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THE DIET AND ECOLOGICAL IMPORTANCE OF *ILLEX COINDETII* AND *TODAROPSIS EBLANAE* (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 euphausids, 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, *Gadiculus argenteus*, *Micromesistius poutassou*, *Argentina* sp. and the euphausid *Meganyctiphanes norvegica*, are also important prey of both species. Data on possible trawlnet-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. coindetti*.

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, 1841) 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, finfish 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 an increasingly important landed component of the catch. Nevertheless, ommastrephid squid catch statistics are currently not available for the area. This is partly attributable to the nature of the multinational fleet fishing there and the fact that cephalopods are nonquota 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 encrasicholus*, *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 dumerelli*, the euphausid *Thysanopoda* sp. and several cephalopod species (Castro and Hernández-García 1995). In South African waters, the diet of

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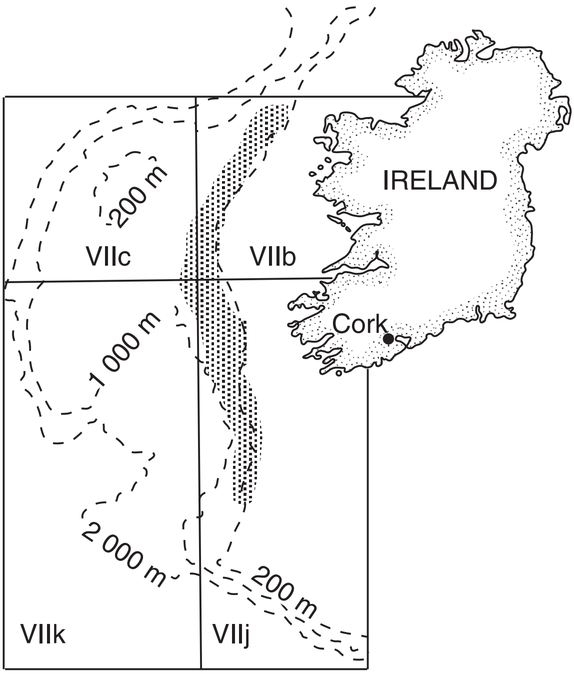

Fig. 1: The sampling area (shaded) on the continental shelf edge from 250 to 600 m deep west and southwest of Ireland. ICES statistical areas marked

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 midwater, 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

Table I: Numbers of squid stomachs sampled from landings of commercial trawlers and at sea on commercial and research vessels between November 1993 and April 1997

Sampling month	Numbers of squid stomachs sampled from the landings of commercial trawlers		Numbers of squid stomachs sampled at sea on commercial and research trawlers		Sea-based sample vessel		
	I. coindetii	*T. eblanae*	*I. coindetii*	*T. eblanae*	Vessel	Sampling dates	ICES area
November 1993	0	0	103	133	M.F.V. *Shannon*	1.11.93–10.11.93	VIIb & VIIc
December 1993	46	106					
January 1994	0	76	7	19	M.F.V. *Shannon*	10.1.94–17.1.94	VIIb & VIIc
February 1994	27	67	352	99	R.V. *Cirolana*	25.2.94–10.3.94	VIIj, VIIh & VIIg
March 1994	120	56					
April 1994	64	104					
May 1994	0	0					
June 1994	0	0					
July 1994	0	0					
August 1994	0	0					
September 1994	0	0					
October 1994	0	0	42	49	R.V. *Thalassa*	27.10.94–4.11.94	VIIh & VIIg
November 1994	108	34					
December 1994	120	77					
January 1995	56	85					
February 1995	0	0	114	189	M.F.V. *Shannon*	7.2.95–14.2.95	VIIj, VIIb & VIIc
March 1995	0	0	274	182	R.V. *Cirolana*	13.3.95–11.4.95	VIIj, VIIh & VIIg
April 1995	59	121					
May 1995	51	189					
June 1995	0	78					
July 1995	0	0					
August 1995	0	0					
September 1995	0	0					
October 1995	0	67					
November 1995	39	88					
December 1995	61	12					
January 1996	108	23					
February 1996	132	78					
March 1996	0	0	104	88	M.F.V. *Shannon*	4.3.96–11.3.96	VIIj, VIIb & VIIc
April 1996	0	0	109	68	M.F.V. *Shannon*	8.4.96–15.4.96	VIIj, VIIb & VIIc
May 1996	0	0	107	107	M.F.V. *Shannon*	8.5.96–14.5.96	VIIj, VIIb & VIIc
June 1996	0	0					
July 1996	77	0					
August 1996	0	0					
September 1996	0	0					
October 1996	0	120					
November 1996	0	0	95	101	M.F.V. *Shannon*	14.11.96–19.11.96	VIIj, VIIb & VIIc
December 1996	0	0	111	138	M.F.V. *Shannon*	5.12.96–12.12..96	VIIb & VIIc
January 1997	0	0	123	131	M.F.V. *Shannon*	7.1.97–17.1.97	VIIj, VIIb & VIIc
February 1997	0	0					
March 1997	0	0	339	50	R.V. *Cirolana*	6.3.97–21.3.97	VIIj, VIIh & VIIg
April 1997	0	0	121	79	M.F.V. *Shannon*	22.4.97–3.5.97	VIIj, VIIb & VIIc

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

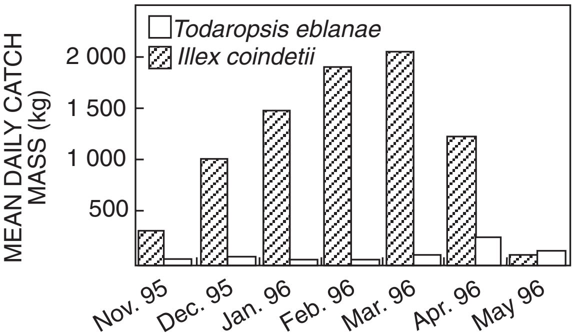

Fig. 2: The mean daily catch rate for the commercial demersal trawler M.F.V. *Shannon* during the 1995–96 season

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, œsophagus 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 χ^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,

Table II: Percentage occurrence of prey items identified in the diet of *I. coindetti* and *T. eblanae* from Irish waters

Taxon	*Illex coindetti*		*Todaropsis eblanae*	
	Percentage occurrence of all taxa	Percentage occurrence of teleosts	Percentage occurrence of all taxa	Percentage occurrence of teleosts
TELEOSTS	74.7	114.9	79.9	125.8
Clupeiformes				
Sprat *Sprattus sprattus*	0.0	0.0	0.5	0.6
Herring *Clupea harengus*	0.0	0.0	0.2	0.6
Family Argentinidae				
Argentine *Argentina* sp.	3.9	4.5	0.7	0.9
Family Sternoptychidae				
Pearlside *Maurolicus muelleri*	48.3	79.5	34.7	61.7
Hatchetfish *Argyropelecus hemigymnus*	0.2	0.2	0.0	0.0
Family Myctophidae				
Diaphus sp.	0.4	0.4	0.0	0.0
Family Gadidae				
Blue whiting *Micromesistius poutassou*	6.3	7.6	0.2	0.3
Silvery pout *Gadiculus argentenus*	7.4	11.1	6.3	9.6
Pouting *Trisopterus* sp.	0.0	0.0	9.7	13.6
Rockling larvae subfamily Lotinae	0.9	1.1	5.3	8.4
Family Gobiidae				
Transparent goby *Aphia minuta* 0.5	0.7	7.9	10.1	
Unidentified goby Gobiidae sp.	0.4	0.4	4.9	6.1
Family Carangidae				
Sead *Trachurus trachurus*	0.9	0.9	0.7	0.9
Family Scombridae				
Mackerel *Scomber scombrus*	0.2	0.2	0.0	0.0
Unidentified teleosts	5.4	8.3	8.8	13.0
CRUSTACEANS	29.9		21.1	
Order Euphausiacea				
Meganyctiphanes norvegica	9.5		7.6	
Unidentified euphausids	9.3		7.4	
Order Decapoda			0.0	
Dichelopandalus bonnieri	0.4		1.2	
Pasiphaea sp.	3.0		0.5	
Unidentified crustaceans	7.7		4.4	
MOLLUSCS				
Order Cephalopoda	10.4		3.7	
Illex coindetti	1.8		0.2	
Todaropsis eblanae	0.4		1.9	
Todarodes sagittatus	0.2		0.0	
Loligo forbesi	0.2		0.5	
Rossia macrosoma	0.4		0.0	
Unidentified cephalopods	7.6		1.2	
Order Gastropoda	6.9		7.4	
Pteropod *Limacina retroversa*	6.9		7.4	

2 532 had no remains or negligible prey remains present in their digestive tract. Another 2 870 *T. eblanae* stomachs were examined and, of these, 2 107 had no remains or negligible prey 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 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 (χ^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 retroversa*. Large numbers of *L. retroversa* 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 (χ^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 *Scomber 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* (χ^2 = 44.06, $df = 6$, $p < 0.001$). Differences between the numbers of stomachs containing identified crustacean (χ^2 = 6.05, $df = 2$, $p < 0.05$) and cephalopod species (χ^2 = 6.07, $df = 2$, $p < 0.05$) were also significant.

Microscopic examination was also used to assess

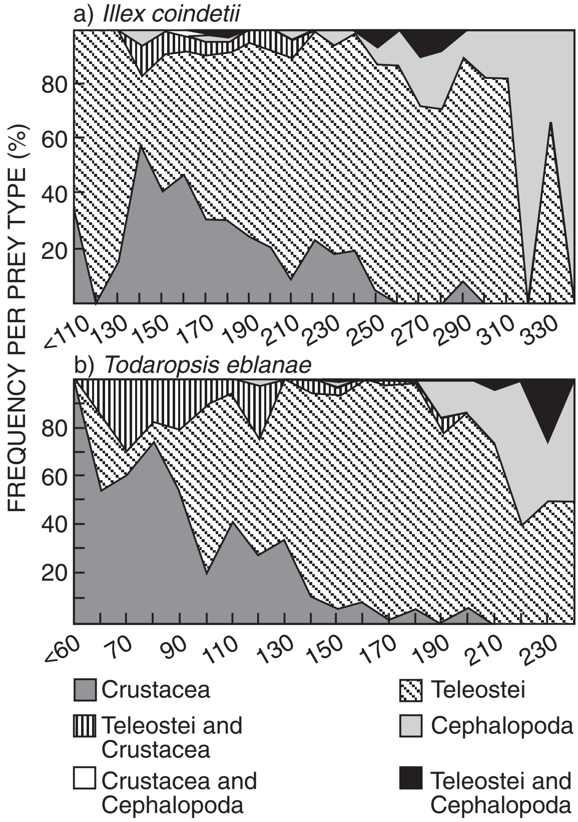

Fig. 3: Variation in the diet of (a) *I. coindetii* and (b) *T. eblanae* with predator size

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 *DML*s 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).

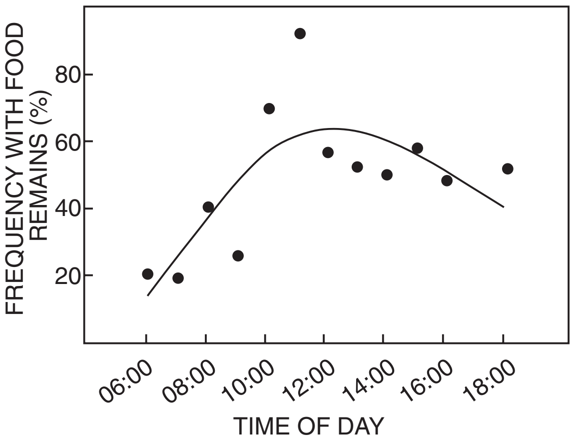

Fig. 4: Percentage of *I. coindetii* with prey remains in their stomachs sampled at hourly intervals in March of 1994, 1995 and 1997 by R.V. *Cirolana*

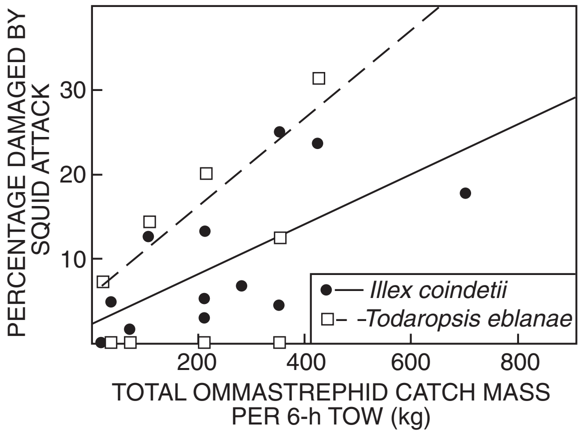

Fig. 5: Relationship between the percentage of *I. coindetii* and *T. eblanae* with damage consistent with squid attack and the total catch mass of ommastrephids in 12 individual hauls

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. argentinus* 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-García 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

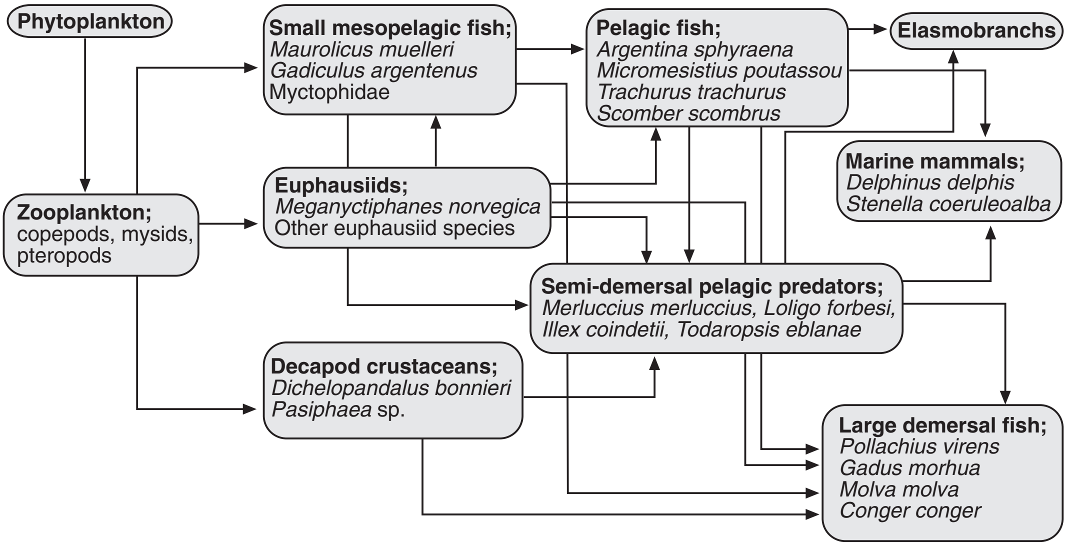

Fig. 6: Simplified trophic web for the continental shelf west and south-west of Ireland

west coast of Ireland (Hardy 1964). 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 the prey types found in stomachs in this and other studies is not proof of prey selection (Dawe 1988). Attempts were made to look at prey teleost size selectivity using the techniques of Collins and Pierce (1996). No patterns of size selectivity of teleost prey was evident in the present study. *I. coindetii* and *T. eblanae* may consume fish smaller than themselves non-selectively, as was 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%. *I. 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 *I. coindetii* 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 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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