Relative growth of paralarvae and juveniles of *Illex argentinus* (Castellanos, 1960) in southern Brazil

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Abstract: Ommastrephid squids undergo remarkable morphological change during the transition from planktonic paralarvae to adults. These changes are characterized by changes in the relative growth of body dimensions and mark phases and stages in post-embryonic development. The following morphometric characters of paralarval and juvenile *Illex argentinus* ranging in size from 1–55 mm ML were measured: dorsal mantle length (ML), mantle width (MW), head width (HW), eye diameter (ED), right arm lengths (AIL) (AIIL) (AIIIL) (AIVL), proboscis length (PL), proboscis division (PD), fin length (FL), fin width (FW), right tentacle length (TL), club length (CIL), dactylus length (DL) and carpus + manus length (CML). The relative growth of AIL, AIIIL, AIIIL, HW and ED, showed discontinuities at *c.* 14 mm ML, while AIL, AIIL, AIIIL, AIVL, FL, and TL showed other discontinuities at *c.* 28 mm ML. These discontinuities seem to be related to the activity and ability of the animal to obtain food and survive in different environments. At an early phase (1–14 mm ML), there is a rapid development of the arms, suckers and fins. In the second stage (14–28 mm ML) there is a rapid development of the tentacles and clubs. In the third (> 28 mm ML), the juvenile grows more in length in relation to other body parts. No morphological change, besides the proboscis division, takes place at the end of rhynchoteuthion stage. This may indicate the necessity for re-evaluation of the paralarval phase in Ommastrephidae.

Introduction

Validity of the terminology larvae is controversial in relation to the cephalopods (Nesis 1979a, Young & Harman 1988, Sweeney *et al.* 1992). Development of cephalopods does not involve metamorphosis as in many marine invertebrates (Boletzky 1974). Young & Harman (1988), have proposed the term paralarvae, to be applied to cephalopods in the post-hatching growth stage, which is pelagic in near-surface waters during the day and has a distinctly different mode-of-life from that of older individuals.

Ommastrephid paralarvae are characterized by fusion of the tentacles into a proboscis and while bearing this proboscis they are termed rhynchoteuthions (Roper & Lu 1979). Rhynchoteuthions are the only cephalopod hatchlings that show sufficiently distinct developmental changes to justify the term "larvae" (Boletzky 1974). Sharp morphological changes during growth are characterized by discontinuities in relative growth, which highlight critical boundaries of phases and stages in development (Nesis 1979a). These discontinuities are related to feeding, mode-of-life, and the animal's behaviour in different habitats. Morphological discontinuities have been found by Kubodera & Okutani (1977), in the allometry of young stages of *Gonatus madokai*. These correspond to the transition between the paralarva and the juvenile. Vecchione (1981) also showed such discontinuities for *Loligo pealei*, and in *Sepioteuthis lessoniana*, seven growth stages have been identified during its life cycle (Segawa 1987). However, some authors divide these stages on an arbitrary basis and not according to ecological,

behavioural or ontogenetic principles (Okutani 1987).

This paper comprises an analysis of the relative growth of the body components of paralarval and juvenile *Illex argentinus*. Growth discontinuities are used to define different growth stages and are associated with the most important events that occur during early development.

Materials and methods

This study was based on the morphometry of 217 paralarvae and juveniles of *Illex argentinus*, collected between Santa Marta Grande Cape (28°30'S) and Chui (34°20'S), in autumn 1984, winter 1980 and spring 1987, and 1989.

Paralarvae and early juveniles were collected with a bongo net with mesh size of 0.33 mm by the RV *Atlantico Sul* during research surveys. The largest juveniles were taken by a 8 m² RMT with a mesh in the cod end of 1 mm from the RV *Meteor* (Anchovy Recruitment Project: SARP) and also by RV *Atlantico Sul* with a midwater trawl. The material was fixed and preserved in 4% formalin for 3–12 years before the measurements were made. To characterize the chromatophore patterns some paralarvae were observed on board before fixation.

Specimens with mantle lengths from 1–55 mm were examined and the following body dimensions measured according to Roper & Voss (1983): dorsal mantle length (ML), mantle width (MW), head width (HW), eye diameter (ED), right arm lengths (AIL), (AIIL), (AIIIL), (AIVL), proboscis length (PL), proboscis

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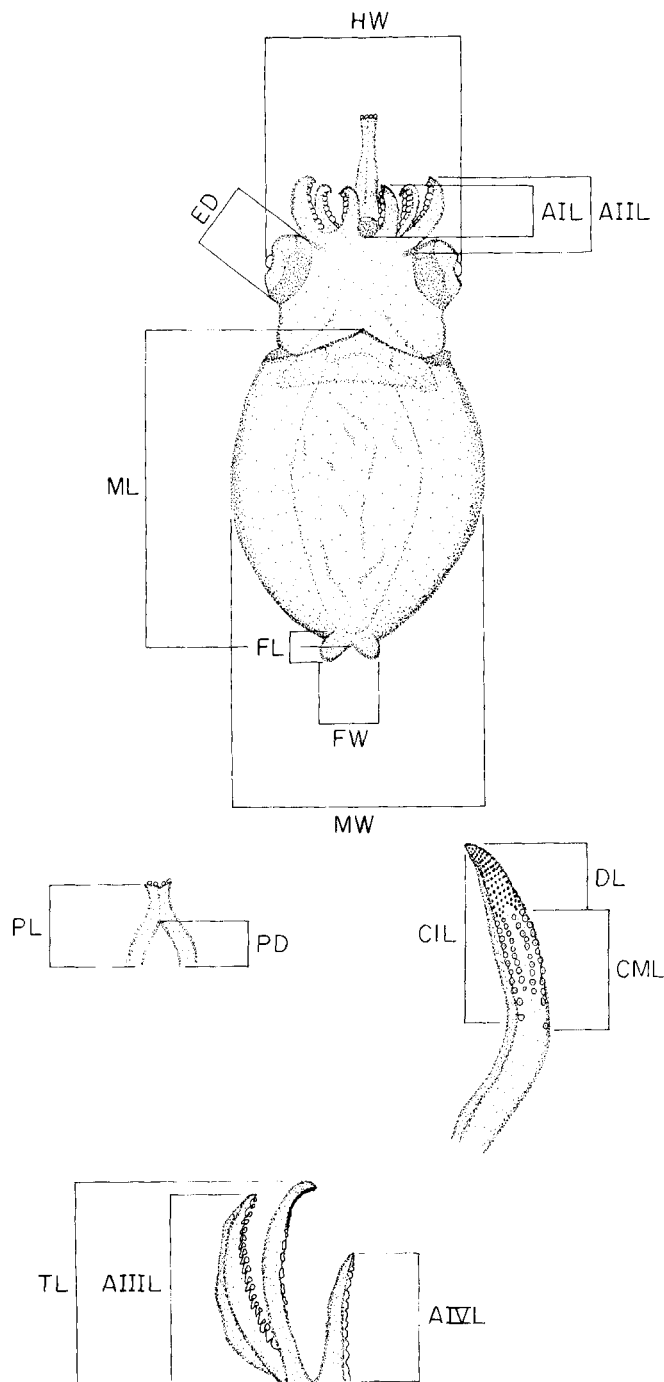
Fig 1. Body dimensions measured: dorsal mantle length (ML), mantle width (MW), head width (HW), eye diameter (ED), right arms length (AI), (AII), (AIII), AIV), proboscis length (PL), proboscis division (PD), fin length (FL), fin width (FW), right tentacle length (TL), club length (CIL), dactylus length (DL), carpus and manus length (CML).

division (PD), fin length (FL), fin width (FW), right tentacle length (TL), club length (CIL), dactylus length (DL), carpus and manus length (CML) (Fig. 1). The proboscis division was measured ventrally from the proboscis base to the maximal height of the splitting part. Small specimens were measured to the nearest 0.05 mm in a stereoscopic microscope equipped with an ocular micrometer, while for the largest ones a paquimeter was utilized to the nearest 0.1 mm.

Changes in body form during growth were analysed by means of the allometric equation, $Y=aX^b$, where Y is the length of each measurement, X is ML, b the allometric constant and a the initial index. After logarithmic transformation of X and Y, a and b are estimated by linear regression. A slope of <1 indicates negative allometry where the dimension grows less rapidly than mantle length. A slope of 1 represents isometric growth, showing where growth rate of the two body components are equal, and a slope >1 indicates positive allometry.

Changes in growth can be observed as discontinuities on plots of body part dimension on ML. However these points may be difficult to determine. In order to test the validity of discontinuities determined by inspection, they were accepted only when the slopes and intercepts between the regression lines either side of the discontinuity showed significant differences by ANCOVA (Snedecor & Cochran 1980), and when slopes were significantly different from zero (Sokal & Rohlf 1981). When one discontinuity was accepted, the same procedure was used to test others on the line, either side of the first, until the slopes and intercepts showed no significant difference. After the data were separated into significantly different lines, parameters of the allometric equation were obtained by linear regression. A significance test for comparison of slopes against 1 was applied (Sokal & Rohlf 1981). The significance level used in all tests and for confidence intervals was 5%.

Results

Description of paralarvae and juveniles of Illex argentinus

The following description shows the changes that paralarvae and juveniles undergo during development. Mantle lengths indicated represent the smallest size in which this was verified.

1.0 mm ML (Fig. 2a): after hatching the head is squarish and wider in the region of the eyes. The funnel is well developed and occupies almost the entire length of the head. The proboscis is highly elastic and on the tip there are eight suckers with the same diameter, according to Brunetti's (1990) description (Fig. 3a). AIL and AIIL have one sucker. AIIIL appears ventrally as a small protuberance, AIVL appears as a tiny point near the base of the proboscis. The arm formula is 2.1.3.4. The mantle is almost as wide as long, the fins are rudimentary and terminal. Chromatophores: *head*: four large ones arranged dorsally, four ventrally, one pair in ventrolateral region, two small ones on lateral surface of funnel; there are two around the buccal mass. *Mantle*: eight dorsal, one anteromedian, six distributed in three lateral bands with two in each one, one above the fin insertion, 13 ventral, four small on the mantle edge, seven divided in two lateral bands and one pair in the posteroventral region.

1.7 mm ML: AIL and AIIL with three suckers and AIIIL with one.

2.5 mm ML: two new large chromatophores on dorsal head,
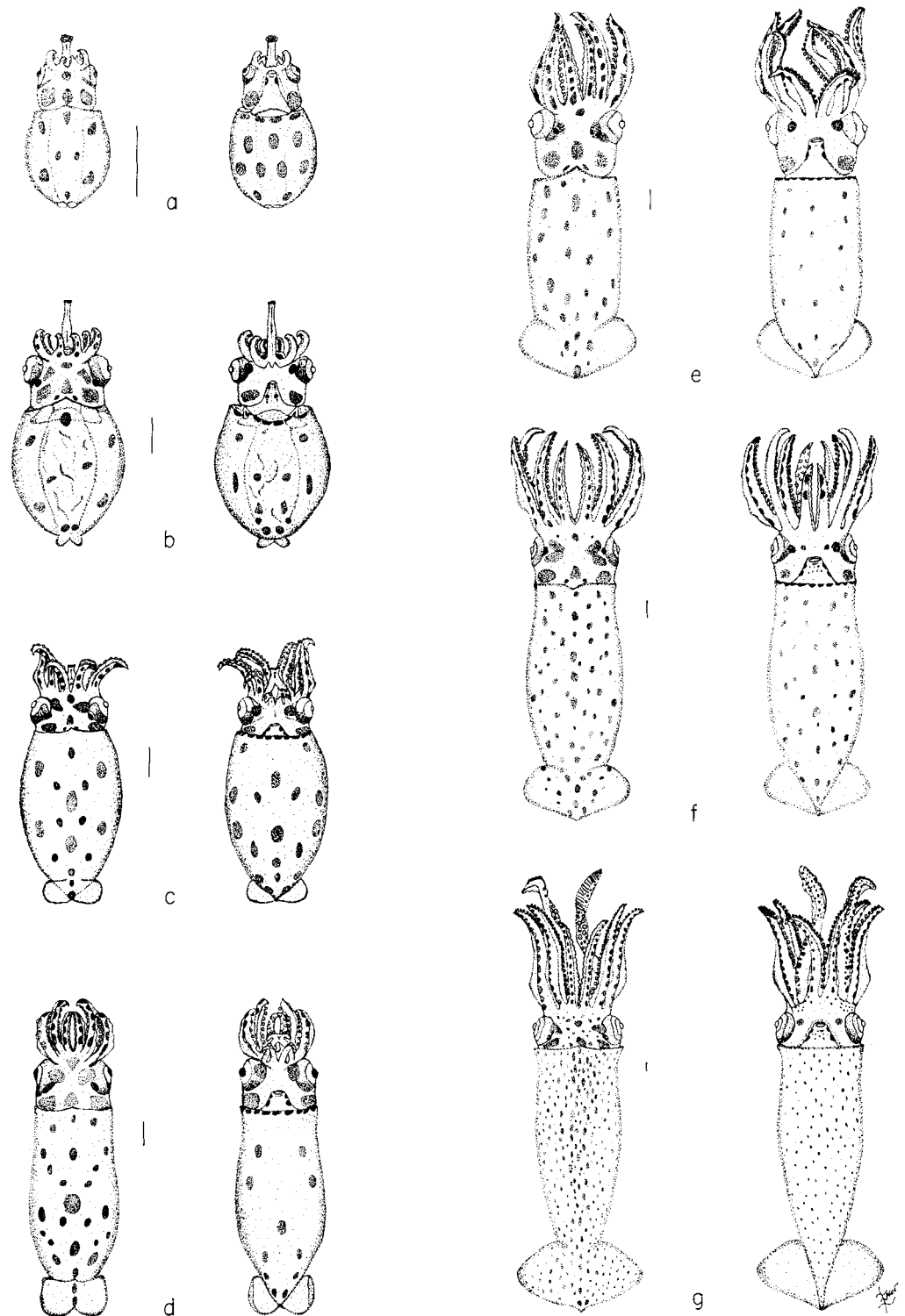
Fig. 2. Morphological and chromatophore pattern changes during growth of *Illex argentinus* (dorsal and ventral views). **a.** 1.4 mm ML, **b.** 3.5 mm ML, **c.** 6.0 mm ML, **d.** 8.0 mm ML, **e.** 11.0 mm ML, **f.** 15.0 mm ML, **g.** 30.0 mm ML. Scale bars= 1.0 mm.

beside each eye. In some specimens the proboscis begins to divide. AIL has about nine suckers, AIIL 11 and AIIIL seven.

3.5 mm ML (Fig. 2b): arm suckers in two rows, with about 15 suckers on AIL, 17 on AIIL, 13 on AIIIL, 1 on AIVL and the number of suckers increases progressively with growth. The fins are wider than long. Chromatophores: *arms*: AIL and AIIL

with three. *Head*: dorsally one small pair appears posterior to or just over each eye and another small pair on posteromedian region; on ventral head one pair appears between and close to the eyes, another one on the sides of the funnel. *Mantle*: nine dorsally, one new appears above the fin insertion; 18 ventrally, six on the mantle edge, one anteroventral pair, four midmantle
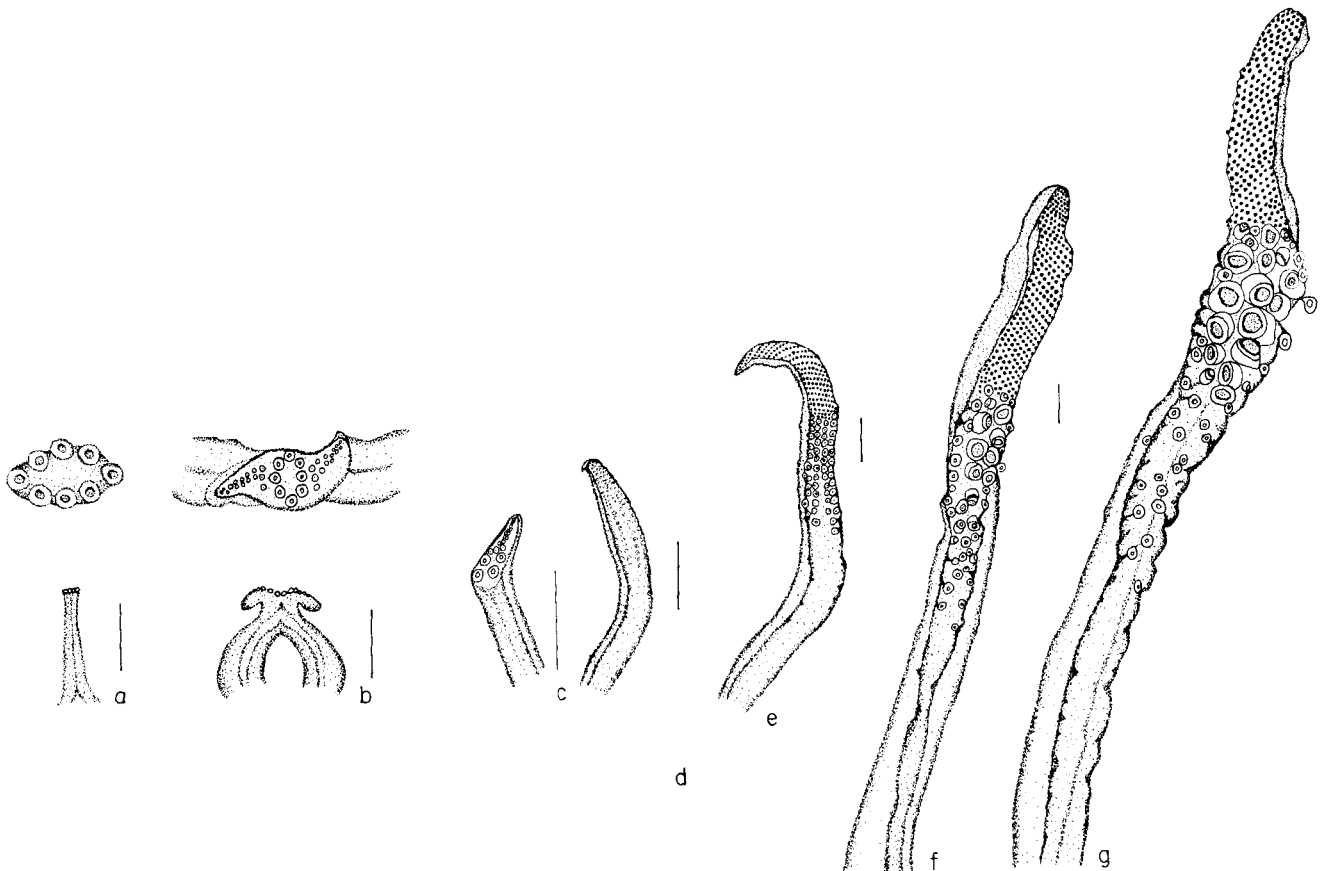
Fig. 3. Sequence of proboscis division (**a.** 3.5 mm ML, **b.** 8.0 mm ML). Developmental sequence of the tentacular club (**c.** 6.6 mm ML, **d.** 11.0 mm ML, **e.** 14.3 mm ML, **f.** 39.7 mm ML, **g.** 53.0 mm ML). Scale bars = 1.0 mm.

and six distributed in a "U" shape on the posterior region.

4.0 mm ML: on the proboscis tip small lateral spreads can be seen.

6.0 mm ML (Fig. 2c): the proboscis is almost completely divided, over each lateral spread 4–6 knobs can be seen. The arm formula changes to the adult 2.3.1.4. Chromatophores: *arms*: AIL and AIIIL 4, AIIL 5. *Head*: there are no changes. *Mantle*: 16 dorsally have a symmetrical scattering; ventrally nine are distributed on mantle edge and 18 scattered.

8.0 mm ML (Fig. 2d): the largest specimen with the proboscis still dividing. The proboscis possesses well developed lateral expansions over which the clubs are beginning to form through the small suckers arranged laterally (Fig. 3b). The mantle is relatively stretched out. After division of the proboscis the tentacles are smaller, slenderer and more fragile than the first three pairs of arms, and apparently do not possess any character to allow species identification. Development can be followed in the proboscis suckers, besides those formed during proboscis division (Fig. 3c). Chromatophores: *arms and head*: there are no changes. *Mantle*: nine form a circle on dorso-anterior region, with a big one in the center, 13 on posterior region and two on the fins, nine ventrally on the mantle edge and in the middle of the mantle a small number were found, on the posterior region

the six in a "U" shape remain.

11 mm ML (Fig. 2e): the club suckers develop so fast they occupy more than half the tentacular length. On the dactylus there are more than four rows of suckers, however the eight rows that characterize the genus *Illex* are still not formed (Fig. 3d). Chromatophores: *arms*: AIL 8, AIIL 7, AIIIL 6, AIVL 2. *Head*: there are no changes. *Mantle*: 29 dorsally and 16 ventrally.

14 mm ML (Fig. 2f): the tentacles are a little longer than the arms, the dactylus occupies almost half the club's length and the eight sucker rows that characterize the genus are already formed and clearly visible (Fig. 3e). Chromatophores: *arms*: AIL 8, AIIL 10, AIIIL 9, AIVL 2. *Head*: two other pairs appear, dorsally over the eyes and ventrally between the eyes. *Mantle*: on the dorsal and ventral mantle there is a major increase in the number of chromatophores.

14–28 mm ML: the main morphological changes verified are: development of the manus suckers on the club, in which the two central sucker rows become larger than lateral ones.

In juveniles >28 mm ML, the resemblance to adults in the shape and proportion of fin, head and eye length became more evident (Fig. 2g). On the club, the relative length of the dactylus is even larger than in the adult (Fig. 3f,g).

Table I. Coefficients and significance of fit for allometric equations between log mantle length (ML) and log body dimensions for paralarvae and juveniles of *Illex argentinus*. Size range in mm ML considering the discontinuity points, slope (b), confidence interval from slope (C.I.), coefficient of correlation (r), and number of regression points *(n)*.

Relation	Size Range	b	C.I.	r	n	
log AI vs log ML	1–17	1.297	0.035	0.989	113	*
	17–28	1.016	0.156	0.893	46	
	28–55	0.773	0.098	0.905	57	*
log AII vs log ML	1–14	1.343	0.038	0.991	100	*
	14–28	0.977	0.091	0.942	60	
	28–55	0.861	0.106	0.909	57	*
log AIII vs log ML	1–16	1.646	0.076	0.973	105	*
	16–28	1.025	0.121	0.924	52	
	28–55	0.857	0.097	0.923	56	*
log AIV vs log ML	1–28	1.745	0.068	0.972	149	*
	28–55	0.884	0.147	0.861	53	
log PL vs log ML	1–8	0.561	0.105	0.807	63	*
log TL vs log ML	7–28	1.488	0.068	0.977	95	*
	28–55	0.862	0.118	0.895	55	*
log ClL vs log ML	7–38	1.630	0.081	0.970	99	*
	38–55	1.054	0.182	0.882	41	
log CML vs log ML	8–55	1.395	0.066	0.965	128	*
log DL vs log ML	8–34	1.703	0.130	0.949	76	*
	34–55	0.600	0.135	0.784	52	*
log MW vs log ML	1–55	0.660	0.017	0.984	188	*
log HW vs log ML	1–17	0.715	0.025	0.983	111	*
	17–55	0.593	0.047	0.937	90	*
log ED vs log ML	1–16	0.888	0.034	0.981	105	*
	16–55	0.780	0.041	0.964	107	*
log FL vs log ML	1–27	1.404	0.041	0.985	146	*
	27–55	1.093	0.107	0.938	59	
log FW vs log ML	1–55	1.196	0.019	0.993	203	*

* $P < 0.05$ for values signicantly different from 1.

Growth stages and allometry

Table I shows the coefficients of the allometric equation calculated for the relationships between log body dimensions and log ML, considering the ML where discontinuity points were determined by ANCOVA to be significant (*F*-test for slope). The plots of log dimensions and log ML are shown in Fig. 4.

Arms (AIL) (AIIL) (AIIIL) and (AIVL): AIL, AIIL and AIIIL showed two discontinuity points, the first between 14–17 mm ML (*F*=6.36 AIL; *F*=13.11 AIIL; *F*=7.62 AIIIL), and the second at 28 mm ML, which also included AIVL (*F*=38.62 AIL; *F*=7.66 AIIL; *F*=12.30 AIIIL; *F*=7.92 AIVL). The first three pairs of arms grew faster than ML up to the first discontinuity, when they reached their largest relative length. Between 17–28 mm ML their growth can be regarded as isometric, however after the second point all the arms showed negative allometry (Table I) (Fig. 4 a,b,c,d).

Proboscis length (PL): no discontinuity point was found (*F*= 0.31), a strong negative allometry was verified and a broad range of lengths occurred for the same ML and vice-versa (Fig. 4e). Proboscis division (PD): the PD began at about 2.5–4.0 mm ML and finished at about 6.5–8.0 mm ML.

Tentacle length (TL): TL showed positive allometry up to 28mm ML, when a discontinuity point was determined (*F*=14.26), and it reached its largest relative length. In squid larger than 28 mm ML, growth in TL slows to less than that of ML (Table I) (Fig. 4f).

Club length (ClL): ClL showed positive allometry up to 38 mm ML, at this ML a discontinuity point was found (*F*=12.67), after which allometric growth became negative (Table I) (Fig. 4g).

Carpus + Manus length (CML) and *Dactylus length* (DL): both CML and DL had fast growth after separation of the tentacles. In squid larger than 34 mm ML, while CML continued growing at the same relative rate, a discontinuity point was found for DL (*F*=113.74), which decreased growth rate in relation to ML (Table I) (Fig. 4h, i).

Mantle width (MW), *head width* (HW) and *eye diameter* (ED): these were characterized by strong negative allometry throughout the size range studied. No discontinuity point was found for MW (*F*=0.20), but HW and ED showed one at about 16–17 mm ML (*F*=18.30 HW; *F*=12.87 ED) (Table I) (Fig. 4j, k, l).

Fin length (FL) and *fin width* (FW): FL showed positive allometry up to 27 mm ML, when a discontinuity was determined (*F*=29.27), and growth became isometric. FW showed positive allometry throughout the size range studied with no discontinuity point (*F*= 0.42) (Table I) (Fig. 4m, n).

Arm sucker counts: All arms had a fast increase of the number of suckers over a short range of length. In all arms this positive allometry was verified up to around 14 mm ML, when the arms had the largest relative number of suckers, after this length the number increased almost constantly with increasing ML (Fig. 4o).

Two main discontinuity points indicate the presence of three growth stages in ontogenetic development of *Illex argentinus*. The first, early stage (1–14 mm ML) was characterized by the predominance of positive allometry, the second (14–28 mm ML) by isometry and the third (> 28 mm ML) by negative allometry (Table I).

Discussion

The developmental pattern in hatchling *Illex argentinus* is characterized by intense growth of arms, suckers and fins, while the width of the mantle and head becomes relatively narrower. No morphological change besides the division of proboscis takes place at the end of the rhynchoteuthion stage. The same developmental pattern of small paralarvae continues up to 14–17 mm ML, when there is a change in rate of relative growth of AIL, AIIL, AIIIL, HW and ED; this event coincides with the formation of the eight rows of suckers on the dactylus, a decrease in the rate of increment of suckers on the arms and an increase in the number of chromatophores .

In juveniles at a ML of 17 mm, AIL, AII, and AIIIL show isometric growth, however AIVL, TL, ClL, DL and CML continue to grow faster than the mantle. The latter are formed later and they reduce their relative growth rate at a large size.
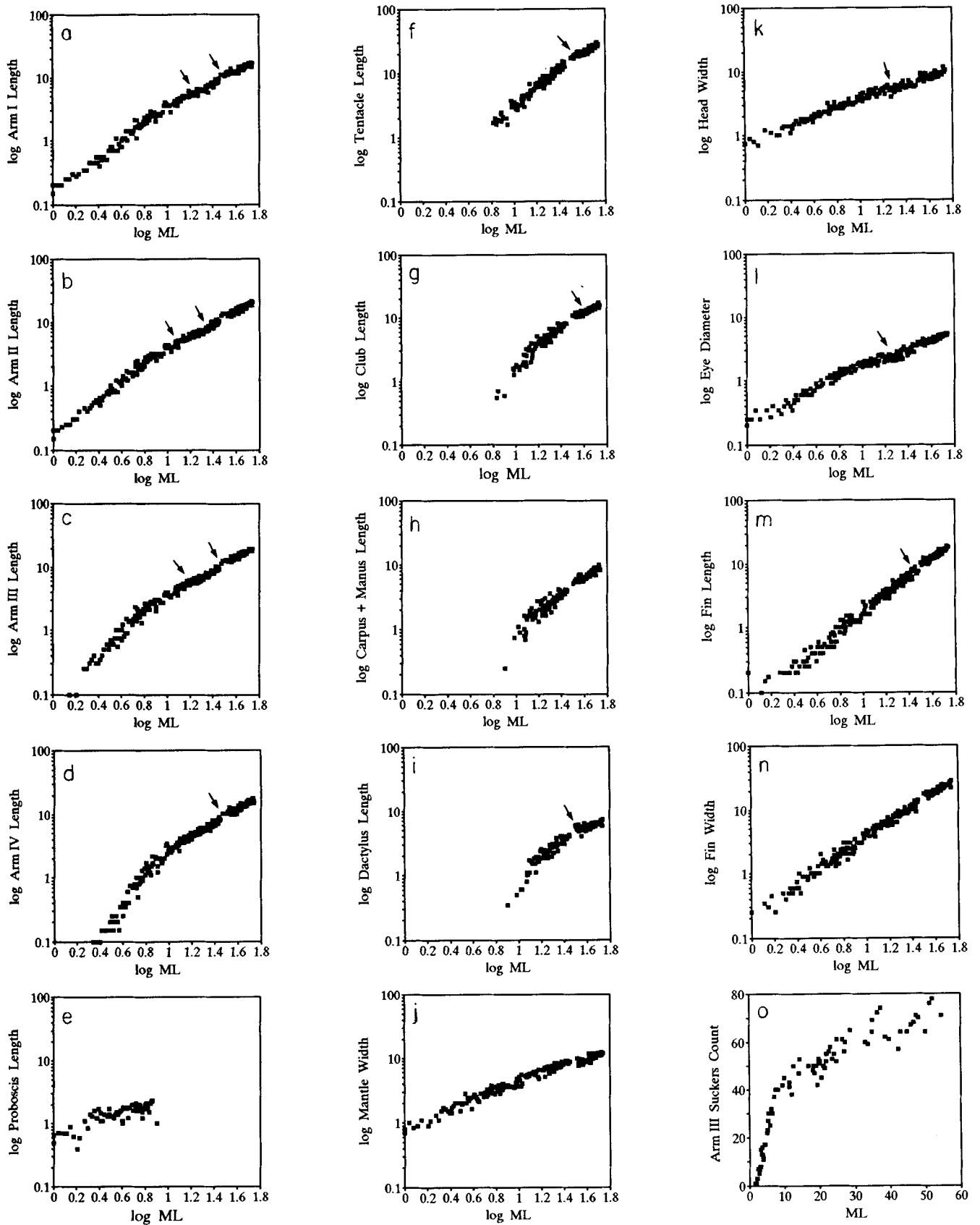
Fig. 4. a–n. Relationship between log body dimensions measured and log ML. **o.** AIIIL suckers count. The discontinuity points are indicated by arrows.

At about 28 mm ML another great change in rate of relative growth of the four pairs of arms, TL and FL, takes place. At this stage the juvenile is growing more in length in relation to body parts which are already well developed and the main changes occur in the club.

The Ommastrephidae possess some of the smallest cephalopod eggs, which produce rhynchoteuthions less than 2 mm total length and with a small yolk reserve at hatching (O'Dor *et al.* 1985, 1986). Therefore they need to rapidly find another food source for their survival. Considering that seizure of prey depends on the prehensile apparatus, which includes the arms with their suckers, and on the propulsory mantle-funnel complex, assisted by fins (Boletzky 1987), the smallest paralarvae lack the minimum morphological development required for effective predation. O'Dor *et al.* (1985) have proposed suspension feeding by the rhynchoteuthion during the critical period after yolk absorption.

So, relatively rapid growth of arms and fins and the progressive increase in the number of suckers is essential for the rhynchoteuthions to become efficient predators. Amaratunga (1983) and Balch *et al.* (1988), have suggested that ommastrephids pass through the rhynchoteuthion stage before predation begins. The results in this paper show that long before the separation of tentacles the first three pairs of arms are relatively well developed and possess a bisserial row of suckers. There is thus no morphological constraint on raptorial feeding and the factor that determines the start of the raptorial feeding mode seems to be development of the prehensile apparatus. As support for this hypothesis, Vecchione (1991) found crustacean fragments in the caecum of rhynchoteuthions of *Sthenoteuthis oualaniensis* of 5.2 mm ML, a species in which division of the proboscis end occurs at about 6–9 mm.

To be efficient predators, rhynchoteuthions must be good swimmers. Fast growth and slendering of the body as a result of relatively slow growth of MW and HW causes loss of the spherical shape and development of the cylindrical shape. This increases the efficiency of jet propulsion (O'Dor 1982).

The discontinuities in allometric growth of *Illex argentinus* seem to be related to activity and ability of the animal to obtain food and survive in different environments. In juveniles of 14 mm ML, the arms are relatively at their longest and the dactylus is already formed, allowing them to capture a broader variety of prey. When they reach 28 mm ML, growth rate of the arms decreases, because they have probably achieved proportions that enable the animal to seize prey of a wide range of sizes. Simultaneously growth in length increases, augmenting efficiency and speed of swimming (O'Dor 1982), moreover, animals this size have long tentacles with a well-developed club, enabling them to seize large, fast swimming prey. Data on the food of juveniles might reflect changes in their external morphology, but no data are available for *Illex argentinus* juveniles.

The transition from the rhynchoteuthion to the juvenile phase in the Ommastrephidae is associated with complete division of the proboscis (Nesis 1979a, 1979b, Roper & Lu 1979,

Amaratunga 1983, O'Dor 1983, O'Dor *et al.* 1985, Okutani 1987, Vecchione 1987, Young & Harmam 1988, Balch *et al.* 1988, Brunetti 1990, Brunetti & Ivanovic 1992); however, no alteration was found in the relative growth of *Illex argentinus* at this stage. After division of the proboscis, the tentacles are fragile and thinner than the arms and the few functional suckers they possess probably do not make them suitable for capture of prey, a fact shown by Naef (1923). The first discontinuity in growth, which seems to coincide with the transition from paralarval to juvenile phase (Young & Harman 1988), was found between 14–17 mm ML. At this size there is a major change in the external morphology of *Illex argentinus*, including the formation of the tentacular dactylus suckers, alterations in relative growth rates and in the pigmentation pattern. The simultaneous occurrence of all these events represents a major change in the life history of this species. The rhynchoteuthion stage can thus be considered an interval in the paralarval phase. Morris & Aldrich (1985), analysing the statolith of *Illex illecebrosus* suggested that the "larval" phase of ommastrephids may extend beyond the rhynchoteuthion interval, since, after division of the proboscis the juveniles still show characteristics considered "larval" in other cephalopods, such as the relative length of arms and tentacles.

Clarke (1966), showed it is common for many forms of oceanic squids and *Spirula spirula* to have one single discontinuity in the growth of the mantle, arms, tentacles and fins, which corresponds to the transition to the juvenile phase. Vecchione (1981), determined this transition to be at 4.5 mm ML for *Loligo pealei*. For *Sepioteuthis lessoniana*, the transition occurs between 7–10 mm ML (Segawa 1987). In *Gonatus madokai*, this transition occurs at around 20 mm ML, when changes in its tentacular armature take place (Kubodera & Okutani 1977). *Onychoteuthis compacta*, shows an increase in the number of mantle chromatophores at the end of the paralarval phase which occurs between 12–16 mm ML (Young & Harman 1987). So, although in Ommastrephidae the formation of club occurs much later, the transition to the juvenile phase seems to happen at sizes close to those of the other oegopsids (14–17 mm ML), which may be because these paralarvae little resemble the adults at hatchling and need a relatively long paralarval phase for the animal to develop the characteristics of the adult, contrary to the myopsids which may be smaller when such a transition takes place.

In general the greater the number and duration of stages or phases of development, the greater the chance for the animal to die from intrinsic factors (Rumrill, 1990). The limits of these phases or stages are defined by size (Nesis, 1979a), that is, the size of body and not the age at which the changes happen is specific. For the same species the age in which the individual will attain the size at which the changes take place, varies according to the environmental conditions. Morris & Aldrich (1985) estimated an age of 58–60 days for juveniles of *Illex illecebrosus* at 14 mm ML and Hurley & Beck (1979), estimated the same age for juveniles at 10 mm ML. For *Illex argentinus*, Arkhipkin (1990) determined age to be between 50–60 days for

juveniles with 15–19 mm ML, and according to Arkhipkin & Scherbich (1991), maximum length in same-age adults is determined by feeding conditions and temperature to which the paralarvae and juveniles are exposed up to 40–60 mm ML.

The growth phases delimited by the morphological changes found in the development of *I. argentinus* may represent important aims for future studies. Using recently developed ageing techniques (for review see Jereb *et al.* 1991) the duration of these phases and their respective growth rates can be estimated. Thus the chances of survival of different cohorts during their early life history may be addressed.

Acknowledgements

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