.</td>
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<td>Unidentified crustaceans</td>
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<td><strong>MOLLUSCS</strong></td>
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<td>Order Cephalopoda</td>
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<tr>
<td><em>Illex coindetii</em></td>
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<td><em>Todaropsis eblanae</em></td>
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<td><em>Todarodes sagittatus</em></td>
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<td><em>Loligo forbesi</em></td>
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<td><em>Rossia macrospum</em></td>
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<td>Unidentified cephalopods</td>
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<td>Order Gastropoda</td>
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<td><em>Pteropod Limacina retroversa</em></td>
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and immature female *T. eblanae* or between mature and immature males of both species.

There was a significant difference between the numbers of empty stomachs and those with prey remains between *I. coindetii* sampled on research cruise surveys aboard the *Cirolana* and those caught by the *Shannon*. There were significantly more full stomachs of *I. coindetii* in the research ship catch ($\chi^2 = 1.239.6, df = 1, p < 0.001$). The ratio of empty stomachs to stomachs with prey in *T. eblanae* was almost identical in research cruise and commercial samples.

In the stomachs examined microscopically, totals of 20 and 19 different prey taxa were identified in *I. coindetii* and *T. eblanae* stomachs respectively (Table II). Teleost fish were the most important prey group in the diet of both species, being found in 74.7% of *I. coindetii* stomachs and 79.9% of *T. eblanae* stomachs. Most of the teleost prey were identified from the sagittal otoliths, vertebrae or scales. The latter were particularly important for identifying *Argentina* sp. The next most important prey group were crustaceans (mainly euphausids), which were found in 29.9 and 21.1% of *I. coindetii* and *T. eblanae* stomachs respectively. Molluscs occurred in 17.3% of *I. coindetii* stomachs and 11.1% of *T. eblanae* stomachs. The molluscan prey included other cephalopod species and the pteropod *Limacina reversa*. Large numbers of *L. reversa* were often found in individual stomachs. Cannibalism was common in both species.

Of the stomachs examined microscopically, significant differences were found between the numbers of stomachs containing the different prey types (i.e. teleost, crustaceans, cephalopods, pteropods) in both species ($\chi^2 = 25.47, df = 3, p < 0.001$). *I. coindetii* had relatively fewer stomachs containing teleost prey, more with crustacean prey and fewer with cephalopod prey than *T. eblanae*. Differences in species composition of the diets was also noticeable. *Diaphus* sp., hatchetfish *Argyropelecus hemigymnus* and mackerel *Scromber scombrus* were found in the *I. coindetii* stomachs, but not in the *T. eblanae* stomachs. Similarly, sprat *Sprattus sprattus*, herring *Clupea harengus* and pouting *Trisopterus* sp. were found in the stomachs of *T. eblanae*, but not in those of *I. coindetii*. There were also significant differences between the numbers of stomachs containing teleost prey in the stomachs of both *I. coindetii* and *T. eblanae* ($\chi^2 = 44.06, df = 6, p < 0.001$). Differences between the numbers of stomachs containing identified crustacean ($\chi^2 = 6.05, df = 2, p < 0.05$) and cephalopod species ($\chi^2 = 6.07, df = 2, p < 0.05$) were also significant.

Microscopic examination was also used to assess the effectiveness of macroscopic identification of prey types. Errors were less than 4.0%, and those were mainly because stomachs classified as having teleost prey also sometimes contained crustaceans. Of the 102 stomachs designated as empty macroscopically, seven had prey remains, in four there were scales or small bones of unidentified fish, two had unidentifiable prey remains and one had a crustacean exoskeleton.

No identifiable relationships were found between the calculated lengths of teleost prey identified in the diet and the *DMLs* of either squid species when plotted and tested with various regressions.

The percentage occurrence of all prey types found in the stomachs containing food remains by 10-mm length-class is presented in Figure 3. The relative importance of crustaceans in the diet of *I. coindetii* decreased as mantle length increased, and cephalopods were more common in the diet of larger animals (Fig. 3a).
The diet of *T. eblanae* <100 mm was dominated by crustaceans, teleosts were most important between 100 and 200 mm, and cephalopods became increasingly important in larger animals (Fig. 3b).

The pooled sample sizes of *I. coindetii* caught at each hourly interval during the *Cirolana* research cruises ranged from a minimum of 23 squid (at 13:00) to a maximum of 183 squid (at 11:00). There was no relationship between sample size and time of day of the tow. The percentages of *I. coindetii* with prey remains in their stomachs is plotted against the time of capture in Figure 4. A curvilinear trend line produced the best fit to the data. The percentage of squid with prey remains in their stomachs was low in the early morning, it then increased to peak at 11:00, then decreased towards the evening. Sample sizes of *T. eblanae* caught during the *Cirolana* research cruises were too small to allow similar analysis.

Cannibalism and predation on other cephalopods was common by both species. Figure 5 reflects the percentage of squid damaged by bites thought to be consistent with attacks by other squid and the total catch mass of ommastrephids in each of the trawls. The trend lines plotted are not statistically significant. There was no apparent relationship between the number of squid with cephalopod remains in their stomachs and either the total catch mass or the percentage of damaged squid sampled in each trawl.

During the study, both *I. coindetii* and *T. eblanae* were found in the stomachs of a number of demersal fish species. Many of these records were attributable to feeding by the fish within the trawl. Well-digested remains and beaks were found in the stomachs of conger eels *Conger conger*, cod, ling and black pollock *Pollachius virens*.

**DISCUSSION**

Heavy fishing effort and the increasing realization of the importance of ommastrephid squid as a resource emphasizes the need for effective fisheries management in Irish waters. Currently, no reliable fisheries statistics for ommastrephids in Irish waters are available. Similar patterns to that seen in 1996 (Fig. 2), i.e. large catches of *I. coindetii* in November or December and a decline in catches in late April or May, were noted but not quantified accurately during 1994, 1995 and 1997. *I. illecebrosus* and *I. argentinus* populations are both known to make extensive seasonal migrations to feeding areas (Hatanaka et al. 1985). There is evidence that such migrations are made to take advantage of more productive but less predictable waters at higher latitudes (Rodhouse and Nigmatullin 1996). The west coast of Ireland is towards the northern limit of the range of *I. coindetii* on the European shelf of the North-East Atlantic (Roper et al. 1984). North of 54°N, the numbers of *I. coindetii* caught in commercial trawls declines dramatically (Lordan in prep.). Therefore, the pattern of recruitment and seasonal catch decline of *I. coindetii* in Irish waters may suggest a
similar type of migration to feeding grounds of higher latitude as do I. argentinas and I. illecebrosus.

The patterns of migration and population fluctuation in T. eblanae are not so obvious. T. eblanae lives commonly in the shelf waters of the Celtic and Irish seas and west of Ireland (Collins et al. 1995, Lordan in prep.). There appears to be a migration to deeper water on the shelf edge to spawn. This feature is evidenced by the increase in sample masses in April 1996, much of which consisted of mated mature females (Fig. 2). The extent of feeding migrations (if any) north and south over the shelf are currently unknown.

The significantly greater numbers of mature female I. coindetii with prey remains in their stomachs found in this study agrees with the findings of Rasero et al. (1996) and may, as they suggest, be related to the increased energetic demands of gonad development. This statement is also supported by the fact that the female I. coindetii had significantly more distended stomachs (Level 5) than males, also suggesting increased levels of feeding by females.

The very significant differences between research and commercial vessels in the numbers of I. coindetii with empty stomachs and stomachs with prey remains was unexpected. It is interesting that no such differences were apparent for T. eblanae (although it must be conceded that the sample size for that species on research cruise surveys was considerably smaller, at n = 379). There are two main differences between the two sample groups. First, research cruise samples were only collected during daylight; second, research cruise tows are all 1-h duration, not the 6–7 h of commercial vessels. Sampling time of day, methods and durations clearly seem to be critical in analysis of levels of feeding.

Cephalopods are opportunistic predators (Nixon 1987). Rasero et al. (1996) demonstrated that the diets of both I. coindetii and T. eblanae vary significantly with area. Other studies on the diets of the two species analysed here have similarly shown different teleost prey in different areas (Sánchez 1982, Castro and Hernández-Garcia 1995). Pearlside M. muelleri, blue whiting M. poutassou, silvery pout G. argenteus, argentines Argentinia sp. and M. norvegica are all common species on the Irish shelf edge. The occurrence of these species in the diets of both ommastrephid species in this study supports the assumption that both I. coindetii and T. eblanae feed primarily on the most abundant pelagic species of appropriate size in the area the squid were sampled.

Although they overlap considerably, there are significant differences between the diets of the two species. Sprat, herring and pouting are found in the diet of T. eblanae, but not in that of I. coindetii. Gobies are also relatively more important in the diet of T. eblanae.

Mackerel, Diaphus sp. and hatchetfish occur in the diet of I. coindetii but not in that of T. eblanae. In general, shallower inshore species (i.e. pouting, sprat and herring) are more common in the diet of T. eblanae in Irish waters. T. eblanae also seem to feed more on demersal species (i.e. pouting and gobies) than I. coindetii. This supports the observations of Rasero et al. (1996). The result may also be influenced by the fact that T. eblanae tends to be more common in shallower waters than I. coindetii (Hastie et al. 1994, Collins et al. 1995, Lordan in prep.).

The diets of both species were dominated by the small mesopelagic sternoptychid, the pearlside, which is known to shoal in very dense concentrations (Gjøsaeter 1981). It is also common in the diet of L. forbesi caught past the shelf-break west of Ireland (Collins et al. 1994). It is also evident from the high percentage occurrence of teleosts (79.5%, Table II) that pearlside remains are also found in great numbers in squid stomachs, e.g. one I. coindetii stomach had 43 pairs of pearlside otoliths.

Interpretations of dietary data should always be treated cautiously. Pearlside have been found in the stomachs of other prey species of both I. coindetii and T. eblanae, most importantly in blue whiting (Bailey 1982). Therefore, it is likely that at least some of the pearlside otoliths found in the stomachs of the ommastrephids analysed here were actually the prey of blue whiting or other primary prey species. Furthermore, observations on feeding behaviour of squid have shown that head, tail and even gut may be selectively rejected (Bidder 1950, Bradbury and Aldrich 1969). Another bias may be introduced by the possible retention of small otoliths of irregular shape, such as those of pearlside, or the selective rejection of large calcareous otoliths and the large vertebrae of blue whiting. Serological techniques can be used to identify prey remains in the absence of otoliths and vertebrae (Boyle et al. 1986). Unfortunately, such techniques cannot be used to determine whether prey are primary or secondary, an important consideration when both blue whiting and pearlside remains are found in the same stomach. The relatively low percentages of unidentified fish remains in the stomachs of I. coindetii when compared to those found in Galician waters (Rasero et al. 1996) may also support the theory that the importance of pearlside has been overstated in the diets of both species in this study. Further investigations need to be made into the diet of blue whiting and other methods of dietary analysis (such as serological techniques) to clarify the overall importance of pearlside in the diets of both species analysed here.

The occurrence of the pteropod L. retroversa in the stomachs of both species was an unexpected result. The species is known to occur in dense swarms off the
In this study, pteropod shells were only found in stomachs where pearlside were also identified. Pteropods were discovered in intact pearlside stomachs inside the squid stomachs and also in the stomachs of whole pearlside selected from the catch. Pearlside are known to feed on pteropods in Norwegian waters, the latter being found in 2% of pearlside stomachs examined (Gjøsaeter 1981). In Irish waters, pteropods may be an important component of pearlside diet and, hence, are likely to be secondary prey of ommastrephid squid.

Ontogenic changes in diet have previously been described in *L. forbesi* in Irish waters (Collins et al. 1994). Similarly, ontogenic changes were described for the ommastrephid species *Todarodes sagittatus* by Breiby and Jobling (1985). In the present study, despite the difference in size between *I. coindetii* and *T. eblanae*, the diet of both clearly shows the same pattern exhibited by most nektonic squid. Crustaceans (in this study, mainly euphausids) are relatively more important in the diet of smaller squid, and other cephalopods become relatively more common in the diet of larger squid. Ontogenic changes in diet have previously been described for captive *I. illecebrosus* by O’Dor et al. (1980).

Bradbury and Aldrich (1969) observed that *I. illecebrosus* in captivity fed most often in the early morning despite food being offered regularly throughout the day. In the wild, *I. illecebrosus* have been observed feeding on surface swarms of euphausids in the early afternoon in the Bay of Fundy (Nicol and O’Dor 1985). Vertical migration by juvenile *I. illecebrosus* is related to feeding intensity as well as to the diurnal movements of euphausids and fish (Arkhipkin and Fedulov 1986). In the present study, the greatest percentage of stomachs with food was recorded during the middle of the day. This may be because *I. coindetii* feed most actively in early morning and adopt a demersal habitat during the day while digestion is taking place. However, this statement cannot be conclusive because no samples of squid were collected at night or higher in the water column and very little is known about diurnal vertical migrations of *I. coindetii*.

Physical damage to both squid and fish caught by trawl has important commercial implications, because most damaged squid and fish are discarded. Net-associated attacks also have important implications for errors in identification of the prey remains in the stomachs of squid. *I. illecebrosus* net-associated attacks on fish in commercial trawls have been reported in the North-West Atlantic by Testaverde (1977). Off the Irish coast, attacks on fish species in trawls also takes place, but it is difficult to quantify this damage.
on commercial fishing vessels. However, by subsampling the ommastrephid squid in the catch in this study, it was possible to quantify damage consistent with squid attack on other squid in the catch. Levels of net-associated damage vary considerably, but occasionally they can reach levels as high as 32.4%. *L. illecebrosus* schools have an internally organized structure and spatial organization (Mather and O’Dor 1984). The trawl will obviously affect this organization and may result in such intraspecific attacks. However, the importance of the attacks as a source of error in dietary studies is currently unquantified.

The short lifespan, fast growth, large interannual fluctuations in recruitment levels and voracious appetite of squid make them unique predators in the marine ecosystem. Several authors have mentioned their potential impact as predators of commercial fish populations (see Rodhouse and Nigmatullin 1996). Many of the teleost prey of *L. illecebrosus* and *T. eblanae* live for several years and are at risk of predation by squid in successive years. It is important to note that this increases the relative ecological importance of both species.

Figure 6 is a simplified foodweb for the continental shelf west and south-west of Ireland, showing the position of both species in the ecosystem and their interactions with species at other trophic levels in the ecosystem. Evaluating the role of *I. coindetii* and *T. eblanae* in the ecosystem quantitatively is currently impossible because of gaps in knowledge specifically of stock size and digestion rates (see Rodhouse and Nigmatullin 1996). However, this study has been able impossible because of gaps in knowledge specifically of stock size and digestion rates (see Rodhouse and Nigmatullin 1996). However, this study has been able to identify important prey species, the trophic position and aspects of predatory behaviour of both *I. coindetii* and *T. eblanae* in Irish waters.

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