

BIOTIC RELATIONSHIPS OF ILLEX COINDETII AND TODAROPSIS EBLANAE (CEPHALOPODA, OMMASTREPHIDAE) IN THE NORTHEAST ATLANTIC: EVIDENCE FROM PARASITES

SANTIAGO PASCUAL, ANGEL GONZALEZ, CRISTINA ARIAS & ANGEL GUERRA

SARSIA



PASCUAL SANTIAGO, ANGEL GONZALEZ, CRISTINA ARIAS & ANGEL GUERRA. 1996 10 15. Biotic relationships of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda, Ommastrephidae) in the Northeast Atlantic: evidence from parasites. – *Sarsia* 81:265-274. Bergen. ISSN 0036-4827.

Parasites were collected from 1,200 short-finned squid (*Illex coindetii*, *Todaropsis eblanae*) caught as by-catch in a multispecies trawling fishery in the northwest Spanish Atlantic waters in 1992-1993. Parasites found included six species of helminths, three tetraphyllidean cestodes (*Phyllobothrium* sp., *Pelichnibothrium speciosum*, *Dinobothrium* sp.), two trypanorhynchidean cestodes (*Nybelinia yamagutii*, *Nybelinia lingualis*), and one ascaridoid nematode (*Anisakis simplex* B). Two of these parasites (*Phyllobothrium* sp., *A. simplex* B), which could be recognised as component species, were used in analyses of host-parasite relationships. Levels of infection varied significantly with host size or stage of maturation for both squid species. Regional variation in infection level seems attributable to geographical variation in availability of prey, discreteness and movements of host populations and to size or age-related changes in the prey selection of their host. Parasite evidences suggest that both ommastrephid squids are sympatric species sharing similar ecomiches, and serve as diet for large top predators (selachians and marine mammals) of Northeast Atlantic. Parasites may also be useful as an indirect indicator of the migratory habits of the squid.

Santiago Pascual and Cristina Arias, Laboratorio de Parasitología, Facultad de Ciencias del Mar, Universidad de Vigo, Ap. 874 Vigo, Spain. – Angel González and Angel Guerra, Instituto de Investigaciones Marinas (CSIC), Eduardo Cabello 6, 36208 Vigo, Spain.

KEYWORDS: *Illex coindetii*; *Todaropsis eblanae*; helminth parasites; biotopic relationships.

INTRODUCTION

Squids are important elements in pelagic food webs and interact with commercial fisheries for finfish (BOYLE & PIERCE 1994). Off the southeast North Atlantic, the short-finned squid *Illex coindetii* (VERANY, 1839) and *Todaropsis eblanae* (BALL, 1841) are an important by-catch in the multispecific trawling fisheries for *Merluccius merluccius* (L.), *Micromesistius poutassou* (RISSO) and *Nephrops norvegicus* (L.). In recent years, annual commercial catches of both squid species together have ranged from 490 to 2,352 metric tons (GONZALEZ & al. 1994a). Management of these fisheries may be based on multispecies models (Mercer 1982), which require detailed knowledge about the trophic connections between the different species concerned.

The alimentary tract of oegopsid cephalopods appears to provide suitable ecological niches for helminth parasites (HOCHBERG 1990), possibly related to the fact that squid also provide an adequate environment for replicated parasite communities (termed 'parasite infracommunities') (ESCH & al. 1990). Many parasites of squid, in particular helminths, are linked at various stages of development to certain groups of hosts by a correspondence of trophic

and parasitic bonds (GAEVSKAYA & NIGMATULLIN 1978; NAIDENOVA & al. 1985; NIGMATULLIN & SHUKHGALTER 1990). Hence, there is undoubted interest in the application of the results of parasitological investigation to the elucidation of the biotic relationships of squid species. The aim of this study was therefore to determine whether analyses of parasite assemblages and host-parasite interactions could clarify biotic relationships of ommastrephid squids in the southeast North Atlantic.

MATERIAL AND METHODS

From November 1992 to November 1993, 1,200 post-recruit *I. coindetii* (♀♀ 334, ♂♂ 266) and *T. eblanae* (♀♀ 304, ♂♂ 296) were collected off the Galician coast between 42°5' - 45°15' N and 7° - 9°20' W. Samples were caught by commercial fishermen working in two areas with different hydrographical characteristics (FRAGA 1981), Ribadeo to Finisterre to the north (ICES VIIIc division), and Finisterre to Miño river to the southwest (ICES IXa division) (Fig.1).

Dorsal mantle length (DML), total body weight (BW), sex and stage of maturation (I-V, LIPINSKY 1979) (Table 1) of each squid were recorded. The digestive tract was then removed and parasites counted. Representative samples of parasites were stained using standard techniques and mounted for identification. To determine

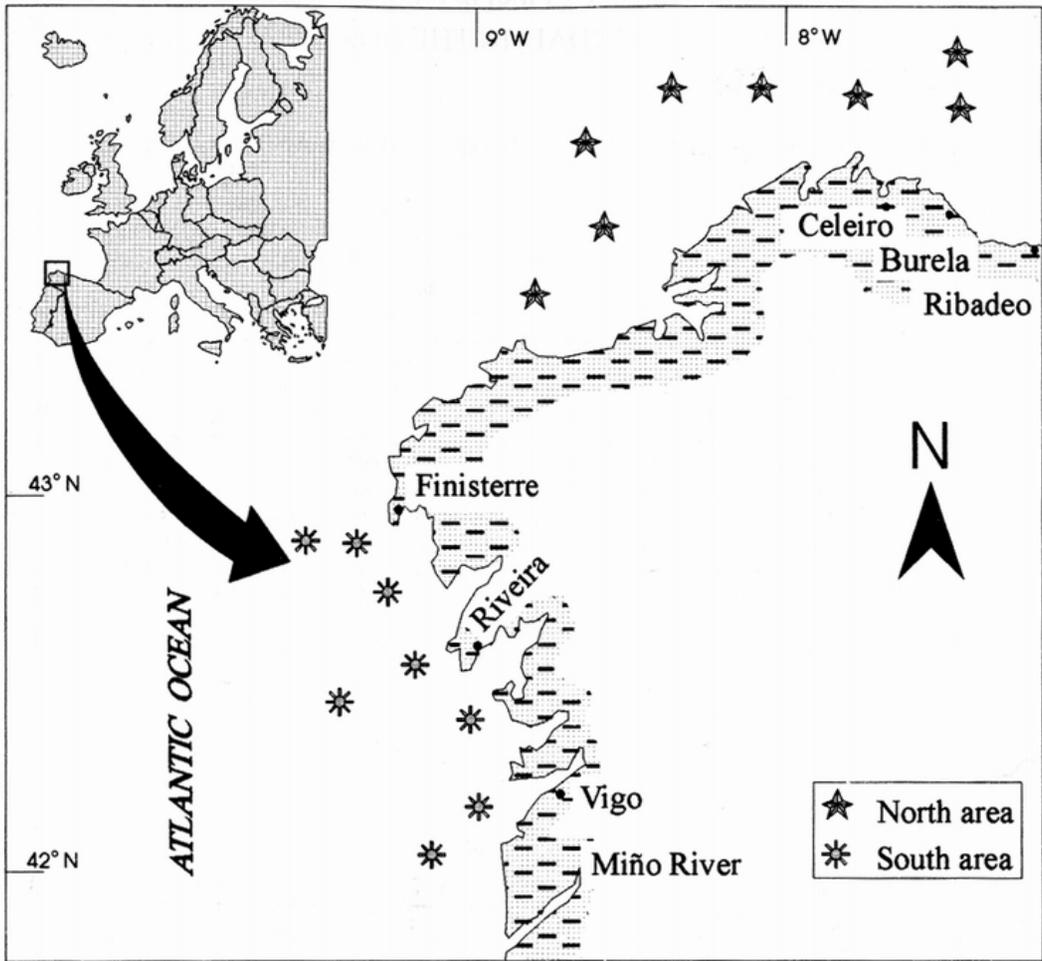


Fig. 1.- Map showing the locations of trawl stations at Galician shelf waters in both sampled areas.

the identity of the *Anisakis simplex* (RUDOLPHI, 1809, det. KRABBE, 1878) L3 within the *Anisakis simplex* complex (see ORECCHIA & al. 1986), we sent several specimens from both squid species to Prof. L. Paggi and co-workers at the University of Rome, 'La Sapienza', Rome, Italy, for analysis using allozyme electrophoresis (for details of electrophoretic procedure see NASCETTI & al. 1986). Voucher specimens of both component helminth species have been deposited in the Department of Invertebrate Zoology, Santa Barbara Museum of Natural History (Santa Barbara, California, USA) (*Phyllobothrium* sp.: 143035-143055; *Anisakis simplex* B: 143034, 143056).

Parasite counts were approximately distributed as a negative binomial, and component species (i.e., those with prevalence

$\geq 10\%$ see below) had a variance greater than the mean, indicating an overdispersed distribution, i.e. the parasites were aggregated. A log transformation [$\log(\text{parasite count} + 1)$] was therefore used to bring the frequency distributions of parasite counts closer to normality (CASSIE 1962). Statistical analysis was performed using SYSTAT (Version 4).

Quantitative terms for parasite infection are according to MARGOLIS & al. (1982), 'prevalence' is defined as the percentage of host individuals in a sample infected by a particular parasite species. The term 'abundance' is defined as the mean number of a particular parasite species per host examined. 'Mean intensity' refers to the mean number of individuals of a particular parasite species per infected host in a sample.

RESULTS

The parasites found were widely distributed throughout the region sampled (Table 2). They were helminths at larval stage, all of them mainly located in the digestive tract of both squid species. Only component parasites

(*Phyllobothrium* sp. Linton, 1922 larvae and *A. simplex* B ORECCHIA & al. 1986 larvae) were chosen for analysis. Routine examination demonstrated the presence of plerocerci of *Phyllobothrium* sp. in 45.9 % and 33 % (mean intensity: 6.13, 2.92) of the examined specimens of *I. coindetii* and *T. eblanae*, respectively. With regard to

Table 1. Mean lengths at different stages of maturity of ommastrephid squids *Illex coindetii* and *Todaropsis eblanae* from the north and south sampling regions. n: number of individuals examined; DML: dorsal mantle length.

Host	Maturity	Sex	n	DML-north	DML-south
<i>Illex coindetii</i>	I	male	37	113.08 ± 20.44	131.31 ± 16.09
		female	50	144.06 ± 32.89	137.36 ± 27.53
	II	male	28	150.73 ± 21.99	140.03 ± 14.28
		female	73	174.75 ± 33.10	149.13 ± 33.27
	III	male	54	170.00 ± 22.56	152.57 ± 23.02
		female	80	221.20 ± 54.61	172.06 ± 32.90
	IV	male	63	190.22 ± 30.10	172.63 ± 23.62
		female	83	216.60 ± 26.77	197.11 ± 48.37
	V	male	84	160.00 ± 14.14	190.00 ± 0.00
		female	48	255.93 ± 67.03	192.25 ± 34.32
<i>Todaropsis eblanae</i>	I	male	80	111.18 ± 18.82	80.06 ± 12.38
		female	89	83.04 ± 14.98	85.00 ± 18.61
	II	male	39	107.71 ± 17.50	110.04 ± 17.18
		female	46	109.08 ± 23.95	106.00 ± 14.56
	III	male	33	128.86 ± 12.65	123.36 ± 8.64
		female	78	125.47 ± 19.59	121.67 ± 18.87
	IV	male	67	137.56 ± 13.11	136.70 ± 9.58
		female	29	146.57 ± 26.12	140.51 ± 15.54
	V	male	77	141.67 ± 7.07	141.00 ± 8.48
		female	53	183.35 ± 26.19	172.33 ± 21.13

Table 2. Parasites found in Ommastrephid squids *Illex coindetii* and *Todaropsis eblanae* at north and/or south sampling areas off Galicia. (Asterisks indicate those component species used in analysis; the remainder species have a prevalence < 1%).

Phylum and identity (order, family)	Site of infection at both squid species	Host	Locality
Cestoidea			
(Tetraphyllidea, Phyllobothriidae):			
<i>Phyllobothrium</i> sp.*	stomach, intestine, caecum, oesophagus	<i>Illex coindetii</i>	north-south
		<i>Todaropsis eblanae</i>	north-south
<i>Pelichnibothrium speciosum</i>	caecum, stomach	<i>Illex coindetii</i>	north
		<i>Todaropsis eblanae</i>	north
<i>Dinobothrium</i> sp.	caecum, stomach	<i>Illex coindetii</i>	north-south
(Athea, Tentaculariidae):			
<i>Nybelinia yamagutii</i>	stomach	<i>Illex coindetii</i>	north
<i>Nybelinia lingualis</i>	stomach	<i>Todaropsis eblanae</i>	north
Nematoda:			
(Ascaridida, Anisakidae)			
<i>Anisakis simplex</i> B*	stomach, gonads, mantle	<i>Illex coindetii</i>	north-south
		<i>Todaropsis eblanae</i>	north-south

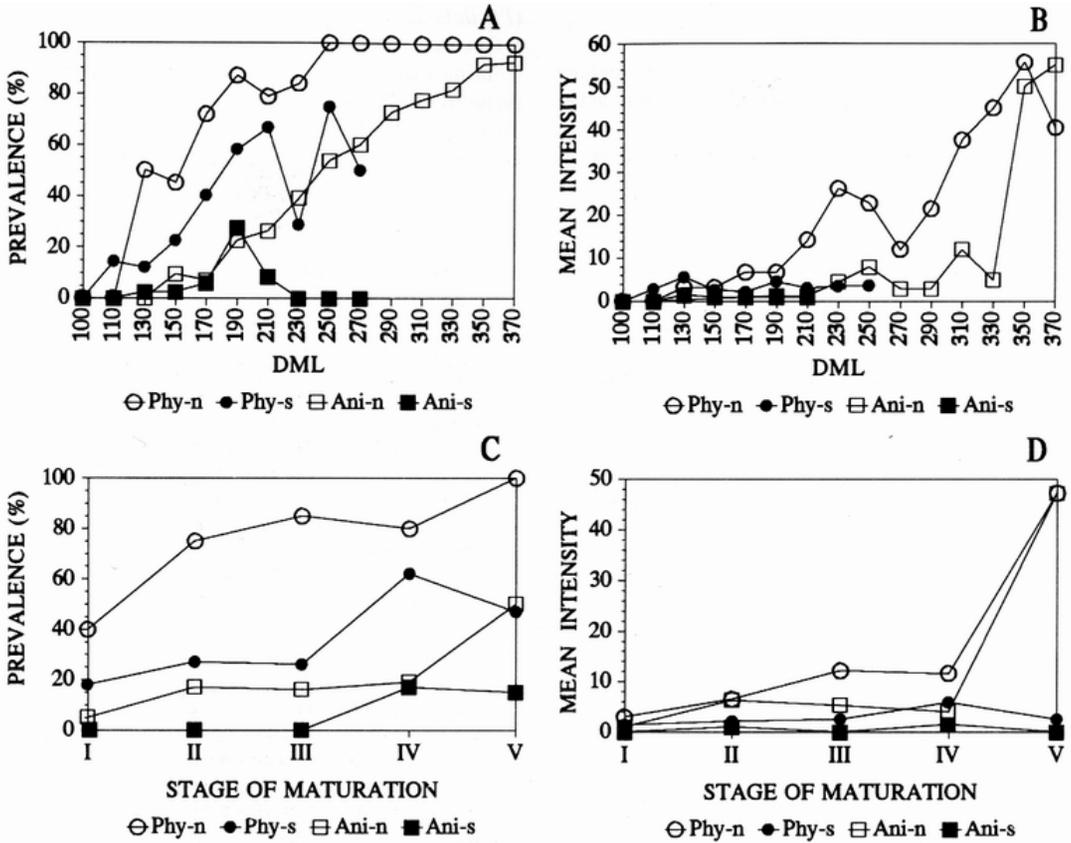


Fig. 2. Prevalence and mean intensity of both helminth component species in relation to *Illex coindetii* length and stage of maturation at both sampled areas. (Phy-n, *Phyllobothrium* sp. from the north area; Phy-s, *Phyllobothrium* sp. from the south area; Ani-n, *A. simplex* B from the north area; Ani-s, *A. simplex* B from the south area).

Table 3. Infection levels of both component helminth species in males and females of short-finned squids *Illex coindetii* (Ic) and *Todaropsis eblanae* (Te) off northwest Spain.

Parasite	Host	sex	Prevalence(%)
<i>Phyllobothrium</i> sp.	Ic	males	43.2
		females	45.9
	Te	males	32.5
		females	33
<i>Anisakis simplex</i> B	Ic	males	9.8
		females	11.3
	Te	males	18.4
		females	19.3

Table 4. Relationship between squid size and gonad maturity and abundance of infection of *Phyllobothrium* sp. and *Anisakis simplex* B in *Illex coindetii* (Ic) and *Todaropsis eblanae* (Te). (ANOVA test, *statistical dependence at P < 0.05).

	Host	F	P*
Size (DML)			
<i>Phyllobothrium</i> sp.	Ic	391.64	< 0.001
	Te	69.74	< 0.001
<i>Anisakis simplex</i> B	Ic	215.42	< 0.001
	Te	463.25	< 0.001
Gonad maturity			
<i>Phyllobothrium</i> sp.	Ic	28.514	< 0.001
	Te	105.84	< 0.005
<i>Anisakis simplex</i> B	Ic	14.192	< 0.001
	Te	21.35	< 0.05

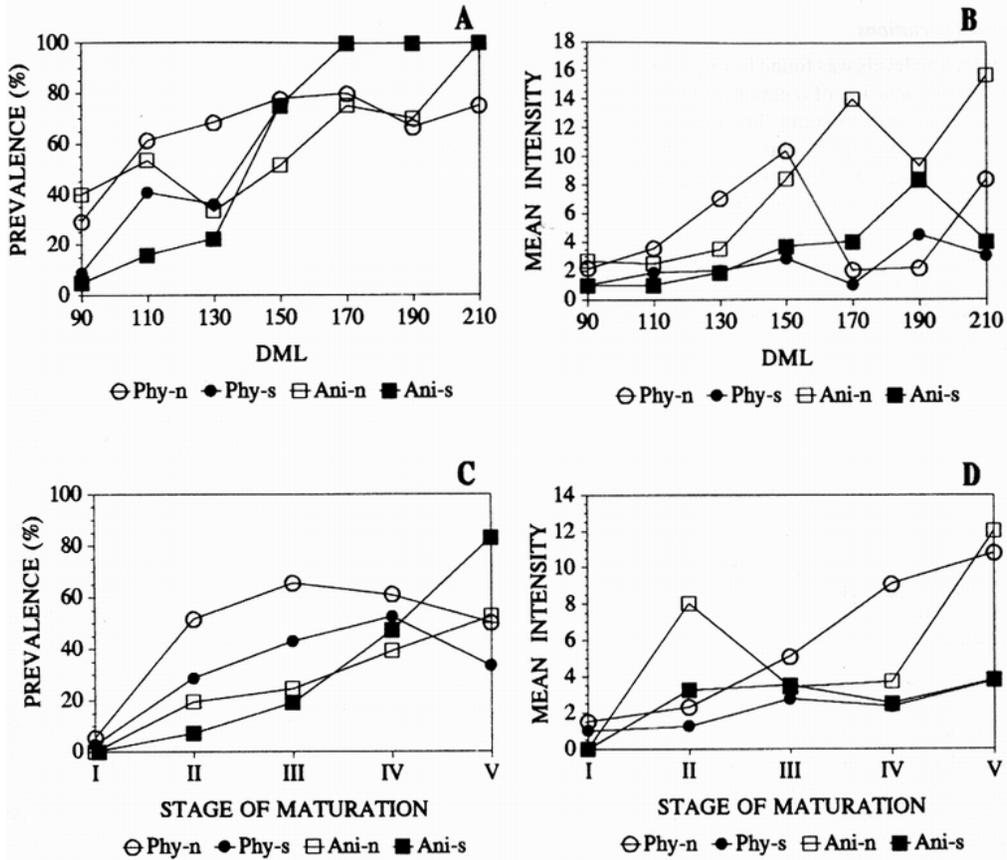


Fig. 3. Prevalence and mean intensity of both helminth component species in relation to *Todaropsis eblanae* length and stage of maturation at both sampled areas. (Phy-n, *Phyllobothrium* sp. from the north area; Phy-s, *Phyllobothrium* sp. from the south area; Ani-n, *A. simplex* B from the north area; Ani-s, *A. simplex* B from the south area).

A. simplex B larvae, infection levels were lower, accounting for the 11.3 % and 19.3 % (mean intensity: 5.57, 3.87) of the *I. coindetii* and *T. eblanae* examined, respectively.

Host-parasite relationships

For both squid species prevalence of infection was slightly higher for females than for males, but differences were not statistically significant (Mann-Whitney U-test, $P > 0.05$ in all cases) (Table 3). A tendency of increased parasite abundance with both increasing host size and maturity was observed for both squid species at both sampling areas (Table 4).

For *I. coindetii* up to 12 cm, only *Phyllobothrium* larvae were found in them. As they grow, specimens 12 to 18 cm long were infected by both component parasite

species in both sampling areas (Fig. 2A), but the sharp rise of infection takes place later, when the squid attain more than 30 cm in length (Fig. 2B).

Plerocercoids of *Phyllobothrium* sp. initially appear in *T. eblanae* of 80-110 mm DML, in connection with their feeding on planktonic invertebrates. Squids at DML greater than 120 mm change to an intermediate diet of fish and squid, and then the larvae of cestodes and nematodes, as well as those satellite species of *Phyllobothriidae*, appear and subsequently accumulate (Fig. 3).

For both squid species variation in infection values was found between different stages of maturation, as prevalence and mean intensity rose gradually from stage I to stage V maturity, increasing markedly in the oldest stages (Figs 2C-D, 3C-D). Statistical analysis confirmed the interdependence between abundance of infection and squid gonad maturity (Table 4).

Regional variations

The infection levels was found to vary on a geographical basis. The proportion of component parasites tended to decline in a north to south direction, from 68 % and 28.3 % off north to 20 % and 26.2 % off the southwest coast for *I. coindetii* and *T. eblanae*, respectively. The abundances of both component helminth species differed significantly among the two geographical groups of *I. coindetii* and *T. eblanae* at stage V of maturation (Table 5). In general, the northern squid group showed higher infection levels than squids from the southwest area at every squid-class examined.

DISCUSSION

Squids as hosts in helminth life cycles

Many reports have recently been published on the important role of squids in the life cycles of different systematic groups of helminths (for review see HOCHBERG 1990). The role of oegopsid Ommastrephidae in the parasite fauna of the Atlantic Ocean has been studied relatively well, but we have only fragmentary information about the helminth fauna of *I. coindetii* and *T. eblanae* (GAEVSKAYA & NIGMATULLIN 1978). The high level of infection in both squid species by plerocerci of *Phyllobothrium* spp. reflects the obligatory participation of squids as intermediate hosts in the life cycle of tetracanthidians of the genus *Phyllobothrium*. The final hosts of these cestodes are large, predaceous sharks of the families Carcharidae and Isuridae (JOYEUX & BAER 1936) and rays (PERIS & al. 1995). Similarly, we may also assume that *I. coindetii* and *T. eblanae* off Galician shelf waters undoubtedly occupies an important function as reservoir or paratenic hosts for *A. simplex* B. The squid position in the life cycle of rare or satellite larval cestodes is presently unclear. However, it appears

that both squid species are accidental hosts and infection is connected to infected prey, mainly mesoplanktonic organisms (copepods, amphipods, ostracods, chaetognaths) and small bony fishes, which are common in the stomachs of medium to large-sized squids.

Biotic relationships of squids

Large active elasmobranch fishes, which can ingest *I. coindetii* and *T. eblanae* both alive and dead (NAIDENOVA & al. 1985; PASCUAL & al. 1994) may prey upon all the stages of maturation found within wild-caught *I. coindetii* and *T. eblanae* (i.e. the 'exploited stocks'). In addition, medium to large-sized individuals of *T. eblanae* (150-210 mm DML) and late-maturing forms of *I. coindetii* are important as food for marine mammals (dolphins and whales) (GONZALEZ & al. 1994b; PASCUAL & al. 1994) (Fig. 4).

Anisakid nematodes are 'open water-types', typically found in predators of nekton and adapted to oceanic environment (OSHIMA 1972; SMITH 1983; NAGASAWA & NAKATA 1984). CANNON (1977) and SMITH (1983) remarked that species of *Anisakis* typically are found in hosts which feed on plankton (*Meganyctiphanes norvegica* having an occurrence of 8.9 % in the diet of *I. coindetii*) and nekton (*Micromesistius poutassou* ranging from 30 to 60 % of the diet of mature individuals of *T. eblanae*).

PIPPY & VAN BANNING (1975), BEVERLY-BURTON & al. (1977), OSHIMA (1979), SMITH (1984), MCGLADDERY (1985) and PAGGI & al. (1985) all suggested that all the *Anisakis* larvae type I found in the North Atlantic are those of *A. simplex* RUDOLPHI 1809, a cosmopolitan species in cold and temperate waters. The closely related *A. typica* DIESING, 1860 is generally found in warmer water from 36° to 40° N (DAVEY 1971). The geographic distribution of *A. simplex* A and *A. simplex* B appears to be mainly Mediterranean for the former, and mainly North Atlantic for the latter

Table 5. Abundance of helminth component species in different stages of maturation of both squid species taken at both sampling areas. Abundances at north and south significantly different at *p < 0.05 and **p < 0.01 (Ic, *Illex coindetii*; Te, *Todaropsis eblanae*). n: number of individuals examined.

Stage of maturation	Host	n	<i>Phyllobothrium</i> sp.		<i>Anisakis simplex</i> B	
			north	south	north	south
immature (I-II)	Ic	188	2.21	0.31	0.30	0.008
	Te	254	1.31	0.24	0.09	0.002
maturing (III)	Ic	134	7.16	0.81*	0.16	0
	Te	111	8.38	1.12*	1.49	0.15
mature (IV-V)	Ic	278	14.57	2.08**	5.20	0.15**
	Te	226	11.79	1.98**	14.37	1.15**

(NASCETTI & al. 1986). Since larval anisakines in squid from northwest Spain have been proved to be *A. simplex* B, it would not be unreasonable to suspect that the squids migrated relatively short distances, or west-east to a yet unknown spawning area, and not north-south, at least not south far than 40° N. This parasitological argument appears consistent with the results of fisheries biology studies (GONZALEZ & al. 1994a; M. Raserio, pers. commn), which show a broad ranges of sizes and stages of maturation during any season within sampled areas off Galicia. In fact, in most ommastrephid squids the onset of maturity is associated with a cycle of migration inshore-offshore in relation to currents, temperature and food supply in the water (BOYLE 1990). On this basis, it is believed that squid spawning are released in offshore deeper waters, close to the shelf edge. This is the principal habitat for teuthivorous species, mainly the common dolphin *Delphinus delphis* (LINNAEUS, 1758), the bottle-nosed dolphin *Tursiops truncatus* (MONTEGU, 1821), the Risso's dolphin *Grampus griseus* (CUIVIER, 1812) (GONZALEZ & al. 1994b), the sperm whale *Physeter macrocephalus* (LINNAEUS, 1758) and the long-finned pilot whale *Globicephala melas* (TRAILL, 1809) (CLARKE & MACLEOD 1974; BALBUENA 1992).

Despite the fact that three species of Ommastrephidae comprise the most important component in the diet of swordfish *Xiphias gladius* (LINNAEUS, 1758) in the North-east Atlantic Ocean (GUERRA & al. 1993), no specimens of *I. coindetii* or *T. eblanae* were found in the stomachs of 113 swordfish. This is in accordance with the absence of trematodes Didymozoidae in our material which is an indicator of the absence of trophic relationships between large predatory fishes (tunnas, sailfishes and swordfish, the final hosts) and both slope-shelf squid species.

The similar trophic relationship of *I. coindetii* and *T. eblanae* with large top predators in local ecosystems, indicates that they both have a key function in the nektonic community in Galician shelf waters.

Regional variations

The composition of the helminth fauna of both squid species appears to be homogeneous throughout the sampled area, with little evidence of regional speciation. Nevertheless, both host species from the south area appeared to a lower level of infection, than these from the north area, although variation was considerable, especially for the later stages of maturation. Latitudinal gradients in the composition of the helminth fauna and the differences in infection frequency has been previously noted for both host species (GAEVSKAYA & NIGMATULLIN 1975), indicating differences in their trophic relationships in various parts of their distribution (GAEVSKAYA & NIGMATULLIN 1978). For both *I. coindetii*

and *T. eblanae* the high intensities and prevalences of infection of northern squids indicate more stable ecological conditions compared with the hydrographically unstable southern part of the range. Despite the short distance between both sampling areas (100 nautical miles), these regions exhibit differences in hydrography, biological productivity, fauna composition and diversity (FARIÑA & AL. 1985; PENAS 1986; VARELA & AL. 1991; VARELA 1992). The physical properties have been suggested as factors influencing the sedimentation rate of *Anisakis* eggs (SMITH 1983), and therefore, causing different degrees of success in parasite transmission patterns in the two sampling areas.

Comparison between *I. coindetii* and *T. eblanae*

According to our data and also suggested by NAIDENOVA & al. (1985) the formation of the helminth fauna of both squid species has proceeded simultaneously. The high similarity of helminth faunas of *I. coindetii* and *T. eblanae* off northwest Spain (Sorensen index: 67 %; 100 % comparing component species) is an indirect evidence that their biotopes are almost identical in the sampled area. Nevertheless, the size-maturity dynamics of the infection are different in the two species indicating a wider participation of *I. coindetii* in the helminth life cycles. In addition, infection levels also suggest that *I. coindetii* is more important as intermediate link from planktonic invertebrates and macroplankton to large predatory sharks, whereas *T. eblanae* is more important as a link ('reservoir') between micronekton (i.e. fish-pisciphagous and small squid) and marine mammals. Higher values of infection by *A. simplex* B in *T. eblanae* may reflect the higher intensity of feeding on *Micromesistius poutassou*, which can accumulate enormous numbers of anisakid larvae (SANMARTIN & al. 1989a).

REFERENCES

- Balbuena, J.A. 1992. *Estudio taxonómico y ecológico de la parasitofauna del calderón común, Globicephala melas* (Traill, 1809), en las aguas de Europa. – Tesis doctoral. Universidad de Valencia. 313 pp.
- Beverly-Burton, M., O.L. Nyman & J.H.C. Pippy 1977. The morphology, and some observations on the population genetics of *Anisakis simplex* larvae (Nematoda: Ascaridata) from fishes of the North Atlantic. – *Journal of Fisheries Research Board of Canada* 34:105-112.
- Boyle, P.R. 1990. Cephalopod biology in the Fisheries context. – *Fisheries Research* 8:303-321.
- Boyle, P.R. & G.J. Pierce 1994. Fishery biology of north-east Atlantic squid: an overview. – *Fisheries Research* 21:1-15.

- Cannon, L.R.G. 1977. Some larval ascaridoids from south-eastern Queensland marine fishes. – *International Journal for Parasitology* 7:233-243.
- Cassie, R.M. 1962. Frequency distribution models in the ecology of plankton and other organisms. – *Journal of Animal Ecology* 31:65-92.
- Clarke, M.R. & N. MacLeod 1974. Cephalopod remains from a sperm whale caught off Vigo, Spain. – *Journal Marine Biological Association of the United Kingdom* 54:959-968.
- Davey, J.T. 1971. A revision of the genus *Anisakis* Dujardin, 1845 (Nematoda: Ascaridata). – *Journal of Helminthology* 45:51-72.
- Esch, G.W., O.A. Bush & J.M. Aho 1990. *Parasite communities: Patterns and Processes*. – Chapman and Hall, New York. 327 pp.
- Fariña, A., F.J. Pereiro & A. Fernández 1985. Peces de los fondos de arrastre de la plataforma continental de Galicia. – *Boletín Instituto Español Oceanografía* 2(3):89-98.
- Fraga, F. 1981. Upwelling of the Galician coast, northwest Spain. – Pp. 176-182. In: Richards, F.A. (ed.). *Coastal Upwelling*. American Geophysical Union.
- Gaevskaya, A.V. & C.M. Nigmatullin 1975. Helminthofauna of Atlantic squids of the family Ommastrephidae (Cephalopoda, Oegopsida) in relationship to features of their ecology. – Pp. 168-171 in: *Molluscs: their systematics, evolution and role in nature*. V Malacol. Congr. Izdvo, Nauka Leningrad (Abstract).
- Gaevskaya, A.V. & C.M. Nigmatullin 1978. The helminth fauna of Atlantic squids of the family Ommastrephidae (Cephalopoda: Oegopsida). – *Malacological Reviews* 11:131-135.
- González, A. 1994. *Bioecología de Illex coindetii (Verany, 1839) (Cephalopoda, Ommastrephidae) de las aguas de Galicia*. – Tesis doctoral. Universidad de Vigo. 237 pp.
- González, A., M. Rasero & A. Guerra 1994a. Preliminary study of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in northern Spanish Atlantic waters. – *Fisheries Research* 21:115-126.
- González, A., A. López, A. Guerra & A. Barreiro 1994b. Diets of marine mammals stranded on north-western Spanish Atlantic coast with special reference to Cephalopoda. – *Fisheries Research* 21:179-191.
- Guerra, A., F. Simón & A. González 1993. Cephalopods in the diet of the swordfish, *Xiphias gladius*, from the Northeastern Atlantic Ocean. – Pp. 159-164 in: Okutani, T. & O' Dor, R.K. (eds). *The recent advances in cephalopod fisheries biology*. Tokai University Press, Tokio.
- Hochberg, F.G. 1990. Diseases of Mollusca: Cephalopoda. – Pp. 47-227 in: Kinne, O. (ed.). *Diseases of marine animals, vol. III. Cephalopoda to Urochordata*. Biologische Anstalt Helgoland, Hamburg.
- Joyeux, C. & J. G. Baer 1936. Cestodes. – *Faune Fr.* 30:1-611.
- Lipinsky, M. 1979. Universal maturity scale for the commercially important squids (Cephalopoda: Teuthoidea). – The results of maturity classification of the *Illex illecebrosus* (LeSueur, 1821). Populations for the years 1973-1977. – *ICNAF Research Document Series* No. 5364 79/83: 40 pp.
- Margolis, L., G.W. Esch, J.C. Holmes, A.M. Kuris & G.A. Schad 1982. The use of ecological terms in parasitology. – *Journal of Parasitology* 68:131-133.
- McGladery, S.E. 1985. Studies of the parasite fauna of Atlantic herring (*Clupea harengus* L.) from the north western Atlantic Ocean. – *Dissertation Abstracts International, B, (Sciences and Engineering)* 45:3142.
- Mercer, M.C. 1982. Multispecies approaches to fisheries management advice. – *Canadian Special Publication of Fisheries and Aquatic Sciences* 59:1-169.
- Nagasawa, N.N. & J. Nakata 1984. Parasite fauna of oceanic squids from the northern North Pacific. – *Fisheries Research Japan Sea Block* 2:83-89.
- Naidenova, N.N., C.M. Nigmatullin & A.V. Gaevskaya 1985. The helminth fauna and host-parasite relations of squids *Stenoteuthis oualiamiensis* (Lesson) (Cephalopoda, Ommastrephidae) in the Indian Ocean and the Red Sea. – Pp. 113-116 in: Hargis, W.J. Jr (ed.). *Parasitology and pathology of marine organisms of the world ocean*. *NOAA Technical Reports, NMFS* 25.
- Nascetti, G., L. Paggi, P. Orecchia, J.W. Smith, S. Mattiucci & L. Bullini 1986. Electrophoretic studies on the *Anisakis simplex* complex (Ascaridida: Anisakidae) from the Mediterranean and the North East Atlantic. – *International Journal for Parasitology* 16:633-640.
- Nigmatullin, C.M. & O.A. Shukhgalter 1990. Helminthofauna y aspectos ecológicos de las relaciones parasitarias del calamar (*Illex argentinus*) en el Atlántico Sudoccidental. – *Frente Marítimo*. 7, Secc. A: 57-68.
- Orecchia, P., L. Paggi, S. Mattiucci, J.W. Smith, G. Nascetti & L. Bullini 1986. Electrophoretic identification of larvae and adults of *Anisakis* (Ascaridida:Anisakidae). – *Journal of Helminthology* 60:331-339.
- Oshima, T. 1972. *Anisakis* and anisakiasis in Japan and adjacent area.- Pp. 305-393 in: Marishita, K. and Y. Koyima (eds). *Progress of Medical Parasitology in Japan*, Vol. 4. Meguro Parasitology Museum, Tokyo.
- Oshima, T. 1979. In vitro development of *Anisakis* larvae collected from fishes caught in Kuroshio current and their identification by the adults.- Pp. 291 in: *XIV Pacific Congress. August 1979, Section FIII, Biological productivity of the Pacific Ocean*. Dept. Parasit. School of Medicine, Yokohama City University.
- Paggi, L., G. Nascetti, P. Orecchia, S. Mattiucci & L. Bullini 1985. Biochemical taxonomy of ascaridoid nematodes. – *Parasitologia* 27:105-112.
- Pascual, S., B. Lores, C. Arias, A. González & A. Guerra 1994. Helminth parasites of *Illex coindetii* (Cephalopoda: Ommastrephidae) off the Galician coast (NE Atlantic). – *Scientia Marina* 58:269-272.
- Penas, E. 1986. Modelo preliminar del ecosistema de la plataforma continental de Galicia. – *Boletín Instituto Español Oceanografía* 3(1):43-56.
- Peris, D., S. Outeiral & M.L. Sanmartín 1995. Estudio parasitológico de la comunidad de helmintos de *Raja undulata* Lacepède, 1802 procedente de la Ría de Muros y Noya (Galicia, N. O. España). – *IV Congreso Ibérico de Parasitología, Santiago de Compostela* (Abstract), 121 pp.

- Pippy, J.H.C. & P. Van Banning 1975. Identification of *Anisakis* larva (I) as *Anisakis simplex* (Rudolphi, 1809, det. Krabbe, 1878) (Nematoda: Ascaridata). – *Journal of the Fisheries Research Board of Canada* 32: 29-32.
- Sanchez-Canals, J.L. & V. Ugorri 1989. Nota sobre la alimentación del caldeirón, *Globicephala melas* (Traill, 1809) en las costas de Galicia. – *Mustela* 4:75.
- Sanmartín, M.L., P. Quinteiro & F.M. Ubeira 1989a. Nematode parasites of commercially important fish in NW Spain. – *Diseases of Aquatic Organisms* 7:75-77.
- Sanmartín, M.L., P. Quinteiro, A. Rodríguez & J.A. Fernández 1989b. Some Spanish cestode fish parasites. – *Journal of Fish Biology* 34:977-978.
- Smith, J.W. 1983. Larval *Anisakis simplex* (Rudolphi, 1809, det. Krabbe, 1878) (Nematoda: Ascaridoidea): morphology and morphometry of larvae from euphausiids and fish, and a review of the life-history and ecology. – *Journal of Helminthology* 57:205-224.
- Smith, J.W. 1984. Larval ascaridoid nematodes in myopsid and oegopsid cephalopods from around Scotland and in the northern North Sea. – *Journal of the Marine Biological Association of the United Kingdom* 64:563-572.
- Varela, M., G. Diaz del Pozo, M.T. Alvarez-Ossorio & E. Costas 1991. Factors controlling phytoplankton size class distribution in the upwelling area of the Galician continental shelf (NW Spain). – *Scientia Marina*, 55:505-518.
- Varela, M. 1992. Distribution of phytoplankton size fractions during the SARP Area cruise (April 1987) off the Galician and Cantabric coasts (NW Spain). – *Boletín Instituto Español Oceanografía* 8 (1):75-85.

Accepted 30 June 1996.