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The paralarvae of two South American sympatric squid: *Loligo gahi* and *Loligo sanpaulensis*

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Two loliginid squid inhabit coastal and continental shelf waters of the south-west Atlantic off Argentina: Loligo gahi D'Orbigny, 1835 and Loligo sanpaulensis Brakoniecki, 1984. Even though L. gahi is associated with colder and deeper waters than L. sanpaulensis, both are sympatric in part of their geographic and bathymetric ranges of distribution. As in many other cephalopod species, there are no detailed descriptions of the 'paralarvae' (planktonic larvae of the cephalopods) of these species useful for identification of individuals captured in plankton samples. In this study, size, morphometry and patterns of chromatophore abundance and distribution were characterized for hatchlings (hatching paralarvae) of these two species obtained in the laboratory after egg incubation at different temperatures. Paralarvae from both species were captured in preliminary plankton surveys conducted off the coast of Central Argentina, and were characterized on the basis of their morphometry. Differences were observed in the dorsal mantle lengths of the hatchlings of L. gahi (2.3–3.7 mm) and L. sanpaulensis (1.4–1.7 mm). Average size and number of dark chromatophores at hatching were negatively correlated with incubation temperature in L. gahi. Although most morphometric indices showed between-species differences, fin length to mantle length ratio was markedly higher in L. sanpaulensis. Patterns of chromatophore abundance and distribution allow the hatchlings of both species to be differentiated from each other and from those of other Loligo species. Hatchlings of L. sanpaulensis have two red chromatophores on the 'cheek patches' areas, while those of L. gahi have three to five. On the dorsal surface, the hatchlings of L. gahi display dark brown chromatophores, which were absent in L. sanpaulensis. Hatchlings of L. gahi were found at outer shelf and costal stations off Northern Patagonia. Paralarvae of L. sanpaulensis were found at coastal stations off the Buenos Aires Province and off Northern Patagonia.

INTRODUCTION

Young cephalopods in their first growth stage after hatching resemble miniature adults with most organs developed, but their planktonic mode of life differs from that of juveniles and adults. This distinguishes them from 'true larvae' like those of other molluscs, and therefore they have been termed 'paralarvae' (Young and Harman, 1988). The collection of paralarvae from plankton samples has allowed inferences on aspects of the cephalopods' ecology, such as the location of the spawning grounds, the drift patterns and areas of aggregation of the early life stages, and the critical size at which individuals complete their planktonic life (Kubodera and Okutani, 1977; Vecchione, 1981; Brunetti *et al.*, 1991; Rodhouse *et al.*, 1992; Filippova and Pakhomov, 1994; Moltschaniwskyj and Doherty, 1994, 1995; Vidal, 1994; Bower, 1996; Bower *et al.*, 1999; Haimovici *et al.*, 2002; Shea and Vecchione, 2002). Although the identification of these organisms to species level is a prerequisite for such a study, their descriptions are scarce and frequently of limited utility to make taxonomic classifications in plankton samples (Vecchione, 1986). Particularly for the paralarvae of squid from the genus *Loligo*, one of the most important in volume of commercial landings [Food and Agriculture Organization (FAO), 1999], only keys to the family level are available (Hanlon *et al.*, 1992). Furthermore, of the 17 species currently recognized within this genus (Sweeney and Vecchione, 1998), detailed illustrations are only available

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for the hatchlings of *L. vulgaris vulgaris* (Naef, 1928), *L. vulgaris reynaudii* (Vecchione and Lipinski, 1995; Blackburn *et al.*, 1998), *L. opalescens*, *L. plei*, *L. pealii* (McConathy *et al.*, 1980; Vecchione, 1988), *L. forbesi* (Hanlon *et al.*, 1992) and *L. bleekerii* (Baeg *et al.*, 1992).

Two *Loligo* species are currently recognized for Atlantic waters off Patagonia: *L. gahi* D'Orbigny, 1835 and *L. sanpaulensis* Brakoniecki, 1984 (Castellanos and Cazzaniga, 1979; Brakoniecki, 1984). The former is distributed in the Pacific Ocean from Peru (6°S) to Tierra del Fuego (55°S), and in the Atlantic Ocean from Tierra del Fuego to coastal (36°S) and slope (38°S) waters of Argentina (Castellanos and Cazzaniga, 1979; Roper *et al.*, 1984). *Loligo gahi* is the loliginid that supported the world's largest catches (in metric tons) during the last decade (FAO, 1999). *Loligo sanpaulensis* is distributed along the Atlantic coast of South America, from Brazil (20°S) to Argentina (~46°S), where it represents an important resource for artisanal fisheries (Castellanos and Cazzaniga, 1979; Vigliano, 1985; Andriguetto and Haimovici, 1991). Both loliginids reproduce in coastal and shelf waters of Northern Patagonia (Barón, 2001; Barón and Ré, 2002a), their juvenile and adult stages being easily recognizable on the basis of morphometry and chromatophore abundance and coloration (Barón and Ré, 2002b). Even though several authors reported the finding of paralarvae from either species (Castellanos *et al.*, 1967; Leta, 1987; Hatfield, 1992; Rodhouse *et al.*, 1992; Andriguetto and Haimovici, 1996; Arkhipkin *et al.*, 2000), their descriptions do not allow their differentiation from each other or from paralarvae of other loliginids. Barón illustrated the most frequent patterns of chromatophore distribution observed in samples of hatchlings from both species (Barón, 2001). However, nothing was reported on the variability that these patterns display, and very little is known about the ecology and distribution of these species in the paralarval stage.

The aims of the present study were: (i) to provide descriptions of the paralarvae of *L. gahi* and *L. sanpaulensis* useful for their identification to the species level; (ii) to assess the variability in their morphometry, abundance of chromatophores and size at hatching; (iii) to record their presence in coastal and shelf waters of Northern Patagonia and other areas of possible distribution; and (iv) to discuss the possible taxonomic affinities between *L. gahi*, *L. sanpaulensis* and other loliginid species on the basis of the morphological characters of their paralarvae.

METHOD

Characterization of hatchlings

During a survey conducted from March 1996 to February 2000, egg masses of *L. gahi* and *L. sanpaulensis* were obtained from coastal waters along the Patagonian coastline (Argentina) (Barón, 2001). Eggs were kept in 100 l aquaria with nearly constant air flow, salinity ranging within 33.6–33.8‰ and temperature regimes (mean ± SD) of 5.0 ± 0.2, 10.5 ± 0.2, 10.7 ± 1.0, 11 ± 0.3, 13.6 ± 1.5 (twice), 14.4 ± 1.6, 15.0 ± 0.4, 16.7 ± 0.4, 16.8 ± 0.5 (twice), 19.0 ± 0.4, 19.1 ± 0.4 and 19.7 ± 1.4°C for *L. gahi*, and 16.2 ± 0.4 and 19.0 ± 1.1°C for *L. sanpaulensis*. Methodological details of incubations are given elsewhere (Barón, 2002, 2003). In each experiment, daily controls were carried out to identify hatchlings. A total of 241 *L. gahi* and 60 *L. sanpaulensis* specimens were taken out of the aquaria within 24 h after hatching, narcotized in chilled water, and preserved in 5% formalin (commercial formaldehyde) in seawater solution in opaque plastic containers. Eleven morphometric variables, including mantle length (ML), head length (HL), head width (HW), fin length (FL), fin width (FW), tentacle length (TL), arm I–IV lengths (AIL–AIVL) and funnel cartilage length (FCL) (Figure 1), were measured with an ocular micrometer under a dissecting microscope in 7–30 randomly chosen hatchlings from each of the egg masses incubated. From these variables, 10 indices (ratios of variables on ML) were calculated. The chromatophores from different body parts were plotted on paper by using a camera lucida, and counted following the

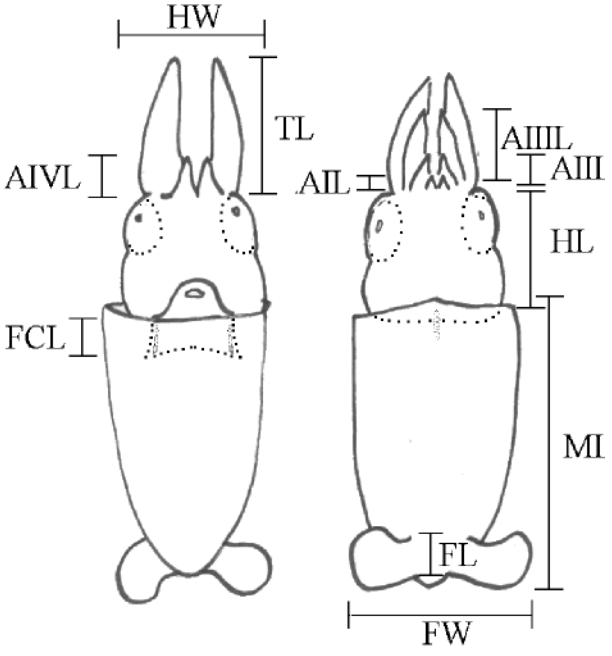

Fig. 1. Morphometric variables recorded on the hatchlings of *L. gahi* and *L. sanpaulensis*. Left, ventral; right, dorsal; AIL, arm I length; AIIL, arm II length; AIIIL, arm III length; AIVL, arm IV length; FL, fin length; FW, fin width; FCL, funnel cartilage length; HL, head length; HW, head width; ML, mantle length; TL, tentacle length.

method employed by McConathy *et al.* (McConathy *et al.*, 1980).

Characterization of paralarvae from plankton samples

In June and September 1997, zooplankton samples were obtained on board the hydrographic vessel A.R.A. 'Puerto Deseado' (CONICET-Armada Argentina) during two oceanographic surveys in coastal and shelf waters of Argentina: 'Buenos Aires–Puerto Madryn' and 'Talud III' (Figure 2). In both surveys, 30 min oblique bottom–surface tows (or 100 m–surface if bottom depth was greater) were performed with a Nansen net 50 cm in diameter and 505 μm in mesh size, equipped with an Ogawa Seiki flow meter. Surface seawater temperature (SST) was registered with a Horiba probe, and in some of the sampling stations bathythermograph profiles were obtained. In summer 1997, fall 1998, winter 1998 and spring 1998, zooplankton samples were obtained with the same sampling gear on board the 'Puerto Madryn' coastguard vessel (Prefectura Naval Argentina) in coastal waters off Conscriptos Point and 25 de mayo lighthouse (Nuevo Gulf; Figure 2). In each of these later samplings, 15-min oblique tows were performed from the bottom to the surface. All samples were preserved in 5% formalin in seawater solution, and

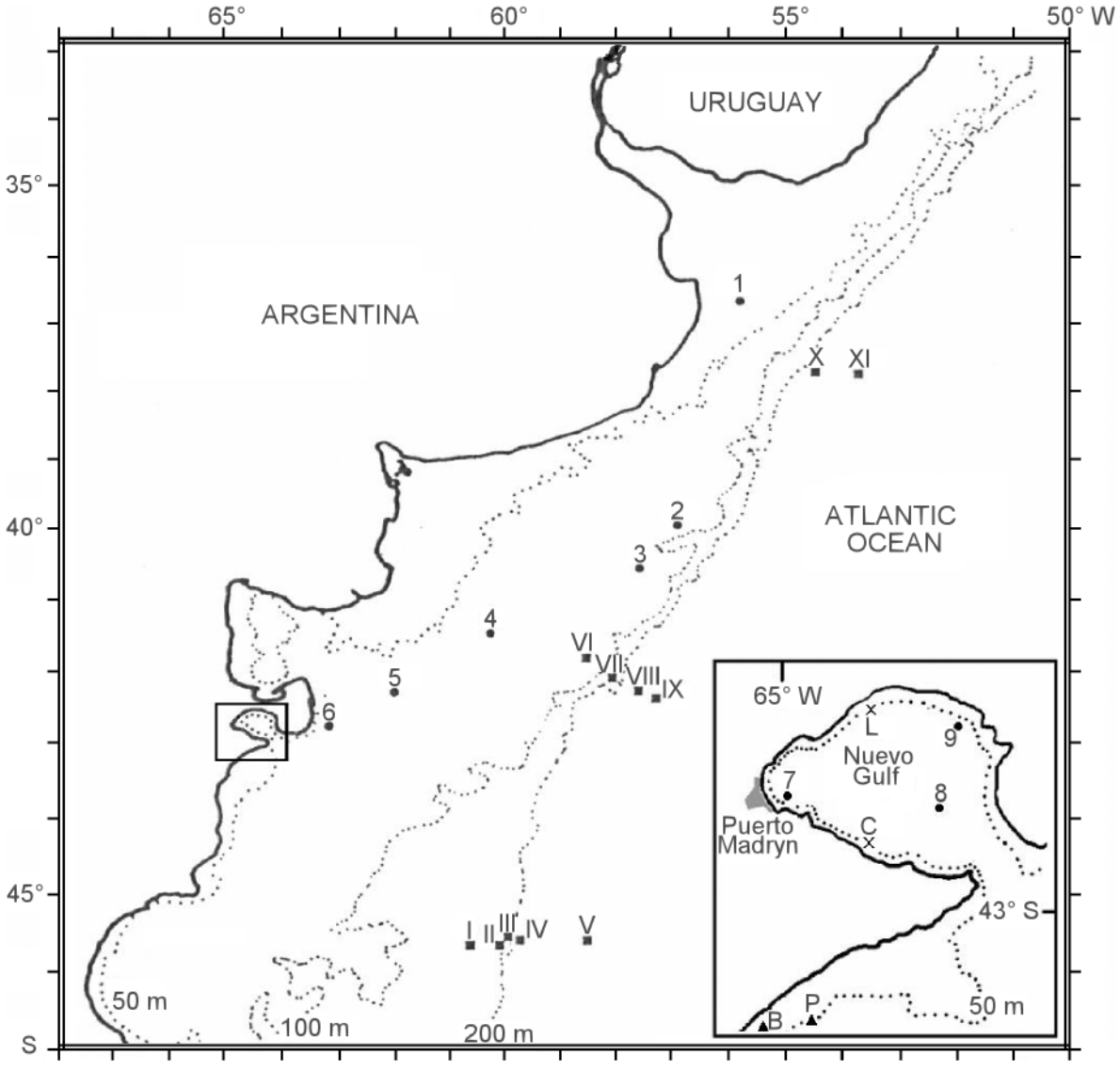

Fig. 2. Map of the zooplankton sampling area. 1–9, sampling stations of the oceanographic survey Buenos Aires–Puerto Madryn (June 1997); I–XI, sampling stations of the oceanographic survey Talud III (September 1997); B, Engaño Bay; C, Conscriptos Point; L, 25 de mayo lighthouse; P, Pozón.

the entire samples were sorted under a light microscope for cephalopod paralarvae. The specimens obtained were identified to the family level with the aid of a taxonomic key for cephalopod paralarvae (Hanlon *et al.*, 1992). The species-level identifications were performed by comparison with the hatchlings obtained in the laboratory and by inference from the area where the individuals were found. Additionally, taking into account the upper size limit adopted for the paralarvae of several other squid species (Kubodera and Okutani, 1977; Nesis, 1979; Vecchione, 1981, 1982; Vidal, 1994), individuals <15 mm in ML captured in Engaño Bay and adjacent fishing grounds (Figure 2) in tows conducted on board the fishing vessel 'Stella Maris', a 19.8-m-long trawler operating with a 60-mm-mesh net, were included in the paralarva collection.

RESULTS

Hatchlings from incubation experiments

Loligo gahi and *L. sanpaulensis* hatchlings displayed a marked positive phototaxy in the aquaria, and swam with swinging movements and the posterior end pointing towards the direction of advance. These movements consisted of a series of short propulsions, during which the paralarvae pointed the funnel openings anteriorly, and repeatedly extended the arms and tentacles as if they were pushing their bodies backwards, and waved the fins antero-ventrally. This was followed by a brief relaxation during which the fins were spread while the paralarvae fell down a short distance until they resumed the propulsion movements again. *Loligo gahi* hatchlings from all experiments (incubated at temperatures within 5–20°C during embryogenesis) ranged between 2.3 and 3.7 mm in ML ($n = 241$), while those of *L. sanpaulensis* (incubated at 16.2 and 19°C) ranged between 1.4 and 1.7 mm ML ($n = 60$). Mean mantle length (MML) of *L. gahi* hatchlings after incubation was negatively correlated with mean incubation temperature (MIT) ($r = -0.91$, $n = 14$, $P < 0.01$) (Figure 3). The regression equation $\text{MML} = -0.05 \times \text{MIT} + 3.54$ ($r^2 = 0.83$) related both variables. MML of *L. sanpaulensis* hatchlings incubated at 16.2°C (1.64 mm) was significantly different to that of hatchlings incubated at 19.0°C (1.59 mm) (*t*-test, $P = 0.005$). The hatchlings of both species show bullet-shaped mantles, longer than wide, sub-terminal fins inserted dorso-laterally and eyes covered by a cornea (Figure 4). Their heads are more or less square, their fins are wider than long and their arm formulae are $3 > 2 = 4 > 1$ (Figure 5). Highly significant between-species differences (Mann–Whitney *U*-test, $P < 0.01$) were found in all morphometric indices of the hatchlings except TL/ML and FCL/ML, the greatest difference being observed in the FL/ML index (Figure 5).

For *L. gahi*, the mean number of dark (red and brown) chromatophores (MNDC) and mean incubation temperature during embryogenesis were negatively correlated ($r = -0.83$, $P < 0.01$, $n = 14$). Both variables were related by the regression equation $\text{MNDC} = 85.86 \times$

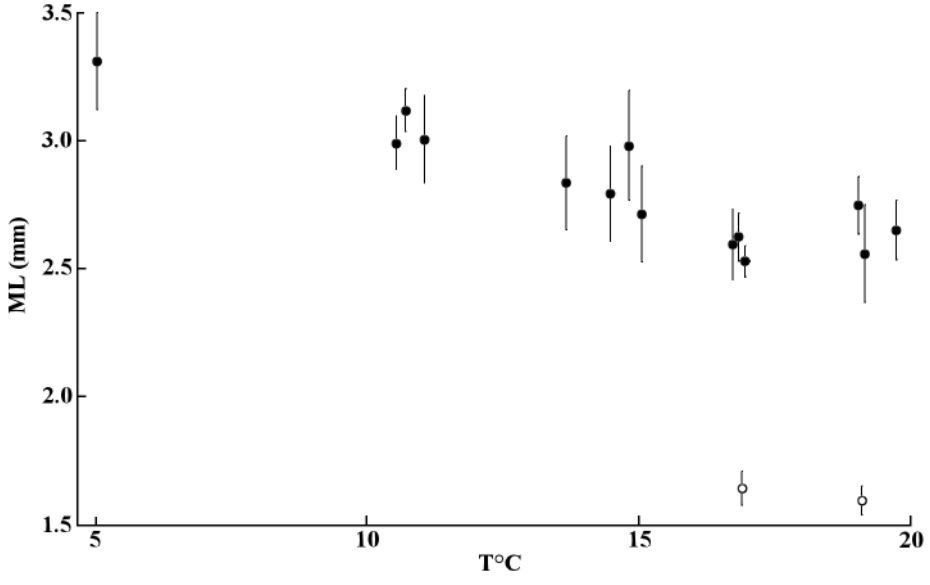

Fig. 3. Relationship between the size of paralarvae at hatching and incubation temperature. Closed circles, mean MLs of *L. gahi* paralarvae; open circles, mean MLs of *L. sanpaulensis* paralarvae. Bars = mean ± SD.

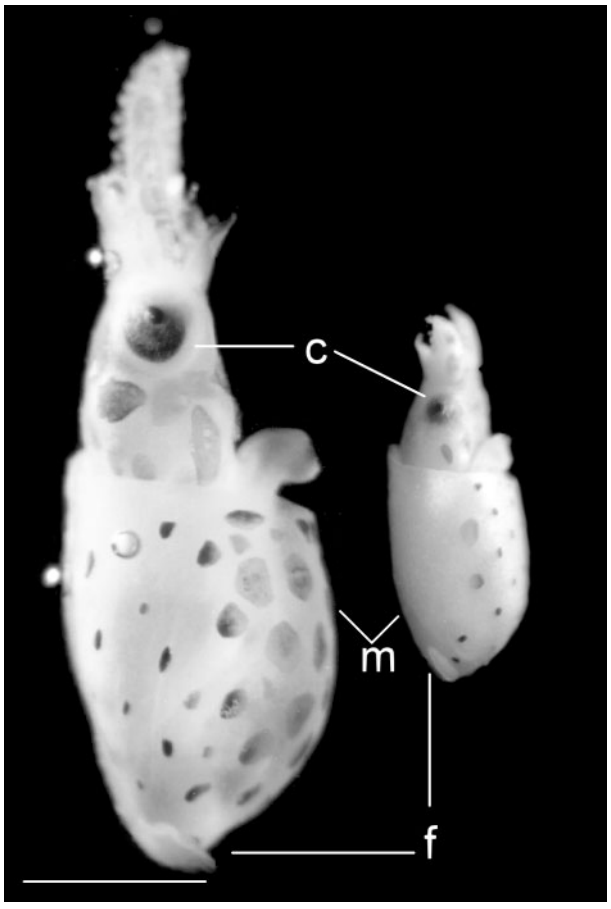

Fig. 4. Lateral aspect of the hatchlings of *L. gahi* (left) and *L. sanpaulensis* (right). c, cornea; f, fins; m, mantle. Bar = 1 mm.

MIT – 1.29 ($r^2 = 0.70$). For *L. sanpaulensis*, no significant difference was found between MNDC of hatchlings incubated at 16.2 and 19.0°C (*t*-test, $P > 0.05$). The most usual patterns of chromatophore arrangement and the frequency distributions of chromatophore abundance recorded in different areas of the hatchlings of both species are represented in Figure 6. The hatchlings of *L. gahi* generally displayed three to four red chromatophores intercalated with a similar number of yellow ones on each tentacle and two red chromatophores on each arm IV. On the areas of the 'cheek patches' (Vecchione and Lipinski, 1995) (two oval areas located at the posterior half of the ventral surface of the head, at both sides of the funnel, slightly separated from the posterior margin of the eyes and extending to the head's posterior and lateral margins; Figure 6), four red chromatophores were generally present, but three chromatophores on each side, or three and four, or five and four, respectively, in each 'cheek patch' were also usual, even for hatchlings that emerged from the same egg capsule. The ventral heads also exhibited two red chromatophores between the eyes, three yellow ones at their anterior margin and two yellow ones at the posterior margin of each eye. The ventral mantle included numerous red chromatophores (22–49) forming a more or less regular grid of oblique lines, and most frequently three to four yellow chromatophores on each side. At the dorsal surface, the head most commonly displayed six brown chromatophores arranged as a hexagon, one yellow one at the anterior margin and another two yellow ones close to the posterior-lateral margins. However, in the smallest hatchlings, the posterior brown chromatophores were yellowish. The dorsal mantle frequently showed five brown chromatophores forming a pentagon in the center, and five to nine yellow ones on the marginal and posterior regions. However, in the largest hatchlings, some of the yellow chromatophores had already turned to brown. For *L. sanpaulensis*, each tentacle displayed four chromatophores, two red intercalated with two yellow, but up to three red ones were observed in the largest hatchlings. Only one red chromatophore was present on each arm IV. On each of the 'cheek patch areas, two red chromatophores were commonly present, but up to three chromatophores were observed. Also on the ventral head, two red chromatophores were always present between the eyes, three yellow ones were placed at the anterior margin of the head, and one or two yellow ones were found close to the posterior margins of each eye. On the ventral mantle, numerous red chromatophores (23–40) were arranged in six horizontal rows, and one longitudinal row of three or four yellow chromatophores was observed on each side. The dorsal surface of the head had eight yellow chromatophores, two between the eyes, two at the posterior margins of the eyes and four at the posterior margin of the head, but sometimes one or two of the latter were absent. The dorsal mantle showed three posterior yellow chromatophores arranged as an arrow pointing out to the posterior end, but a fourth yellow chromatophore was also frequently present at one of the lateral margins. Dark chromatophores were always absent from the mantle's dorsal surface.

Paralarvae from plankton collections

Loligo spp. paralarvae were found in three sampling stations of the survey conducted in June 1997, out of 28 stations sampled throughout this study. Seven *L. sanpaulensis* specimens (ML = 2.7–7.3 mm) were obtained at dawn at a coastal station (36°36′S–56°05′W, depth = 17 m) characterized by homogeneous temperatures through the water column (15°C) (Station 1; Figure 2). Two *L. gahi* paralarvae (ML = 2.51 and 2.67 mm) were captured at night at an outer shelf station (40°34′S–57°03′W, depth = 86 m) characterized by a

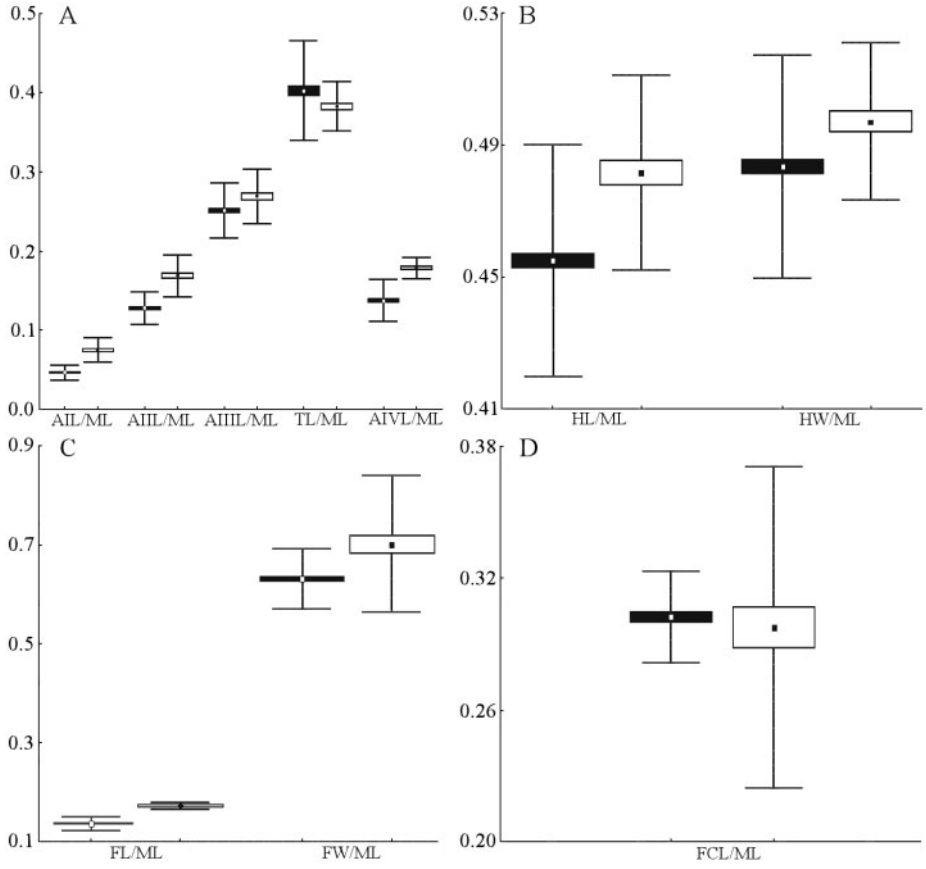

Fig. 5. Box plot diagrams of the morphometric indices (ratios of morphometric variables to ML) of the paralarvae of *L. gahi* (closed boxes) and *L. sanpaulensis* (open boxes). (**A**) Indices of arms and tentacles. (**B**) Indices of head. (**C**) Indices of fins. (**D**) Indices of funnel cartilage. Point, mean; box, mean ± SE; whiskers, mean ± SD.

SST of 10.2°C, a marked thermocline at 43–56 m depth and bottom temperatures of ~7.5°C (Station 3; Figure 2), and another one (ML = 3.4 mm) was obtained at dusk at a station located in Nuevo Gulf (42°46′S–64°28′W, depth = 165 m) characterized by a SST of 14°C (bottom temperatures are unavailable) (Station 8; Figure 2). Additionally, five *L. sanpaulensis* specimens (ML = 9.3–14.8 mm) were captured in March 1998 on board the fishing vessel 'Stella Maris' at the fishing ground called Pozón (43°14′S, 64°46′W, depth = 53 m) (P; Figure 2), and another five (ML = 12.9–15.9 mm) were obtained during hauls performed in February, March and June 1998, and April 1999 in Engaño Bay (43°20′S, 64°04′W, depth = 10 m) (B; Figure 2). Only one cephalopod paralarva, belonging to *Illex argentinus* (ML = 6.5 mm), was obtained during the Talud III oceanographic survey, in one tow conducted near the slope (depth = 86 m) (Station XI; Figure 2).

The regressions of the main morphometric variables of *L. sanpaulensis* paralarvae on their ML are shown in Figure 7. Given that the sizes of *L. gahi* paralarvae found in the zooplankton samples (ML = 2.5–3.4 mm) and of those hatched after incubation in the laboratory were similar, they did not provide additional information on the species morphometry. *Loligo sanpaulensis* paralarvae were easily distinguished from *L. gahi* hatchlings of similar sizes because of their proportionately longer head, fins, arms and tentacles, and the marked differentiation between stalk and club of the tentacles (Figure 8). Owing to the partial fading of chromatophores in the paralarvae from plankton samples, their chromatophore arrangement is not reported here.

DISCUSSION

For *L. gahi*, egg length and ML at hatching are comparable with those of *L. opalescens*, *L. bleekeri* and *L. vulgaris*, while for *L. sanpaulensis* they are similar to those of *L. plei* and *L. pealei* (Table I). Such well-defined size differences between the hatchlings and eggs of both groups suggest a closer phylogenic relationship between *L. sanpaulensis* and other species from the Western Atlantic Ocean such as

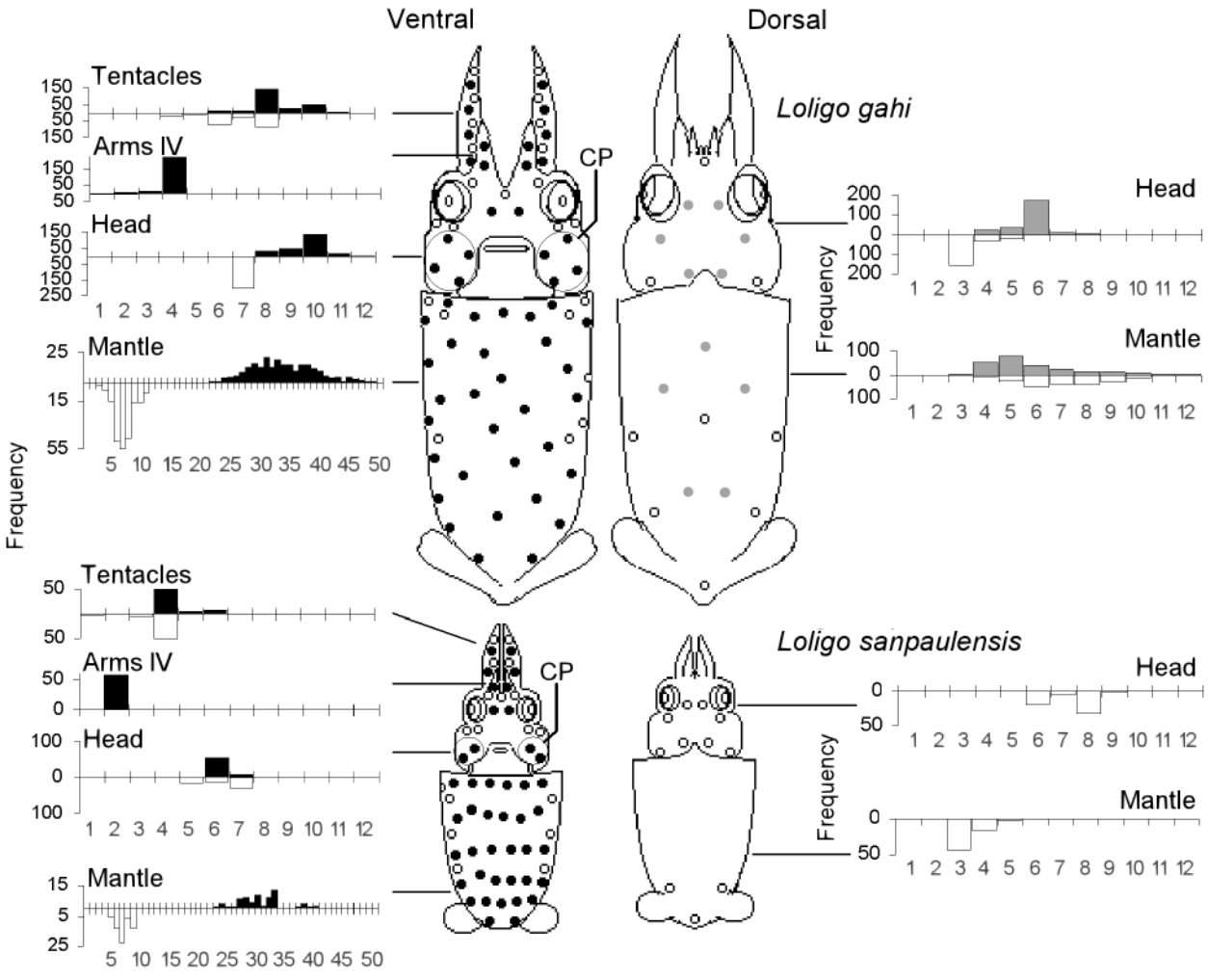

Fig. 6. Typical patterns of chromatophore distribution and frequency distributions of chromatophore abundance on ventral (both tentacles, both arms IV, head and mantle) and dorsal (head and mantle) areas of *L. gahi* ($n = 241$) and *L. sanpaulensis* ($n = 60$) hatchlings. Black bars/dots, red chromatophores; white bars/circles, yellow chromatophores; grey bars/dots, brown chromatophores; CP, cheek patch area.

L. pealei and *L. plei* on the one hand, and between *L. gahi* and other species from the Pacific Ocean such as *L. opalescens* and *L. bleekeri* on the other. These relationships contrast with those proposed by Brakoniecki on the basis of the hectocotylus morphology: *L. sanpaulensis*, *L. gahi*, *L. plei*, *L. opalescens* and *L. bleekeri* in one group, and *L. pealei* in another (Brakoniecki, 1986).

Recent experiments conducted by Vidal *et al.* with *L. opalescens* show that the weight and volume of yolk reserves in hatchlings vary with the temperature during embryogenesis (Vidal *et al.*, 2002). The marked negative correlation found in this study between the average size of *L. gahi* hatchlings and the incubation temperature can be related to their ecology by considering two aspects. First, given that the paralarval stage is the phase of the life cycle in which the greatest mortality rates are observed (Vecchione and Hand, 1989; Venter *et al.*, 1999), the sooner an individual reaches the critical size to acquire the juvenile mode of life the greatest are the chances it should have to survive. Secondly, during the first days of their lives, cephalopod paralarvae show high growth rates (Villanueva *et al.*, 1995, 1996), which are directly related to temperature (Forsythe, 1993; Hatfield, 2000). Therefore, for warm-environment paralarvae hatching at relatively small sizes, high temperatures should provide comparatively high growth rates to reach the critical size rapidly. In contrast, the low growth rates of cold-environment paralarvae should be compensated by relatively large size at hatching in order to attain the critical size promptly.

The chromatophore arrangements in the hatchlings of *L. gahi* are similar to those reported for *L. opalescens* (McConathy *et al.*, 1980), *L. v. vulgaris* (Naef, 1928; Hanlon *et al.*, 1992) and *L. v. reynaudii* (Vecchione and Lipinski, 1995; Blackburn *et al.*, 1998). However, the chromatophore

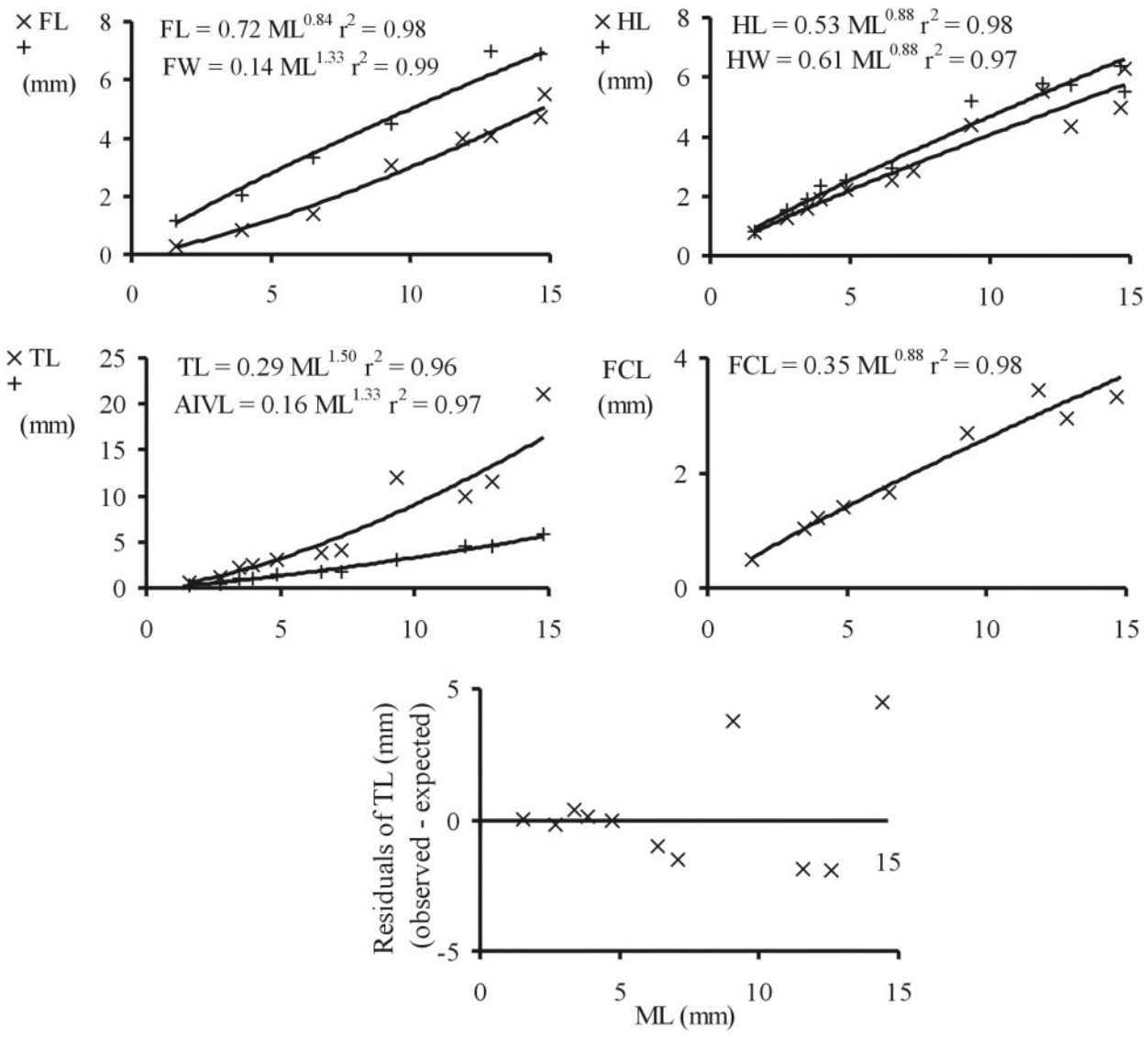

Fig. 7. Regressions of different morphometric variables of the paralarvae of *L. sanpaulensis* on ML, and residuals plot of the regression of TL on ML. AIVL, arm IV length; FCL, funnel cartilage length; FL, fin length; FW, fin width; HL, head length; HW, head width; ML, mantle length; TL, tentacle length.

arrangement of the ventral mantle and the absence of chromatophores on the dorsal arms make the hatchlings of *L. gahi* and *L. opalescens* (McConathy *et al.*, 1980) particularly similar. The pattern of chromatophore distribution in the hatchlings of *L. sanpaulensis* shows some unique features that differentiate it from those of other *Loligo* species, such as the presence of only two red chromatophores in the 'cheek patches', only two red chromatophores intercalated with two yellow ones on each tentacle and only one red chromatophore on each arm IV. In contrast, it resembles the chromatophore arrangement reported for *Lolliguncula brevis* Blainville, 1823 (McConathy *et al.*, 1980). It is interesting to note that in spite of the marked size differences between the hatchlings of *L. gahi* and *L. sanpaulensis*, both present similar numbers of red and yellow chromatophores on the ventral surface of their mantles. Therefore, the paralarvae of *L. sanpaulensis* can be expected to show more red chromatophores than the hatchlings of *L. gahi* when they reach the size of the latter because the yellow chromatophores become red as they mature and new chromatophores are formed as individuals grow.

The abundance and distribution of chromatophores of the 'cheek patches' have been used as diagnostic characters to differentiate the hatchlings of sympatric loliginids (McConathy *et al.*, 1980; Vecchione and Lipinski, 1995; Blackburn *et al.*, 1998). Blackburn *et al.* highlighted the need

Fig. 8. General aspect of a 3.6 mm ML *L. sanpaulensis* paralarva. c, tentacle club; s, tentacle stalk. Bar = 1 mm.

for careful use of this character by pointing out that if hatching occurs prematurely, some chromatophores of the 'cheek patches' can be absent (Blackburn *et al.*, 1998). The present observations on normal hatchlings of *L. gahi* suggest that this character is more variable than previously considered, even for those emerging from the same egg capsule. Variability in hatchlings from the same egg capsule can be associated with intrinsic factors like multiple paternities (Buresch *et al.*, 2001), or with extrinsic factors such as the possible differences in the oxygen availability to embryos. Variability between hatchlings from different egg masses can be related to incubation temperature, hatchlings incubated at cold temperatures displaying a higher abundance of chromatophores than those incubated in warmer conditions.

During the survey conducted as part of the present study, *Loligo* spp. paralarvae were only found in three tows out of 28 performed with the plankton net. This low capture rate could be related to the diameter of the net's ring (50 cm), which is smaller than that commonly used in other surveys [100 cm; (Vecchione, 1981, 1982, 1991; Rodhouse *et al.*, 1992; Bower, 1996)]. Also, the capture rate could have been influenced by the type of tow. As an example, Vecchione (Vecchione, 1981) reported the greatest *L. pealei* paralarva abundance in surface and sub-surface tows, while Rodhouse *et al.* (Rodhouse *et al.*, 1992) reported that the paralarvae of *L. gahi* were captured only when the nets were towed close to the bottom. The absence of paralarvae in the zooplankton samples taken seasonally from waters of Nuevo Gulf could also be the result of the low number of tows performed. Haimovici *et al.* mentioned that some of the possible causes for the low captures of cephalopod paralarvae in zooplankton samplings are the patchy distribution of these organisms, their low densities and the underestimation of their ability to elude the nets (Haimovici *et al.*, 2002).

All of the *Loligo* paralarvae captured during this study were associated with coastal and shelf waters and depths <100 m, which is common for several *Loligo* species (Vecchione, 1981; Rodhouse *et al.*, 1992; Hatfield and Rodhouse, 1994; Rocha *et al.*, 1999). Egg masses of *L. gahi* have been frequently located in coastal waters off Northern Patagonia (Barón, 2001). The presence of hatchlings of this species at Station 3 (June 1997, depth = 86 m) suggests that the spawning grounds can extend to depths of several tens of meters, at least in the northern part of its distribution. On the other hand, the presence of paralarvae of *L. sanpaulensis* at Engaño Bay confirms that this species can reproduce at latitudes as high as 43–44°S.

The present study provides the first regression functions for the morphometric variables of *L. sanpaulensis* paralarvae on their MLs. The limited number of paralarvae included in the analysis prevented me from finding morphometric discontinuities (changes in the growth rate of a morphometric variable relative to another) like those reported for the paralarvae of other cephalopod species (Kubodera and Okutani, 1977; Vidal, 1994; Shea and Vecchione, 2002). However, it was possible to observe an increased variability in TL for specimens >5 mm ML (Figure 7), similar to that reported for *L. pealei* (Vecchione, 1981), probably associated with a change in the mode of life of *L. sanpaulensis* at this size. Further studies on the paralarvae of *L. gahi* and *L. sanpaulensis* are necessary to analyse possible morphological discontinuities and to recognize the association of these organisms with particular oceanographic conditions and with other zooplankton taxa.

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Table I: Egg length, mantle length (ML) and patterns of chromatophore abundance on each 'cheek patch' area (CP), tentacle (T), arm IV (AIV), arm III (AIII) and arm II (AII) of several species/subspecies of the genus Loligo

Species/subspecies	Egg length (mm)	ML at hatching (mm)	Chromatophore abundance					
			CP	T	AIV	A III	AII	DH
Loligo gahi	2.1–3.0[1]	2.3–3.7[6]	3–5d	3–4d 3–4y	2d	0	0	4–8d[6] 3–5y
Loligo opalescens	2.0–2.5[2]	2.5–3.2[7]	3d	4d 4y	2d	0	0	6d 4y[7]
Loligo bleekeri	2.6–2.7[3]	3.0–3.3[3]	5d	10d 4y	2d 1y	1d	1d 1y	9d 6y[3]
Loligo vulgaris vulgaris	2.3–2.7[4]	2.8–3.3[8]	4d	5d 4y	2d ?	1d	0	6d ?y[8][9]
Loligo vulgaris reynaudii		2.2–2.4[9]	4d	13d 5y	2d 1y	3d	2d	4d 5y[10]
Loligo sanpaulensis	1.2–1.3[1]	1.4–1.7[6]	2–3d	2d 2y	1d	0	0	6–9y[6]
Loligo plei		1.3–1.7[7]	4d	3d 3y	2d	0	0	9y[7]
Loligo pealei	1.1–1.6[5]	1.4–1.7[7]	4d	3d 3y	2d	0	0	9y[7]

References: (1) Barón (2001); (2) Fields (1965); (3) Baeg *et al.* (1992); (4) Worms (1983); (5) Summers (1983); (6) this study; (7) McConathy *et al.* (1980); (8) Hanlon *et al.* (1992); (9) Vecchione and Lipinski (1995); (10) Blackburn *et al.* (1998).
d, number of dark chromatophores; y, number of yellow chromatophores; ?, not reported.

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