

# Ontogenic changes in diel vertical migration patterns compared with known allometric changes in three mesopelagic squid species suggest an expanded definition of a paralarva

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Shea, E. K., and Vecchione, M. 2010. Ontogenic changes in diel vertical migration patterns compared with known allometric changes in three mesopelagic squid species suggest an expanded definition of a paralarva. – *ICES Journal of Marine Science*, 67: 1436–1443.

Planktonic and newly hatched cephalopods are routinely called paralarvae. Currently, the onset of diel vertical migration (DVM) marks the end of the paralarval phase, although changes in ontogenic growth trajectories may also be used. Patterns of DVM are reported for the first time for three poorly understood mesopelagic squid species. Discrete-depth samples taken during the Amsterdam Mid North Atlantic Plankton Expeditions (AMNAPE) of 1980–1983 are used to examine the timing of ecological and morphological changes in *Ctenopteryx sicula*, *Mastigoteuthis magna*, and *Brachioteuthis* sp. 3. DVM patterns are species-specific, and ontogenic changes in DVM coincide with allometric changes in the arm, fin, and funnel characters of *C. sicula* at 7 mm mantle length. *Mastigoteuthis magna* is not concentrated in the upper 250 m of the water column during the day, and no clear DVM pattern is found in *Brachioteuthis* sp. 3, meaning that the endpoint of the paralarval phase cannot be defined ecologically in these species. Other ecological transformations, e.g. changes in prey-capture ability, are therefore explored as alternatives to DVM. The pad-shaped club and long neck are proposed as visual markers of the end of the paralarval phase of *C. sicula* and *Brachioteuthis* sp. 3, respectively.

**Keywords:** allometry, diel vertical migration, oegopsid, paralarva, squid.

Received 13 November 2009; accepted 7 June 2010; advance access publication 4 August 2010.

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## Introduction

Cephalopods are frequently described as developing directly (Ruppert and Barnes, 1994; Nielsen, 1995), but in many families, newly hatched and adult conspecifics have radically different morphologies, e.g. the brachial pillar in the Chiroteuthidae, the eye stalks in the Cranchiidae, and the fused tentacles in the Ommastrephidae. Because of this variability, and because no single morphological change is common to all cephalopods (cf. notochord flexion in fish), referring to newly hatched cephalopods as “larvae” is controversial (Boletzky, 1974; Nesis, 1979). Young and Harman (1988) proposed using the term paralarva to describe newly hatched cephalopods that live in the plankton. Their definition uses a daytime niche change from epiplanktonic to nektonic to mark the end of this ecologically important early life-history stage. Morphological change is predicted to coincide with the end of the paralarval phase of life in most oceanic squid species and, in the absence of ecological data, is substituted for habitat differences in defining the endpoint of that phase of life (Young and Harman, 1988).

The term paralarva has been readily accepted as shorthand for planktonic or newly hatched cephalopods, but the concept has not been critically examined within the oegopsids. The term has been criticized, however, because it does not apply across all cephalopod taxa. Many species of benthic octopods, all sepiids, and most sepiolids have hatchlings that immediately adopt a benthic lifestyle and therefore do not meet the primary ecological requirement of

the definition, although they may meet the secondary morphological criteria. No single size or morphological change can be universally applied to all cephalopods, requiring the end of the paralarva phase to be identified on a species-by-species basis.

When single species are examined, the expected relationships are not always supported. For example, the fused tentacles, or proboscis, of newly hatched ommastrephid squid has regularly been used to identify a so-called larval stage (Harman and Young, 1985; Wormuth *et al.*, 1992), and separation of the tentacles was identified as a convenient marker of the end of the paralarval stage (Young and Harman, 1988). This dramatic morphological change has never been linked to changes in depth distribution, but it has been correlated with changes in arm characters (Vidal, 1994), and therefore with ecological function related to obtaining food.

The three mesopelagic oegopsid squid species analysed here were selected based on their abundance during day- and night-time sampling, a variety of capture depths, a relatively stable taxonomy in the study area, and anticipated variation in the extent of ontogenic change in morphology. *Ctenopteryx sicula*, the comb-finned squid, is a warm-water species (Lu and Roper, 1979) with a worldwide distribution between 40°N and 40°S (Clarke, 1966). Specimens hatch at ~1 mm dorsal mantle length (DML; Jefferts, 1992); they grow to 90 mm (Nesis, 1987). Very little is known about the life cycle or ecology of this family. *Mastigoteuthis magna* is one of the 13 species in the family

Mastigoteuthidae (Vecchione *et al.*, 2007), all of which have characteristically long, thin tentacles, with minute suckers in >15 series along the length, and large, robust fourth arms (Roper *et al.*, 1969). Mastigoteuthid squid are a worldwide, deep-water family (Roper and Young, 1975) with daytime distributions at 500–1000 m (Roper *et al.*, 1969) and shallower night-time distributions at 200–700 m (Roper and Young, 1975). Brachioteuthids are found worldwide (Roper and Sweeney, 1992), and there are seven commonly accepted species, but their taxonomy is unsettled. Two new species were recently described by Lipiński (2001) from the South Atlantic and Southern Ocean, and more are likely to be described from the Southern Ocean and off Bermuda (K. Bolstad, pers. comm. and EKS, pers. obs.). North Atlantic specimens are generally identified as *Brachioteuthis riisei*, but the type locality for *B. riisei* is in the South Atlantic near Tristan da Cunha. Shea (1995) found evidence for four species in the North Atlantic. *Brachioteuthis* sp. 3 (Figure 1) is likely *Brachioteuthis beanii* (type locality western North Atlantic), but it is maintained here as *Brachioteuthis* sp. 3 pending taxonomic revision of the family. Newly hatched brachioteuthids are characterized by their unusually long neck (Young *et al.*, 1985). Most reach adult size between 35 and 90 mm DML (Roper *et al.*, 1984), but *Slosarczykovia circumantarctica* grows to 170 mm DML (Lipiński, 2001). Brachioteuthids are often caught in relatively large numbers, indicative of aggregating behaviour (EKS, pers. obs.).

No recent synthesis of the vertical distribution of newly hatched species exists, and understanding the diel vertical migration

(DVM) patterns of oegopsid squid has not progressed dramatically since the mid-1970s (Clarke and Lu, 1974, 1975; Lu and Clarke, 1975a, b; Roper and Young, 1975). The AMNAPE data (Amsterdam Mid North Atlantic Plankton Expeditions) are ideally suited to describing the patterns of DVM because the nets sampled discrete depths, and because of the depth horizons sampled. We describe for the first time the DVM patterns of three species of mesopelagic oegopsid squid whose life cycles are poorly known. We also compare the ontogenic changes in depth distribution with known discontinuities in morphological growth trajectories (Shea and Vecchione, 2002) to identify the end of the paralarval stage using the strict ecological definition. When depth distributions are uninformative, alternative ecological shifts are inferred from the previously identified allometric changes. Once an endpoint has been identified, simple presence/absence or other visual markers of the endpoints are sought to facilitate identification.

## Material and methods

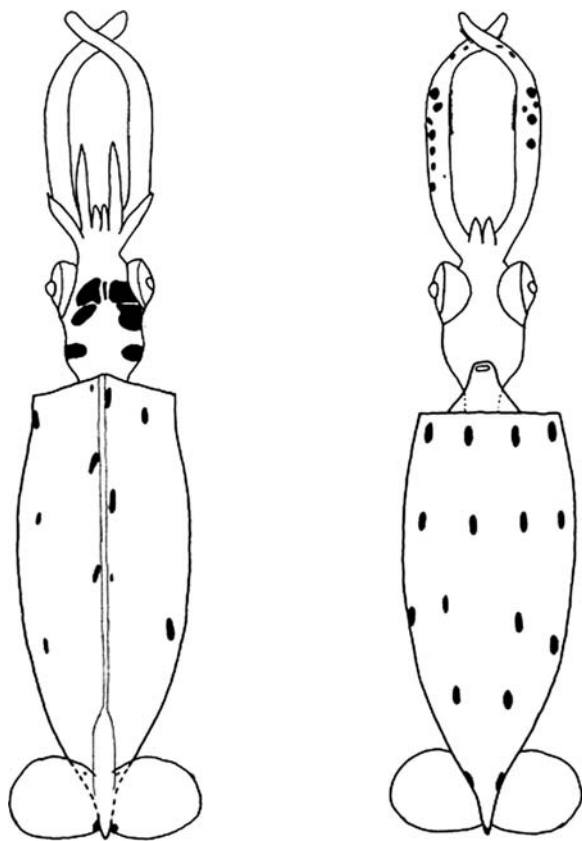
Specimens were collected with discrete-depth open-net hauls during the AMNAPE surveys of 1980–1983 (see van der Spoel, 1981, 1985, and van der Spoel and Meering, 1983, for collection details). Stations were generally located between 55 and 25°N along the 30°W longitude. Rectangular midwater trawls (RMT1 + 8) were opened at the top of the discrete-depth range (0–50, 50–100, 100–200, 200–300, 300–400, 400–500, and 500–1000 m), and the layer was sampled in a downward direction. The specimens analysed here were examined previously for breakpoints in growth trajectories using a Model II piecewise linear regression (Shea and Vecchione, 2002). Not all characters (Figure 2) were measured in all species (see Table 1 in Shea and Vecchione, 2002). The specimens were fixed in formalin and preserved in 50% isopropyl alcohol until they were measured in 1992.

Average catch per haul at depth (Figure 3) and day and night depth-distribution data (Figure 4) were compiled for each species. To define a consistent time for day and night, crepuscular periods were determined for each station using a marine navigation program (Twilight, ©Microsoft 1982–1987) based on month, day, and year of the sampling effort and the latitude and longitude at the sampling station.

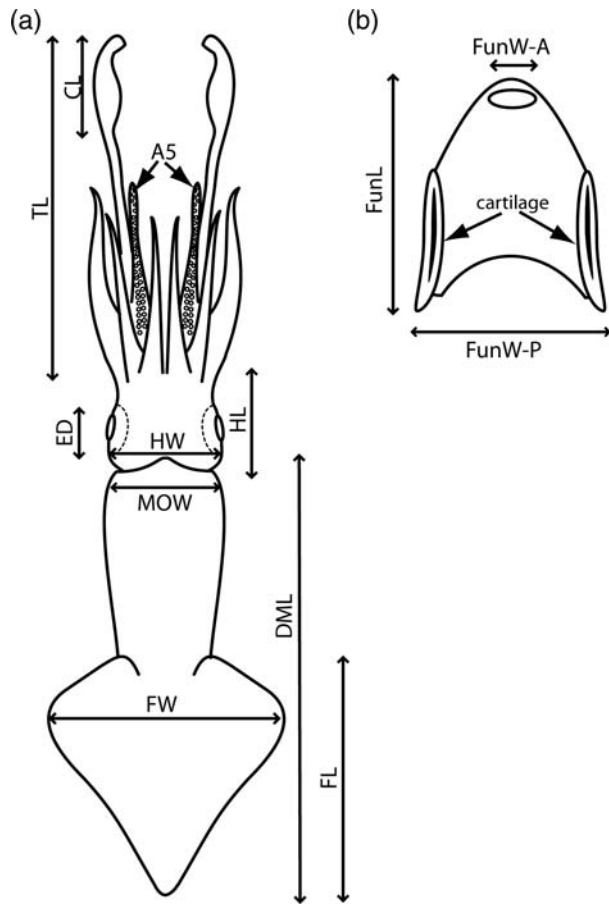
## Results

### *Chtenopteryx sicula*

Specimens ( $n = 144$ ; size range 2–25 mm DML) were sparsely collected in the upper 300 m in both day and night hauls. Daylight hauls between 50 and 100 m were most successful at capturing the species, with an average capture rate of four specimens per haul (Figure 3). The daytime depth distribution shows a gradual, ontogenic descent into deeper water with increasing DML (Figure 4). The smallest specimens (3.2–9.8 mm DML) were caught in the upper 200 m, and the larger specimens were found progressively deeper, with the two largest (18.5 and 21.5 mm DML) caught between 500 and 1000 m. The smallest daytime specimen reliably collected other than in the top 100 m was ~7 mm DML. A single 5 mm specimen was collected at 500–1000 m, but was likely net contamination. At night, all specimens regardless of size were caught in the upper 300 m, and 43 of the 48 specimens collected were from the upper 200 m.



**Figure 1.** *Brachioteuthis* sp. 3. Dorsal (left) and ventral (right) view of a 9.5-mm DML specimen.



**Figure 2.** Key to measurements, adapted from Roper and Voss (1983). (a) External characters: CL, club length; ED, eye diameter; FL, fin length; FW, fin width; HW, head width; HL, head length; DML, dorsal mantle length; MOW, mantle opening width; TL, tentacle length; A5, ventral arms. (b) Funnel characters: FunL, funnel length; FunW-A, width of the anterior funnel opening; FunW-P, width of the posterior funnel opening.

### *Mastigoteuthis magna*

Specimens ( $n = 62$ ; size range 3–12 mm DML) were sparsely collected by day at all depths except 200–300 m. Night-time catches were concentrated between 50 and 400 m, with a maximum catch per haul between 50 and 100 m (Figure 3b). The species occupies the entire water column by day, but is confined to the upper waters by night. Of the 17 specimens caught by day, 13 were caught shallower than 200 m, and 4 deeper than 350 m (Figure 4). Smaller specimens (<7 mm DML) were found as deep as 400–500 m, with larger specimens (>7 mm DML) in the deepest (500–1000 m) layer. At night, specimens of all sizes were caught in the upper 200 m, with 27 of 31 in the upper 100 m.

### *Brachioteuthis* sp. 3

The rate of capture of *Brachioteuthis* sp. 3 ( $n = 114$ ; size range 3–50 mm DML) was distinctly different from the other taxa considered. Daytime catches were large. In the upper 100 m, 10–30 specimens were collected on average per haul, indicative of aggregating behaviour (Figure 3). Night-time hauls yielded considerably fewer specimens per haul, and no specimens were collected between 300 and 500 m (Figure 3c). All specimens were taken at

depth shallower than 200 m by day and shallower than 300 m by night (Figure 4), indicating modest nocturnal vertical spreading. All specimens >30 mm DML were collected in malfunctioning nets, so were not included in subsequent analysis.

## Discussion

### *Chtenopteryx sicula*

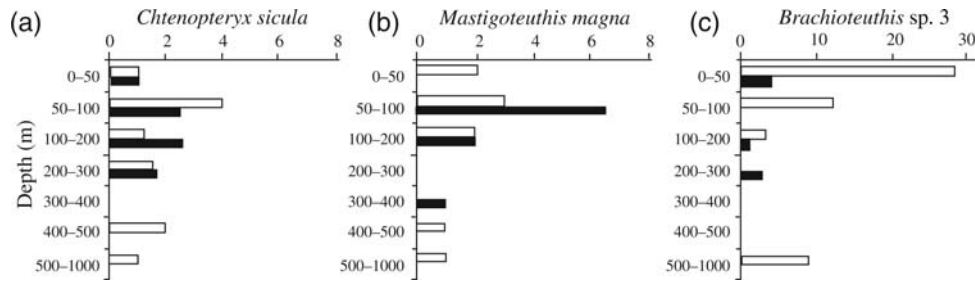
The AMNAPE data corroborate a daytime habitat of 0–100 m for specimens of <6.5 mm DML (Clarke and Lu, 1974, 1975; Lu and Clarke, 1975b), but extend the night-time range at these sizes to 0–300 m. An overall pattern of gradual ontogenic descent is evident in the daytime distribution (Figure 4a). In contrast, Roper and Young (1975) categorized *C. sicula* as first-order diel vertical migrators, moving from 600 to 800 m by day into the upper 150 m at night (size range 12–83 mm DML), but that conclusion was based on just a few specimens collected from multiple locations around the world. Nesis (1977) agrees that *C. sicula* young are found between 50 and 200 m and that the few adults he collected were meso- and bathypelagic. Multiple Atlantic species likely exist (Naef, 1921–1923b) and may have different vertical migration profiles. Pacific *C. "sicula"* have a night-time distribution of 600–1000 m and a daytime distribution in the upper 200 m over a 10–50-mm size range (Young, 1978).

The allomorphy in feeding (TL and A5) and locomotion (FL, MOW, and FunL) characters at ~7–9 mm (Table 1) corresponds to the smallest specimens found outside the upper 100 m by day. Specimens as small as 11 mm DML (Young, 1978) or 12.1 mm DML have previously been identified as the smallest sizes collected deeper than 100 m (Clarke and Lu, 1975). This migration out of the euphotic zone may mark the first step in many different patterns of DVM, in this case, gradual ontogenic descent. Gradual ontogenic descent was expected to confound the delineation of a paralarva (Young and Harman, 1988), because there is no rapid onset of DVM. In our analysis, it provides a good example of ecological change coincident with allometric change.

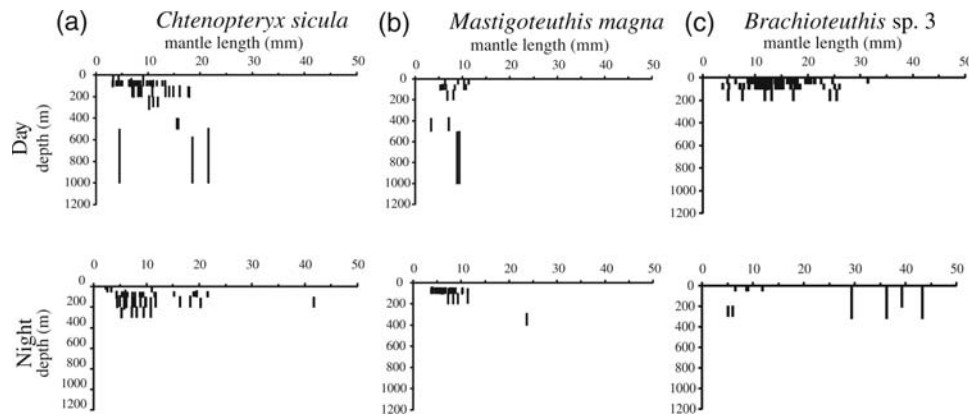
At sizes greater than the 7–9 mm allomorphy, daytime specimens were collected between 200 and 300 m, slightly shallower than the daytime depth of >250–300 m proposed by Young and Harman (1988) as a vertical migration marker in oligotrophic Hawaiian waters. The smallest daytime specimens caught deeper than 300 m were 15 mm DML, a size that corresponds to a single allometric change in the posterior funnel width (FunW-P). This character affects jetting ability, because as the size of the FunW-P increases, the speed at which water can be expelled through the FunW-A increases, along with the jetting speed. According to the strictest definition, two endpoints of the paralarval phase are possible: 7–9 or 15 mm. The first is chosen here because the allometric change is found in multiple characters and is coincident with an ecological change in distribution as proposed by Young and Harman (1988).

### *Mastigoteuthis magna*

Depth-distribution data for *M. magna* are sparse, but specimens 17–130 mm DML have been found below 500 m by day and at 200–500 m at night (Lu and Roper, 1979). The AMNAPE data show a shallower night-time distribution in the eastern North Atlantic than previously reported, with most specimens collected between 50 and 100 m (Figures 3 and 4). Specimens <10 mm DML are caught throughout the water column (0–1000 m) by



**Figure 3.** Average number of specimens caught per haul, by species. White bars are daytime hauls and black bars are night hauls. Note the scale difference for *Brachiooteuthis* sp. 3.



**Figure 4.** Day and night depth distributions for three species of oegopsid cephalopod. Each solid line represents the depth range over which one individual was collected. (a) *Ctenopteryx sicula*; (b) *Mastigoteuthis magna*; (c) *Brachiooteuthis* sp. 3.

day, likely a consequence of deep-hatching animals gradually coming towards the surface.

Although evidence of a sudden onset of DVM is not found in *M. magna*, four characters had discernible inflection points in their growth trajectories, and three of the four (FL, FW, FunW-P) were between 4 and 7 mm DML. These characters are all involved in locomotion, and the dramatic decrease in the scaling exponent after the inflection point (Table 1) suggests that the fins grow rapidly to 3–4 mm long and 4–5 mm wide. Increase in FunW-P size concomitantly increases the speed at which water can move through the funnel, potentially increasing jetting speed. Together with changes in the fin shape, this may mark a change in the propensity to maintain the fins up, head down “tuning-fork” vertical position documented *in situ* (Roper and Vecchione, 1997).

At sizes smaller than the 4–7 mm allomorphy, one specimen was collected at 400–500 m by day, well exceeding the Young and Harman (1988) >250–300 m daytime criterion. Above 7 mm DML, specimens were collected as deep as 500–1000 m by day and rose to 50–400 m by night, suggestive of DVM, but as deep-mesopelagic and bathypelagic species, mastigoteuthids are not expected to undergo major migration (Nesis, 1977). More large specimens are needed to confirm whether this pattern holds.

### *Brachiooteuthis* sp. 3

Daytime specimens were narrowly distributed in the upper 200 m, and all night-time specimens were collected between 0 and 300 m, suggesting that *Brachiooteuthis* sp. 3 is a night-time vertical spreader (*sensu* Roper and Young, 1975) at sizes <45 mm DML (Figure 4). This result is similar to the previous reports of hatchlings and

juveniles (1.7–32 mm DML) found between 0 and 300 m by day and night (Clarke and Lu, 1974, 1975; Lu and Clarke 1975a, b). Irrespective of size, daytime captures were all between 0 and 200 m and night-time captures between 0 and 300 m. This modest night-time spreading out vertically is similar to the previous reports in which specimens <5.6 mm DML were documented as being collected between 10 and 300 m, and those >5.6 mm being found shallower, in the upper 50 m (Lu and Clarke, 1975a).

This species had the most specimens in the dataset ( $n = 114$ ), and 12 of the 14 measured characters had an identifiable inflection point. Individual characters changed at different points throughout the size range examined, and neck characters changed twice over the size range (Table 1). However, two clusters of inflection points were found: five characters of the arm crown, head, and neck (TL, A5, HL, HW, NL) changed between 11 and 12 mm DML, and four characters of the head, neck, and funnel (HW, HL, NW, FunW-P) changed at ~25–27 mm.

Both suites of characters clearly relate to changes in feeding ability more directly than locomotion. Brachiooteuthid paralarvae have been observed hanging head down in the water and using their neck to move the arm crown towards prey (Young *et al.*, 1985). Perhaps the allomorphy reflects a shift from this “neck-mediated” to a more common “tentacle-mediated” method of prey capture. Multiple changes in neck measurements may suggest several methods of prey capture as in the ommastrephids (Shea, 2005; Uchikawa *et al.*, 2009) or may be an artefact of the highly contractile nature of the neck.

Larger brachiooteuthids are regularly caught deeper by day (0–1000 m, Roper and Young, 1975; Lipiński, 2001; >32 mm,

**Table 1.** Characters with breakpoints in their growth trajectory, modified from Shea and Vecchione (2002).

Character	n	Breakpoint (mm DML)	Function	Growth rate after breakpoint
<i>Chtenopteryx sicula</i>				
TL	20	8.2	Predation	—
A5	21	7.4	Predation	—
FL	67	6.7	Movement	++
MOW <sup>a</sup>	81	8.2–9.0	Movement	—
FunW-A	77	4.1	Movement	—
FunW-P <sup>a</sup>	79	14.9–16.4	Movement	—
FunL	78	7.4	Movement	+
<i>Mastigoteuthis magna</i>				
A5	50	10	Predation	—
FL	58	4.1	Movement	—
FW	53	6.7	Movement	—
FunW-P	45	6.7	Movement	—
<i>Brachioteuthis</i> sp. 3				
TL	146	11.0	Predation	+
A5	152	12.2	Predation	++
ED	138	20.1	Predation	++
FL	152	14.9	Movement	+
FW	141	16.4	Movement	+
FunW-A	138	13.5	Movement	+
FunW-P	134	27.1	Movement	++
FunL	138	8.2	Movement	—
HW	145	24.5	Predation	++
HL <sup>b</sup>	146	11 and 24.5	Predation	+
NW <sup>b</sup>	156	12.2 and 27.1	Predation	+
NL <sup>b</sup>	156	11 and 36.6	Predation	+

After the breakpoint, changes in the scaling exponent show that the rate of growth of the character either increases (+) or decreases (–) compared with before the breakpoint. Changes >50% are marked as ++ or –. Characters as in Figure 2. n, number of specimens measured for the character. Function is a presumed major ecological function of the character.

<sup>a</sup>The breakpoint was equally good across the size range given.

<sup>b</sup>The scaling exponents increased after each of the two breakpoints.

0–1250 m haul, EKS, pers. obs.). In the AMNAPE data, there are no reliable daytime captures of animals >27 mm DML, so coincident DVM change cannot be addressed at that size. However, as *B. beanii* reaches adult size between 35 and 90 mm (Roper *et al.*, 1984), a length of 27 mm may represent a later life-history stage than is intended by the term paralarva. The 11–12-mm cluster of allometric change likely reflects the end of the paralarval phase.

### Morphological markers

Circular fin shape, large chromatophores in species-specific patterns, and a sac-shaped mantle are common characteristics of newly hatched cephalopods (Sweeney *et al.*, 1992). Many oegopsids have additional family-specific morphological characters, e.g. stalked eyes in cranchiids, fused tentacles in ommastrephids, or Kölliker organs in octopodids, and the loss of these characters, or the growth of new ones, e.g. the central club hook in gonatids, is often assumed to be associated with the end of the paralarval phase of life (Young, 1972; Young and Harman, 1988; Falcon *et al.*, 2000). A reliable morphological marker that distinguishes paralarvae from other stages of life would be useful, especially if it develops concomitant with allometric and ecological change, e.g. the development of the club hook in *Gonatus steenstrupi* (Falcon *et al.*, 2000), or chromatophore numbers in *Lolliguncula brevis*

(Vecchione, 1982), but commonly cited markers may not meet this criterion. For example, in ommastrephids, tentacle separation has been assumed to mark the end of the paralarval phase. Depending on species, tentacle separation takes place between 6 and 13 mm DML, and the tentacles are probably not used for prey capture then (Wormuth *et al.*, 1992; Vidal, 1994; Wakabayashi *et al.*, 2002; Shea, 2005; Uchikawa *et al.*, 2009). In *Illex argentinus*, discontinuities in the growth of the arms, suckers, and fins at ~14 mm DML (Vidal, 1994) suggest that post-separation changes in feeding ability are more relevant ecological changes than tentacle separation.

Newly hatched *C. sicula* have a characteristic circular club. As the tentacle grows at the distal tip, the club assumes a more traditional shape until the circular carpal pad is only a remnant of the proximal club. At 6 mm DML, the length of the distal tip is roughly equal to the diameter of the circular club (Jefferts, 1992), and this marker has been proposed as a conveniently identified endpoint of the paralarval stage. This size is slightly smaller than the 7–9 mm allomorphosis, although in the AMNAPE dataset, the growing distal tip was often broken at the point where it intersected the circular pad, making measurements unreliable for statistical analysis. The presence of a circular club would be a robust indicator of a paralarva, but would not necessarily mark the end of the phase. As the allometric change starts at ~7 mm and changes in feeding are predicted to be ecologically important, it remains a feasible, but untested, marker.

Adult *M. magna* have been photographed in a characteristic fins up/arms down “tuning-fork” posture in the water column (Roper and Vecchione, 1997). No morphological marker of a paralarva has been proposed for mastigoteuthids, but based on the allometric inflection points, useful markers may be found in the fins; fin undulation is necessary to maintain the “tuning-fork” posture. Although no clear allometric change was found in the ventral arms in the AMNAPE collection, additional arm characters related to the tuning-fork posture need to be examined, e.g. the size at which the protective membranes on the ventral arms develop.

“Elongate neck becomes short” was proposed as a morphological marker in *Brachioteuthis* (Young and Harman, 1988), and neck length and width did show marked allometric changes at four points: NL at 11 and 36.6 mm DML, and NW at 12.2 and 27 mm DML (Shea and Vecchione, 2002). Reliably quantifying when the neck has shortened is problematic, however, because it is very contractile (Young *et al.*, 1985). Arm and club sucker morphology would be reasonable characters to examine as alternative markers, along with the development of the characteristic tripartite sucker arrangement on the club.

### Redefining the term paralarva

The term paralarva has been widely adopted in the cephalopod literature to refer to newly hatched cephalopods, but the concept has rarely been critically applied to individual taxa (Vidal, 1994; Shea, 1995).

None of the three species examined had a sudden, obvious onset of DVM, and no clear pattern was found in the size of the specimens collected deeper than 250 m by day, the main benchmark for having left the paralarval niche (Young and Harman, 1988). In *M. magna*, the smallest animals were found in deep water, possibly migrating from deep-hatching locations to the plankton. This behaviour is known or suspected in many

deep-spawning species (Nesis, 1977) and makes it difficult to identify the onset of DVM.

Using DVM to mark the end of the paralarval stage presents additional problems. Micro-migrations have been documented in many marine larvae, and microhabitat usage coincides with saltatory changes in fish growth trajectories (Sagnes *et al.*, 1997; Kováč *et al.*, 1999). Similar vertical micro-migrations of cephalopods are possible within the 0–50 m depth range for the smallest specimens, so this would be undetected by the AMNAPE specimens because of the relatively coarse sampling regime. A depth range 0–1000 m is 10 000 body lengths for a 100 mm (0.1 m) adult brachioteuthid. For a 5-mm specimen, a 50 m depth range represents a similar distance. Second, like the tentacle strike (Messenger, 1968; Chen *et al.*, 1996; Kier, 1996; Shea, 2005), DVM is a complex behaviour that likely requires a suite of coordinated morphological and behavioural changes, including well-developed fin, mantle, and funnel musculature and the presence of functional light sensing vesicles (Young, 1978). Attainment of the full behaviour may not be complete until the animals are larger than expected when the term paralarva is typically being used (post-hatchling). The broadly variable depths of capture for the smallest specimens may reflect this lack of coordination.

In these three species in the AMNAPE dataset, changes in prey-capture ability and the use of fins for maintaining position in the water column are clearly important. Broadening the definition to include alternative ecological niche shifts would potentially allow the term to encompass all cephalopod species, unlike the current usage, which is most appropriate for oegopsid squids.

We propose a single, revised definition of a paralarva: newly hatched cephalopods that have a distinctly different mode of life from the adults, with an endpoint identified by ecologically significant allometric changes in morphological characters. Inflection points in the growth trajectories of morphological characters (Shea and Vecchione, 2002) provide an unambiguous, testable endpoint of the paralarval phase. This expanded definition is more broadly applicable across all cephalopod taxa because it decouples the definition of the term paralarva from DVM. In benthic octopods with a post-hatching planktonic phase, settlement is an important ecological function that may be coincident with allometric changes in the arms (Villanueva and Norman, 2008). After settlement in *Octopus vulgaris* (33–40 d post-hatching), there is a marked increase in arm length and mantle length (ML; Figure 3 of Nixon and Mangold, 1996) as well as increases in weight, and development of the nervous system. These morphological changes reflect the transition from being a diurnally active, visual, swimming paralarva to being a nocturnal, tactile, sedentary juvenile. In large egged benthic octopods with crawl-away hatchlings (Hochberg *et al.*, 1992), behavioural changes such as the onset of parachuting behaviour at 2 weeks post-hatch, a decline in activity and swimming, or declines in crowding tolerance (Forsythe and Hanlon 1988) may be a more relevant marker of this life-history stage.

*Sepia officinalis* hatches from a benthic egg and assumes many adult behaviours soon after hatching. Richard and Declair (1969) defined several post-hatchling phases in that species according to changes in blood proteins related to yolk utilization. At 10 d post-hatch, there is an obvious inflection point in the growth trajectory of ML (at 17°C), which is coincident with changes in final absorption of the yolk reserves (see Figure 3.6 of Boletzky, 1983). This may be a significant milestone in the ontogeny of the species. Other ecologically relevant changes may be the full assumption

of burrowing behaviours, a loss in the ability to attach to hard structures, or the attainment of a full suite of chromatophore patterns. In *S. officinalis*, multiple coincident changes in morphology and ecology may be identified in the life cycle.

The AMNAPE specimens reveal inflection points in multiple characters for each of the three species, and groups of inflection points in related characters can be interpreted as an allomorphosis. The characters included in these groups point to shifts other than DVM that should be considered (Vidal, 1994; Shea and Vecchione, 2002). The presence of family-specific morphological markers may positively identify a paralarva, but their loss (or attainment) may not be sufficient to identify the end of the paralarval phase. The duration of the paralarval phase of life has, therefore, to continue to be defined on a species-by-species basis.

## Acknowledgements

We thank Clyde Roper and Mike Sweeney, National Museum of Natural History, Smithsonian Institution, for access to the AMNAPE collection. The work was completed while the senior author was a graduate student at the Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA, USA. Particular thanks go to the committee members John Olney, Roger Mann, John Brubaker, and Mark Patterson and to Clyde Roper for their help and guidance during that time. Finally, we thank Leslie Skibinski, Delaware Museum of Natural History, and three anonymous reviewers who improved the manuscript through critical reading and thoughtful comments.

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doi:10.1093/icesjms/fsq104