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Article

Development and Length Frequency Distribution of Larvae of Some Mesopelagic Fishes Near Coral Reefs in the Red Sea

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Abstract: This work aims to describe the early life history and the length frequency distribution of larval stages of three mesopelagic species collected near coral reef areas in the Red Sea. Larvae were collected monthly using a plankton net (500 μ) from three coastal coral reef areas surrounding Sharm El-Shekikh on the Egyptian Red Sea coast between January and December 2015. The identification of larvae was based on the author's experience and other literature. The larvae of this species were divided into preflexion, flexion, and postflexion based on the flexion of the notochord and they were also categorized according to their size into relevant size classes. Mesopelagic fishes were represented in the collection by four species belonging to four families; *Vinciguerria mabahiss* (Family: Phosichthyidae), *Benthosema pterotum* (Family: Myctophidae), *Astronesthes martensii* (Family: Stomiidae; subfamily: Astronesthidae) and *Trichiurus* sp. (Family Scombridae). In general a total of 3678 larvae were collected, of which 1191 belonged to mesopelagic species. The most abundant species was V. *mabahiss* with 677 larvae that constituted 18% of total larvae collected. The second most abundant species was *B. pterotum* that was represented by 485 larvae (13%). *A. martensii* was represented by the lowest number of larvae (29 larvae, 2%). Most larvae of the three species were in preflexion stage and more abundant in the cooler months of the year between November and April. The high number of preflexion larvae at the time may indicate the spawning of the three species in the colder times of the year.

Keywords: mesopelagic fish; larvae; development; Red Sea; spawning

Key Contribution: The breakthroughs or highlights of the manuscript. Authors can write one or two sentences to describe the most important part of the paper.

1. Introduction

Mesopelagic (or midwater) fish live in the intermediate pelagic water masses between the euphoric zone at 100 m and the deep bathypelagic zone at 1000 m where no light is found (Kaiser et al., 2011; Clavel-Henry et, 2020). Most mesopelagic species undergo vertical migration into the epipelagic zone at night to feed and later return to mesopelagic depths during the day (Olivar et al., 2012).

Mesopelagic species are the most abundant marine vertebrates in the world oceans (Mann, 1984) with a total biomass of billions of tons of which about 300 million tons occur in the Indian Ocean. These estimates represent approximately 10 times the biomass of the world's total fish catch. Due to the high proportion of wax-esters of limited nutritional value, however, only a few species, such as *Benthosema glaciale* in the Oman Sea (Valinassab et al., 2007), are potentially abundant enough for commercial purposes. Although most species lack commercial importance, mesopelagic fishes play essential roles in the ocean's pelagic and benthic food webs and are able to affect the dynamics of their zooplankton prey (Williams et al., 2001; Saunders et al., 2019), and predators, such as some commercially important pelagic fishes (Würtz, 2010), marine mammals (Giménez et al., 2017), seabirds (Barrett et al., 2002), and benthic predators (Herring, 2002), and are important in transferring energy between ocean ecosystems.

Due to their small size, mesopelagic fish are characterized by low fecundity, and average from a few hundred to few thousand eggs over the spawning season. Most species are oviparous with plankton eggs and larvae and some exhibit batch-spawning characteristics (i.e., spawn eggs in batches over several months). Eggs are released either during the day in mesopelagic waters, or at night in the epipelagic zone where larvae hatch and may remain until metamorphosis during which the light organs or photophores develop; thereafter, they return to deeper water juvenile and adult habitat. Some mesopelagic species are distributed worldwide, and many are circumpolar, especially in the Southern Hemisphere (Salvanes and Kristofersen, 2001).

Much of the research on the distribution and natural history of mesopelagic fishes was conducted in the 1970s' when FAO (Food and Agriculture Organization) searched for new unexplored commercial resources. Interest in mesopelagic fishes has been renewed since the 1990's after the discovery that the sound-scattering layers (SSL's) in the ocean was high densities of mesopelagic species, which formed the basis for studies of the life history and adaptations of mesopelagic fish in the context of general ecological theory.

Investigations of the midwaters of the Red Sea have shown that the deep-water fauna in general is quite limited (Marshall, 1963; Marshall and Bourne, 1964; Aron and Goodyear, 1969; Halim, 1969; Weikert, 1982) due to the unusually isothermal structure of the waters below the sill level that makes the Red Sea unsuitable for all but a very few adaptable species.

Sixteen species of mesopelagic fish occur in the Red Sea (Table 1) with little known about their spawning seasonality. This work aims to describe the developmental stages of three mesopelagic species whose larvae are abundant near coral reefs in the Red Sea. Larvae of two species, *V. mabahiss and A. martensii* are described for the first time.

Table 1. Orders, families, and species of mesopelagic fish in the Red Sea.

Order	Family	Species
Stomiiformes	Phosichthyidae	*Vinciguerria mabahiss* Johnson & Feltes 1984
	Stomiidae Subfam: Astroneshthinae	*Astronesthes martensii* Klunzinger 1871
	Subfam: Stomiinae	*Chauliodus sloani* Bloch & Schneider 1801
		Stomias affinis Günther 1887
	Sternoptychidae	*Maurolicus mucronatus* Klunzinger 1871
Myctophiformes	Myctophidae	*Benthosema fibulatum* (Gilbert & Cramer 1897)
		Benthosema pterotum (Alcock 1890)
		Diaphus coeruleus (Klunzinger 1871)
Ateleopodiformes	Ateleopodididae	*Ateleopus japonicus* Bleeker 1853
Scombriformes	Trichiuridae	*Evoxymetopon moricheni* Fricke, Golani & Appelbaum-Golani 2014
		Tentoriceps cristatus (Klunzinger 1884)
		Trichiurus auriga Klunzinger 1884
		Trichiurus lepturus Linnaeus 1758
	Gempylidae	*Thyrsitoides marleyi* Fowler 1929
Aulopiformes	Paralepididae	*Lestidiops jayakari* (Boulenger 1889)
		Lestrolepis luetkeni (Ege 1933)

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2. Material and methods

2.1. Study area

The present study was carried out at three coastal sites along Gulf of Aqaba coast (Figure 1), Naama Bay (NAM), Sharm El-Maya Bay (SMB) and Port Bay (PRT), each with different ecological conditions. Naama Bay is located approximately 15 km south of the Strait of Tiran at 27° 55' N and 34° 20' E with a maximum depth of 100 m and is exposed to touristic stress from its many resorts, sailing, and diving activities. This bay is bordered by a fringing reefs characteristics of the Red Sea. Sharm El-Maya Bay is a semi-enclosed bay at 27° 51.8' N and 34° 18.1' E and is divided into two water bodies, a small, near-shore, sub-tidal area (mean depth: 9 m) and a larger area with a maximum depth of 90 m connected to the Red Sea through an opening 200 m wide. The bottom is covered mainly with seagrass patches. Port Bay lies at the entrance of Sharm El-Sheikh City at 27° 51' N and 34° 16.7' E with a maximum depth of 35 m and is subjected to less stress by tourism and other human activities than the other two sites. Borders of this bay are characterized by coral reefs whereas the bottom is sandy with many reef and seagrass patches.

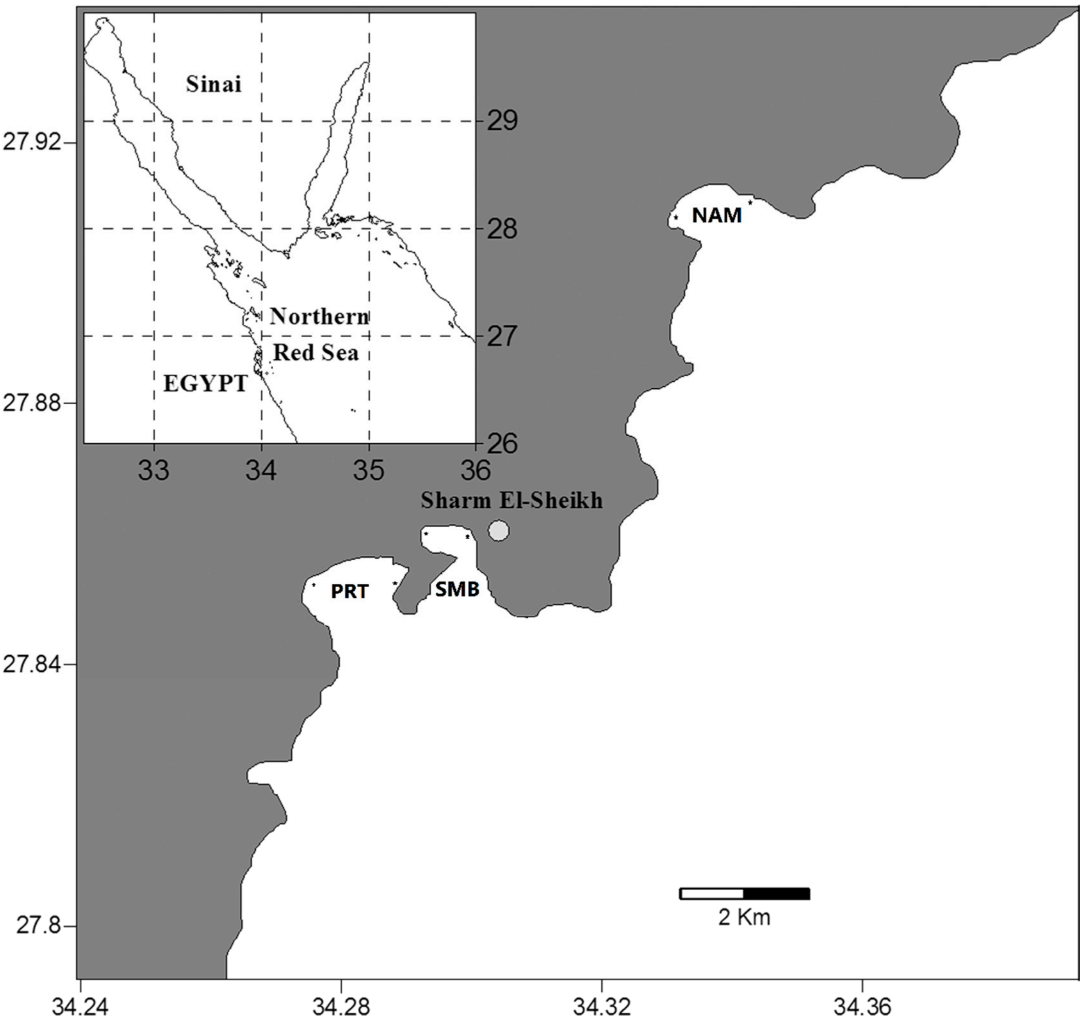


Figure 1. Sampling sites of fish larvae.

2.2. Field work

Each site was sampled with a 100 cm mouth diameter and 500 µm mesh plankton net. The net was hauled horizontally parallel to the reef with the top of the net at the water's surface for 10 minutes at a speed of 1.5 to 2.5 knots. Two stations were sampled monthly with three replicates each site from

January to December 2015, which resulted in collection of 216 plankton samples. The sampling process was conducted in the morning just before sunrise and in the afternoon just before sunset. A flowmeter fitted in the mouth of the net was used to estimate the volume of water filtered, which was calculated. Samples were fixed in buffered 5% formalin solution in seawater on board ship and later preserved in 90% ethanol for further examination in the laboratory.

2.3. Laboratory work

The samples were examined under a stereomicroscope and larvae were sorted and separated by group. The larvae of mesopelagic fishes were separated, counted, and measured under the stereomicroscope with an eyepiece micrometer. Measurements were expressed as proportions of the body length (BL) and rounded to the nearest 0.1 mm. Here, we consider BL equivalent to standard length (SL) and use both interchangeably. Larvae were identified to species level, where possible, using relevant identification guides (Abu El-Regal, 2000 and 2008), and were divided into preflexion, flexion and postflexion stages based on degree of notochord flexion. Larvae were placed in separate labeled vials by life stage and preserved in 70% ethanol for further examination and description.

2.4. Data analysis

Abundance of fish larvae was expressed as number of larvae in 1000 m^3 based on the following equation:

$$A=N/V$$

where ‘A’ is the abundance of larvae of a given taxon; ‘N’ is the number of larvae of said taxon collected; and ‘V’ is the volume of water filtered. A correlation between the standard length and other measurements was tested by SPSS 22. Univariate statistics were done in SPSS 22 using analysis of variance (ANOVA) to determine differences in number of individuals and number of species between months and sites. All data were tested for homogeneity of variance. Where the samples were not homogeneous, data were either transformed or the non-parametric Kruskal-Wallis test was used (Zar, 1999; Dytham, 2003). Graphs were illustrated in GraphPad Prism 8.

2.5. Ethical statement

Samples are collected by plankton net, and they are only plankton samples and there are no rules to follow.

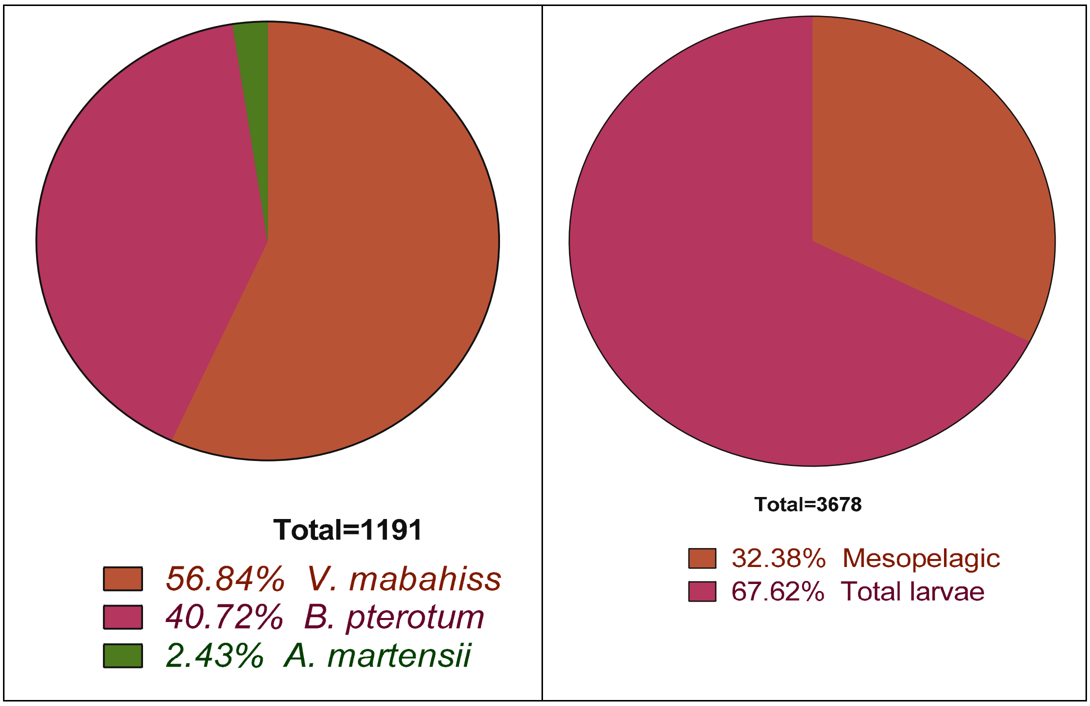
3. Results

3.1. General abundance of larvae of mesopelagic fish

Mesopelagic fish in the current study were represented by four species in four families and three orders, Stomiiformes, Myctophifiormes, and Scombriformes. Order Stomiiformes was represented by two species in two families (Phosichthyidae, *V. mabahiss*, and Stomiidae, *A. martensii*). Order Myctophiformes was represented by *B. pterotum* (Myctophidae). Scombriformes were represented by one family, Trichiuridae, and one species, likely *T. auriga*. The larvae of mesopelagic fishes constituted about 32% of all larvae (1191 of 3678 total larvae collected). The most abundant mesopelagic species was *Vinciguerria mabhaiss* with 677 larvae, which represents 18% of all fish larvae collected and 57% of larvae of mesopelagic species, followed by *Benthosema pterotum* with 485 larvae (13% of all larvae and 41% of all mesopelagic larvae) (Table 2). The larvae of *Astronesthes martensii* (n = 29) accounted for 2% of all mesopelagic larvae (Figure 2). A 5 mm trichiurid larva (likely *Trichiurus auriga*) was also collected in Sharm El-Maya Bay during July but was excluded from further analyses.

Table 2. General abundance of larvae of mesopelagic fish from Sharm El-Shaeikh during the sampling period from January to December 2015.

Month	*V. mabahiss*			*B. Pterotum*			*A. martensii*		
	NA	MPR	TSMB	NA	MPR	TSMB	NA	MPR	TSMB
Aug	0	0	0	0	2	6	0	0	0
Sep	2	0	0	0	0	0	0	0	0
Oct	0	0	0	0	0	0	0	0	0
Nov	39	68	93	0	15	11	0	0	0
Dec	42	33	32	9	10	2	5	1	2
Jan	3	117	108	4	195	82	1	7	11
Feb	9	7	53	4	9	50	0	0	0
Mar	0	0	0	0	0	5	2	0	0
Apr	14	28	29	0	55	24	0	0	0
May	0	0	0	0	0	0	0	0	0
Jun	0	0	0	0	1	0	0	0	0
Jul	0	0	0	0	1	0	0	0	0
Sum	**109**	**253**	**315**	**17**	**288**	**180**	**8**	**8**	**13**



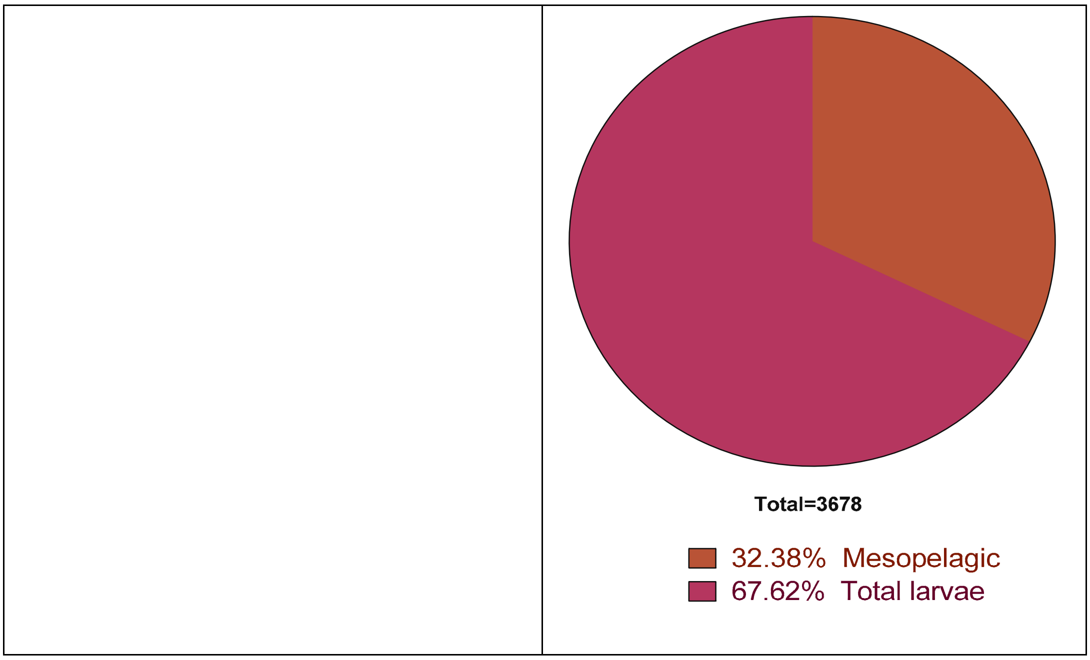


Figure 2. Percent contribution of mesopelagic larvae to all fish larvae collected.

The ANOVA showed that the abundance of *V. mabahiss* differed significantly among months (F=4.94, P<0.05), but not among bays (F=0.89, P>0.05). The abundance of *B. pterotum* also differed significantly among months (F=4, P<0.05), but not among bays (F=1.2, P>0.05), as did *A. martensii* among months (F=2.4, P<0.05), but not among bays (F=0.1, P>0.05).

3.2. *Vinciguerria mabahiss*

3.2.1. Description of larvae

The larvae are elongate with 37-39 myomeres and have a long gut (70%-80% BL). The head has an elongated snout, large mouth, and elliptical eye; larvae also lack fin and head spines (Table 3). Preflexion larvae of 5 mm have pectoral and pelvic fin buds, but lack anlage in the dorsal, anal, and caudal fins. Head length is about 20% BL, and body depth is 8% BL at this size (**Figure 3, Table 4**). Notochord flexion occurs between 6 mm and 7 mm, after which early postflexion larvae have a well-formed caudal fin. By 8 mm, rays begin to develop in the dorsal fin. By about 9 mm, rays begin to develop in the anal fin, which originates below mid-base of the dorsal fin; canine teeth are also visible in both jaws at this size, but pectoral fin rays remain undeveloped. Larvae also have pigment at the base of the caudal fin (hypurals area), and three melanophores along the ventral margin of the caudal peduncle. By 12.5 mm, the dorsal and anal fins have 14 rays each, and rays are developing in the pectoral fins. At this size, *V. mabahiss* typically have a melanophore above the cleithrum, one above the hindgut near the vent, one to three melanophores along the ventral margin of the caudal peduncle, and pigment dorsally above the caudal fin base.

Table 3. Meristics of mesopelagic species collected from the Red Sea.

Meristics	***V. mabahiss***	***B. pterotum***	***A. martensii***
Myomeres	37	30	50
Preanal	25	19	35
Postanal	12	11	15
Doral fin spines	0	0	0
Doral fin rays	13	12	10-21*
Anal fin spines	0	0	0
Anal fin rays	13	18	12-22*

Pelvic	7	8	5-9*
Pectoral	10	19	5-9*
Caudal	19		NA

*Moser, 1996.

Table 4. Morphometrics of the mesopelagic species collected from the Red Sea.

	V. mabahiss		*B. pterotum*		*A. martensii*	
	Preflexion	**Postflexion**	**Preflexion**	**Postflexion**	**Preflexion**	**Postflexion**
Snl/HL	37%	33-40%	33-40%	25-30%	25%	30%
ED/HL	25%	22-26%	33-40%	16-20%	18%	35%
HL/BL	26%	16-20%	20-25%	25-26%	16%	36%
PAL/BL	83%	74-77%	50-60%	55-60%	trailing gut	trailing gut
PDL/BL	---	61-63%	---	44-50%	----	61%
BD/BL			13-15%	15-17%	%	6%

Snl, snout length; ED eye diameter; HL, head length; PAL, Preanal length; PDL, predorsal length; BD, body depth; BL, body length.

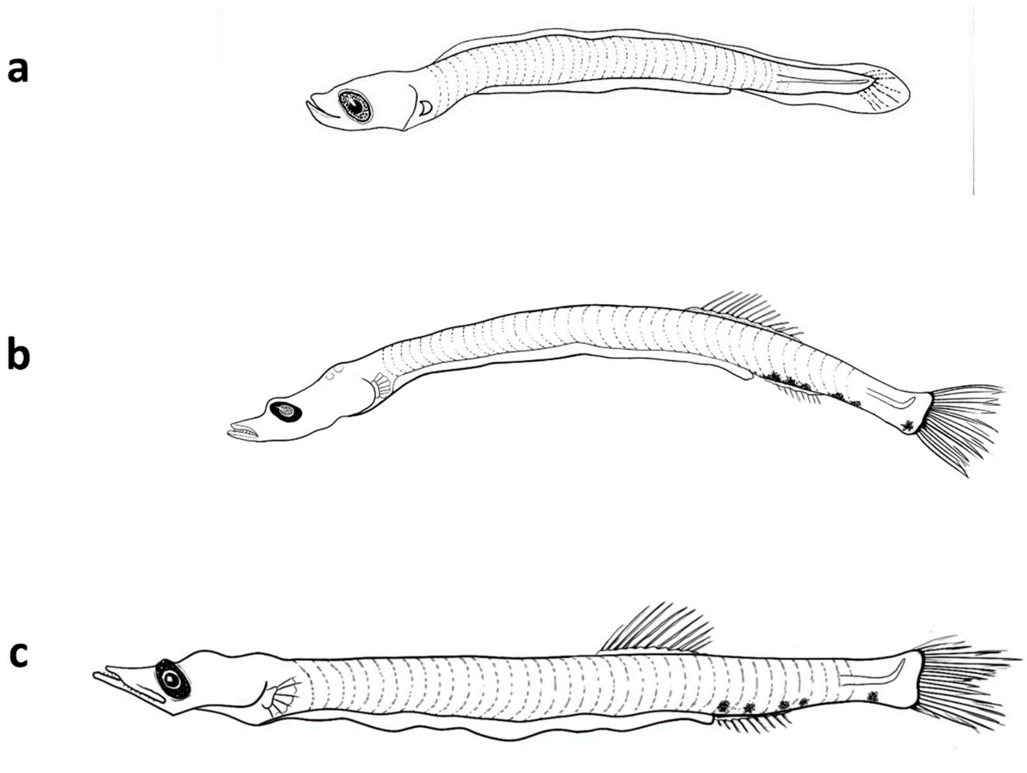


Figure 3. Larvae of *V. mabahiss* collected form the Red Sea. A.5 mm, B. 9 mm, C. 13 mm.

Distinguishing characters of *V. mabahiss* include an elongate body; elliptical eyes and duck-like snout; the anal fin originates below the middle of the dorsal fin base; myomere count of 37-39; and unusual pigmentation pattern. *V. mabahiss* can be confused with larvae of members of Clupeiformes; however, clupeids and engraulids have round eyes and a longer preanal length (typically >80% compared to <80% in *V. mabahiss*) and differ in pigmentation pattern and in the relative positions of the dorsal and anal fins. Clupeids and engraulids also lack the canine teeth of *V. mabahiss*. Larvae closely resemble those of *V. nimbaria* (Ahlstrom et al., 1984; Watson, 1996a), which occur in the Indian Ocean, but not Red Sea.

The study of morphometrics showed that the ratios of head length (HL), body depth (BD, preanal length (PAL) and pre-dorsal length (PDL) increase linearly with the standard length (Figure 4, Table 4).

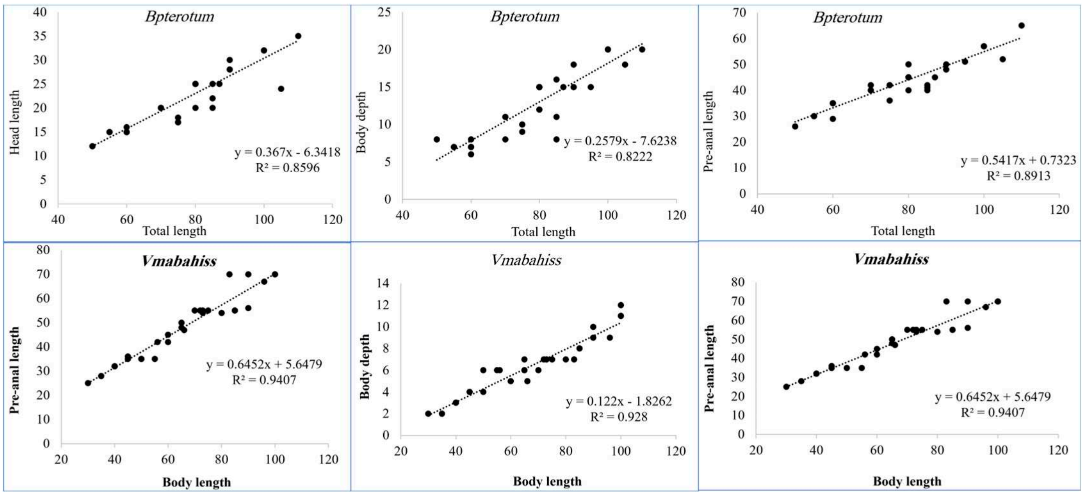


Figure 4. Morphometrics of *V. mabahiss* and *B. pterotum* collected from the Red Sea.

3.2.2. Abundance and spawning season of V. mabahiss

Larvae occurred in 39% of all samples collected and were the most abundant larvae of any mesopelagic species collected with an overall abundance of 19/1000 m^3). Larvae occurred mostly during the cooler months from November to April with peaks of abundance during November (200/1000 m^3) and January (228/1000 m^3). Larvae were rare in September (2/1000 m^3) and totally absent during the summer month (June-August) and in October and March. Larvae were collected at all sites sampled but were most abundant in Sharm El Maya Bay (315/1000 m^3) and least abundant in Naama Bay (109/1000 m^3). Larvae reached their maximum abundance in Port Bay (PRT)in January (192/1000 m^3) and Sharm El-Maya Bay (SMB) in November (140/1000 m^3) (Figure 5).

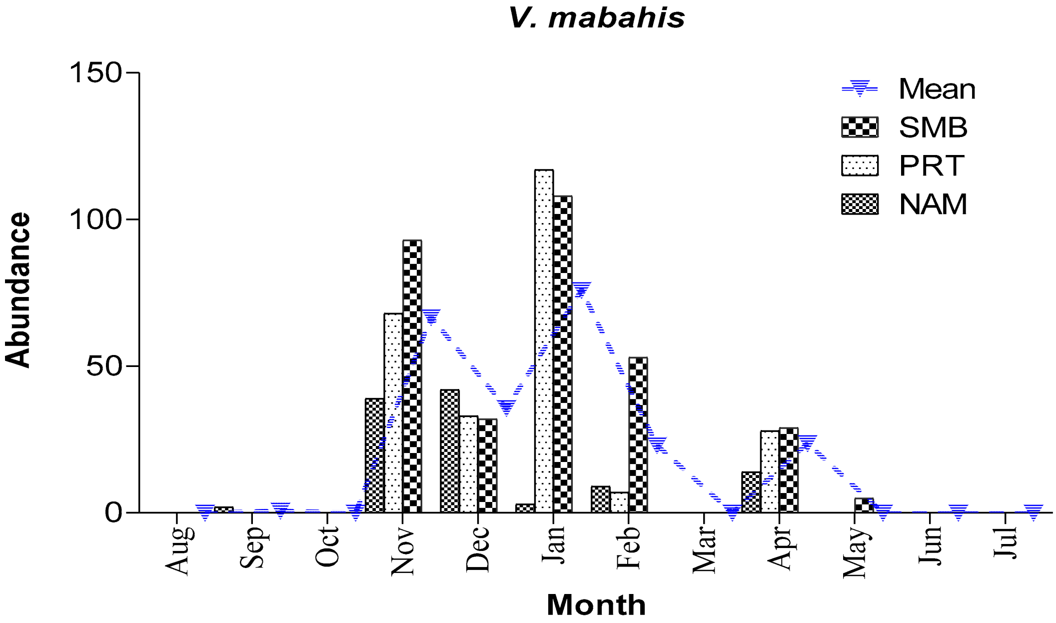


Figure 5. Mean monthly abundance of *V. mabahiss* (number/ 1000 m^3) at different bays throughout the sampling period.

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3.2.3. Length frequency distribution of V. mabahiss larvae:

The larvae of *V. mabahiss* occurred primarily from September through May with a total of 339 larvae collected (Figure 6) *V. mabahiss* larvae ranged in size from 3 to 13 mm SL and were divided into six size classes at two-millimeter (mm) length intervals: I: 3-4.9 mm; II: 5-6.9 mm; III: 7-8.9 mm, IV: 9-10.9 mm, V: 11-12.9 mm; and VI: 13-14.9 mm. Overall, most larvae were preflexion stage (Figure 6) with size classes I-III (<8.9 mm) accounting for about 97% of all *V. mabahiss* larvae collected, while larvae >8.9 mm only contributed 3%. Although *V. mabahiss* larvae collected in November (n = 119) ranged in size from 3 to 10.9 mm SL, most were in size classes I or II with one larva > 9 mm SL. December contained 66 larvae between 3 and 8.9 mm SL, but 48% were in the two smallest size classes, while January collections contained 86 larvae between 3 and 12.9 mm SL with 48% in size class II (5-6.9 mm); 9% of *V. mabahiss* larvae collected in January were >8.9 mm SL (Figure 6). During February, 89% of all larvae were in size classes I and II (<6.9 mm) with two larvae in the largest between 13 and 14.9 mm SL. Of the 22 larvae collected in April between 3- and 10.9-mm SL, 86% were <4.9 mm SL. All larvae collected in May (n = 5) were <4.9 mm SL. Collection of larvae <4.9 mm SL during all months in which *V. mabahiss* occurred suggests that spawning may have occurred near the reef at those locations.

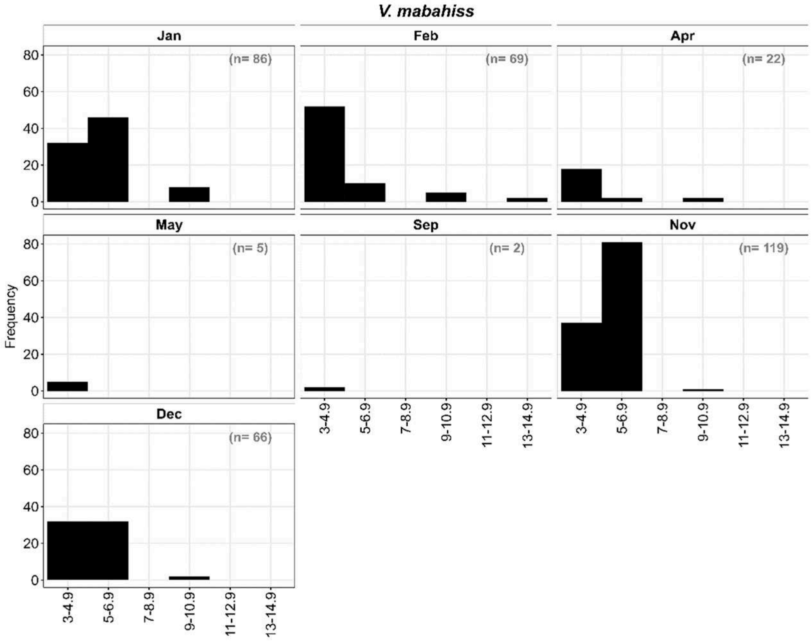

Figure 6. Length frequency distribution of *V. mabahiss* larvae.

3.2.4. Description of larvae

The larvae of *Astronesthes martensii* ranged in size from 6 to 13.5 mm SL with all larvae <8 mm preflexion stage. In general, larvae of *A. martensii* are elongate and moderately slender with >50 myomeres, and have a small head with small elliptical eyes, and both jaws have fang-like teeth. The long gut extends about 70% SL and the posterior portion of the hindgut trails the body. The finfold along the dorsal and ventral margins of the body are peppered with small melanophores, and stellate, brown melanophores line the dorsal and ventral margins of the tail and extend forward onto the trunk. Head length is about 16% SL and body depth about 6% SL. Notochord flexion begins at about 8 mm and is completed by 13.5 mm when the caudal fin is well-formed, and the dorsal and anal fins are beginning to form; however, the pectoral fins still lack rays. The anal fin originates well behind the dorsal fin and is slightly longer than the dorsal fin base (Figure 7). The larvae of *A. martensii* are distinguished from those of other mesopelagic fish in the Red Sea by the trailing gut, finfold pigmentation, relative position of the dorsal and anal fins, and high myomere count.

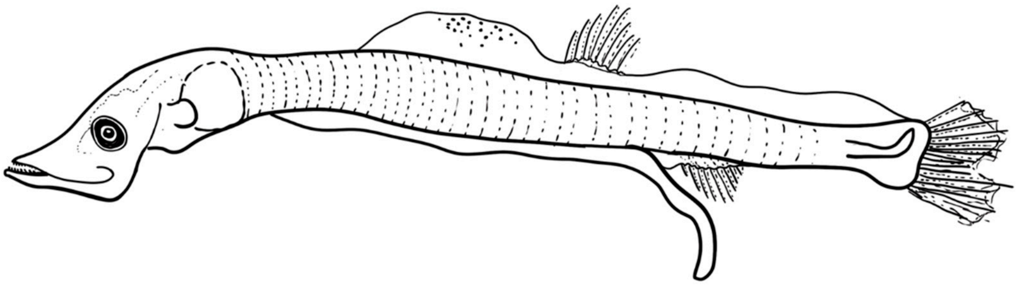

Figure 7. Larvae of *A. martensii* collected from Sharm El-Sheikh during the sampling period.

3.2.5. Abundance and spawning season of A. martensii

To our knowledge, information on the spawning seasonality of *A. martensii* has not been reported, until now. All 29 larvae were collected during December, January, and March with a peak in January (Figure 8), whereas March samples contained only two larvae. A. martensii accounted for <2% of all larvae of mesopelagic fishes, at a mean overall abundance of 1/1000 m^3. Larvae occurred in all bays sampled but were most abundant in SMB (Figure 8). Even though collections contained few larvae, our data suggest that *A. martensii* spawn during the winter months, although we cannot exclude the possibility that they may also spawn during other months and seasons.

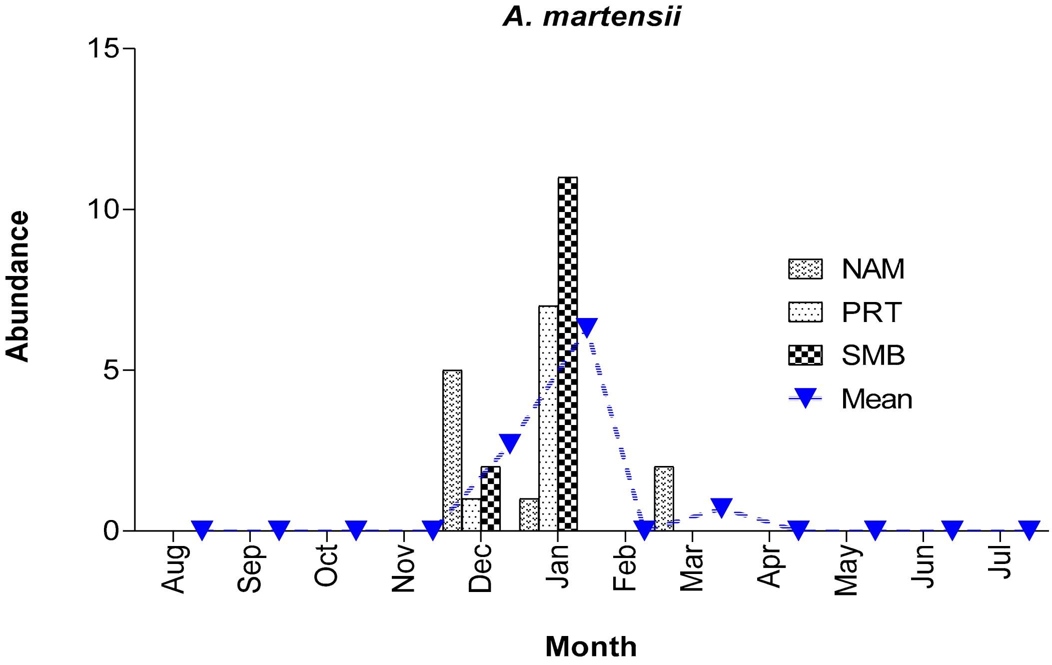

Figure 8. Mean monthly abundance of *A. martensii* (no/1000 m^3) at different bays throughout the sampling period.

3.2.6. Length frequency distribution of A. martensii

Larvae were divided into four size classes at two mm length intervals: I: 6-7.9 mm; II: 8-9.9 mm, III: 10-11.9 mm, and IV: 12-13.9 mm SL with most preflexion larvae in the smallest size class. December collections contained eight preflexion larvae, as were 15 of 19 larvae collected in January. Both larvae collected during March, however, were between 12- and 13.9-mm SL, which is also consistent with primary spawning during the winter months (Figure 9).

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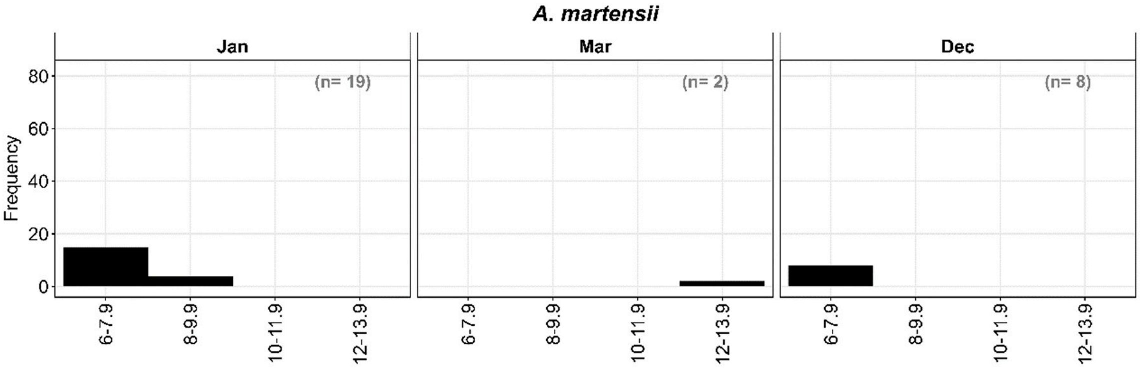

Figure 9. Length frequency distribution of *A. martensii*.

3.3. *Benthosema pterotum*

3.3.1. Description of larvae:

The larvae of *B. pterotum* (Figure 10) have robust bodies, elliptical eyes with a small, lunate choroid mass ventrally, a sigmoid-shaped gut with transverse mucosal folds that extend to mid-body. A gap between the anus and anal fin origin closes between 9- and 10-mm SL as the anal fin develops. The body becomes shorter and deeper as larvae develop, and the gut narrows posteriorly. The sequence of fin formation is as follows: pectoral-primary caudal-anal and dorsal-secondary caudal-pelvic fin rays. Larvae begin to transform at about 10 mm SL.

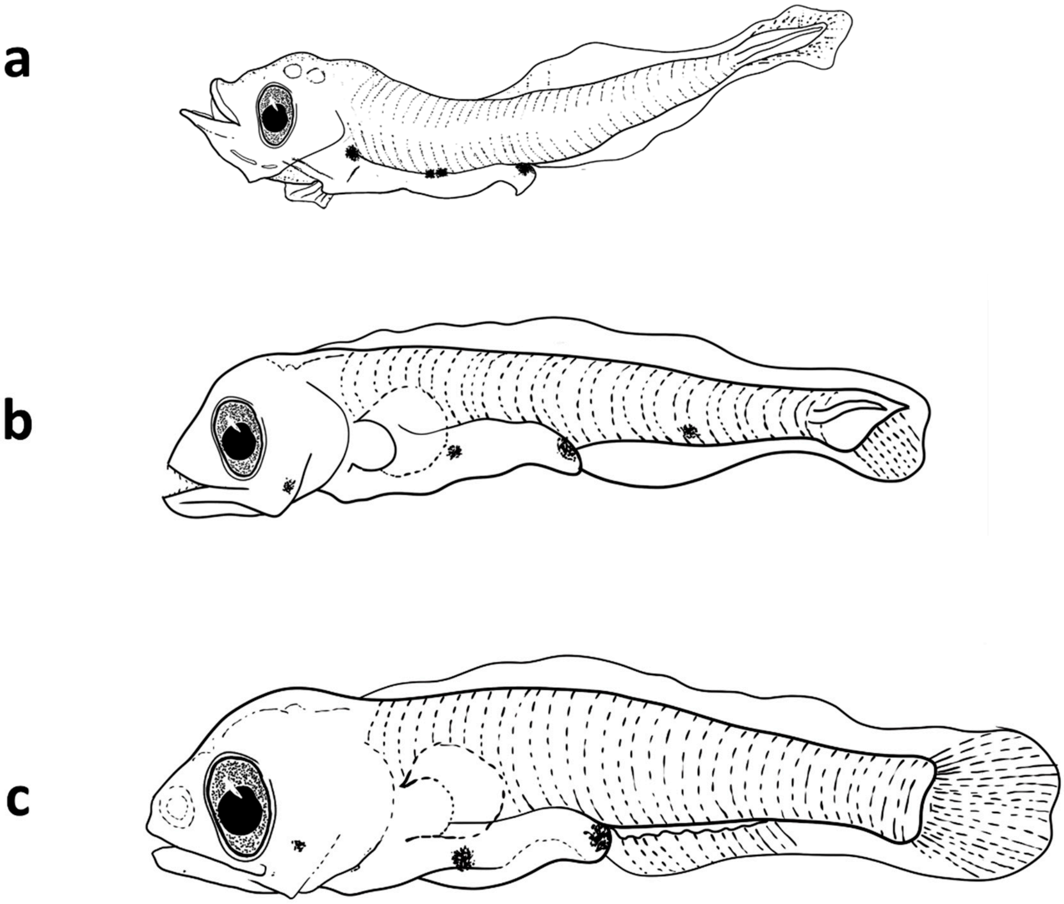

Figure 10. larvae of *B. pterotum.* A. 2.1 mm *Benthosema pterotum*, B. 4 mm and C. 6 mm.

Small preflexion larvae have 12-15 preanal myomeres and 30-32 total myomeres. The gut terminates near mid-body (preanal length about 55% SL) and larvae have pigment along the ventral margin of the gut and over the dorsal margin of the vent. The larvae have a relatively large head (25% SL), and moderately deep body (depth 15% SL), which deepens to 19% by 4 mm SL. The notochord begins to flex by 5 mm, and flexion is complete by about 5.5 mm SL or shortly thereafter. Rays begin to develop in the dorsal and anal fins of early postflexion larvae, and by 7.5 mm SL, all fins have a full complement of primary elements. Postflexion larvae lack pigment ventrally on the body, except on the ventral surface of head, and on the dorsal and ventral margins of the pectoral fin base.

3.3.2. Abundance and Spawning season of B. pterotum

Larvae occurred in 43% of all samples taken and accounted for 14.8% of all fish larvae collected at an **overall average concentration** of 14/1000 m^3. Larvae were collected during all months, except September and October, and most abundant between November and April with a peak in January (Figure 11). In fact, January accounted for >50% of all *B. pterotum* larvae collected (255 of **485** larvae). Although not significantly different among bays, abundance was somewhat higher in Naama Bay (180/1000 m^3), than Port Bay (161/1000 m^3), and Sharm El-Maya Bay (137/1000 m^3).

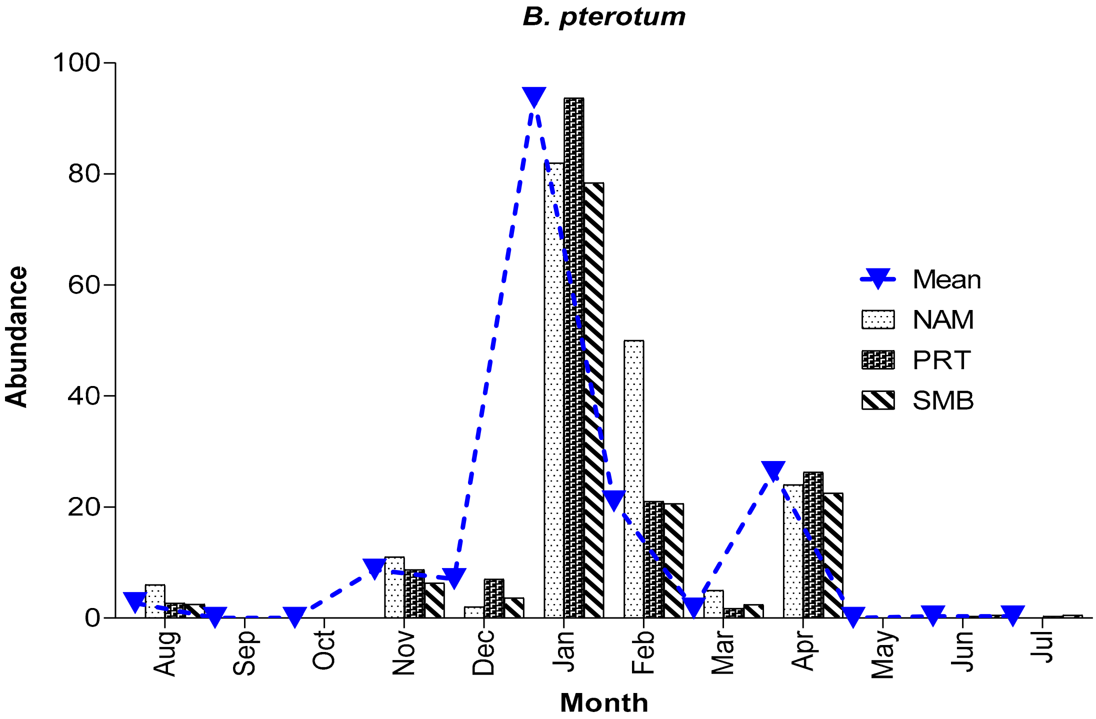

Figure 11. Mean monthly abundance of *B. pterotum* (per 1000 m^3) at different bays throughout the sampling period.

3.3.3. Length frequency distribution of B. pterotum larvae:

Larvae ranged in size from 2.3 to 7.5 mm SL and were divided into six size classes in one mm length intervals from I: 2-2.9 mm to VI: 6-6.9 mm. Larvae <5 mm (i.e., size classes I, II, III) accounted for nearly 75% of all *B. pterotum* collected, and those between 5 and 6.9 mm for about 25%. The smallest larva was collected during December in Port Bay as was the largest larva during January. Based on monthly length frequency distributions, small larvae were collected in every month, except September and October, which suggests that spawning may occur year-round with peak spawning in January and February, and at much lower levels during late spring through early fall (Figure 12).

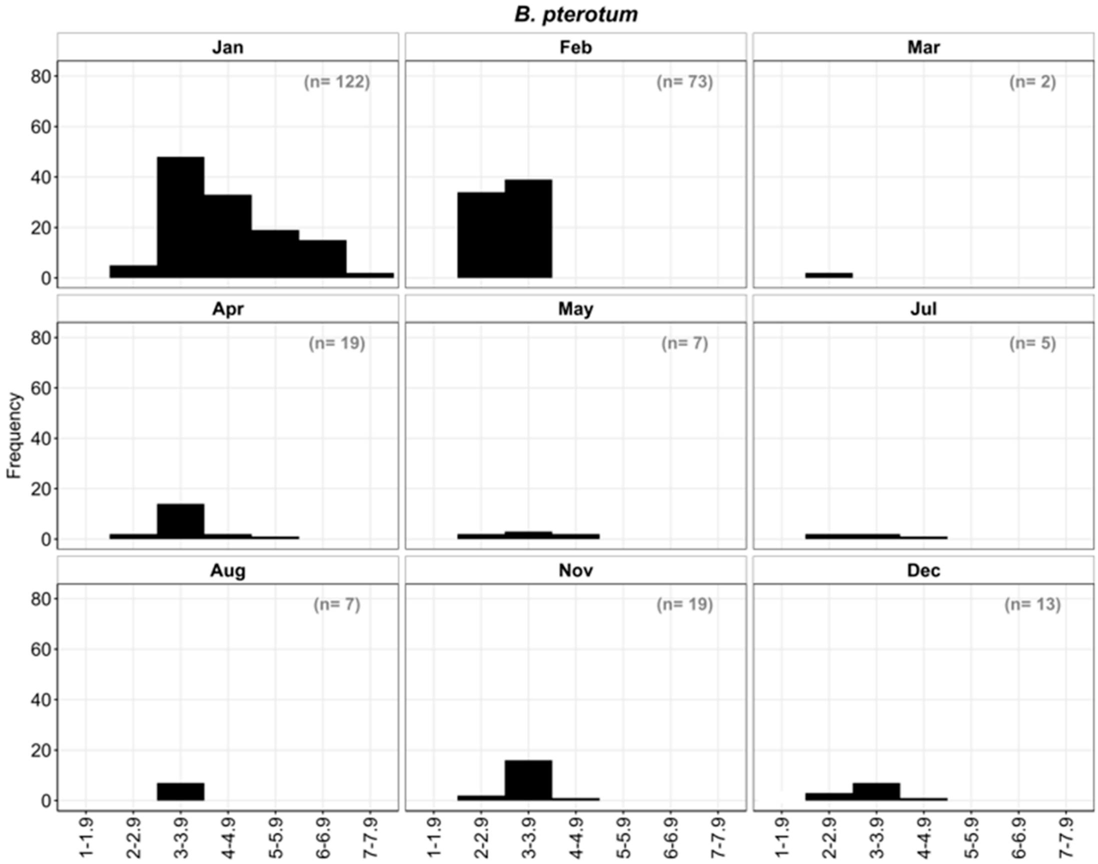

Figure 12. Length frequency distribution of *B. pterotum*.

In August, seven larvae of the same size class III (3-3.9 mm) were collected. In November, the length varied between 2 mm to 4.9 mm with nearly 93% of all larvae in size classes I and II (2-3.9 mm). In December, 13 larvae were collected, all <5 mm SL (preflexion). About 54% of these larvae were in size class II (3-3.9 mm). In January, 122 larvae representing all size classes (I-VI) were collected with about 70% <5 mm SL. In February, one peak was observed representing size groups I, II with 47% and 53% respectively. The March sample contained only two larvae, both of similar length. A total of 19 larvae were collected in April and ranged in size between 2-5.9 mm. SL with most in size class II (3-3.9 mm). The seven larvae collected in May ranged from 2-4.9 mm SL and belonged to size classes I, II, III, as did the five larvae taken in July.

4. Discussion

4.1. Diversity and distribution of mesopelagic fish larvae

The Red Sea, an area characterized by high endemism (Klevjer et al., 2012), contains 16 species of mesopelagic fishes in 9 families and 6 orders (Table 1). Despite the unusual environmental conditions of its mesopelagic waters (warm, stable water temperatures (~ 22°C); high salinities (40.5 ppt); and low zooplankton concentrations (Dypvik and Kaartvedt, 2013), the Red Sea reportedly has abundant populations of some mesopelagic fishes during the day (Klevjer et al., 2012) dominated by *V. mabahiss* at ~ 500 m (Isari et al. 2017). These aggregations of mesopelagic fishes later disperse as they migrate vertically into warmer near-surface waters in the early evening to feed and return to cooler waters before sunrise.

Although patterns of abundance vary by location, larvae of *V. mabahiss* and *B. pterotum* dominate collections of mesopelagic fishes in the Red Sea (Abu El-Regal et al., 2008; Abu El-Regal et al., 2014; Isari et al. 2017; this study) and are important components of the ichthyoplankton community (Isari et al. 2017). We found small *V. mabahiss* larvae most abundant from November through April with peaks in November and January and are absent from collections taken during June through August. By comparison, Isari et al. (2017) showed a gradual increase in abundance for *V. mabahiss* at the offshore station from January through April, a decline in abundance thereafter through August, and a low secondary peak in September. At the inshore station, monthly estimated abundances were consistently low throughout the year with a minor peak during June (Isari et al 2017). However, *Vinciguerria mabahiss* was weakly represented and B. pterotum was completely absent in a coastal reef lagoon at Hurghada coast Red Sea (Abu El-Regal, 2013) compared to the current results and previous ichthyoplankton surveys in the area. Differences in sampling methodologies and locations may help to explain this discrepancy in seasonal abundance patterns because Gulf of Aqaba waters were sampled off Egypt by horizontal tows within one meter of the sea surface in this study, whereas Isari et al. (2017) sampled waters down to 50 m off central Saudi Arabia with oblique tows. Otolith-derived back-calculated hatch dates between June and October for *V. mabahiss* larvae collected in the central Red Sea (Aldanondo et al. 2023), however, when combined with our findings and those by Isari et al. (2017) is consistent with the suggestion that *V. mabahiss* spawn continuously throughout the year (Isari et al. 2017) at least in some parts of the Red Sea.

Although larvae of V. *mabahiss* were the most abundant mesopelagic species collected in this study, and second in total abundance among all taxa collected near coral reefs in the Indo-Pacific (Leis, 1991), this was a somewhat surprising result. The Island Mass Effect may help to explain these findings, however, as physical processes near island and other underwater structures can enhanced input of nutrients in the euphotic layer, which favors biological productivity, as nutrient rich deeper waters are brought up towards the surface through upwelling and mixing (De Falco et al. 2022).

Larvae of *Astronesthes martensii* were the least abundant mesopelagic species collected in this study (n = 29 total larvae) and are rare to absent from other ichthyoplankton collections (Abu El-Regal et al. 2014; Isari et al. 2017), as are juveniles and adults in deep-water trawl collections taken in the southeast Arabian Sea (Renjith at al. 2020). This finding should not be surprising, as *Astronesthes martensii* typically inhabit waters at depths >1000 m and ichthyoplankton surveys rarely sample waters at that depth.

Larvae of *B. pterotum* were collected during all months sampled in this study, except September and October, with larvae most abundant between November and April, and peak abundance during January; larvae were collected at relatively low abundance levels from May through October. By comparison, Isari et al. (2017) collected larvae in the smallest size classes during all months, except during July and August. Although larvae were consistently less abundant in collections taken by Isari et al. (2015) than in this study, Isari et al. (2017) show a small spike in abundance about every three months throughout the year at their offshore stations. Back-calculated hatch dates for *B. pterotum* in the Sea of Oman suggest a primary spawning season from May to September (Hosseini-Shekarabi et al. 2015), which is generally consistent with that of *B. pterotum* in the East China Sea that spawn primarily during August and September (Gjs̈ؤter & Tilseth, 1988; Sassa et al. 2015), although based on the gonadosomatic index (GSI), a small percentage of mature females occur from May through January based on the gonadosomatic index (GSI; (Sassa et al., 2014). Dalpadado and Gjesaeter, (1987) studied the reproduction of *B. pterotum* in the Red Sea and found no direct evidence of a second spawning in the Red Sea, although in a few females a second mode of ova was observed, which is similar to the ones observed by Dalpadado (1985) from other areas.

Benthosema pterotum eggs are spawned in deep waters (200 to 300 m in the Gulf of Oman); yolk sac larvae were found between 100 and 300m, and older larvae were generally found between 5 and 200m (Gjs̈ؤter and Tilseth, 1983). If time to hatching is about 10-12 hrs at water temperature of 21°C as is common for the Red Sea, and larvae hatch at about 1.5 mm SL (Gjs̈ؤter & Tilseth 1988), if daily growth rates approach those for *B. pterotum* larvae in the East China Sea (mean absolute growth rate 0.26 mm; Sassa et al. 2015), larvae in the two smallest size classes (2-3.9 mm SL) in this study suggest collection within 7 to 10 of spawning. A mean absolute growth rate of 0.26 mm (Sassa et al. 2015) appears reasonable given an overall mean absolute growth rate of 0.21 mm per day based on growth rates for eight other species of myctophids (see Sassa et al. 2015; Table 4). Therefore, an estimated hatch date for the largest *B. pterotum* larva collected in this study (7.5 mm SL) is 23-25 days prior to

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collection date, which is consistent with an estimated larval duration period of 42 days for the smallest juvenile (12 mm SL) collected by Sassa et al. (2015).

4.2. The diagnostic features of Vinciguerria species, B. pterotum and A. martensii

V. mabahiss, endemic to the Red Sea and Gulf of Aqaba (Johnson and Feltes, 1984), are one of five species of *Vinciguerria* currently described. *V. mabahiss* is most similar to its congeners, *V. nimbaria* and *V. lucetia* from the Indian Ocean and elsewhere as all three species possess a pair of symphyseal photophores (just behind the mandibular symphysis), which *V. attenuate* and *V. poweriae* lack (Johnson and Feltes 1984). *V. mabahiss* differs from *V. nimbaria* and *V. lucetia* without overlap by having 58 to 63 total photophores (vs. 64-73) and 37 to 38 vertebrae (vs. 39-44, typically 40-41).

All species of *Vinciguerria* larvae have an enlarged pigment medially or near the ventral margin of the caudal complex. *Vinciguerria mabahiss* larvae like those of *V. nimbaria and V. lucetia* have pigment near the ventral margin of the tail and pigment above the anal fin base, whereas *V. poweriae* have the caudal pigment medially and lack pigment above the anal fin. *V. attenuata* also has pigment above the gas bladder (Johnson and Feltes 1984). *V. mabahiss* larvae lack pigment typically found at three locations in *V. nimbaria and V. lucetia*: post-pectoral, anal, and precaudally, whereas larvae of all three species have pigment in front of the pectoral fin base, along the base of the anal fin, on the tail, and pigment at the base of upper and lower caudal rays (Ahlstrom & Counts, 1958; Johnson and Feltes 1984).

Only two species within Myctophidae (*Benthosema pterotum* and *Diaphus coeruleus*) are reported in the Red Sea (Goren & Dor, 1994), and all collected in this study were identified as *B. pterotum* based on the pigment patterns and myomere counts. Myctophid larvae are characterized by the presence of an adipose fin and can be distinguished by differences in the number and placement of photophores and the size at which photophores develop. Larvae collected in this study (2.3 to 7.5 mm SL) are generally consistent with the description of the smallest *B. pterotum* larva (5.75 mm SL) by Lee et al. (2020), who observed pigment on the gut, and on the dorsal margin of the hindgut near the vent as noted here. Lee et al. (2020) also suggests that metamorphosis and photophore development is complete and the juvenile life stage attained by 12–13 mm SL in *B. pterotum*. *Benthosema pterotum* larvae can be confused with the larvae of other myctophids due to the elliptical eye in some species, and with some scarids, but scarids have <27 myomeres and a row of melanophores along or beneath the base of the anal fin that typically extend onto the caudal peduncle, which *B. pterotum* lack. Larvae of *A. martensii* are highly diverse and have a great number of morphological specializations; however, no complete developmental series, with transformation specimens, has been described and identifications in the literature are tentative (Kawaguchi and Moser 1984).

Larvae of mesopelagic fishes collected during this study from the Red Sea have some common characteristics including the absence of spines both in fins and head, the early forming teeth in one or both jaws the long snout and the elliptical eyes. The elongated body and elongate gut in *V. mabahiss* and *A. martensii* characterized them from larvae of many other families such as Clupeidae. The trailing gut of *A. martensii* is a very distinctive feature of the species.

5. Conclusion

This study contains valuable information about the early stages of mesopelagic fish, which have rarely been described worldwide in general and in the Red Sea in particular. The larvae of *V. mabahiss* and *A. martensii* are described for the first time in the Red Sea. Moreover, the spawning seasons and grounds of these deepwater fish are described for the first time. The presence of their larvae in large numbers, which outnumber the larvae of coastal fish, indicates that sea currents play a major role in transporting these larvae. However, more studies on the life history of mesopelagic fish are required.

Author Contributions: Methodology, Mohamed Ahmed Abu El-Regal; Investigation, Mohamed Ahmed Abu El-Regal and James G. Ditty; Data curation, Mohamed Ahmed Abu El-Regal; Writing – original draft, Mohamed Ahmed Abu El-Regal and James G. Ditty; Writing – review & editing, Mohamed Ahmed Abu El-Regal.

Institutional Review Board Statement: Samples are collected by plankton net, and they are only plankton samples and there are no rules to follow.

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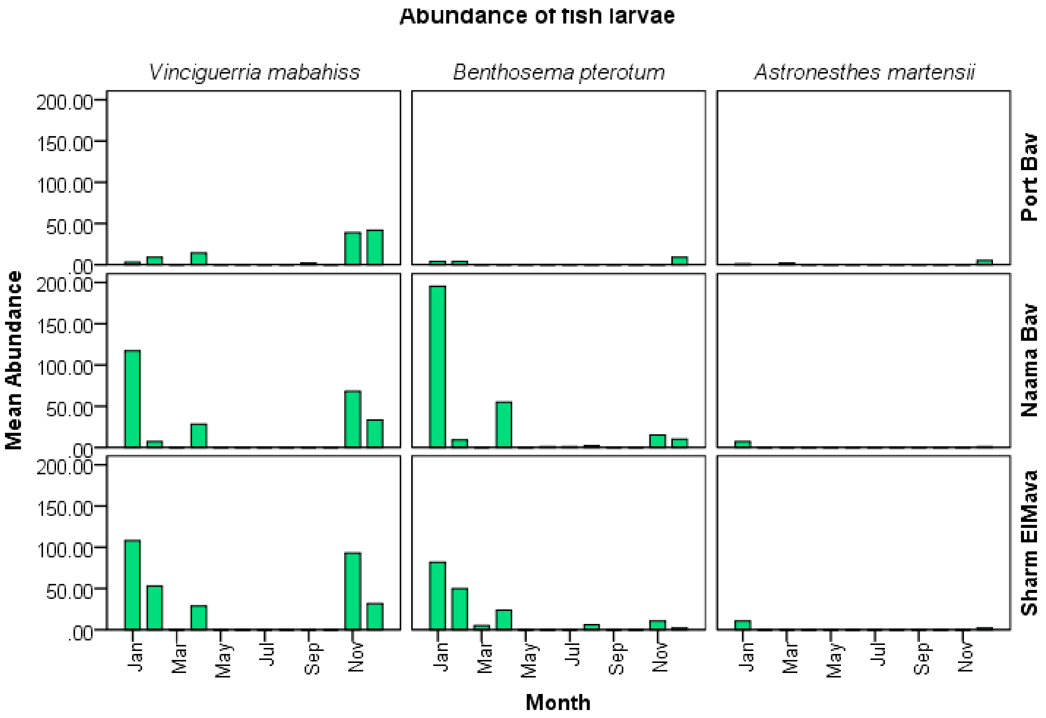
Conflicts of Interest: The authors declare no conflict of interest.

Appendix A



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