BROTULOTAENIA (TELEOSTEI: OPHIDIIFORMES) LARVAL DEVELOPMENT REVISITED: AN APPARENTLY NEW TYPE OF MIMETIC RESEMBLANCE IN THE EPIPELAGIC OCEAN

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ABSTRACT. – Numerous examples of the mimicry of inanimate objects by living animals have been well-documented, mainly in the terrestrial realm. The epipelagic ocean, with its cover-deficient properties would seem to be a less suitable habitat for the development of such defensive strategies. Thus, the main tactic utilized by many planktonic organisms, including fish larvae, is to become virtually transparent. Despite the recent descriptions of the early life history of the ophidiid species *Brotulotaenia nielseni*, the form-function relationships during early ontogeny of this rare deep-sea species have never been addressed. The recent find of a larval *B. nielseni* in near-perfect condition allowed further observations on its morphology which led to a hypothesis regarding its mimetic resemblance to a bird feather, an apparently new defense strategy in the pelagic environment. In this paper, I approach the unusual Bauplan of larval *Brotulotaenia* from a functional morphology standpoint and show how a suite of larval features facilitates the resemblance to an inanimate model, thus offering possible protection against visual predators. The numerous similarities between the hypothesized model (bird feather) and the mimic (fish larva), as well as certain basic requirements for the development of such a mimetic resemblance are reviewed and discussed.

KEY WORDS. – *Brotulotaenia*, mimetic resemblance, Batesian mimicry, epipelagic ocean, fish larvae, Ophidiiformes.

INTRODUCTION

The genus *Brotulotaenia* Parr, 1933 represents an unusual case among other representatives of the diverse teleost Order Ophidiiformes. Four species of this genus: *B. brevicauda* Cohen, 1974, *B. crassa* Parr, 1934, *B. nielseni* Cohen, 1974 and *B. nigra* Parr, 1933 seem to have abandoned the benthopelagic lifestyle that is favoured by the majority of other ophidiiform representatives and have successfully invaded the mesopelagic and bathypelagic realms in the tropical-subtropical regions of the world's oceans. The adoption of a pelagic lifestyle has apparently resulted in some morphological changes in the adults such as loss of pelvic fins and modification of scales into small prickles (Cohen, 1974; Nielsen et al., 1999).

Interestingly enough, the early ontogeny of this genus has received much recent attention. This is rather surprising because the early life history information on almost 90 known ophidiiform genera is rather scarce and scattered, focusing mainly on the shallow-living, coastal species (Gordon et al., 1984). However, two detailed works describing the early development of *B. nielseni* were recently published (Okiyama & Kato, 2002; Fahay & Nielsen, 2003), complementing earlier information on *B. crassa* (Aboussouan, 1980).

An exceptionally well-preserved larva of *B. nielseni* was recently found in the fish collection of the P. P. Shirshov Institute of Oceanology, Moscow, Russia. Upon closer examination, it became apparent that some important larval characters were not reported in the earlier studies and this justified an additional morphological description of the new specimen. More importantly, the new morphological information has prompted a consideration of the unusual Bauplan of larval *B. nielseni* in terms of its possible adaptive significance. Thus, the objectives of this study are to: 1) refine and update the information on the early development of *B. nielseni* and 2) discuss a hypothesis that a suite of larval characters possibly facilitates a new type of protective resemblance in the pelagic environment.

MATERIALS AND METHODS

The description is based on a single uncatalogued specimen of 30.0 mm standard length (SL), deposited in the P. P. Shirshov Institute of Oceanology, Moscow, Russia. [Research vessel 'VITYAZ', cruise 50, station 6493 (500), 3 Jul.1971,

1900 hours, plankton net 80 cm in diameter, sampling depth 0 - 10 m, West of the Tinian, Saipan and Aguijan Islands in the Northern Marianas group (13°31'2"N 139°57'6"E)]. The specimen was fixed in formalin, so body shrinkage has probably not occurred. Measurements were taken to the nearest 0.1 mm with an ocular micrometer on an MBS-1 standard stereomicroscope. After the specimen was illustrated and measurements taken, it was cleared and stained with alizarin-red to facilitate counts of vertebrae, dorsal and anal fin rays, as well as to reveal details of the osteology. A contour feather (37 mm in length) illustrated for comparative purposes in Figure 3 was collected on the beach of Fort Pierce, Florida, USA in April 2006 and probably belonged to a common species of seagull (family Laridae).

RESULTS

General morphology. – Dorsal fin rays - 89, anal fin rays - 68, pectoral fin rays - 26, pelvic fin rays - I 2, vertebrae 72 (13 + 59). Body proportions, in % SL: 1) preanal length, 35.5%; 2) head length, 17.0%; 3) maximum body depth (at base of pelvic fin origin), 33.6%; 4) body depth at origin of anal fin, 20.3%; 5) caudal peduncle depth, 2.3%; 6) length of pectoral fin, 11.5%. Head proportions, in % of head length: 1) head depth at anterior portion of eye to dorsal fin origin, 124.3%; 2) eye diameter, 21.6%; 3) postorbital length, 55.4%; 4) snout length, 20.3%; 5) upper jaw length, 51.4%.

Body is strongly-compressed, with greatest depth at the level of pelvic fin origin, tapering gradually to a very narrow and extremely short caudal peduncle (Fig. 1). The body is divided into four distinct muscular bands delineated by chevron-shaped myomeres. Two central myomere portions stand out as being thicker while two outer portions are less thick and semi-transparent. There are relatively broad semi-transparent areas, occupied by pterygiophores.

Head depth is greater than length and is also strongly compressed laterally. Dorsal head profile is very steep, with the origin of dorsal fin at the level of the anterior margin of orbit. Enlarged rostral cartilage of premaxilla forming a distinct stub just anterior to the eye and short snout has a distinct snub-nosed appearance. Mouth is large and oblique, forming a ~ 45° angle, with posterior margin of upper jaw reaching the level of posterior margin of orbit. Minute teeth are present on premaxillae. The eye is moderate in size, round, nearly filling the orbit and situated close to dorsal profile of the head. A small single nostril is found in front of each eye.

The origin of dorsal fin is displaced extremely to the anterior, with first dorsal ray originating at the level slightly behind the anterior margin of the eye. Dorsal fin rays 1 - 7, 10, 16, 22, 26, 29 and 36 extremely elongated, with elongated parts protruding well beyond the fin membrane. These free parts of elongated rays are enveloped in a transparent sheath, in some places forming distinct swellings, peppered with fine melanophores. Most elongated rays bear one swelling, but rays 1 and 6 have two. In addition to the extremely elongated rays, several less elongated, as well as rather short rays, are

present in the anterior portions of dorsal and anal fins giving the outer margins very distinct, uneven outlines. Posterior to dorsal fin ray 36, the rays become nearly equal and gradually decrease in length thereby forming a confluent portion with caudal fin. All extremely elongated dorsal rays, except the first one, appear to be broken at their tips, thus original length prior to capture may have been longer. The first dorsal fin ray (49.8% SL) is intact and terminates with a pigmented swelling.

The anterior portion of anal fin is very similar morphologically to that of dorsal fin. Anal fin rays 1 - 4, 7 - 8, 14, 22 and 27 are elongated and enveloped in a transparent sheath with pigmented swellings present in some rays (1, 3 and 7). Several less-elongated rays, connected by the fin membrane, are found between the elongated rays. Depths of the opposing portions of the dorsal and anal fins are nearly identical.

The caudal fin is small, with nine rays. Pelvic fins are placed below the origin of pectoral fin base and start with a small spine. The two pelvic fin rays are very elongated but both were broken so the original lengths could have been longer. However, the second pelvic ray bears a pigmented swelling similar to those found on some rays of the dorsal and anal fins. The pectoral fin is fan-like, on a relatively narrow base. The elongate coracoid process, extending posteroventrally below the pectoral fin base, was visible prior to staining.

Features of internal anatomy. – The abdominal region is short (18% SL) and strongly compressed, with gut and surrounding liver lobes clearly visible through the transparent body wall. The gut is long and narrow, making a few distinct loops before ending as a freely protruding distal portion on the right side. The diameter of the gut is nearly uniform along its entire length. Its middle lower part is tilted away from the main body plane at an angle of approximately 90°, creating a distinct three-dimensional appearance (Fig. 2).

The distinctly-curved and strongly-compressed anterior lobe of the liver is found anterior to the gut region, following closely to the outline of the gut. Other liver lobes are visible in between the gut loops. A well-developed network of hepatic veins and ducts is clearly visible in the liver lobes, which is better seen from the right side. The large heart with well-separated oval ventricle and atrium is situated below the pectoral fin base and is partly obscured by the branchiostegal membrane. A small swim bladder is present above the gut approximately in the middle of the abdominal region. The very elongated process of the coracoid runs posteroventrally from below the pectoral fin base and passes between the gut loops (Fig. 2).

Pigmentation. – Elongated longitudinal pigment spots are found along the dorsal and ventral profiles of the two central myomere portions: nine along the dorsal profile and five along the ventral. In addition, smaller pigment spots are present between some of these distinct pigment streaks. Similar elongated pigment spots are found along dorsal and ventral profiles of the outer myomere zones. The head pigmentation
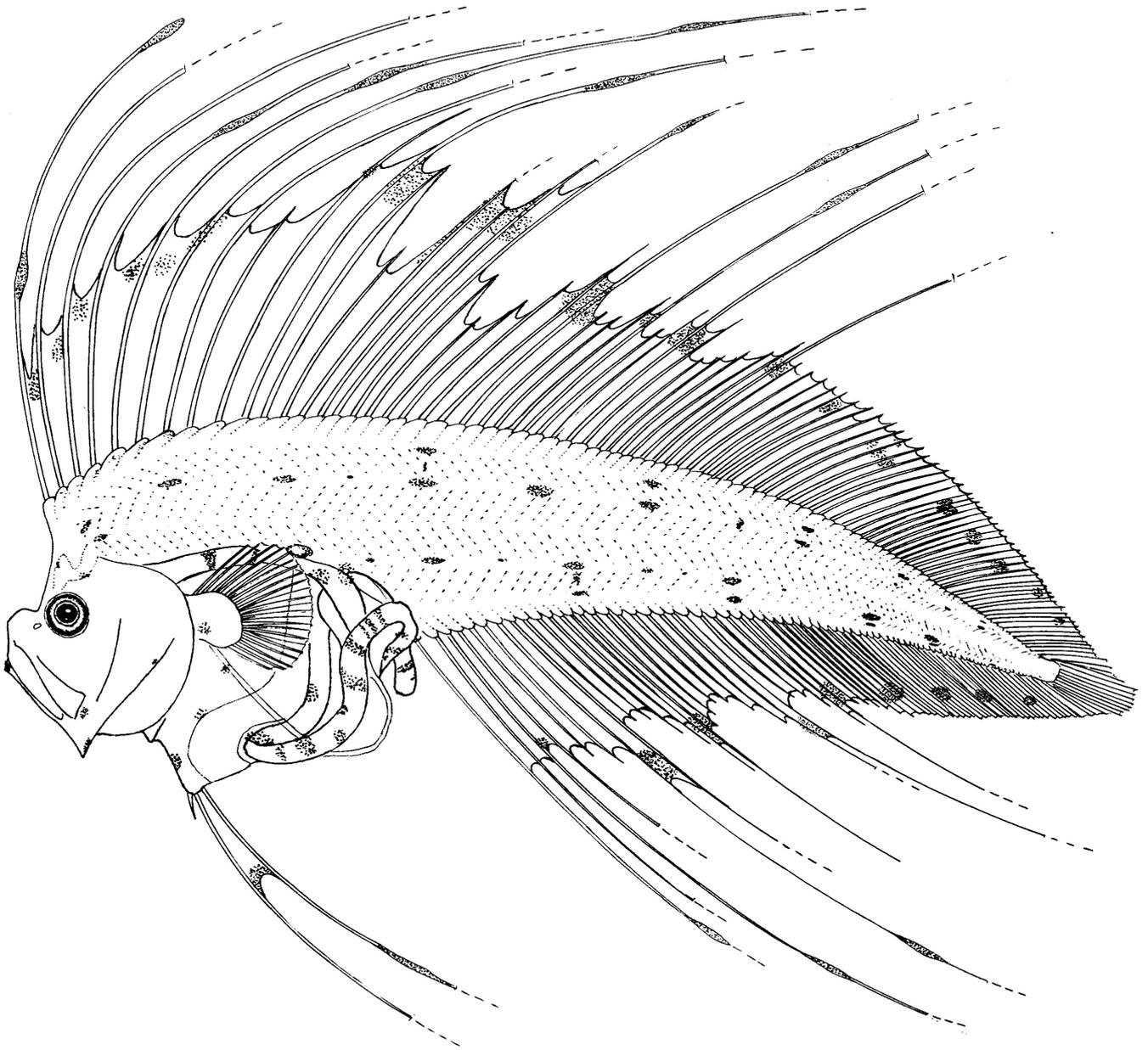
Fig. 1. *Brotulotaenia nielseni* larva, 30.0 mm SL, lateral view.

consists of spots behind the posterior end of the maxilla, on the symphysis of lower jaw, interopercle and retroarticular. Internal head pigmentation consists of small spots above the midbrain, below the anterior portion of hindbrain, near the proximal end of the maxilla and behind the supracleithrum (Figs. 1 & 2).

Gut pigmentation consists of numerous pigment patches and rings of varying widths. Other pigment spots in the abdominal region include pigmentation over the swim bladder, anterior to the pelvic fin base, on the internal surface of pectoral fin bases and two small spots between the anterior lobe of liver and the heart (Figs. 1 & 2).

In addition to pigmented swellings on the elongated rays, pigmentation on the dorsal and anal fins consists of more or less regularly-spaced distinct pigment spots near the margin of the dorsal and anal fin membranes (Fig. 1).

Internal pigmentation of the body consists of a row of small pigment spots along the dorsal surface of the vertebrae. Such spots are found below neural spines 1, 6, 9, 12, 14, 17, 22, 25, 28, 32, 35, 41 and 46.

DISCUSSION

Based on meristic counts and numerous other morphological similarities with published information, this larva is confirmed as *Brotulotaenia nielseni* (Okiyama & Kato, 2002; Fahay & Nielsen, 2003). However, there are certain important differences from previously described material. The most striking feature is the variable length of the rays on the dorsal and anal fins of the present specimen. Fahay & Nielsen (2003) illustrated the morphology of the dorsal and anal fins rays in a 15.5 mm larval *B. nielseni* as being very long anteriorly and decreasing in length posteriorly. Okiyama & Kato (2002) noted extreme elongation of the three anterior-most dorsal rays in the 10.0 mm larva specimen they examined. Notably, their 21.0 mm specimen showed uneven elongation of dorsal

and anal fin rays ending at about the same level as in the larva described presently. All of these rays, however, appear to be broken and the actual ray length could not be inferred. The distal parts of the elongated rays in larval fishes are fragile and are easily broken during collecting. Thus, it is possible that the tips of the elongated rays in the previously illustrated larvae of *B. nielseni* were missing.

Pigmentation in the present specimen also differs significantly from previous reports. The specimen displayed prominent pigment spots along the entire outer margins of the dorsal and anal fins. No such pigmentation was evident in earlier illustrations of *B. nielseni* larvae, although Okiyama & Kato (2002) noted several patches of pigment on the distal portions of the dorsal and anal fin rays/membranes in their largest specimen (69.5 mm SL). In addition, no pigmented swellings on fin rays were reported in earlier descriptions, which could be the result of poor preservation (Okiyama & Kato, 2002; Fahay & Nielsen, 2003).

***Hypothesis on mimetic resemblance in* Brotulotaenia *larvae.* –** Mimicry and crypsis are important evolutionary phenomena and their widespread occurrence in nature suggests that they are of great selective advantage for living organisms (Cott, 1940; Wickler, 1968). Numerous examples of mimicry of inanimate objects such as leaves, sticks, blades of grass, stones and even bird droppings are well-known. They are mainly found in the terrestrial realm and have been documented most extensively in arthropods (Cott, 1940; Edmunds, 1974). Far fewer examples exist among vertebrates (and for fishes in particular) and several reviews summarize the available information mainly from coastal habitats (Randall & Randall, 1960; Randall, 2005).

The epipelagic ocean would seem like a less suitable environment for developing mimetic resemblances to inanimate materials. However, the larval development of the majority of pelagic organisms occurs primarily in this habitat. The defense strategies utilized by animals in this
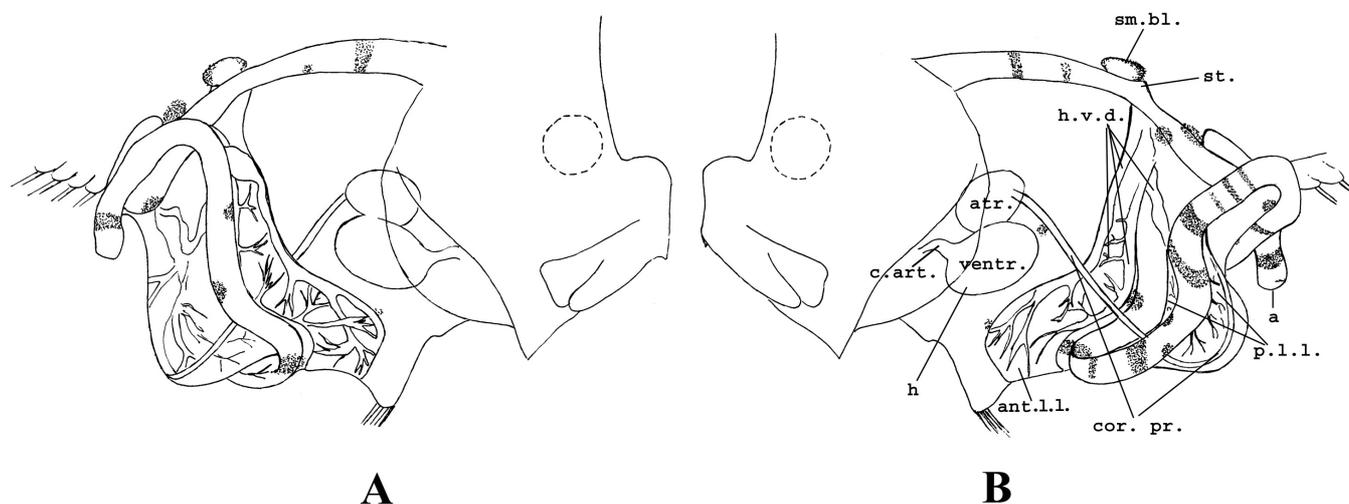

A   **B**

Fig. 2. Morphology of the abdominal region in *Brotulotaenia nielseni* 30.0 mm SL. A) right-side lateral view, B) left-side lateral view. a = anus; ant.l.l = anterior lobes of liver; atr. = atrium; c. art. = conus arteriosus; cor. pr. = ventral process of coracoid; h = heart; h.v.d. = hepatic veins and ducts; p.l.l. = posterior lobes of liver; sm. bl. = swim bladder; st. = stomach; ventr. = ventricle.

homogeneous, three-dimensional environment are rather limited. Numerous planktonic animals have converged on a handful of defensive characteristics, such as small size, invisibility due to tissue transparency, diel vertical migration and exploitation of the sea surface (Zaret, 1975; McFall-Ngai, 1990; Hamner, 1995). For example, numerous fish larvae developing in the productive surface layers are nearly transparent as an adaptation for predator avoidance (Breder, 1962). However, transparency is certainly not a panacea to avoid predation, since some species are well capable of detecting transparent objects via polarized vision (Shashar et al., 1998). Imitation of inanimate objects to escape predators, a method widely-utilized in terrestrial habitats, is practically unknown in the marine pelagic domain. The apparent lack of such examples is likely related to a much lower abundance of non-living matter at sea and also to paucity of inanimate models with conserved shapes and properties, which would be of little interest to a potential predator.

The resemblance of live animals to inanimate objects was once regarded as protective resemblance or crypsis (Cott, 1940), mimesis (Pasteur, 1982), or Batesian mimicry (Wickler, 1968; Wiens, 1978). Subsequently, it was proposed that imitation of inanimate objects by live animals is based on the broadcasting of false information, a fundamental property shared with Batesian mimicry (Robinson, 1981). At present, the imitation of inanimate objects is not regarded as crypsis or camouflage, where a close relationship is established between the mimic and its background, but as masquerade, in which a deception depends on a similarity to a specific object and not the background (Endler, 1981).

The hypothesis in this study is that the unusual Bauplan of larval *B. nielseni* could, in fact, be a passable imitation of a bird feather (a conspicuous, inanimate object with conservative morphology among different species). It is commonly present in the pelagic environment and due to its low nutritional value, should be ignored by active visual predators. As stated earlier, this type of mimetic resemblance conforms to a definition of masquerade rather than crypsis or camouflage and thus should satisfy several theoretical tenets of Batesian mimicry (Endler, 1981). Below, several intrinsic properties of certain bird feathers, making them suitable objects for mimicry are detailed. Similarities of the larval *B. nielseni* to a hypothetical model are also examined and then considered if criteria for Batesian mimicry of the mimic/model system are met.

Of the several distinct types of feathers (e.g., contour feathers, semiplumes, down feathers) present in modern birds, only body contour feathers appear as the appropriate models for the proposed mimetic resemblance. The majority of body contour feathers are symmetrical tapering structures with a distinct central part, the rachis and a broad flat vane on each side. This simple design shows little variation in modern birds. Specialized flight feathers on wings and remiges and rectrices on tail (which are also included in the contour feather category), are unlikely to be such models due to their larger
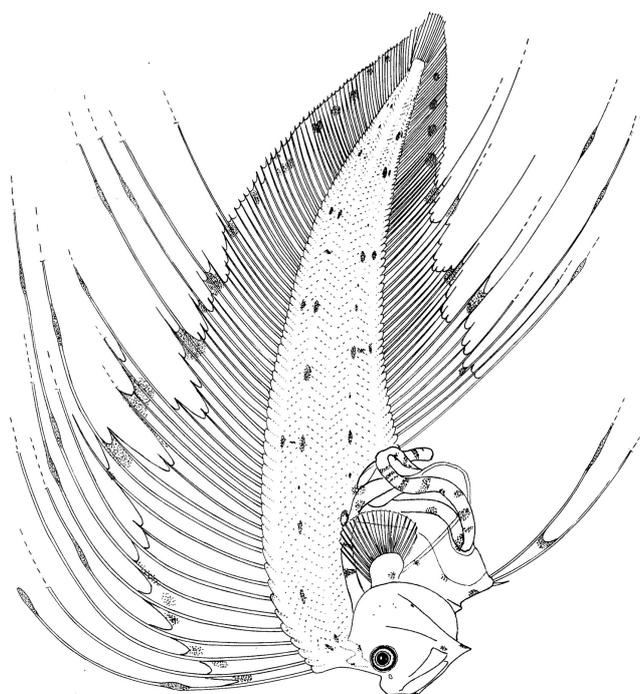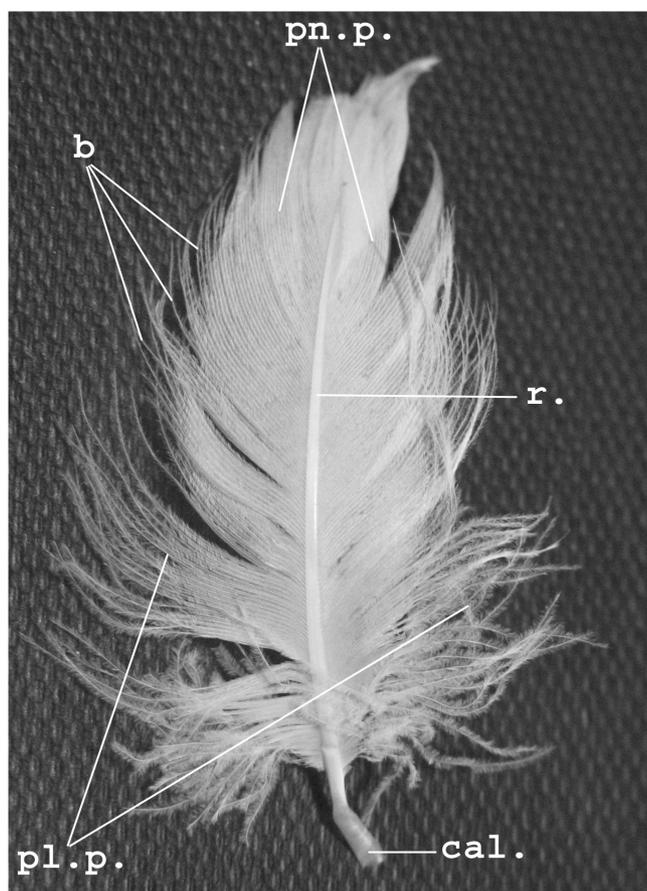

Fig. 3. Comparison of a larva of *Brotulotaenia nielseni* 30.0 mm SL and a contour feather (37 mm) of an unidentified seabird. b = barbs; cal. = calamus; pl.p. = plumulaceous portion, pn.p. = pennaceous portion; r. = rachis.

size, fewer numbers and other morphological features which would be difficult to imitate (e.g., long quill protruding from the anterior end). On the other hand, body contour feathers and some wing coverts in seabirds are much more numerous in number and have size ranges similar to length of the *B. nielseni* larvae prior to metamorphosis, which can grow up to 70 mm (Okiyama & Kato, 2002). The larval specimen of *B. nielseni* described herein resembles a body contour feather in the following characters (Fig. 3):

1) Deep, continuous dorsal and anal fins, matching the position and tapering appearance of vanes attached to rachis. The metameric and oblique dorsal and anal fin rays, incidentally nearly identical to the structure and position of feather's barbs. The extremely compressed body and head rendering the two-dimensional appearance of the model.

2) Narrow and tapering middle portion of the body, distinctly outlined by streaks of pigment is similar to central position of a rachis. The broad semi-transparent pterygiophore and outer myomere zones emphasizing the thicker, central portion of the larval body.

3) Very short and stubby snout, steep dorsal and ventral head profiles and extreme forward displacement of dorsal fin, appearing as a stumpy proximal end of a typical contour feather.

4) Extremely elongated and uneven rays in anterior portions of dorsal and anal fins, resembling the proximal plumulaceous part of a feather, in which elongated barbs of unequal length, not connected by barbules, form a bushy aggregation. The uniform and short posterior rays in the median fins match the distal pennaceous portion of a feather.

5) Symmetrical pigmentation of the body and median fins, emphasizing the bipinnate larval morphology and strengthening the basic outlines of a bipinnate contour feather. Distinct pigmented swellings present in most elongated fin rays, enhancing their visibility and contrast and simulating resemblance to the plumulaceous part of a feather.

Some morphological constraints. – Despite the numerous similarities to the proposed inanimate model (the feather), this larva displayed some morphological features that potentially decrease this resemblance. The abdominal region, devoid of fin rays, represents a clear problem in creating a similarity to a symmetrical bipinnate structure such as a bird feather. In addition to the abdominal region being relatively short, two very elongated pelvic fin rays, similar morphologically and in pigmentation to elongated rays in median fins, could partially obliterate the visual appearance of such a gap.

More interestingly is that this larva, similar to some other larval ophidiiforms, is an example of an exterilium type (*sensu* Fraser & Smith, 1974), with the ventral middle portion of

the gut projecting beyond the lower body profile. In this specimen, this protruding gut part is tilted at about 90º to the main body plane, which is a likely indication of the ongoing process of intestinal shrinkage. At a less advanced stage, this portion of the intestine would seem to extend further from the ventral body profile, thus partially filling the gap between membranous portions of pelvic and anal fins, the condition seen in earlier descriptions (Okiyama & Kato, 2002; Fahay and Nielsen, 2003). When fully extended, this intestinal loop with distinct concentric bands of pigments would extend to the level of the outer margin of the anal and pelvic fin membrane and at such a position, its distinct pigmentation would form a continuous line with the pigment spots present over the distal portions of anal and pelvic fin membrane.

A certain constraint to the proposed mimetic resemblance could also be the color of the model. In general, the plumage of seabirds is less colorful than that of land birds and their colors are mainly white, gray, black and/or brown (Schreiber & Burger, 2001). It is not known how durable the pigments are in a shed feather found in an aquatic environment. Nevertheless, considering that significant color differences are found in feathers of even a single species, it seems unlikely that selection would favor resemblance to just one particular color morph, which would greatly decrease the number of available models. On the other hand, if overall morphological similarity between the model and mimic is at a premium and color information has less significant imprinting value, development of such mimetic resemblance is more likely.

Relevant to the current discussion, are the numerous cases of Batesian mimicry where the similarity between mimic and model is far less than perfect (Edmunds, 2000; Sherratt, 2002). Morphological constraints are not uncommon in the evolution of mimetic relationships, especially if the mimic and model are distantly related. Imitation of inanimate objects by living organisms presents an even more serious challenge. A number of known examples among fishes are often crude versions of their inanimate models (Breder, 1946; Randall & Randall, 1960; Randall, 2005), which probably indicate a less strict selection for precise resemblance in the aquatic environment. Fishes, for example, are less advanced than birds in terms of their sight and memory. However, the outstanding visual capabilities of land birds as predatory organisms still permits the evolution of imperfect mimicry in insects (Dittrich et al., 1993). Thus, the deviation from the "perfect" replica of a model in the marine pelagic environment, where a potential mimic would be subject to scrutiny by aquatic (fishes) or aerial (seabirds) predators, appears to be acceptable.

Batesian mimicry is recognized on the basis of several criteria (Rettenmeyer, 1970):

1) *The model is undesirable or ignored by predators.* Feathers are composed mainly of keratin, an inert and durable biological material with little nutritional value, resistant to break-down by the proteases of microbes and fungi. To date, no known vertebrate species is capable of digesting keratin and no higher animal specializes in the consumption of feathers.

2) *The mimic is desirable to predators*. Larvae of *B. nielseni* probably experience the same high predation rate as any other pelagic larvae. Early fish larvae are highly subjected to invertebrate predation (Baier & Purcell, 1997; Purcell & Arai, 2001). More advanced larval stages experience significant mortality both from opportunistic and specialized feeding by active epipelagic predators such as scombrids and carangids and in particular, the juveniles of these families (Aoki, 1999; Roux & Conand, 2000; Tanabe, 2001; Shoji & Tanaka, 2005). The importance of surface dwelling fishes as prey for seabirds is well known and many species have a high proportion of juvenile fish (less than 8 - 10 cm) in their diet (Ashmole & Ashmole, 1968). In addition, several studies report feeding on fish larvae by diving petrels (Zavalaga & Jahncke, 1997), frigatebirds (Diamond, 1973), black noddies (Ashmole & Ashmole, 1968), storm-petrels (Pitman & Ballance, 1990), terns (Taylor & Roe, 2004) and gannets, which even successfully prey on transparent leptocephali (Figueroa, 1997). In rare cases, some larval fishes possess toxins and are avoided by predators, but these larvae belong to species where the adults are also highly poisonous (Gladstone, 1987). At present, there is no evidence for poisonous species in the Order Ophidiiformes or any other closely related group of fishes. Although the possibility that *B. nielseni* larvae are toxic and are avoided by potential predators cannot be excluded with certainty, the available evidence indicates that this is probably not the case.

3) *The models are more abundant than the mimics*. The larvae of *B. nielseni* are rare in ichthyoplankton collections and this probably reflects a general rarity in the wild as well, since few adults have been reported to date. Thus, Okiyama & Kato (2002) based their description on seven larvae of *B. nielseni*, while Fahay & Nielsen (2003) had only two larvae of this species. On the other hand, numerous species of seabirds are known to form huge colonies and aggregations reaching into millions of individuals (Schreiber & Burger, 2001). Most seabirds molt at least once a year and molting timings vary among different species (Howell et al., 2003). This feature of the avian annual life cycle could be a persistent and significant supply of models (feathers) to the surface of the ocean. In addition to regular molts, some feather loss in seabirds could occur due to other reasons such as during fights over food, preening and grooming.

4) *Both mimics and models are found in the same place and time*. The geographic co-occurrence of models and mimics is self-evident, considering the widespread tropical-subtropical distribution of *B. nielseni* in the Indo-Pacific and the numerous and abundant seabird species found in same area. Due to their high surface area to volume ratio, light weight and poor wettability, feathers are likely to be carried for long distances either by currents or wind, contributing to their long-range dispersal. These same properties would also contribute to their slow sinking rates, ensuring their long-term presence in the upper levels of water column, the predominant habitat of larval fishes. Although the exact vertical distribution of *B. nielseni* larvae is not known due to the current paucity of records, it appears that development takes place in the upper levels of the water column. The specimen described herein was
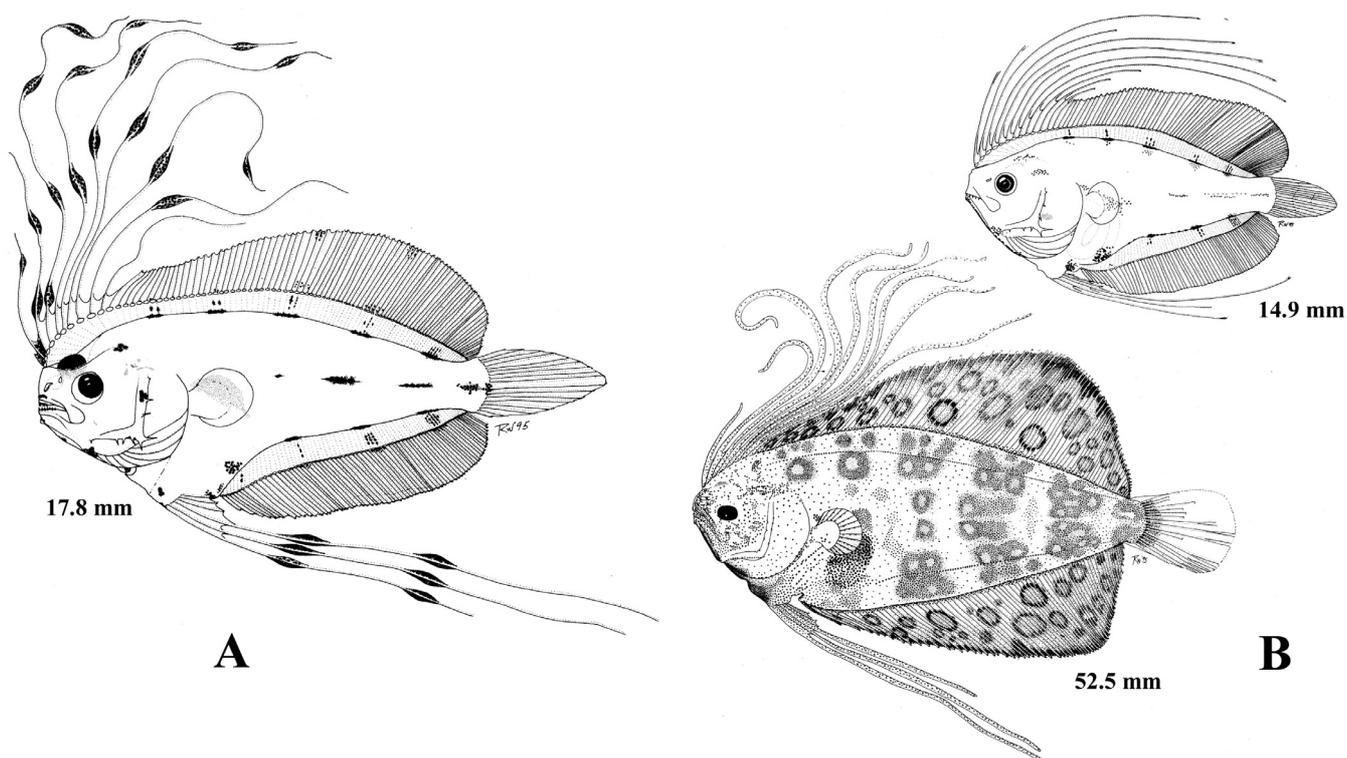

Fig. 4. Possible convergence towards mimetic resemblance of certain bird feathers in some pleuronectiform larvae. A) *Cyclopsetta panamensis,* 17.8 mm SL, B) *Cyclopsetta querna,* 14.9 and 52.5 mm SL (from Moser & Sumida, 1996).

collected by plankton net sampling in the upper 10 m of the water column. Okiyama & Kato's (2002) larvae were collected with oblique tows in surface waters down to depths 354 m. More collections are clearly needed to determine exact vertical range of larval *Brotulotaenia*.

5) *Both mimic and model are conspicuous or readily seen by potential predators*. The extremely compressed, leaf-like body of larval *B. nielseni* is probably an indication that the larva is semi-transparent in life. However, its characteristic pigmentation, with numerous melanistic streaks and patches found on its body, head, fin membrane and free-ending parts of the fin rays accentuates the larval outlines and generally does not seem to promote transparent camouflage. The characteristic white color in many seabirds is in fact a "structural coloration", produced by reflection of light by irregularly spaced air-filled cavities and not by presence of pigments. Such "whiteness" would be less apparent in a medium with a different refractive index than air and a feather found in the water will likely appear less conspicuous and probably semi-transparent (Tickell, 2003). On the other hand, melanistic pigments in dark feathers would make them more conspicuous underwater. Although the conspicuousness of such models underwater is difficult to quantify, their two-dimensional, delicate structure will also likely render the models (feathers) semi-transparent. Nevertheless, considering the good visual capabilities of potential predators (epipelagic fishes and birds), the detection of such objects is probably not a problem.

6) *The predators learn or associate undesirability with appearance of the model*. This tenet is currently open and unsubstantiated for the hypothesized type of mimetic resemblance, as it would require experiments and detailed observations.

Some anatomical features of the larva (such as a very long undifferentiated intestine) are probably indicative of its opportunistic feeding habits. This is also a feature not in disagreement with the hypothesized passive lifestyle of the larvae. Observations of live larvae could yield more information relevant to the current hypothesis. Thus, if the larva's similarity to the proposed inanimate object is not incidental, some characteristic behaviour of the mimic is likely to be present. Freezing or very little movement would be expected responses in such larvae if threatened or in the presence of potential predator.

CONCLUSIONS

Interestingly, there are a number of pronounced morphological similarities between some strongly compressed larval ophidiiforms and larvae of certain flatfishes. Such similarities are often so significant that ophidiiform larvae have been mistakenly identified as pleuronectiforms (Nielsen, 1963; Fourmanoir, 1976). Certain larvae in both Orders share characteristics such as strongly compressed elongate bodies, continuous long dorsal and anal

fins, narrow abdominal regions, long and convoluted intestines, short heads and exterilium guts (Ahlstrom et al., 1984; Gordon et al., 1984). Basic morphological similarity can possibly result in convergent evolution towards similar protective resemblances. In fact, the shared larval Bauplan in both unrelated groups could simply be a suitable pre-adaptation for the development of mimetic resemblance to the symmetrical bipinnate structure of a bird feather.

Several pleuronectiform larvae are surprisingly similar in their external morphology to larval *Brotulotaenia nielseni* described herein (Fig. 4). The most striking similarity is found with the larvae of *Cyclopsetta panamensis* (Moser & Sumida, 1996), especially the specimen 17.8 mm SL (CALCOFI, TO 61-01, Station 32). Apart from the similarity in general body shape, the larvae of *C. panamensis* display extreme elongation of the anterior dorsal fin rays, coupled with similarly elongated pelvic fin rays, which also bear very distinct, pigmented swellings. Body pigmentation, consisting of elongated pigment streaks, as well as round patches of pigment on the dorsal fin membrane, appears to be very similar to pigmentation of *B. nielseni* larvae. Larvae of *C. querna* are also characterized by pronounced elongation of the anterior dorsal and pelvic fin rays. However, this species displays rather different pigmentation and lacks pigmented swellings in fin rays (Moser & Sumida, 1996).

Brotulotaenia larvae reach a significant size prior to metamorphosis (between 62 and 78 mm) (Fahay & Nielsen, 2003). This feature is probably indicative of the long pelagic duration and is concurrent with the very broad geographic distribution of *B. nielseni*. However, prolonged existence in the epipelagic habitat increases the exposure to potential predators and the possibility of a successful predation event. A number of teleost larvae with long pelagic durations and large sizes prior to metamorphosis display unconventional morphologies and larval specializations to possibly counter predation effects. Some examples include the leaf-like bodies and high-transparency in certain bothids (Amaoka, 1971) and anguilliforms such as *Talassenchelys* type leptocephali (Castle & Raju, 1975). Another specialization is the extreme development of spines in the fins and on head bones in larval acanthurids, holocentrids, epignepheline serranids and other larvae (Moser, 1981). Some larval ophidiids (Fraser & Smith, 1974; Moser, 1981) and serranids (Hubbs & Chu, 1934; Baldwin et al., 1991; Suntsov, 2005) might possibly mimic the stinging tentacles of pelagic coelenterates. Mimicry of inanimate objects could be yet another strategy to increase chances for survival in the epipelagic habitat.

Alternatively, more conventional interpretations are possible for the spectacular morphology of larval *B. nielseni*. However, it is expected that the remarkable morphological diversity in marine teleost larvae allows for the evolution of less common types of defense (e.g., the type of mimetic resemblance proposed here). A greater emphasis on functional morphology and adaptive significance of unusual larval morphotypes is desirable in future studies if we are to better understand the ecology of the epipelagic zone, intra- and interspecific interactions of the pelagic biota and the diversity of anti-predator adaptations available during early ontogeny.

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LITERATURE CITED

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