

Parasitic helminths of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) in open waters of the central east Pacific

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Abstract

During 1981–1989, 849 jumbo squid, *Dosidicus gigas*, from four open ocean regions of the east Pacific (from 11°N to 22°S) were examined for parasitic helminths. The samples were collected from the Peruvian (9–21°S and 82–87°W), east equatorial (2°N–6°S and 84–87°W), west equatorial (1°N–3°S and 96–100°W) and Nicaraguan (9–11°N and 88–91°W) regions. Nine species of parasitic helminths were found, with a total prevalence of infection of 75.5%. Trematoda: metacercaria of Didymozoidae indet (prevalence: 13%, intensity: 1–35, abundance: 0.51); Cestoda: *Pelichnibothrium speciosum* (75.2%, 1–63 000, 664.5); *Phyllobothrium* sp. (1.2%, 1–2, 0.02); *Tentacularia coryphaenae* (6.6%, 1–5, 0.16); Nematoda: *Anisakis simplex* (9.2%, 1–16, 0.23); *Anisakis physeteris* (24.2%, 1–26, 1.22); *Porrocaecum* sp. (29.4%, 1–17, 0.30); *Contracaecum* sp. (0.5%, 1–41, 0.22); *Spinitectus* sp. (0.4%, 1–3, 0.01). All these parasites occurred in the larval stage. The composition of helminths and quantitative infection indexes were similar for males and females of similar mantle length (ML). Four size groups of *Dosidicus* were recognised. The helminths of the first size group, 30–89 mm ML comprised metacercaria of Didymozoidae and larvae of *Porrocaecum* sp. In the second size group, 90–139 mm ML, the prevalence of didymozoids increased to 47.5% and the majority of the parasite fauna (four species) occurred at this stage. All nine species were present in the third size group, 140–359 mm ML, but with a sharp decrease in the prevalence of didymozoids (5.8%). In the fourth size group, 360–431 mm ML, didymozoids were absent while the prevalence and intensity values for the other helminth species were maximal. The helminth fauna of similar sized squid (190–300 mm ML) from different regions was similar and the levels of infection corresponded closely. However, a comparison of ontogenetic infection dynamics between the Peruvian and east equatorial waters showed that the prevalence and intensity data for the main and secondary helminth species differed. This may support the hypothesis of isolated populations in these two regions. *D. gigas* is a paratenic (transport) host for the helminth species studied, with scombroid and xiphoid fishes, sharks and marine mammals as the definitive hosts. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Jumbo squid; *Dosidicus gigas*; East Pacific; Helminth fauna; Ecology

1. Introduction

Dosidicus gigas (Ommastrephidae) is widely distributed within the pelagic realm of the east Pacific, from the Gulf of California to central Chile. This

species is abundant and plays an important role within the pelagic ecosystems of the continental slope and the adjacent offshore waters (Nesis, 1983). To date, metacercaria of didymozoid trematodes, plerocercoids of phyllobothriid and trypanorhynch cestodes and anisakid nematode larvae have been found (Riser, 1956; Dollfus, 1964; Overstreet and Hochberg, 1975; Hochberg, 1969, 1990; Chiclla and Verano, 1997). However, these were mainly collected from the northern

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part of the distribution range for *D. gigas* and are based on a very limited number of squid samples without quantitative data on infection rates.

In addition, in a sample of *D. gigas* obtained from the open waters of the Peruvian region (200 specimens of 180–300 mm mantle length (ML)) in a separate study, the ectoparasitic copepod *Lepeophtherius* sp. (Caligidae) was found on the inner surface of the mantle wall (prevalence, 1.0%; intensity, 1–2) (Nigmatullin et al., 1985). These were probably accidental parasites.

Within the AtlantNIRO programme of *D. gigas* biological/fishery studies in the 1980s, parasitic helminths were collected from *D. gigas* samples from the central and southern oceanic parts of its distribution range. Preliminary results have been published (Gaevskaya et al., 1982, 1983, 1987; Gaevskaya and Nigmatullin, 1983; Gaevskaya and Shukhgalter, 1992; Nigmatullin et al., 1985; Shukhgalter, 1985,

Table 1

Sample data

Study region	Sample size	ML (mm)
Peruvian region (I)	620	30–431
East equatorial region (II)	119	90–360
West equatorial region (III)	24	170–325
Nicaraguan region (IV)	86	120–403
Total	849	30–431

1986, 1988a,b, 1990a,b, 1992), but these texts are in Russian and mainly in the form of abstracts. The aim of the present paper is to report on the helminth fauna of *D. gigas* from Nicaraguan, equatorial and Peruvian waters and to examine its ecological variability. As all the parasites found in this study occurred in the larval stage, which causes difficulties for identification, helminth morphology is also described.

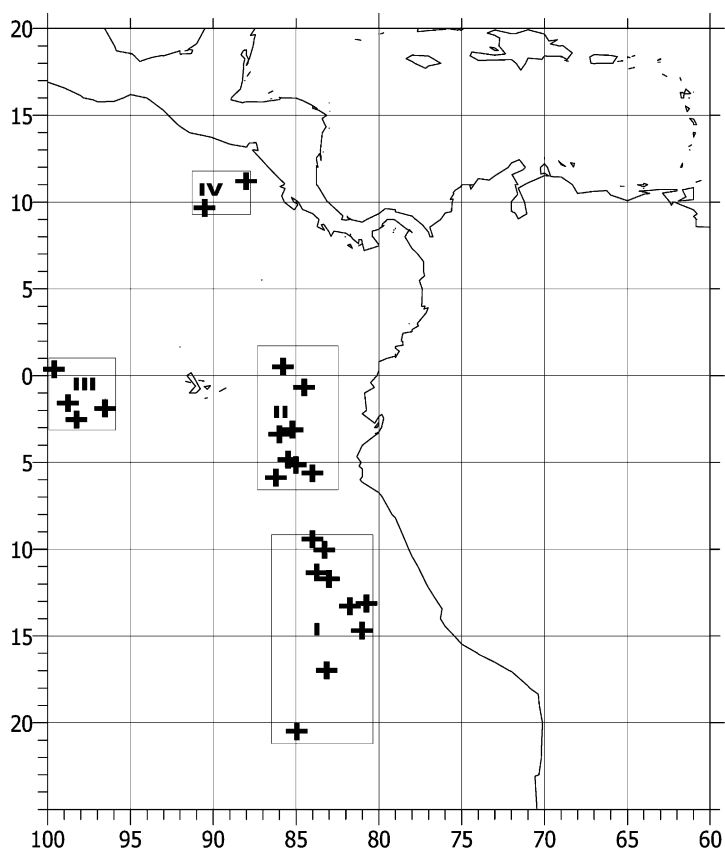


Fig. 1. Study areas: Peruvian region (I), east equatorial region (II), west equatorial region (III) and Nicaraguan region (IV).

2. Materials and methods

During 1981–1989, 849 *D. gigas* individuals of 30–431 mm ML from four open ocean regions of the east Pacific between 11°N and 22°S were examined for parasitic helminths (Table 1). The ML, sex and maturity stage of each squid were recorded. The four sample areas are shown in Fig. 1 and comprise the Peruvian region (I, 9–21°S and 82–87°W), the east equatorial region (II, 2°N–6°S and 84–87°W), the west equatorial region (III, 1°N–3°S and 96–100°W) and the Nicaraguan region (IV, 9°30'–11°N and 88–91°W).

In all four regions, the samples obtained included males and females at different stages of maturation ranging from juveniles and immature individuals to mature squid.

The methods used follow the standard approach (Zuev et al., 1985). All worms were collected from frozen squid. As plerocercoids of *Pelichnibothrium speciosum* were so numerous that the intensity of plerocercoids encysted in the rectum wall was obtained by multiplying up the mean number of cysts in 1 mm² of rectum wall surface. Trematodes and cestodes were fixed in 10% formalin and stored in

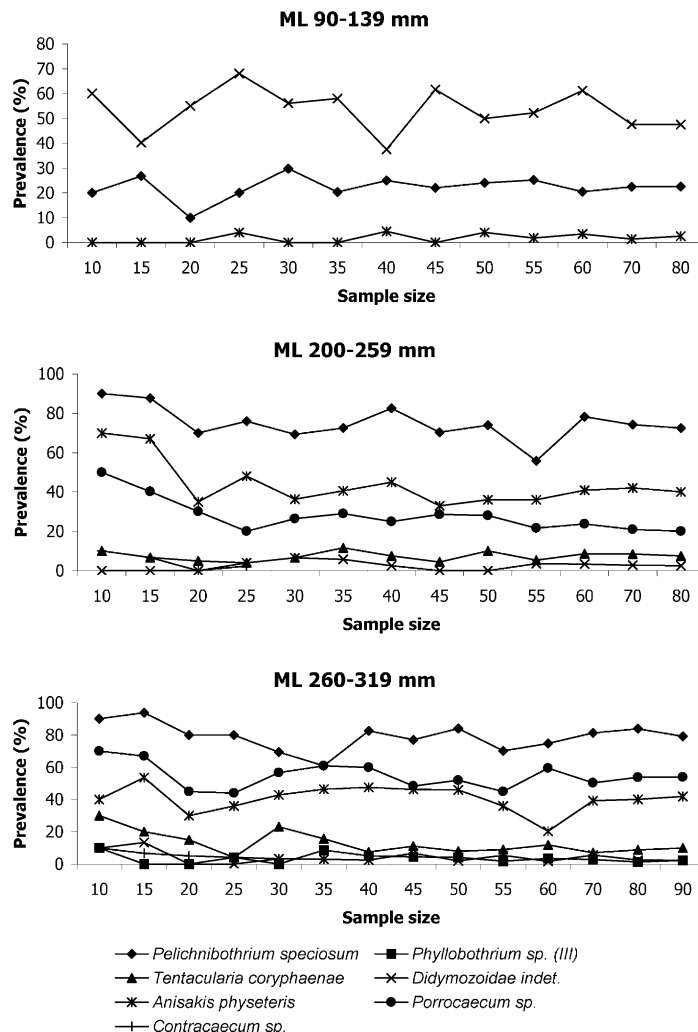


Fig. 2. Variability in species composition and prevalence data (*P*) for parasitic helminths in relation to sample size for three size groups of squid.

70% alcohol. These worms were stained in alum carmine after washing in distilled water, dehydrated in alcohol, cleared in oil of cloves and mounted in Canada balsam. Nematodes were preserved in formalin and cleared in a mixture of glycerol and milk acid. All measurements are given in millimetres.

The cestode larvae were identified according to Joyeux and Baer (1936), Dollfus (1942), Yamaguti (1959), Stunkard (1977), Gaevskaya (1977), Palm (1995) and Scholz et al. (1998); the didymozoid trematode larvae according to Yamaguti (1942), Overstreet and Hochberg (1975) and Gaevskaya (1977), and the anisakid nematode larvae according to Berland (1961), Koyama et al. (1969), Smith and Wootten (1978), Smith (1983) and Matsuura et al. (1992).

The ecological terms — prevalence, intensity, density and abundance — were used in accordance with the recommendations of Margolis et al. (1982). Thus, 'prevalence', which is expressed as a percentage, reflects the number of hosts infected by a particular parasite species relative to the number of all hosts in the sample; 'intensity' the number of individuals of a particular parasite species in each infected host in the sample. 'Density' (mean intensity) is the mean number of individuals of a particular parasite species per infected host in the sample, and 'abundance' is the mean number of individuals of a particular parasite species per host examined (infected and uninfected) in the sample.

The minimum sample size (20–25 specimens) for comparative analyses of sexual, ontogenetic and geographical variability was determined from an empirically supported hypothesis. Prevalence data for the main and secondary helminths in three squid size groups are compared in Fig. 2. A further increase in sample size (to more than 20–25 specimens) did not influence the precision of the estimates of species numbers or the prevalence index values.

3. Results and discussion

3.1. Composition of the helminth fauna and its description

Nine different species of cestode, trematode and nematode were found.

3.1.1. Cestoda

3.1.1.1. Family: *Phyllobothriidae* Braun, 1900. *P. speciosum* Monticelli, 1889, larva (Fig. 3A). Prevalence: 75.2%; intensity: 1–63 000; density: 879.4; abundance: 664.5.

Site. Small larvae were encysted in the epithelium of the rectum and large larvae occurred free (without cysts) within the cavity of the rectum, caecum and stomach (intensity: 1–20 usually 2–6).

Description. Measurements based on 20 specimens. Size range of small larvae was 0.04–0.18 mm and large larvae 0.13–0.22 mm. Size of cysts was 0.04–0.22 × 0.03–0.15 mm. Scolex has one apical sucker (diameter 0.03–0.05 mm) and an accessory sucker (diameter 0.04–0.05 mm) in front of the anterior border of each bothridium. Bothridia (size 0.03–0.04 × 0.04–0.05 mm) of dorsal and ventral pairs sessile with free posterior ends.

These cestodes were initially identified as *Dinobothrium* sp. (Gaevskaya et al., 1982, 1983; Nigmatullin et al., 1985) and as *Scolex pleuronectis* (Shukhgalter, 1985). But more detailed study of the morphology of encysted plerocercoids made it possible to define more precisely the peculiarities of bothridia structure and this turned out to be bilocular. Plerocercoids of *P. speciosum* (*S. pleuronectis bilocularis*) were found in *D. gigas* from the eastern north Pacific (California) (Riser, 1956; Hochberg, 1990) and the eastern south Pacific (Gaevskaya et al., 1982, 1983, 1987; Gaevskaya and Shukhgalter, 1992; Shukhgalter, 1985, 1988a,b, 1992; Nigmatullin et al., 1985).

Phyllobothrium sp. larva (III) (Fig. 3B). Prevalence: 1.2%; intensity: 1–2; density: 1.7; abundance: 0.02.

Site. Plerocercoids occurred free in the stomach, caecum and rectum. Some larvae moved in the mantle cavity and buccal cone.

Description. Measurements based on 25 specimens. Size range of larvae was 4.3–15.5 mm. Scolex with apical sucker (0.21–0.25 × 0.24–0.35 mm) and one accessory sucker (0.14–0.28 × 0.15–0.32 mm) in front of the anterior border of each bothridium. Bothridia (0.31–0.52 × 0.77–0.83 mm) with smooth surface and slightly curled border.

Plerocercoids of *Phyllobothrium* sp. were marked in *D. gigas* from the eastern north Pacific (MacGinitie and MacGinitie, 1949; Riser, 1956) and from the eastern south Pacific (Dollfus, 1964; Gaevskaya

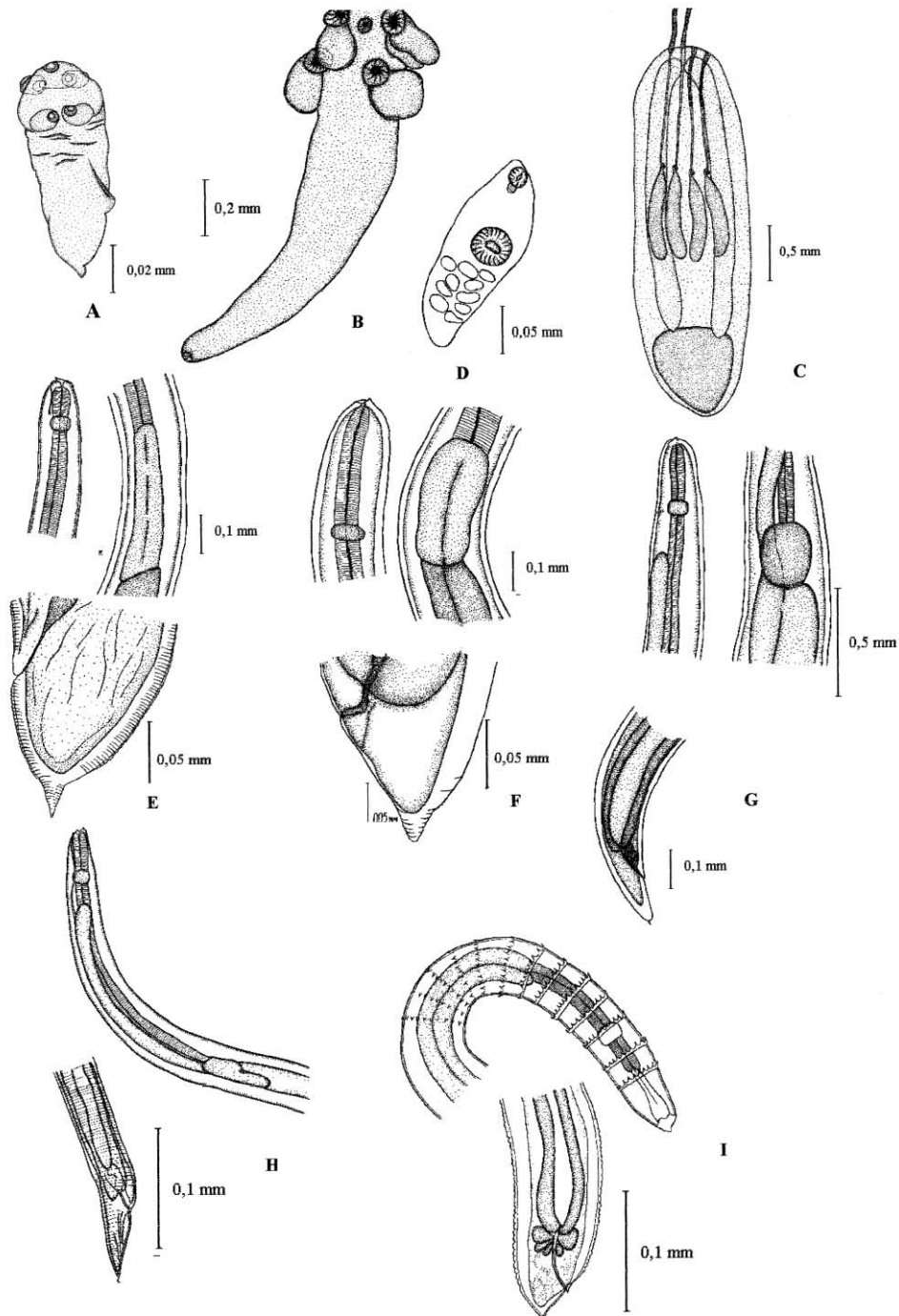


Fig. 3. Parasitic helminths of *D. gigas*: (A) *P. speciosum*, (B) *Pyllobothrium* sp., (C) *T. coryphaenae*, (D) Didymozoidae indet. (E) *A. simplex*, (F) *A. physeteris*, (G) *Porrocaecum* sp., (H) *Contracaecum* sp. and (I) *Spinitectus* sp.

et al., 1982, 1983, 1987; Gaevskaya and Shukhgalter, 1992; Nigmatullin et al., 1985; Shukhgalter, 1985, 1988a,b, 1992). These postlarvae were classified conditionally as type III (Shukhgalter, 1992) because they differed from the types I and II described from *Stenoteuthis pteropus* (Gaevskaya, 1977) in the form of their bothridia.

3.1.1.2. Family: *Tentaculariidae* Poche, 1929. *Tentacularia coryphaenae* Bosc, 1802 (Fig. 3C). Prevalence: 6.6%; intensity: 1–5; density: 2.4; abundance: 0.16.

Site. Postlarvae occurred within the internal organs of the mantle cavity, sometimes penetrating the ventral mantle musculature and very mobile.

Description. Measurements based on 15 specimens. Size range 5.0–14.0 mm, maximum widths at level of pars bothridialis 1.7–2.9 mm. Postlarvae possess four tentacles armed with hooks. Armature homeoacanthous homeomorphous with characteristic tridentate basal hooks. Size of metabasal hooks: 0.031 mm, size of basal hooks: 0.01–0.014 mm. Pars bothridialis: 3.8–5.8 mm, pars vaginalis: 1.12–1.19 mm, pars bulbosa: 0.98–1.52 mm, pars postbulbosa: 2.01–5.60 mm, appendix: 2.80–3.78 mm and velum: 2.52–2.80 mm.

Postlarvae of *T. coryphaenae* were found in *D. gigas* from the eastern south Pacific (Gaevskaya et al., 1982, 1983, 1987; Gaevskaya and Shukhgalter, 1992; Nigmatullin et al., 1985; Shukhgalter, 1985, 1988a,b, 1992).

3.1.2. Trematoda

3.1.2.1. Family: *Didymozoidae* (Monticelli, 1888), Poche, 1907. *Didymozoidae* indet. mtc. (Fig. 3D). Prevalence: 13.0%; intensity: 1–35; density: 3.9; abundance: 0.51.

Site. Metacercaria localised in cysts on the inner wall of stomach and occasionally in oesophagus and caecum along major blood vessels, sometimes free in stomach cavity.

Description. Measurements based on 20 specimens. Length range 0.224–0.504 mm, maximum widths 0.15–0.24 mm. Oral sucker almost terminal (0.021–0.045 × 0.028–0.061 mm). Pharynx placed close to or under the oral sucker, 0.11–0.020 × 0.014–0.028 mm in size. Ventral sucker (0.045–0.084 × 0.053–0.098 mm) larger than oral sucker. Ventral

sucker situated just anterior to mid-body. Eighteen to 20 ‘vesicular’ cells.

Larval didymozoids were found in *D. gigas* from the Gulf of California (Hochberg, 1969, 1990; Overstreet and Hochberg, 1975) and the eastern south Pacific (Gaevskaya et al., 1982, 1983, 1987; Gaevskaya and Shukhgalter, 1992; Nigmatullin et al., 1985; Shukhgalter, 1986, 1988b).

3.1.3. Nematoda

3.1.3.1. Family: *Anisakidae* Skrjabin et Karokhin, 1945. *Anisakis simplex* (Rudolphi, 1802) larva (Fig. 3E). Prevalence: 9.2%; intensity: 1–16; density: 2.5; abundance: 0.23.

Site. The third-stage larvae were encysted in coelomic membranes and the ovary.

Description. Measurements based on 12 specimens. Size range 18.0–37.5 mm, maximum body widths 0.484–1.0 mm. Length from anterior end of body to nerve ring 0.273–0.414 mm. Length of oesophagus 1.156–2.235 mm. Size of stomach 0.142–0.327 × 0.523–0.624 mm. Tail length 0.218–0.327 mm, length of tail mucron 0.022 mm.

Anisakis physeteris (Baylis, 1923) larva (Fig. 3F). Prevalence: 24.2%; intensity: 1–26; density: 5.0; abundance: 1.22.

Site. The third-stage small-sized larvae were encysted in the stomach wall and the large-sized larvae in coelomic membranes and ovary.

Description. Measurements based on 15 specimens. Size range 22.5–35.0 mm, maximum body widths 0.709–0.774 mm. Length from anterior end of body to nerve ring (position of nerve ring) 0.338–0.360 mm. Length of oesophagus 1.679–1.908 mm. Size of stomach 0.234–0.30 × 0.468–0.512 mm. Tail length 0.185–0.272 mm, length of tail mucron 0.004 mm.

Larvae of *Anisakis* sp. (Gaevskaya et al., 1982, 1983, 1987; Nigmatullin et al., 1985; Hochberg, 1990) and *A. simplex* (Chiclla and Verano, 1997) were found in *D. gigas* from the eastern south Pacific and the Gulf of California area (our data). This is the first record of *A. physeteris* in this squid. Previously (Shukhgalter, 1988b, 1990b; Gaevskaya and Shukhgalter, 1992), this species was known as *Anisakis* sp. larva (II).

The third-stage larvae of *A. simplex* are morphologically characterised by a relatively long ventriculus

with an oblique ventriculus–intestinal junction and a short, rounded tail with a mucron (Berland, 1961; Smith, 1983). At the same stage *A. physeteris* have a relatively short ventriculus with a horizontal ventriculus–intestinal junction and a long, conical tail without a mucron (Berland, 1961; Smith and Wootten, 1978; Koyama et al., 1969; Matsuura et al., 1992).

Porrocaecum sp. larva (Fig. 3G). Prevalence: 29.4%; intensity: 1–17; density: 1.0; abundance: 0.3.

Site. The third-stage larvae were encysted in stomach and rectum walls.

Description. Measurements based on 10 specimens. Size range 8.2–23.0 mm, maximum width 0.240–0.480 mm. Length from anterior end of body to nerve ring 0.220–0.338 mm. Length of oesophagus 1.624–2.518 mm, size of stomach $0.163\text{--}0.184 \times 0.232\text{--}0.294$ mm and length of intestinal caecum 1.415–2.289 mm. Excretory pore situated at the level of nerve ring. Tail length 0.136–0.162 mm, length of tail thorn 0.008–0.01 mm.

Larvae of *Porrocaecum* sp. were observed in *D. gigas* from the eastern south Pacific (Gaevskaya et al., 1982, 1983, 1987; Gaevskaya and Shukhgalter, 1992; Nigmatullin et al., 1985; Shukhgalter, 1988b, 1990b; Hochberg, 1990).

Contracaecum sp. larva (Fig. 3H). Prevalence: 0.5%; intensity: 1–4; density: 4.2; abundance: 0.02.

Site. The third-stage larvae were encysted in stomach, caecum and rectum walls.

Description. Measurements based on 15 specimens. Size range 4.4–6.5 mm, maximum widths 0.162–0.262 mm. Length from anterior end of body to nerve ring 0.108–0.135 mm. Length of oesophagus 0.601–0.923 mm, size of stomach $0.035\text{--}0.059 \times 0.068\text{--}0.108$ mm and length of intestinal caecum 0.049–0.737 mm. Length of ventricular appendix: 0.049–0.081 mm. Tail length 0.108–0.173 mm, length of tail thorn 0.005 mm.

Larvae of *Contracaecum* sp. have been recorded in *D. gigas* from the eastern south Pacific (Shukhgalter, 1988b, 1990b; Gaevskaya and Shukhgalter, 1992).

3.1.3.2. Family: Ascarophididae Trofimenko, 1967. *Spinitectus* sp. larva (Fig. 3I). Prevalence: 0.4%; intensity: 1–3; density: 2.8; abundance: 0.01.

Site. Larvae encysted in stomach and caecum walls.

Description. Measurements based on three specimens. Size range 1.8–2.6 mm, maximum width

0.07–0.08 mm. Length of pharynx 0.04–0.05 mm and oesophagus 0.108–0.49 mm. Cuticle has 23 rings of thorns. First seven rings are prominent. Position of first ring, 0.054 mm from anterior end. Distance between first and second rings 0.027 mm, second and third rings 0.03 mm, third and fourth rings 0.022 mm, further rings 0.024, 0.028, 0.024, 0.022, 0.019 mm, etc. Number of thorns in ring 20–22. Size of thorns in first to fifth rings 0.005 mm, sixth to eighth rings 0.008 mm, further rings 0.005 mm. Nerve ring situated at the level of third thorn ring (0.097–0.108 mm). Length of tail 0.041–0.054 mm.

Larvae of *Spinitectus* sp. are marked in *D. gigas* from the eastern south Pacific (Shukhgalter, 1988b, 1990b; Gaevskaya and Shukhgalter, 1992).

3.2. Groups of helminths by infection rates

Nine species and larval forms of helminth were found in *D. gigas* from the four study areas of the east Pacific; three species of cestode, one trematode species and five species of nematode. The prevalence of infection in the total sample was 75.5%.

Three groups of helminths were distinguished on the basis of the rates of infection and for each of these groups the squid play various roles in their respective life cycles. Subsamples of the various size groups of squid were analysed taking into account the maximum infection rate for the particular helminth. This is due to well-pronounced ontogenetic variations for squid infestation by the various helminth groups (see Section 3.4, Table 3 and Fig. 4). Thus, juvenile and adult squid play different roles in the life cycles of the various helminth species; for didymozoids juvenile squid are responsible for their transfer to the final host, and for cestodes and nematodes, this role is taken by adult squid.

The main helminths (defined by a prevalence in some squid size groups of >45%, see Table 3 and Fig. 4) comprised metacercaria of didymozoids, larvae of the cestode *Pelichnibothrium speciosum*, and larvae of the nematodes *Porrocaecum* sp. and *A. physeteris*. The secondary helminths (defined by a prevalence of between 10 and 45%) comprised *T. coryphaenae* and *A. simplex*. The rare helminths (defined by a prevalence of <10%) comprised *Contracaecum* sp., *Spinitectus* sp. and *Phyllobothrium* sp. (III).

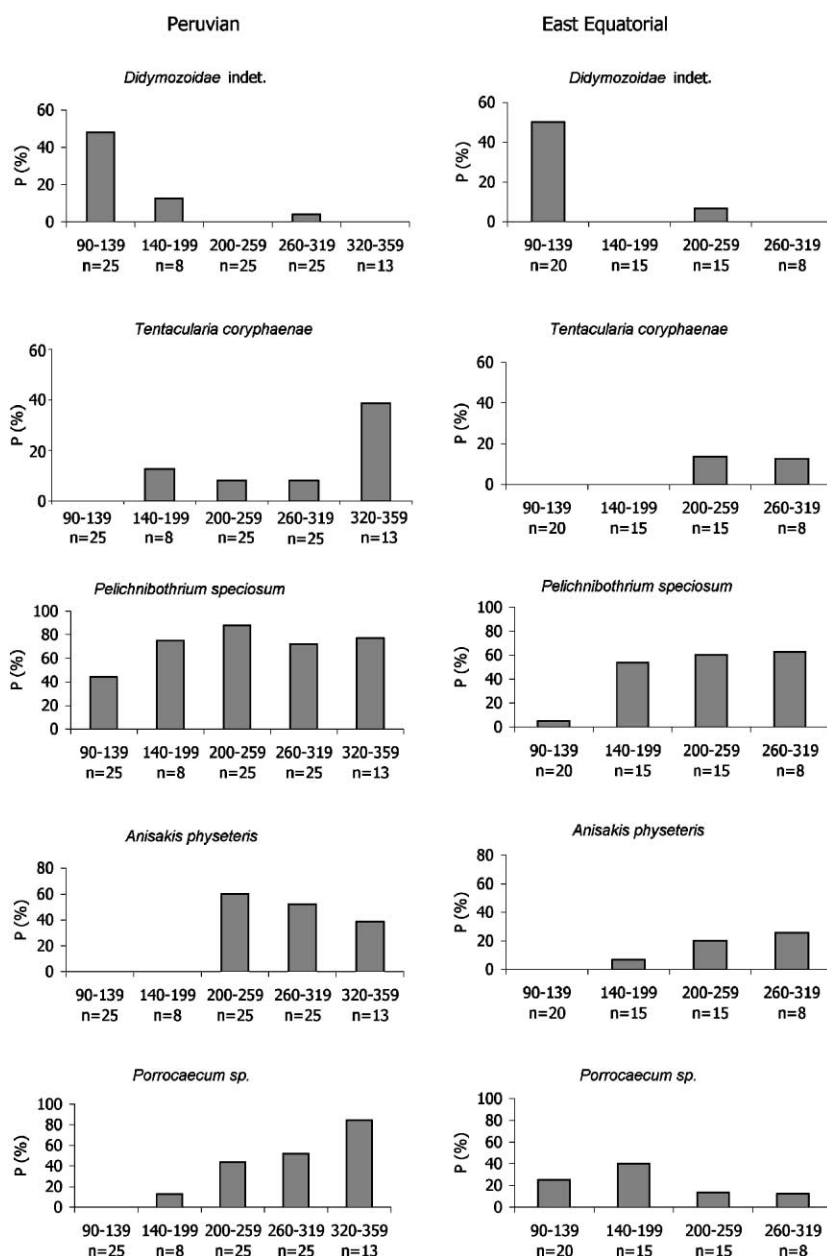


Fig. 4. Ontogenetic variability in helminth composition and prevalence values (P) for squid from the Peruvian and east equatorial regions.

3.3. Infection in relation to sex and age of squid

Samples of mature females and males of 250–300 mm ML from the Peruvian area were examined to determine whether infection rates vary with sex. The species composition of the two samples was

similar and the infection rate of males slightly higher than females (Table 2). Immature and adult females of 250–300 mm ML from the Peruvian region were used to determinate the effect of age on helminth fauna in squid of equal size. Helminth composition in the samples was similar and the infection rate in immature

Table 2

Prevalence (*P*), with confidence limits ($p = 0.95$), and intensity (*I*) of helminth infection in squid by sex, age group and season

	Peruvian region, March–April 1981			East equatorial region			
	Females (immature), <i>P</i> (%) ^a	Females (mature), <i>P</i> (%) ^b	Males (mature), <i>P</i> (%) ^c	February 1982		September 1981	
				Males and females, <i>P</i> (%) ^d	Males and females, <i>I</i> (specimens) ^d	Males and females, <i>P</i> (%) ^e	Males and females, <i>I</i> (specimens) ^e
<i>Didymozoidae</i> indet.	–	–	–	3 (0.5–15.7)	1–5		
<i>T. coryphaenae</i>	8.7 (2.3–23.7)	28.6 (13.6–50.4)	23.1 (10.9–42.5)	6 (1.6–20.0)	1–2	4.3 (0.8–21.4)	1–2
<i>P. speciosum</i>	65.2 (44.5–81.5)	71.4 (49.6–86.4)	92.3 (75.4–98.0)	66.7 (49.3–80.5)	100–25 000	77.4 (57.7–90.5)	50–1000
<i>A. physeteris</i>	30.4 (15.4–51.5)	38.1 (20.5–59.5)	34.6 (19.2–54.2)	18.2 (8.5–34.7)	1–3	38.7 (21.8–59.6)	1–6
<i>Porrocaecum</i> sp.	13.0 (4.4–32.6)	23.8 (10.5–45.5)	42.3 (25.2–61.4)	3 (0.5–15.7)	1–5	17.2 (6.8–37.6)	1–5

^a *n* = 23, 250–300 mm.^b *n* = 21, 250–300 mm.^c *n* = 26, 250–300 mm.^d *n* = 33, 200–300 mm.^e *n* = 23, 200–300 mm.

females was slightly lower (Table 2). These minor differences probably reflect the greater age of males relative to females for a given size, and immature squid being younger than adult squid for a given ML (Arkhipkin and Murzov, 1986).

Although in both cases, the composition of the helminth fauna and the infection rates were similar, some differences were evident principally due to the different ages of squid of equal size. However, the level of the differences is not large and so allows data to be pooled for further comparative analyses. The similarity revealed is largely explained by the common habitats of males, females and different maturity stages (Nesis, 1983; Nigmatullin et al., 1991) and the similarity of food consumed by squid of equal size (Shchetinnikov, 1989).

3.4. Ontogenetic variations

Ontogenetic variations were investigated by examining data for four size groups of squid from the Peruvian region (Table 3). These groups were selected (Nigmatullin, 1987a) on the basis of size variations in prey and predator composition (Shchetinnikov, 1989) and sexual maturity in ontogenesis (group I comprises juveniles, II immature squid, III mainly maturing and IV comprises mature adult squid). Since *D. gigas* is monocyclic and has a 1 year life cycle in the Peruvian region (Arkhipkin and Murzov, 1986; Nigmatullin

et al., 1991), this series almost covers (with the exception of larvae and fry) the entire life cycle of the middle size intraspecific group. Each size group is characterised by a particular composition of helminths and particular rates of infection for the different species (Table 3). Thus, the ontogenetic series actually represents successive stages in the formation of the helminth fauna.

Stage I. Metacercaria of didymozoids penetrate the smallest squid and generally have relatively high infection rates in juveniles. Isolated larvae of *Porrocaecum* sp. occurred in young of >50–60 mm ML. The main prey items of this size group are crustaceans (copepods, euphausiids and amphipods) and chaetognaths (Shchetinnikov, 1989), which are the common second intermediate hosts of didymozoids (Hochberg, 1990).

Stage II. Larvae of *P. speciosum* occur in squid of around 100 mm ML, and both the prevalence and intensity of infection quickly reach relatively high values for this narrow size range. This size of squid also has isolated larvae of *A. physeteris*, and infection rates for *Porrocaecum* sp. are stable. The prevalence of metacercaria of didymozoids reach maximum values for ontogeny. This size group is characterised by a transition from feeding mainly on crustaceans to feeding mainly on small fish and squid (Shchetinnikov, 1989); the fish are mainly myctophids and *Vinciguerria* and become significantly more important with

Table 3

Prevalence (P) with confidence limits ($p = 0.95$) and intensity (I) of helminth infection in squid of different ontogenetic groups in the Peruvian region

Stage	Number of species	ML (mm)	Species	P (%)	I (specimens)
I	25	30–89	Didymozoidae indet.	24.0 (12.0–44.8)	1–50
			<i>Porrocaecum</i> sp.	8.0 (2.3–25.9)	1–5
II	25	90–139	Didymozoidae indet.	48.0 (29.3–66.3)	1–50
			<i>Porrocaecum</i> sp.	4.0 (1.1–21.3)	1–5
			<i>P. speciosum</i>	24.0 (12.0–44.8)	1–10 000
			<i>A. physeteris</i>	4.0 (1.1–21.3)	1–3
III	25	140–359	Didymozoidae indet.	4.0 (1.1–21.3)	1–5
			<i>Porrocaecum</i> sp.	20.0 (7.9–38.1)	1–10
			<i>P. speciosum</i>	68.0 (48.3–83.1)	1–25 000
			<i>A. physeteris</i>	4.0 (1.1–21.3)	1–10
			<i>Contracaecum</i> sp.	4.0 (1.1–21.3)	1
			<i>T. coryphaenae</i>	4.0 (1.1–21.3)	1–2
IV	15	360–431	<i>Porrocaecum</i> sp.	66.7 (39.7–83.9)	1–15
			<i>P. speciosum</i>	73.4 (49.1–90.3)	1–63 000
			<i>A. physeteris</i>	53.4 (28.7–74.5)	1–10
			<i>A. simplex</i>	13.3 (4.4–40.4)	1–7
			<i>T. coryphaenae</i>	40.0 (18.4–63.4)	1–5
			<i>Contracaecum</i> sp.	6.7 (0.9–29.3)	1–16
			<i>Phyllobothrium</i> sp. (III)	6.7 (0.9–29.3)	1–5
			<i>Spinitectus</i> sp.	6.7 (0.9–29.3)	1–3

significant decreases in the quantity of crustaceans taken. The fish are paratenic hosts for these cestodes and nematodes and the main transmitter to squid (Gaevskaya and Nigmatullin, 1981; Smith, 1983; Hurst, 1984; Hochberg, 1990; Nagasawa, 1990).

Stage III. In this size group, there is a sharp decrease in infection by metacercaria of didymozoids and an increase in infection by the other helminth species. The cestode *T. coryphaenae* and the nematode *Contracaecum* sp. are observed for the first time. Myctophids are the main prey item for this size group, other squid are minor prey items, and *Vinciguerria* and other fishes and planktonic crustaceans are absent (Shchetinnikov, 1989). The decrease of infection by metacercaria of didymozoids is due to the absence of crustaceans in the diet of *D. gigas* of this size group and to the limited life span of metacercaria generally around 4–6 months (Gaevskaya and Nigmatullin, 1981; Naidenova et al., 1985). An increase in infection by cestodes and nematodes and the appearance of new species, are connected with the feeding of *Dosidicus* on small fish and squid.

Stage IV. Mature squid have no metacercaria of didymozoids. The eight helminth species observed are

all characterised by maximum infection rates for the ontogeny period as a whole. Purely oceanic species and nerito-oceanic helminths are evident (*Phyllobothrium* sp. larva (III), *A. simplex* larva). The main prey items for this size group are squids, myctophids and flying fishes (Shchetinnikov, 1989).

Thus, juvenile squid play the most important role in the life cycles of didymozoid trematodes, while sub-adult and adult squid are most important for the life cycles of the cestodes and nematodes studied. These variations in the host–parasite relationship depend directly on ontogenetic variations in *D. gigas* food relations.

3.5. Geographic variability

Geographic variations were examined using data on the infection rates of equal-sized immature and maturing squid of 190–210 to 300–320 mm ML from the four regions of the east Pacific (Fig. 1 and Table 4).

As a generalisation, the species composition of the main and secondary helminths was similar in squid from all four areas. The only exception was the absence of *Porrocaecum* sp. from the west equatorial

Table 4

Prevalence (P) with confidence limits ($p = 0.95$) and intensity (I) of helminth infection in squid from the four study areas

	Peruvian region ^a		East equatorial region ^b		West equatorial region ^c		Nicaraguan region ^d	
	P (%)	I (specimens)	P (%)	I (specimens)	P (%)	I (specimens)	P (%)	I (specimens)
Didymozoidae indet.	2 (0.4–10.8)	1–5	4.3 (0–23.3)	1–5	4.2 (0.7–20.7)	1–5	5 (1.7–13.9)	3–10
<i>T. coryphaenae</i>	8 (3.1–19.1)	1–2	12.9 (2.0–35.0)	1–2	16.8 (6.5–36.9)	1–2	10 (4.6–20.4)	1–2
<i>Phyllobothrium</i> sp.	2 (0.4–10.8)	1–5	–	–	–	–	1.7 (0.3–9.1)	1
<i>P. speciosum</i>	84 (71.2–91.8)	1–25 000	77.9 (55.3–93.7)	1–50 000	58.8 (38.4–75.8)	1–10 000	86.6 (75.3–93.1)	1–10 075
<i>A. physeteris</i>	56 (42.1–69.1)	1–6	21.5 (6.6–45.2)	1–6	29.4 (14.7–49.5)	1–6	10 (4.6–20.4)	1–3
<i>Porrocaecum</i> sp.	24 (14.1–37.7)	1–15	12.9 (2.0–35.0)	1–10	–	–	6.7 (2.6–16.2)	1–2

^a 210–320 mm ML, $n = 50$.^b 210–320 mm ML, $n = 23$.^c 190–300 mm ML, $n = 22$.^d 190–320 mm ML, $n = 60$.

region, while infection by larvae of this species in the neighbouring southern and western areas was more than 10% (Table 4). Squid from both equatorial regions effectively contained no 'rare' larvae of *Phyllobothrium* sp. (one larva of *Phyllobothrium* sp. was found in a mature female of ML 340 mm ML in the west equatorial region).

Total infection rates in all four areas were similar and ranged between 73.8 and 98%. There was also similarity between the prevalence and intensity rates, and these are characteristic features for each main and secondary species of helminth (Table 4). These data reflect the similar position of *D. gigas* with respect to the parasite community within the areas investigated, which include more than 50% of the species range.

Despite the general similarity in the composition of the helminth fauna and the infection rates in the different regions, there were geographic variations in the helminth fauna related to its formation in ontogeny. Thus, significant differences were found when comparing ontogenetic infection dynamics of squid of 90–360 mm ML from the Peruvian and east equatorial areas (Fig. 4). Main and secondary helminth species begin to infect squid at different MLs (for four species) and curves describing infection dynamics differ for all five species. The shape of the curves is considerably different between the two regions for four of the species, and although they are similar for *P. speciosum* the prevalence of infection is different varying by 30–70%.

The data obtained (Fig. 4) suggests earlier and greater mass infection of squid and, thus, squid participation in helminth life cycles, in the Peruvian region relative to the east equatorial region. This is probably due to the distribution of the final helminth hosts in these regions — tuna, xiphoid fishes, sharks and marine mammals — and thus differences in the infection of the planktonic crustaceans and small fish upon which the squid prey. These data do not contradict the hypothesis of the isolation of the squid populations of the Peruvian and equatorial areas and the absence of extensive interchange of specimens between them (Nigmatullin et al., 1983, 1991).

3.6. Seasonal variations

To study seasonal variability in the helminth fauna of *D. gigas*, two samples of immature squid

of 200–300 mm ML were obtained from the east equatorial area in September 1981 and February 1982 (Table 2). Comparison of these data did not reveal any significant qualitative or quantitative differences. Some differences in the rate of infection by larvae of *A. physeteris* and *Porrocaecum* sp. were not considered important. The presence or absence of didymozoid trematodes is normal as these are rare in squid of this size range. So, seasonal parasite–host interactions are relatively stable for *D. gigas*. But, nevertheless seasonal variability in the size composition and abundance of squid within the different age and size groups may affect the role of squid population in the parasite structure as a whole.

4. Conclusion

Nine species of helminth were found in *D. gigas* from the open waters of the central part of its species range, trematodes, cestodes and nematodes. These species were all represented by larval stages. The structure of the helminth fauna and its larval composition are in principle similar to those for other ecologically and taxonomically similar nektonic ommastrephid squid, such as *Ommastrephes bartrami*, *S. pteropus* and *S. oualaniensis* (Gaevskaya and Nigmatullin, 1976, 1981; Naidenova et al., 1985; Zuev et al., 1985; Nigmatullin, 1987b). This indicates a closeness in terms of their ecological niches. Some differences in infection rates by didymozoid trematodes (their rates of infection are considerably higher for the three latter species), the absence in *D. gigas* larvae of cestodes of the genus *Nybelinia* (which are common parasites of *Ommastrephes* and *Sthenoteuthis*) and acantocephales, as well as a poorer helminth composition in *D. gigas*, indicate that the parasite structure of the pelagic system in the central and southeastern Pacific may be somewhat different to that observed in earlier studies of oceanic waters in the Atlantic and Indian Oceans.

All the helminths (metacercaria of didymozoids, larvae of *Pelichnibothrium* sp., *Phyllobothrium* sp., *T. coryphaenae* and *Anisakis* sp.) found in *D. gigas* at the northern limit of its species range near California (Riser, 1956; Overstreet and Hochberg, 1975; Hochberg, 1969, 1990; our data on *Anisakis*) were also found in *D. gigas* from the four study areas

considered here. Together with all the other data on geographical and seasonal variability in the rates of infection, this indicates consistency in the helminth fauna and relative spatial and temporal stability in terms of the position of *D. gigas* within the parasite structure of the pelagic ecosystem of the east Pacific.

The comparative ontogenetic approach to the ecological analysis of parasite relations used in the present study is an effective addition to the traditional approach of using samples of equal-sized hosts for studying the geographic variability of parasitological parameters. This new approach is process orientated and more system based.

There are two opposing situations in the formation of the helminth fauna in ontogeny. The first concerns metacercaria of didymozoids. These are the first helminths to infect *D. gigas*, and the squid become infected by consuming small crustaceans. Young squid of 130–150 mm ML are most affected; in larger squid, the metacercaria have died and in adult specimens of >300–350 mm ML the metacercaria are absent. The second situation is typical for the cestodes and nematodes. In this latter case, the squid first become infected at around >150–200 mm ML with adult squid the most infected. The squid become infected by consuming fish and other smaller squid. The main predators of young squid (<100–150 mm ML) are scombroid fishes (mainly tunas) (Nigmatullin, 1986; Shchetinnikov, 1986), which are the definitive hosts of didymozoid trematodes (Yamaguti, 1971). Many species feed on subadult and adult squid, active sharks (e.g. *Carcharinus obscurus*, *Prionace glauca*), xiphoid fish, fur seals, dolphins and sperm whales (Clarke et al., 1976, 1978; Clarke and Trillmich, 1980; Nesis, 1983; Shchetinnikov, 1986; Robertsons and Chivers, 1997; Abita-Gardenas et al., 1997; Markaida and Sosa-Nishizaki, 1998). Sharks are the definitive hosts for the cestodes found in this study; for nematodes (except *Contracaecum* sp.) the definitive hosts are marine mammals (for *Anisakis*) and xiphoid fishes (for *Porrocaecum* and *Spinitectus*), while seabirds are the definitive hosts for *Contracaecum* sp. (see review by Hochberg, 1990). So, the trophic and parasite relations of *D. gigas* are well synchronised, which is a pattern peculiar to stable trophic–parasitic systems (Kennedy, 1975). An analogous situation was described for the squid *S. pteropus*

and *S. oualaniensis* (Gaevskaya and Nigmatullin, 1981; Naidenova et al., 1985).

All the helminths observed are characterised by a very broad specificity: they use various planktonic invertebrates, small fishes and squid at the same stages of their life cycles. Squid are infected by eating infected prey — crustaceans, small fish and squid — which represent second and paratenic intermediate hosts for these helminth species (Gaevskaya and Nigmatullin, 1976, 1981, 1983; Naidenova et al., 1985; Zuev et al., 1985; Nigmatullin, 1987b; Hochberg, 1990; Nagasawa, 1990). Further transfer of these helminths to definitive hosts occurs by consuming infected squid. Thus, the life cycles of all these helminths are facilitated by the trophic interactions of the pelagic ecosystem (Nigmatullin, 1987b).

As is clear from the close trophic relations with definitive hosts and relatively high infection rates, *D. gigas* plays different roles in the life cycles of the helminths. However, its role in the life cycle of the nematode *Contracaecum* sp. is not yet clear. On one hand, the definitive hosts for this nematode are seabirds, while on the other hand *Contracaecum* sp. only infects large adult squid. When these large squid are alive, they are not available to seabirds, so the squid is the deadlock host for *Contracaecum* sp. But it is possible that seabirds may be infected by these nematodes when eating hardly moving or dead squid after spawning, which at some periods of the day are near the surface (A.A. Baral, pers. commun.). In this case, *D. gigas* is one of the paratenic hosts for *Contracaecum* sp.

In the life cycles of the helminths in the present study, *D. gigas* is a cyclogenic transport host and a member of the secondary host structure. This is an ecologically driven group of intermediate hosts between the primary (obligatory intermediate and definitive hosts) and tertiary (deadlock hosts and hosts-killers) host structures (Nigmatullin, 1995). *D. gigas* is one of the paratenic hosts. In the didymozoid life cycles, *D. gigas* is positioned between the second intermediate hosts (copepods, euphausiids, chaetognaths) and the definitive hosts, and for cestodes and nematodes, it is positioned between other paratenic hosts (mainly small fish and squid) and definitive hosts. This transport role for the completion of the helminth life cycles, due to the extended range, high abundance, short 1 year life cycle, and numerous and

stable trophic relations of *D. gigas*, is important and often ecologically necessary, especially for *P. speciosum*, *Porrocaecum* sp., *A. physeteris*, didymozoids and *T. coryphaenae*.

In conclusion, it must be stressed that our results relate to small- and mainly medium-sized intraspecific groups of *D. gigas* from the open waters of the central part of its species range. To provide a complete picture of parasite relations for *D. gigas*, it would be necessary to study the helminth fauna of squid from the coastal waters of the EEZs, as well for large-sized groups (with adults of >500–600 to 1000–1500 mm ML) from the northern and southern peripheries of the species range.

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