

PREDATORY RELATIONSHIPS OF TWO SYMPATRIC SQUID, *TODAROPSIS EBLANAE* AND *ILLEX COINDETII* (CEPHALOPODA: OMMASTREPHIDAE) IN GALICIAN WATERS

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The natural feeding of the two most abundant ommastrephid squid (Cephalopoda: Ommastrephidae) in Galician waters was studied and compared. A sample of 334 stomach contents of *Todaropsis eblanae* (34–222 mm ML) and 267 stomach contents of *Illex coindetii* (50–379 mm ML) caught by commercial trawlers was examined. A total of 21 (*T. eblanae*) and 23 (*I. coindetii*) different prey items, belonging to three zoological groups (Teleostei, Crustacea and Cephalopoda), were taken by these cephalopods. However, 43% of the *T. eblanae* diet comprised only one fish species, *Micromesistius poutassou*. The diet of these squid species was significantly influenced by the geographical area (both species), size (*T. eblanae*) and maturation (*I. coindetii*). Feeding rate of both species decreased with size, but the percentage of stomachs with food remains increased in maturing and mature females. Weight of prey captured was dependent on available prey sizes and, in small individuals, maximum prey weight was very close to the squid weight. Both squid species are mainly neritic nekto-benthic predators, but *I. coindetii* seems to have a broader and more pelagic diet.

INTRODUCTION

Cephalopods are fast-growing carnivorous molluscs that play an important role in the trophic webs of marine ecosystems (Amaratunga, 1983). Among them, fast-swimming muscular squid are considered the most voracious predators (O'Dor et al., 1980). Daily feeding rates of some species of the family Ommastrephidae (e.g. *Illex illecebrosus* (Lesueur), *Dosidicus gigas* (d'Orbigny)) have been estimated to be over 10% of the total body weight (O'Dor et al., 1980; Ehrhardt, 1991). *Todaropsis eblanae* (Ball) and *Illex coindetii* (Vérany) are the only two ommastrephid squid which are relatively abundant off the Galician coast (north-western Spain), an area with a high primary production due to an important upwelling of nutrient-rich water (Fraga, 1981). Total average capture (1980–1991) of both squid species together was 1000 tonnes per year. However, a high interannual variability (range 500–2500 tonnes) was observed (González et al., 1994). Both species are captured as a by-catch of a multispecies trawling fishery on the Galician shelf and continental slope (100–500 m depth). Target species of this fishery are blue whiting (*Micromesistius poutassou* (Risso)), hake (*Merluccius merluccius* (L.)) horse-mackerel (*Trachurus trachurus* (L.)), monkfish (*Lophius* spp.) and Norway lobster (*Nephrops norvegicus* (L.)).

Management of this fishery requires a detailed knowledge of the trophic relationships between the species involved as predation has a significant influence on community structure and population dynamics (Paine, 1980). Information about the diet of the main species of fish present in the fishery is available at the present time (Robles Pariente, 1970; Olaso & Pereda, 1982; González et al., 1985). However, nothing is known about the feeding biology of *T. eblanae* and *I. coindetii* in the Atlantic waters off the Iberian peninsula. Fish are the most important prey of *T. eblanae* in the Benguela ecosystem (Lipinski, 1992) and of *I. coindetii* in eastern Mediterranean waters (Sánchez, 1982) and north-west Africa (Hernández-García, 1992). In the latter area, there is a similar occurrence of crustaceans and fishes in the diet of *T. eblanae* (Hernández-García, 1992).

These two species inhabit the same fishing grounds and have nearly the same range of bathymetric distribution in Galician waters. As they are close in morphology and size, and cephalopods are considered opportunistic predators (Nixon, 1987), an important overlap may be expected in their diets.

There are many factors that affect the diet of a species. Some are intrinsic to the species, and others depend on the habitat. Among the intrinsic factors, sex, size and maturity stage have been reported to affect the diet of cephalopods (Castro & Guerra, 1990). There is little information on the influence of these factors in the diet of *T. eblanae* and *I. coindetii*. Only the size and/or maturity have been reported to affect the diet of *I. coindetii* in the Catalanian Sea and north-west Africa, with small/immature individuals preying mainly upon crustaceans and large/mature squid upon fish species (Sánchez, 1982; Hernández-García, 1992). In *T. eblanae*, an increase in cephalopod prey has been reported in large/mature animals from north-west Africa (Hernández-García, 1992).

Habitat influences diet mainly through the availability of prey that can be related to oceanographic factors. Two main areas can be considered in oceanographic terms in Galicia (Figure 1), where the circulation systems of the north and west coasts are dissimilar and subsurface waters (75–400 m depth) in each area have different origins. In addition, the circulation system of the western area intensifies upwelling and favours the accumulation of nutrients (Fraga, 1981). As a result of this, the availability of prey may be different in the two areas. Higher densities of decapod crustaceans and demersal fishes have been reported in the western area than in the northern area (González-Gurriarán & Olaso, 1987; Fariña et al., 1985).

In this paper the natural feeding of *T. eblanae* and *I. coindetii* is studied and compared. Size, sex and maturity stage of squid, and the area of capture, are tested as factors which may affect their diets. Estimates of the predatory activity of both species is based on their feeding rates.

MATERIAL AND METHODS

A total of 1372 *Todaropsis eblanae* and 618 *Illex coindetii* were sampled from commercial vessels trawling on the continental shelf and slope off Galicia. *Todaropsis eblanae* specimens ranged from 34 to 222 mm dorsal mantle length (ML). The range of *I. coindetii* individuals was 50–379 mm ML. Samples were taken monthly between November 1991

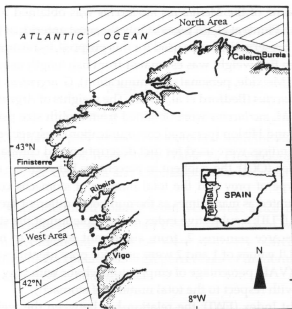


Figure 1. Map showing the approximate areas (north and west) where the squid samples were taken.

and November 1992 at three ports: Burela, Celeiro and Ribeira (Figure 1). Trawlers from Burela and Celeiro fish in northern fishing grounds, whereas vessels based at Ribeira fish in the western area.

For each specimen, ML, total body weight (BW), sex and maturity stage (according to Lipinski, 1979) were noted, the stomach was then removed and assigned to a fullness index category (see below). The stomach contents of a randomly selected subsample of *T. eblanae* (N=334) and all the stomachs containing food of *I. coindetii* (N=267) were weighed and stored in 70% ethanol before prey analysis.

Prey were identified to the lowest possible taxon. When a prey item was clearly distinguishable from others, but impossible to identify, it was placed in a separate arbitrary category.

Teleostean fishes were identified from otoliths, vertebrae and scales, after comparison with a reference collection and the drawings, pictures and descriptions appearing in Bauzá-Rullán (1962); Schmidt (1968); Härkönen (1986) and Pierce et al. (in press).

Cephalopods were identified from statoliths, beaks and gladii, using reference collections and according to guidelines by Clarke (1966) and Pérez-Gándaras (1986).

Crustaceans were identified by comparison of hard remains with the illustrations of the published guides of Zariquiey (1968), McLaughlin (1980) and González-Gurriarán & Méndez (1985). Identification of euphausiaceans was carried out by comparison of their mandibles with the drawings of Lagardère (1972).

Cephalopod weight was estimated from beaks using equations found in Pérez-Gándaras (1986). Estimation of length of *Micromesistius poutassou*, *Gadaculus argenteus*

Guinochet and some of the *Merluccius merluccius* was obtained from vertebrae using equations given in Pierce et al. (in press). Only the most anterior of the caudal vertebrae in a good state of preservation were used for this purpose, as recommended by Pierce et al. (in press). Then fish weight was estimated from fish length using specific equations for: *M. poutassou* (Meixide, personal communication), *G. argentus* (Pereda & Villamor, 1991) and *M. merluccius* (Bedford et al., 1986). The weights of *Argentina sphyraena* L. and of the rest of the *M. merluccius* were obtained from otolith size using the equations of Härkönen (1986) and Hislop (personal communication), respectively.

The following indices were used for diet description and comparison:

Occurrence Index (OCI): the quotient in percentage between the number of stomachs containing one type of prey and the total number of stomachs containing prey, each stomach being counted as many times as the number of different prey types it contained.

Fullness Index (FUI): a subjective index of the repletion of the stomach. 0, empty; 1, containing very scarce remains; 2, from significant remains to maximum repletion. Stomachs with FUI values of 1 and 2 were used for prey identification.

Vacuity Index (VAI): percentage of empty stomachs or with very scarce remains (FUI values 0 and 1), with respect to the total number of stomachs.

Fullness Weight Index (FWI): the relationship between the weight of the stomach content (g) multiplied by 100, and the BW (g) less the weight of the stomach content. An estimation of the maximum FWI by squid weight was obtained. The method employed was as follows: (1) to sort the FWI data by squid BW classes. Body weight classes for *T. eblanae* were: (a) in the north, one class each 40 g for specimens between 10 and 430 g; (b) in the west, one class for each 40 g, for specimens between 0 and 320 g. Body weight classes for *I. coindetii* were: (a) in the north, one class for each 50 g, for specimens between 10 and 460 g; (b) in the west, one class for each 40 g, for specimens between 10 and 290 g. (2) To obtain the mean of the three maximum FWI values of each BW class. Only weight classes with at least three FWI values were considered. (3) To take the successive maxima of these means, from the highest to the lowest BW class. (4) A regression line was fitted to these successive maxima, taking the midweight of the respective BW class as abscissa values.

In order to test the effect of squid size and maturity on diet, different predator groups were considered in each case: (a) study of squid size effect: $ML \leq 120$ mm and $ML > 120$ mm for *T. eblanae*; and $ML \leq 150$ mm and $ML > 150$ mm for *I. coindetii*. Size ranges were selected according to maximum size of species and adequate sample size; (b) study of maturity stage effect: immature and mature individuals were grouped separately in both species. Immature individuals correspond to stages I and II of the scale of Lipinski (1979). Mature individuals correspond to stages III, IV and V of the same scale.

Comparisons of the diet between *T. eblanae* and *I. coindetii*, and between different groups of each species were made using a χ^2 test (Crow, 1982), followed by a test of percentage comparison (Sokal & Rohlf, 1969) between clusters of prey. Four clusters of prey were considered for *T. eblanae*: *Micromesistius poutassou* (Risso), other teleosteans (including unidentified fishes), crustaceans and cephalopods. For *I. coindetii*, three clusters of prey were considered: teleosteans, crustaceans and cephalopods. Prey clusters were made to fulfil the requirements of the statistical tests employed, on the basis of

taxonomic affinities.

Vacuity indices of different predator groups were compared using a test of percentage comparison (Sokal & Rohlf, 1969).

RESULTS

General description of diets

A total of 21 and 23 different prey items were identified from the stomach contents of *Todaropsis eblanae* and *Illex coindetii*, respectively (Table 1). Prey belonged to three main zoological groups, Teleostei, Crustacea and Cephalopoda, in decreasing order of occurrence.

Teleostean fishes were identified mainly from vertebrae, since the occurrence of otoliths was very low in both species (less than 10% of the stomachs with fish remains). Moreover, hard remains including vertebrae were also very scarce in the stomach contents of *I. coindetii*, which explains the high percentage of unidentified teleosteans.

Cannibalism was observed in both species.

Feeding by geographical areas

Table 2 shows the diet comparison by prey clusters between the north and the west for both species. The feeding of each species was significantly different between the two geographical areas considered.

The occurrence of fish was significantly higher for both squid species in the northern area. On the contrary, crustaceans were significantly more abundant in the west.

The vacuity index (VAI) showed an opposite tendency in the two species. Significantly higher values were found in *T. eblanae* from the west, and in *I. coindetii* from the north.

Feeding by sex and maturity stage

There were no significant differences between sexes for either species or areas ($P > 0.05$). Therefore, males and females were always grouped in further comparisons.

The diet of *T. eblanae* showed significant differences between immature and mature individuals in both areas (Table 3A). *Micromesistius poutassou* was the predominant prey of mature individuals from the north, while 'other Teleostei' were predominant in immature individuals. The differences found in the west were due to the higher occurrence of cephalopods in immature animals. The vacuity index was always higher in immature individuals.

No diet differences were found due to maturity in *I. coindetii* from the north (Table 3B). In the west, there was a higher percentage of crustaceans and cephalopods in the stomachs of immature and mature specimens, respectively. The vacuity index was higher in immature animals from both areas.

The decrease of VAI values in mature animals of both species was mainly due to the differences between mature and immature females (Figure 2).

Table 1. Occurrence index of prey items in the diet of *Todaropsis eblanae* and *Illex coindetii* in the north and west of the Galician Coast.

Prey items	<i>Todaropsis eblanae</i>		<i>Illex coindetii</i>	
	North	West	North	West
Teleostei	89.0	66.7	77.2	65.0
Clupeidae	-	-	1.5	1.2
<i>Sprattus sprattus</i> (L.)	-	-	-	3.0
<i>Trachurus trachurus</i> (L.)	0.5	1.6	-	-
Gadidae	0.5	-	2.2	1.8
<i>Micromesistius poutassou</i> (Risso)	49.5	34.8	9.6	7.8
<i>Gadiculus argenteus</i> Guinochet	7.5	9.3	2.2	1.8
<i>Antonogadus macrophthalmus</i> (Günther)	1.5	-	-	-
<i>Merluccius merluccius</i> (L.)	6.5	0.5	0.7	0.6
<i>Mauroliscus muelleri</i> (Gmelin)	-	-	1.5	-
<i>Gaidropsarus vulgaris</i> (Cloquet)	-	-	-	0.6
<i>Zeus faber</i> L.	-	-	-	0.6
<i>Cepola macrophthalma</i> (L.)	7.0	0.5	-	1.2
<i>Diplodus</i> sp.	-	-	0.7	0.6
<i>Gymnamodites semisquamatus</i> Jourdain	-	-	-	0.6
<i>Argentina sphyraena</i> L.	4.5	1.1	1.5	1.8
<i>Callyonimus</i> sp.	2.0	-	-	-
Gobiidae	-	1.6	0.7	-
<i>Aphya minuta</i> (Risso)	-	1.6	2.2	5.4
<i>Gobisculus flavescens</i> (Fabricius)	-	-	-	0.6
Pleuronectiforms	0.5	-	-	1.2
Teleostei A	-	1.6	-	-
Teleostei B	1.0	-	-	-
Not identified	8.0	14.1	54.4	36.2
Crustacea	3.5	18.0	11.8	22.3
<i>Gammaridea</i>	-	-	0.7	-
<i>Meganyctiphanes norvegica</i> (M. Sars)	-	0.5	2.2	14.5
Decapoda	-	1.0	-	-
Natantia	-	2.1	-	-
<i>Sergestes robustus</i> S. I. Smith	-	-	-	1.8
<i>Pasiphaea</i> sp.	1.0	4.2	-	0.6
<i>Plesionika martia</i> (A. Milne Edwards)	-	-	-	1.2
Reptantia	-	0.5	-	-
Galatheidae	-	1.0	-	-
Brachyura	-	2.1	-	-
<i>Polybius henslowii</i> Leach	-	-	1.5	-
Not identified	2.5	6.6	7.4	4.2
Cephalopoda	7.0	14.8	11.0	12.7
<i>Loligo</i> sp.	0.5	0.5	-	0.6
<i>Alloteuthis</i> sp.	-	1.6	-	-
<i>Alloteuthis subulata</i> (Lamarck)	-	-	0.7	1.2
Ommastrephidae	4.0	2.2	-	-
<i>Todaropsis eblanae</i> (Ball)	1.5	3.4	1.5	2.4
<i>Illex coindetii</i> (Vérany)	-	1.6	4.4	3.0
<i>Eledone cirrhosa</i> Lamarck	1.0	-	-	-
Not identified	-	5.5	4.4	5.5
Not identified	0.5	0.5	-	-

Table 2. Prey clusters used for total comparison of the diet between areas within each squid species, OCI values, VAI, significance levels of the differences and results of the χ^2 test.

Prey cluster	<i>Todaropsis eblanae</i>		<i>Illex coindetii</i>	
	North	West	North	West
<i>Micromesistius putassou</i>	49.8	**	35.0	} 65.0
Other Teleostei	39.7	ns	32.0	
Crustacea	3.5	***	18.1	} 22.3
Cephalopoda	7.0	**	14.9	11.0 ns 12.7
Total 100%	197		182	136 166
No.	174		160	110 132
VAI	67.4	***	78.0	75.9 * 66.8
No. VAI	641		731	
χ^2		33.34		6.61
df		3		1
P		<0.001		<0.05

No., total number of specimens with food in the stomach; No. VAI, number of stomachs utilized for *Todaropsis eblanae* VAI calculation (see Material and Methods).

Table 3. Prey clusters used for total comparison of the diet between immature and mature individuals of each species and area, OCI values, VAI, significance levels of the differences and results of the χ^2 test.A. *Todaropsis eblanae*.

Prey cluster	North		West	
	Immatures	Matures	Immatures	Matures
<i>Micromesistius putassou</i>	38.3	**	31.2	39.7
Other Teleostei	50.0	**	30.3	35.6
Crustacea	4.3	ns	15.6	21.9
Cephalopoda	7.4	ns	22.9	2.8
Total 100%	94		103	73
No.	83		91	62
VAI	71.4	*	63.3	70.3
No. VAI	322		319	128
χ^2		9.66		17.26
df		3		3
P		<0.05		<0.001

B. *Illex coindetii*.

Prey cluster	North		West	
	Immatures	Matures	Immatures	Matures
Teleostei	80.9	ns	75.5	69.0
Crustacea	11.9	ns	11.7	15.1
Cephalopoda	7.2	ns	12.8	15.9
Total 100%	42		94	126
No.	33		77	95
VAI	82.4	*	72.3	55.9
χ^2		1.01		19.19
df		2		2
P		>0.05		<0.001

No., total number of specimens with food in the stomach; No. VAI, number of stomachs utilized for *Todaropsis eblanae* VAI calculation (see Material and Methods).

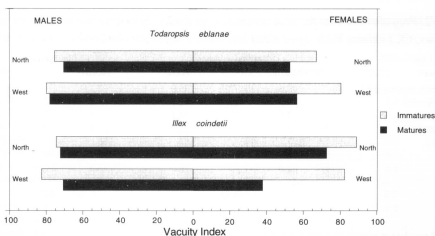


Figure 2. Variation of the vacuity index (VAI) in immature and mature males and females of *Todaropsis eblanae* and *Illex coindetii* in both areas.

Table 4. Prey clusters used for total comparison of the diet between size classes of *Todaropsis eblanae* within areas, OCI values, VAI, significance levels of the differences and results of the χ^2 test.

Prey cluster	North		West			
	ML \leq 120	ML>120	ML \leq 120	ML>120		
<i>Micromesistius poutassou</i>	37.8	**	59.8	25.2	**	48.0
Other Teleostei	51.1	**	30.8	34.6	ns	29.3
Crustacea	} 11.1	ns	} 9.4	15.9	ns	21.4
Cephalopoda				24.3	***	1.3
Total 100%	90		107	107		75
No.	78		96	97		63
VAI	71.6	*	64.0	80.3	**	66.7
No. VAI	285		356	605		126
χ^2		10.08				27.74
df		2				3
P		<0.01				<0.001

No., total number of specimens with food in the stomach; No. VAI, number of stomachs utilized for *Todaropsis eblanae* VAI calculation (see Material and Methods).

Feeding by size

The diet of *T. eblanae* showed significant changes with growth in both areas (Table 4). Changes in the occurrence of prey clusters presented similar tendencies in the north and the west. The occurrence index of *M. poutassou* was significantly higher in the larger animals, while occurrence of 'other Teleostei' decreased with squid size increment. In the western area, individuals with ML \leq 120 mm showed a significantly higher occurrence of cephalopoda in their stomach contents. Vacuity index was higher in the group of small squid.

Feeding of *I. coindetii* did not vary with size ($P>0.05$), comparing individuals with

Table 5. Prey clusters used for total comparison of the diet between both squid species for each area, OCI values, VAI, significance levels of the differences and results of the χ^2 test.

Prey cluster	North		West	
	<i>T. eblanae</i>	<i>I. coindetii</i>	<i>T. eblanae</i>	<i>T. coindetii</i>
Teleostei	89.5	**	77.2	67.0
Crustacea	3.5	**	11.8	18.1
Cephalopoda	7.0	ns	11.0	14.9
Total 100%	197		136	182
No.	174		110	160
VAI	67.4	**	75.9	78.0
No. VAI	641		731	***
χ^2		10.55		1.10
df		2		2
P		<0.01		>0.05

No., total number of specimens with food in the stomach; No. VAI, number of stomachs utilized for *Todaropsis eblanae* VAI calculation (see Material and Methods).

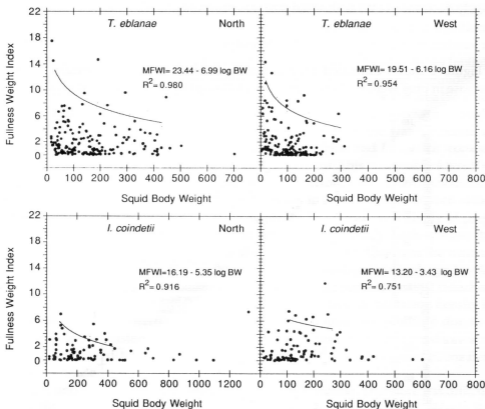


Figure 3. Variation of fullness weight index (FWI) with respect to the body weight (g) of *Todaropsis eblanae* and *Illex coindetii* in both areas. Solid lines represent the estimated maxima of the fullness weight indices by squid weight (see Material and Methods). Equations of these lines are also shown. MFWI, maximum fullness weight index; BW, squid body weight.

ML \leq 150 mm and ML $>$ 150 mm. The vacuity index was higher in the smaller animals from both areas: 74.1% vs 57.6% in the west and 81.3% vs 72.0% in the north.

Comparison of the diet of Todaropsis eblanae and Illex coindetii

The diet of the two species was significantly different in the north, but similar in the west (Table 5). Northern dissimilarities were due to the differences in occurrence of teleosts and crustaceans in the two squid species.

From the comparison of VAI between species, an opposite tendency was displayed in each area. Empty stomachs of *I. coindetii* from the northern area were consistently more numerous than those of *T. eblanae*. Conversely, empty stomachs of *T. eblanae* were significantly more abundant than those of *I. coindetii* in the west (Table 5).

Relationship between fullness weight index and body weight index

Figure 3 shows the relationships between FWI and BW for both species and areas. A steady decrease of FWI with squid size was observed in each case.

Size of prey

Figure 4 shows estimated prey weight in relation to predator weight. A steady increase in prey weight of small predators followed by a flattening out in larger squid

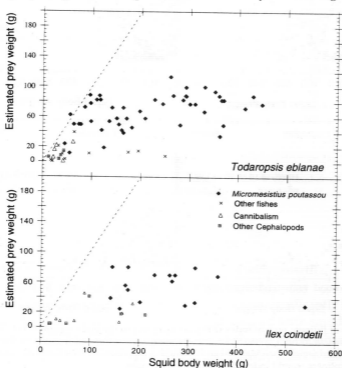


Figure 4. Relation between body weight of *Todaropsis eblanae* and *Illex coindetii* and estimated weight of their prey.

sizes was observed in both species. In order to clarify the illustration three cases were eliminated: one *M. poutassou* of 50 g and one *I. coindetii* of 32 g eaten by two *I. coindetii* of 645 and 853 g, respectively. Also one *Merluccius merluccius* of 252g eaten by one *T. eblanae* of 314 g.

DISCUSSION

Teleostean fishes are by far the most important prey of *Illex coindetii* and *Todaropsis eblanae*. *Micromesistius poutassou* shows the highest occurrence overall, comprising nearly 50% of the diet of *T. eblanae*. Similar results were found for this species in South Africa, where 49% of its diet was comprised of the fish *Lampanyctodes hectoris* (Gunther) (Lipinski, 1992). The importance of *M. poutassou* in the diet of both squid species reflects the high biomass of this species in the fishery, where it constitutes almost half of the total available fish biomass (Sánchez & Pereiro, 1992). Other fish species present in the diet of both squid species (*Merluccius merluccius*, *Trachurus trachurus*, *Argentina sphyraena*) are also target species of important abundance in the demersal fishery off the Galician coast. Among non-commercial fish species, *Gadiculus argenteus* represents a significant proportion of the diet of both squid species, as could be expected from its abundance in the ecosystem (Sánchez & Pereiro, 1992). The low occurrence of benthic fishes (mainly pleuronectiforms) and nekto-benthic cephalopods (*Eledone cirrhosa* and Sepioidea) in the diet of both squids is noticeable. Since these prey are abundant in the area (Sánchez & Pereiro, 1992; Guerra, 1992), it seems that, although the two squid species are caught near the bottom, their predatory activity is exerted mainly in the water column, as pointed out by Sánchez (1982). Overall, the diet of *T. eblanae* and *I. coindetii* consists mainly of demersal fishes, co-occurring in the same habitat. This is probably a result of the opportunistic predator character of cephalopods (Nixon, 1987). This opportunistic behaviour could also be the origin of the differences in diet detected between areas, since these differences were probably a consequence of unequal availability of prey. This hypothesis is supported by the similar tendency observed in both species; the abundance of crustaceans increased in the diet of both squid species from the western area, while fish were more common in the north. The main fish prey of both species (*M. poutassou*) showed similar abundances in both areas during September 1992 (Sánchez, personal communication). Therefore, although further studies on crustacean density in each habitat are necessary, differences in diet between areas are probably due to a dissimilarity in the crustacean prey density, as the biomass of decapod crustaceans of the west is estimated to be two or three times that of the northern area (González-Gurriarán & Olaso, 1987).

Maturity and size are strongly linked, especially in *T. eblanae*. Therefore it is difficult to study the effect of each variable on diet independently. In the case of *T. eblanae*, the OCI of *M. poutassou* increased in both mature and larger individuals. No proof of the effect of maturation on diet has been presented to date for cephalopods, but size is usually considered to produce changes in the prey taken (Nixon, 1987). *Micromesistius poutassou* >14 cm are caught together with small and large squids. Smaller *M. poutassou*

are pelagic (upper 30 m) and live off the edge of the shelf (Raitt, 1968). This makes them unavailable to *T. eblanae*. Estimated sizes of *M. poutassou* preyed upon by *T. eblanae* were mainly between 20 and 26 cm. This size range fits narrowly within the most frequent sizes of *M. poutassou* found in this habitat throughout the year (Robles Pariente, 1970). Conversely, although *T. eblanae* <50 g consume an important amount of fish (OCI=55%), they hardly prey upon *M. poutassou* (OCI=7.9%). Based on all these facts, it can be concluded that size and not maturity is responsible for the high occurrence of *M. poutassou* in the stomachs of large/mature *T. eblanae*. Small squid are probably incapable of capturing the available *M. poutassou* and, as the squid grow, this abundant fish becomes more available to them. A similar conclusion could be drawn for *I. coindetii* (Figure 4B), in spite of the small number of identified occurrences of *M. poutassou*.

The large number of cephalopods in the diet of small/immature *T. eblanae* from the west is another significant result. At least 22% of these cephalopod prey are of their own species. This percentage is probably higher as more than 50% of the cephalopod prey consisted of unidentified ommastrephids or other cephalopods. The high incidence of cannibalism in small/immature animals from the western area could have been produced by the high density of small *T. eblanae* in that area (López-Veiga et al., 1977; apparently segregated from the large specimens (unpublished data).

Maturity, not size, seems to be responsible for the change in the diet of *I. coindetii*. Since these differences were detected only in the western area, conclusions about the effect of maturity needs a further broader-based study.

The decrease of VAI values in mature females of both species is probably related to their increased energetic demand concentrated on reproductive products. Similar results have been found for *Loligo vulgaris* and *L. forbesi* (Rocha et al., 1994) and *Sepia officinalis* and *S. elegans* (Castro & Guerra, 1990).

Diet differences between the two species were dependent on the area. *Illex coindetii* seemed to forage in a wider area, since both coastal (e.g. *Diplodus* sp., *Gobisculus flavescens* (Fabricius), *Zeus faber* L., *Aphia minuta* (Risso)) and epipelagic (Clupeidae) species were present in its diet. Moreover, the main occurrence of bathypelagic and benthic Decapoda (*Pasiphaea* sp., Galatheidae, Reptantia) and fishes (*Cepola macrophtalma* (L.), *Callyonimus* sp.) was in the diet of *T. eblanae*. This also suggests that the species has a predatory activity which is more related to the bottom than that of *I. coindetii*.

The FWI decrease with size in both species (Figure 3) could be closely related to the decrease of cephalopod metabolic rate with growth (O'Dor & Wells, 1987). The line relating maximum FWI and size could be taken as a default approximation of the daily ration. For other ommastrephid squids, daily rations between 13.1% in *Dosidicus gigas* (Ehrhardt, 1991) and 5.2% in *Illex illecebrosus* (Hirtle et al., 1981) have been estimated. Results obtained in this study are between these estimations (Figure 3). Actual daily rations could be higher since digestion is very fast in these species (Boucher-Rodoni, 1975), and more than one meal could be taken per day. Although no reliable estimates of total biomass of the two squid species in the ecosystem are available, considering their voracity and relative abundance, their impact over the population of prey should be appreciable.

The line estimating FWI with size of *I. coindetii* is clearly below that obtained for *T. eblanae*. The opposite result should be expected since *I. coindetii* seems to be more active than *T. eblanae*. However, both facts are undoubtedly related to the absence of hard remains in the stomach contents of *I. coindetii*. This could reflect a strategy of this species, based on optimizing energy input and minimizing costs by not ingesting undigestible materials to be carried in the stomach during digestion. Similar behaviour has been observed in aquaria by O'Dor et al. (1980).

Maximum size of prey increased steadily, approaching the size of *T. eblanae*, itself up to ~100 g squid weight (Figure 4). In squid >100 g no further increase in prey size was detected, except in the case of one *Merluccius merluccius* not included in the Figure (see Results). This could be due to the fact that the main prey of *T. eblanae* was *Micromesistius poutassou*, and larger sizes of this species (BW>100g) are almost unavailable in the habitat (Robles Pariente, 1970). Even when large individuals of other species were available in the habitat, they were not found as prey. Since hard remains are used to estimate prey size, a partially incorrect picture of real prey size range could be obtained if large otoliths and/or vertebrae were not ingested. This phenomenon could have even more influence in the case of *I. coindetii*, since this species rarely ingests hard parts of its prey. Prey/predator size relationships of *I. coindetii* were similar to those of *T. eblanae* (Figure 4). Maximum prey size also increased steadily with squid size, but the slope seemed to be lower, and prey size was stabilized at a larger size than in *T. eblanae* (~140 g). These differences in slope could also be due to different behaviour patterns of the two species in relation to the ingestion of hard remains.

In summary, post-recruit *T. eblanae* and *I. coindetii* are very voracious opportunistic predators, with noticeably overlapping diets, preying mainly upon nekto-benthic fish species. Both squid species are the main nektonic cephalopod predators on the edge of the continental slope and the adjacent continental shelf (100–500 m depth) off the Galician coast.

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