

DEVELOPMENT OF LARVAE AND JUVENILES
OF THE ALFONSINS, *BERYX SPLENDENS* AND
B. DECADACTYLUS (BERYCIDAE, BERYCIFORMES)

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ABSTRACT

The larval development of the alfonsins, *Beryx* spp., is described from specimens collected from the central North Pacific Ocean (29°N, 179°E) during July 1984, primarily in the upper 50 m. Yolk-sac larvae, 1.5–3.0 mm standard length (SL), have pigment at the forebrain and midbrain, the anterior end of the oil globule, over the intestine above the anus, and around the tip of the notochord. Pelvic buds form at 1.5–3.0 mm SL; flexion occurs between 3.7 and 6.0 mm SL. Fin ray formation is complete and scales are formed by 15 mm SL. Characters useful for identifying *Beryx* larvae include very elongate, early forming pelvic rays and anterior dorsal spines; a slightly S-shaped intestine about half the standard length; and sparse pigment restricted to internal pigment at the gas bladder, over the posterior intestine, and a spot located asymmetrically on the forebrain. Spines on the first lower infraorbital, characteristic of adult *Beryx*, develop at 3.8–4.5 mm SL. Juvenile *B. splendens* and *B. decadactylus*, from the North Atlantic, differ from each other in dorsal fin ray count.

The alfonsins (Berycidae) are moderately large, usually bright red fishes found in tropical and temperate shelf or slope waters of all oceans (Busakhin, 1982). The family contains two genera, *Beryx* and *Centroberyx*, which are easily distinguished by meristics and head spination (Zehren, 1979). *Beryx* contains two species: *B. decadactylus* from the Atlantic, Mediterranean, southern Indian Ocean, western Pacific rim, and Hawaii in the central Pacific plate; and *B. splendens* from all temperate and tropical areas except the Mediterranean Sea and the eastern Pacific Ocean north of the Equator (Busakhin, 1982). *Beryx mollis* is a synonym of *B. splendens* (Heemstra, 1986). Commercial fisheries for alfonsin exist where they are abundant (Woods and Sonoda, 1973), particularly in the central and western Pacific (Uchida and Tagami, 1984; Seki and Tagami, 1986). Although both species of *Beryx* are abundant and commercially important, relatively little is known of their early life history (Keene and Tighe, 1984). Onishi (1966; 1968) described the eggs, yolk-sac larvae, and preflexion larvae, and Okiyama (1988) described a single 10.0 mm larva of *B. splendens*. Juvenile *Beryx* have been described, first as a separate genus, *Actinoberyx* (Roule, 1924), and more recently under both generic names (Fourmanoir, 1976; Krefft, 1976) as reviewed by Busakhin (1982).

This paper presents the first complete ontogenetic description of *Beryx* species. Large larvae and small juveniles of *B. splendens* are compared to those of *B. decadactylus*, and developmental features of *Beryx* pertinent to future phylogenetic studies of the Beryciformes are reviewed.

MATERIALS AND METHODS

Larvae were collected at the Southeast Hancock Seamount (29°48'N, 179°04'E) during 9–28 July 1984. Stepped, oblique plankton tows were taken over the seamount and at areas approximately 20 km to the west during day and night. A three-net Tucker trawl (1 m² effective mouth opening and 0.333 mm bar mesh), containing calibrated flowmeters, was towed at 2–3 kn for 14–38 min per net. Samples were taken at depth strata of 0–25, 25–50, 50–100, and 100–200 m, with additional oblique tows taken at 0–50 and 0–100 m as the trawl was retrieved from the deeper strata. Samples were fixed in 10% buffered formalin. In the laboratory, samples were processed by the methods of Smith and

Richardson (1977). *Beryx* larvae (133 specimens) were removed from sorted lots of fish larvae and preserved in 70% ethanol (Lavenberg et al., 1984) approximately 18 months after collection. Additional specimens of large larvae and small juveniles of *B. splendens* and *B. decadactylus* from the Atlantic Ocean were borrowed from the Woods Hole Oceanographic Institution (WHOI) collections housed at the Museum of Comparative Zoology, Harvard University (MCZ); the U.S. National Museum of Natural History (USNM), and the Atlantic Reference Center, Huntsman Marine Laboratory (ARC).

Yolk-sac larvae of *B. splendens* were obtained by artificial fertilization using gametes from identified adults caught by handline at the Hancock Seamount on 30 July 1984. The eggs and larvae were held in seawater at 23°–25°C. The eggs hatched after 27.5 h, and larvae, which were not fed, were preserved in 5% buffered formalin 60 h after hatching.¹

The developmental series from the plankton samples was established using the serial technique of Moser and Ahlstrom (1970). Terminology of developmental stages follows Ahlstrom et al. (1976). That of head spination follows Johnson and Washington (1987), except the lacrimal is referred to here as the first infraorbital, the small spines that form secondarily on larger spines are called accessory spines, and the spines of the preopercle are distinguished as being on anterior and posterior ridges. In this paper, SL refers to standard length in flexion and postflexion specimens, and to notochord length in preflexion larvae. Measurements were taken with an ocular micrometer in a dissection microscope as defined by Moser and Ahlstrom (1970) and Leis and Rennis (1983). Illustrations were made using a camera lucida. Specimens were stained lightly with alizarin red S to enhance visibility of head spines and fin elements.

DESCRIPTION

Distinguishing Features.—Yolk-sac *Beryx* from plankton samples were initially identified by reference to the reared specimens (Fig. 1A). The combination of characters that allows identification of preflexion larvae from plankton samples includes 23 myomeres, an uncoiled intestine, a preanal length approximately 50% SL, early forming pelvic fin buds indicating early development of the pelvics, and an unusual pigment pattern consisting of melanophores restricted to the forebrain and midbrain, the anterior edge of the oil globule, the end of the intestine, and around the notochord tip. Larger *Beryx* larvae are characterized by very long, early forming pelvic rays and anterior dorsal elements, a slightly curved intestine, a preanal length 45–56% SL (Table 1), and sparse pigment (restricted to internal pigment located asymmetrically over the forebrain, pigment on the cranium in postflexion larvae, internal pigment at the gas bladder and over the posterior intestine, and external pigment at the anus) (Figs. 1–3).

Larvae with elongate dorsal and pelvic fins which superficially resemble *Beryx* in preflexion and flexion stages are described by Leis and Rennis (1983), Ahlstrom et al. (1984), Keene and Tighe (1984), Olney (1984), Okiyama (1988), and Leis and Trnski (in press). *Beryx* larvae show the greatest similarity to melamphaid larvae, particularly *Melamphaes*. Both genera are very similar in body shape, intestine shape and length, and in the sequence of fin formation (Keene and Tighe, 1984). Melamphaid differ from berycids in pigment pattern, meristics, and head spination (Ebeling, 1962; Ebeling and Weed, 1963; 1973; Keene and Tighe, 1984).

Postflexion *Beryx* larvae and juveniles have 10+9 principal caudal rays, characteristic of the Beryciformes in the Percomorpha, and develop the unpaired, procurent caudal fin spines of the Beryciformes (Lauder and Liem, 1983). Postflexion *Beryx decadactylus* larvae have 16–18 dorsal rays versus 13–15 in *B. splendens* (Woods and Sonoda, 1973). No other character identifies larvae of the two species, although the presence of internal branchial pigment in *B. decadactylus* may prove useful in identifying postflexion larvae (see comparison of the two species later in this paper). Identification of small *B. decadactylus* is not possible at this time. Larvae of the confamilial *Centroberyx* are undescribed and are ex-

¹ Y. Lamadnd-Rose, Hawaii State Division of Aquatic Resources, Honolulu, Hawaii 96813 (pers. comm., April 1986).

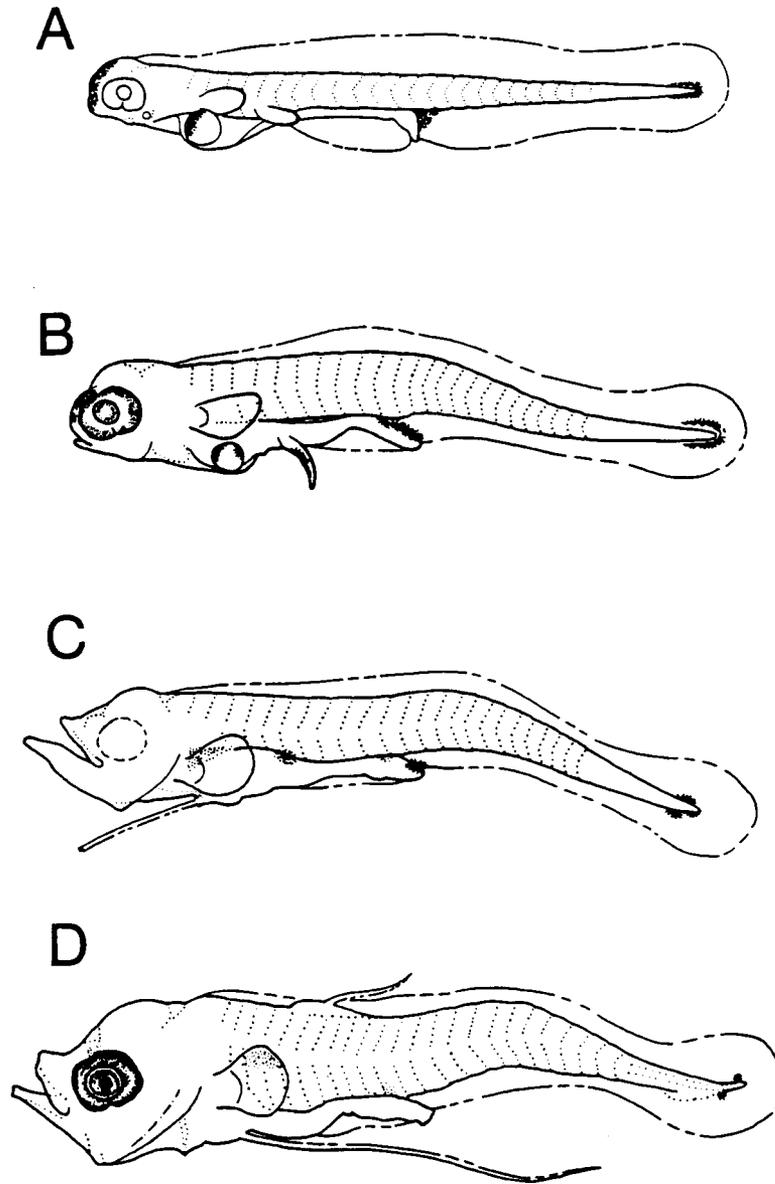


Figure 1. Preflexion larvae of *Beryx* spp. All except A were collected at Southeast Hancock Seamount. (A) reared larva of *B. splendens*. 3.0 mm SL. (B) 2.1 mm SL. (C) 3.0 mm SL. (D) 3.3 mm SL.

pected to be very similar to *Beryx*. Postflexion *Centroberyx* will have fewer anal rays (IV, 12–16) than *Beryx* (III–IV, 25–32) (Busakhin, 1982). Postflexion *Beryx* larvae from the Hancock Seamount with 14–15 dorsal soft rays and all fin rays formed (Fig. 3) were identified as *B. splendens*. North Atlantic specimens with 17–18 dorsal rays were identified as *B. decadactylus*. With the exception of the reared and largest specimens, the material described from the Hancock Seamount

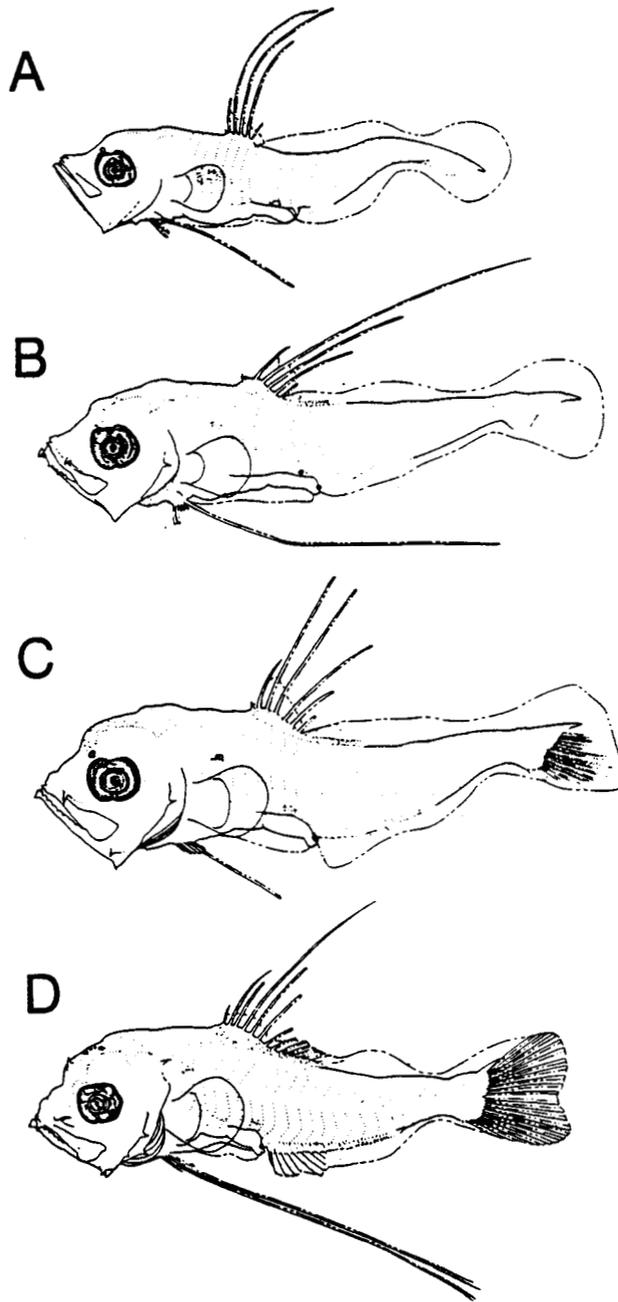


Figure 2. Flexion larvae of *Beryx* spp. collected at the Southeast Hancock Seamount. (A) 4.0 mm SL. (B) 4.6 mm SL. (C) 5.0 mm. SL. (D) 5.2 mm SL.

could include *B. decadactylus* as well as *B. splendens*. No differences were found among the larvae to indicate that more than one species was present in collections from the Hancock Seamount.

Morphology (Tables 1, 2).—Recently hatched larvae (Fig. 1A) have a large oil globule (mean diameter = 0.15 mm, 0.03 SD, N = 6) at the anterior end of the ovoid yolk, unpigmented eyes, and an unformed mouth. The yolk measures 0.34 mm in mean length (0.13 SD) and 0.15 mm in mean depth (0.03 SD). The intestine is straight until the downward bend before the anus. Pelvic and pectoral buds form before the yolk is absorbed. The mouth forms, the eyes become pigmented, and the pelvic buds begin to elongate as the yolk and oil globule disappear (Fig. 1B). After the yolk is absorbed, the body deepens, the snout becomes pointed, and the head assumes a characteristically concave dorsal profile (Figs. 1C–D, 2A–B); this profile may be due to tissue shrinkage caused by preservation. The intestine becomes slightly curved and develops a distinct midgut and hindgut. Late preflexion larvae become laterally compressed, remaining so through transformation.

During flexion, the body deepens and the gut becomes more differentiated (Fig. 2B–D). The profile of the head remains concave with a pointed snout, which becomes rounded near the end of flexion. In flexion and postflexion larvae, the body depth, head depth, and head length increase relative to the SL, and a prominent gas bladder is present (Figs. 2, 3). In postflexion *Beryx* larvae the dorsal profile of the head becomes strongly convex (Fig. 3). Preanal length shortens with development, from 56 to 45% SL, but lengthens to 53% SL in juveniles (Table 1; Fig. 4), the midgut and hindgut become more distinct, and the midgut becomes coiled.

A preanal finfold is present. The preanal and remnant dorsal finfolds, midway between the dorsal and caudal fins, are the last parts of the finfold to persist before transformation (Fig. 3B). The remnant dorsal finfold, seen on all postflexion larval specimens, is curiously like the precursor of the adipose fin seen in myctophids (Moser and Ahlstrom, 1970) and percopsids (Auer, 1982). The finfolds are gone at 9.2 mm SL.

Head Spines (Table 3; Fig. 5).—Head spines begin to develop at flexion (Fig. 2A, B). All head spines of *Beryx* are bilateral. The first to appear are spines at the anterior end of the maxilla and at the retroarticular, at 2.8–4.3 mm SL. The large spine on the first infraorbital, characteristic of *Beryx* (Zehren, 1979), develops in midflexion at 3.8–4.5 mm SL, when spines appear along the anterolateral ridge of the preopercle (Fig. 2B). Teeth form on the premaxilla in early flexion and remain prominent through larval development. The frontals develop a rugose texture, and a spine appears posteriorly on the anguloarticular, above the retroarticular, at 3.3–5.0 mm SL (Fig. 2B, C). During late flexion (5.0–6.0 mm SL), other spines appear on the preopercle, interopercle, and posttemporal (Fig. 2D). An unspined supraorbital ridge and a prominent anteromedial spine, both on the frontal, develop at sizes greater than 5.0 mm SL. In postflexion specimens (> 7.0 mm SL; Fig. 3B), all spines previously seen are present, and additional spines appear at the tip and along the lateral edge of the dentary. More spines are present on the preopercle and interopercle, including a row of spines on the posterior margin of the preopercle. A small spine is present anterior to the large, first infraorbital spine, and there is a spine on the posterior margin of the dorsal part of the opercle.

In juveniles (≥ 15 mm SL), additional spines appear at the retroarticular, near the anteromedial frontal spine, on the infraorbitals, and along the supraorbital ridge (Figs. 4A, 5). Several small spines form on the posttemporal, but there are

Table 1. Mean body proportions (mm divided by SL) of larval and juvenile *Beryx* spp., except for classes with only single specimens. N = numbers of specimens. Developmental stages for each size class are 1 = yolk sac, 2 = preflexion, no yolk sac, 3 = flexion, 4 = postflexion, 5 = juvenile

SL	N	Stages	Prenatal length	Predorsal length	Prepelvic length	Head length	Head width	Snout length	Eye diameter	Body depth	Pectoral fin ray length	Pelvic fin ray length	Dorsal fin ray length
<i>Beryx</i> spp.													
1.0-1.9	12	1	0.54	—	0.30	0.16	0.13	0.03	0.10	0.18	0.06	0.08	—
2.0-2.9	8	1	0.55	0.41	0.26	0.25	0.14	0.06	0.11	0.18	0.07	0.29	0.09
3.0-3.9	25	1-2	0.56	0.40	0.27	0.32	0.14	0.09	0.10	0.22	0.08	0.48	0.34
4.0-4.9	72	2-3	0.54	0.39	0.26	0.32	0.14	0.09	0.10	0.22	0.08	0.39	0.36
5.0-5.9	4	2-4	0.49	0.39	0.28	0.33	0.14	0.09	0.09	0.27	0.09	0.38	0.39
<i>Beryx splendens</i>													
7.0-7.9	4	4	0.45	0.36	0.29	0.29	0.12	0.09	0.09	0.35	0.15	0.76	0.56
9.0-9.9	3	4	0.49	0.38	0.36	0.29	0.17	0.08	0.08	0.38	0.18	0.62	0.25
10.32	1	5	0.45	0.42	0.34	0.30	0.16	0.08	0.09	0.37	0.22	0.83	0.30
15.00	1	5	0.46	0.40	0.34	0.25	0.16	0.07	0.10	0.41	0.22	0.94	2.07
21.72	1	5	0.50	0.43	0.34	0.28	0.18	0.07	0.09	0.40	0.21	0.25	0.32
27.48	1	5	0.53	0.46	0.40	0.27	0.19	0.07	0.10	0.41	0.26	0.75	0.22
<i>Beryx decadactylus</i>													
8.52	1	4	0.46	0.44	0.42	0.32	0.12	0.11	0.08	0.37	0.14	0.63	0.37
10.08	1	5	0.45	0.42	0.34	0.29	0.18	0.09	0.08	0.40	0.21	1.20	0.31
11.52	1	5	0.48	0.33	0.39	0.26	0.17	0.08	0.07	0.38	0.30	1.16	1.20
16.38	1	5	0.53	0.41	0.40	0.26	0.19	0.08	0.10	0.44	0.23	0.93	1.88
21.38	1	5	0.51	0.45	0.42	0.27	0.15	0.09	0.08	0.47	0.23	1.46	1.69
23.28	1	5	0.58	0.44	0.48	0.31	0.18	0.10	0.08	0.46	0.24	2.19	2.26

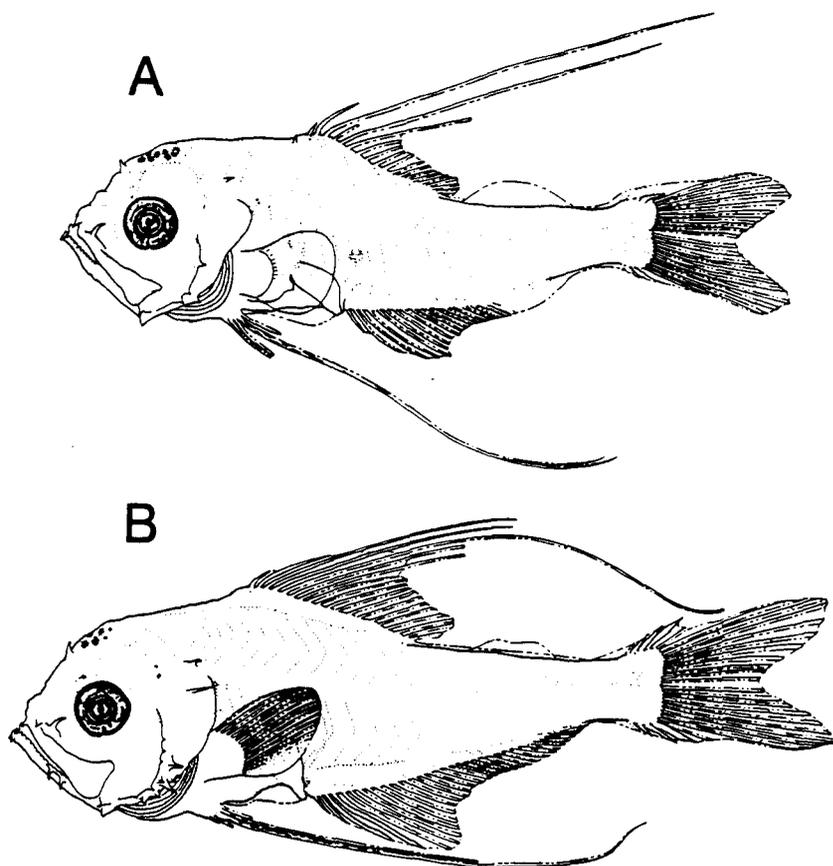


Figure 3. Postflexion larvae of *Beryx splendens* collected at the Southeast Hancock Seamount. (A) 6.0 mm SL. (B) 7.5 mm SL.

no spines on the cleithrum or other pectoral bones. A second opercular spine forms ventral to the first. As many as 13 spines appear on the posterior margin of the interopercle (Table 3). Small accessory spines appear along the upper opercular spine, and on the largest spines near the angles of both preopercular series. In the bones of the jaws, the dentary bears two ridges of spines with a series of large pores between them. The upper jaw bears two spiny ridges on the posterior supramaxilla. Maxillary and retroarticular spines are absent on the largest juvenile (Table 3). The rugose area of the frontal in juveniles bears three serrate ridges. Juveniles also develop a serrate ridge incorporating the anteromedial frontal spine. The bony supraorbital ridge develops small spines. *Beryx* larvae and juveniles lack spines on the parietals and supraoccipital.

With the exception of the spines on the first infraorbital and upper opercle, the larval spines are incorporated into serrate ridges or crests in adult *Beryx* (Woods and Sonoda, 1973; Busakhin, 1982). See Zehren (1979) for a detailed description of adult osteology.

Meristics/Fin Formation (Table 4).—All specimens have 23 myomeres, not including the urostylar segment and the muscle segment anterior to the first myo-

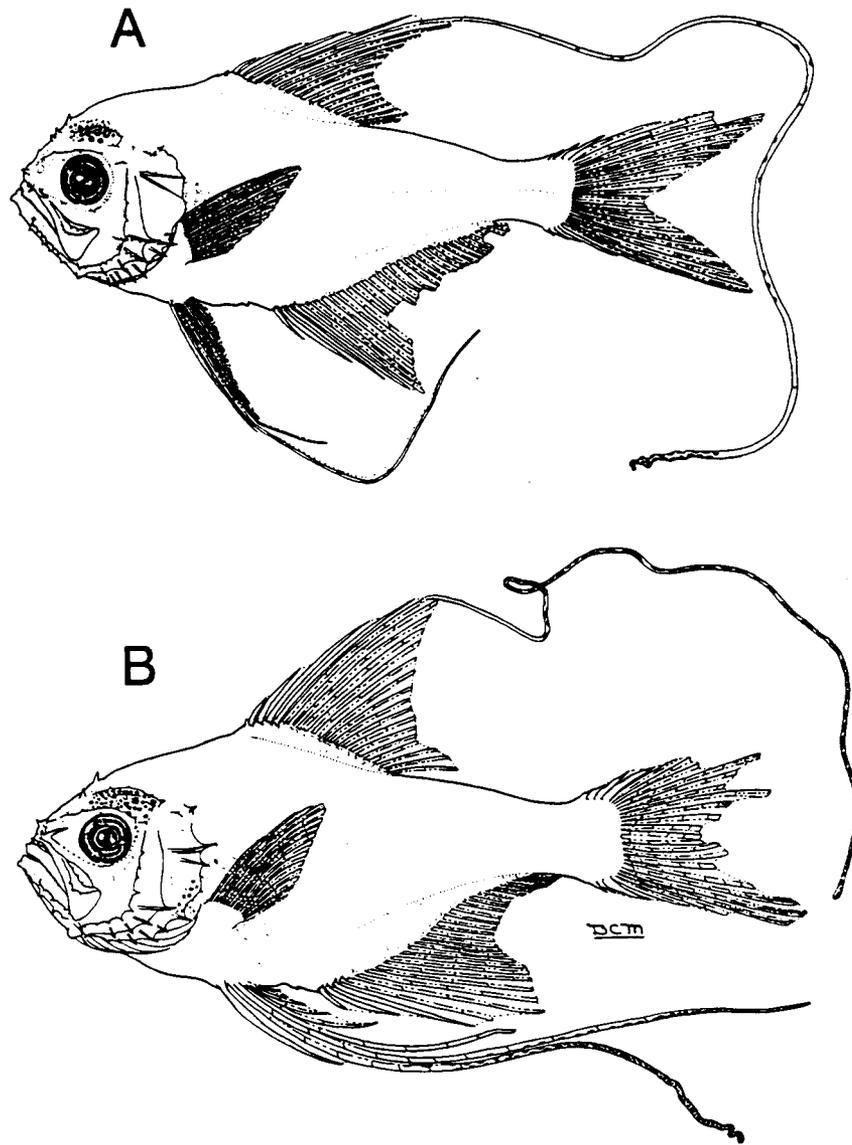


Figure 4. Pelagic juveniles of *Beryx* spp. collected in the North Atlantic. (A) *B. splendens*, 15.0 mm SL (MCZ 068672). (B) *B. decadactylus*, 16.4 mm SL (MCZ 064863). Scales are completely formed on these specimens but are not shown.

septum. Onishi's (1966) count of 30 is clearly an error; the myomere count of teleosts, including the urostylar and anterior segments, is one more than the vertebral count (Fuiman, 1982), which, in *Beryx*, is 24 (Starks, 1904; Woods and Sonoda, 1973; Zehren, 1979). As the intestine shortens, the precaudal myomere number decreases from 11 to 9.

In contrast to most other fishes, the pelvic fin rays are the first to ossify in

Table 2. Measurements (mm) of larval and juvenile *Beryx* spp. Means and standard deviations are given for measurements within each size class, except for classes with single specimens. (See Table 1 for sample sizes and developmental stages for each size class)

SL	Precanal length x (SD)	Predorsal length x (SD)	Prepelvic length x (SD)	Head length x (SD)	Head width x (SD)	Snout length x (SD)	Eye diameter x (SD)	Body depth x (SD)	Pectoral fin ray length x (SD)	Pelvic fin ray length x (SD)	Dorsal fin ray length x (SD)
<i>Beryx</i> spp.											
1.0-1.9	0.91 (0.10)	— (—)	0.50 (0.04)	0.27 (0.06)	0.22 (0.04)	0.05 (0.03)	0.16 (0.02)	0.30 (0.06)	0.09 (0.03)	0.13 (0.04)	— (—)
2.0-2.9	1.37 (0.28)	1.18 (0.09)	0.66 (0.15)	0.64 (0.19)	0.34 (0.09)	0.17 (0.06)	0.27 (0.07)	0.47 (0.15)	0.18 (0.07)	0.79 (0.54)	0.27 (0.10)
3.0-3.9	2.06 (0.21)	1.47 (0.16)	0.98 (0.15)	1.19 (0.18)	0.52 (0.07)	0.35 (0.09)	0.37 (0.04)	0.80 (0.13)	0.30 (0.06)	1.75 (0.53)	1.29 (0.70)
4.0-4.9	2.34 (0.11)	1.68 (0.09)	1.14 (0.09)	1.41 (0.10)	0.60 (0.04)	0.41 (0.04)	0.41 (0.03)	0.97 (0.09)	0.33 (0.07)	1.69 (0.79)	1.58 (0.67)
5.0-5.9	2.63 (0.15)	2.08 (0.14)	1.48 (0.20)	1.74 (0.14)	0.76 (0.08)	0.50 (0.05)	0.49 (0.05)	1.43 (0.18)	0.47 (0.05)	2.05 (1.13)	2.14 (1.14)
<i>Beryx splendens</i>											
7.0-7.9	3.32 (0.07)	2.66 (0.14)	2.17 (0.03)	2.15 (0.08)	0.86 (0.12)	0.63 (0.02)	0.64 (0.04)	2.55 (0.28)	1.11 (0.13)	5.62 (0.51)	4.19 (1.05)
9.0-9.9	4.66 (0.66)	3.64 (0.11)	3.46 (0.73)	2.72 (0.20)	1.56 (0.10)	0.82 (0.08)	0.80 (0.11)	3.56 (0.43)	1.73 (0.13)	5.94 (2.32)	2.34 (0.85)
10.32	4.68	4.38	3.48	3.12	1.62	0.87	0.90	3.84	2.28	8.52	3.06
15.00	6.96	6.00	5.16	3.72	2.40	1.08	1.44	6.12	3.36	14.04	31.08
21.72	10.92	9.36	7.44	6.12	3.96	1.62	1.98	8.64	4.92	5.34	6.96
27.58	14.64	12.66	11.04	7.44	5.28	1.92	2.70	11.40	7.08	20.64	6.12
<i>Beryx decadactylus</i>											
8.52	3.96	3.72	3.60	2.70	1.03	0.96	0.66	3.12	1.22	5.40	3.12
10.08	4.50	4.20	3.42	2.94	1.80	0.90	0.84	4.08	2.10	12.12	3.12
11.52	5.52	3.84	4.44	3.00	1.92	0.91	0.86	4.32	3.48	1.38	13.32
16.38	8.64	6.72	6.60	4.32	3.12	1.32	1.56	7.20	3.72	15.31	30.84
21.00	10.68	9.36	8.76	5.76	3.24	1.80	1.68	9.84	4.92	30.60	35.52
23.28	13.44	10.20	11.28	7.32	4.20	2.28	2.16	10.80	5.64	51.00	52.56

Table 3. Development of head spines in *Beryx* spp. Minimum-modal-maximum numbers of spines are given when a range of spine numbers was found within a size class; + = presence, - = absence. Only minimum and maximum numbers are given when no modal number was found. (See Table 1 for sample sizes and developmental stages for each size class)

Sl. (mm)	Maxilla	Retro-articular	First infra-orbital	Anterior preopercle	Rugose frontal	Angulo-articular	Interopercle	Frontal	Post-temporal	Supraorbital ridge	Dentary	Opercle	Posterior pre-opercle	Nasal
<i>Beryx</i> spp.														
1.0-1.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2.0-2.9	-	0-0-1	-	-	-	-	-	-	-	-	-	-	-	-
3.0-3.9	0-1-1	0-1-1	0-0-1	0-0-1	or 1	0-0-1	-	-	-	-	-	-	-	-
4.0-4.9	1	0-1-1	0-1-1	0-0-2	or 1	0-0-1	-	-	-	or +	-	-	-	-
5.0-5.9	1	1	1	1-3-3	1	0-1	0-1-1	0-1-1	0-1-1	or +	-	or +	-	-
<i>Beryx splendens</i>														
7.0-7.9	1	1	2	5-5-7	1	1	2-5-5	1	1	+	2-2-3	1	3-4	-
9.0-9.9	1	1	1-2-2	4-4-6	1	1	3-5	1	1-1-2	+	2-3-3	1-1-2	2-3-3	-
10.32	1	1	2	2	1	1	4	1	1	+	4	1	3	-
15.00	1	2	2	8	1	1	10	3	1	+	8	2	4	1
21.72	2	1	2	6	1	2	8	6	1	6	22	2	7	1
27.48	-	-	2	8	1	1	13	5	2	11	20	2	8	2
<i>Beryx decadactylus</i>														
8.52	1	1	2	5	?	1	3	1	1	+	3	+	4	-
10.08	1	1	2	5	1	1	5	1	2	1	3	1	4	1
11.52	1	1	2	3	1	1	3	2	2	+	3	1	2	-
16.38	1	1	2	7	1	1	4	2	2	2	9	2	5	1
21.00	1	1	2	9	1	1	5	3	2	4	9	3	5	1
23.28	-	-	2	11	1	1	7	2	2	5	10	1	6	1

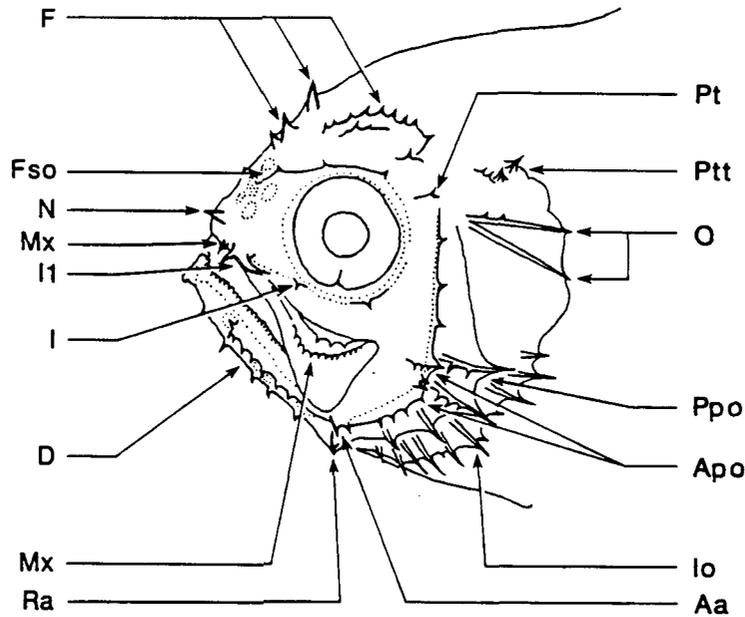


Figure 5. Head spines of *B. decadactylus*, 16.4 mm SL (MCZ 064863). (Aa) anguloarticular; (Apo) anterior preopercle; (D) dentary; (F) frontal; (Fso) supraorbital ridge of frontal; (I) infraorbital; (I1) first infraorbital; (Io) interopercle; (Mx) maxilla; (N) nasal; (O) opercle; (Ppo) posterior preopercle; (Pt) pterotic; (Ptt) posttemporal; and (Ra) retroarticular.

Beryx, at 1.5–3.0 mm SL (Fig. 1B, C). The full adult complement of I, 10–12 pelvic elements (Woods and Sonoda, 1973; Zehren, 1979) is not seen in larvae. Juveniles (≥ 15 mm SL) have all pelvic elements developed. Pelvic rays are almost invariably broken and difficult to see in the larvae. Only a few specimens have even one or two pelvic rays intact. The greatest pelvic ray length of any of the *Beryx* specimens is over twice the SL (Tables 1, 2); even this ray may have been damaged.

Dorsal fin elements also begin to develop early, at about 2.8 mm SL (Fig. 1D). As with the pelvic rays, the anterior dorsal spines and soft rays are elongate and rarely intact. The pigmented swelling at the distal end of the first dorsal ray of the largest specimens (Fig. 4) suggests that the rays may be longer and more highly ornamented than seen in these specimens, a condition similar to that seen in larval carapids (Govoni et al., 1984) and some larval serranids (Kendall et al., 1984). The greatest dorsal ray length is over twice the SL (Tables 1, 2). Fin element formation proceeds posteriad from the first spine, and the fourth element forms initially as a soft ray, becoming a spine by 6.0 mm SL. The adult complement of IV, 14–15 is formed at sizes greater than 5.9 mm SL (Fig. 3A, B).

Other fin elements form after the dorsal and pelvic elements first appear. Flexion, with formation of the principal caudal rays, begins at about 3.7–4.0 mm SL, and is complete by about 6.0 mm SL when the full complement of 10+9 principal rays is present (Figs. 2D, 3). The four large procurent spines and single, unsegmented procurent ray on each caudal lobe are present in specimens larger than 7.0 mm SL (Fig. 3B). The anal fin develops with the caudal, from 4.0 to 7.0 mm SL (Figs. 2, 3). As with the dorsal fin, anal fin element formation proceeds posteriad from the first spine, and the fourth element develops as a soft ray, becoming a

Table 4. Development of fin elements and branchiostegals in *Beryx* spp. Minimum-modal-maximum numbers of elements are given when a range of element number was found within a size class; ? = structures not entirely visible. Only minimum and maximum numbers are given when no modal number was found. (See Table 1 for sample sizes and developmental stages within each size class)

SL (mm)	Dorsal spines	Dorsal rays	Anal spines	Anal rays	Pectoral rays	Pelvic rays	Upper prominent caudal rays	Upper principal caudal rays	Lower principal caudal rays	Lower prominent caudal rays	Branchiostegals
<i>Beryx</i> spp.											
1.0-1.9	0	0	0	0	0	0-0-1	0	0	0	0	0
2.0-2.9	0-1	0	0	0	0	1-1-3	0	0	0	0	0-0-1
3.0-3.9	I-IV-IV	0-0-3	0	0	0	1-2-3	0	0-0-4	0-0-4	0	0-0-5
4.0-4.9	I-IV-IV	0-2-8	0-0-IV	0-0-5	0	2-3-6	0-0-i	0-5-10	0-4-8	0-0-ii	0-4-6
5.0-5.9	IV	3-15	III-IV-IV	5-9-23	0-0-9	2-6	0-iv	9-10-10	8-9-9	0-iii-iv	4-4-5
<i>Beryx splendens</i>											
7.0-7.9	III-IV-IV	14-15	III-IV	28-28-29	15-16-17	5-5-9	iv-v-v	10	9	iv-v-v	5-7
9.0-9.9	IV	13-14-14	III-IV-IV	27-30	17-17-19	6-8	v	10	9	iv-v-v	7-8
10.32	IV	14	IV	29	17	6	v	10	9	v	?
15.00	IV	14	IV	28	19	13	v	10	9	vi	?
21.72	IV	14	IV	28	15	14	v	10	9	v	?
27.58	IV	14	IV	27	17	12	v	10	9	iv	?
<i>Beryx decadactylus</i>											
8.52	IV	18	III	28	14	7	iv	10	9	iv	7
10.08	IV	18	III	28	16	12	v	10	9	iv	?
11.52	IV	18	III	26	17	6	v	10	9	iv	8
16.38	IV	17	IV	26	17	9	v	10	9	iv	8
21.00	IV	18	IV	30	16	11	v	10	9	iv	8
23.28	IV	20	IV	29	16	12	v	10	9	iv	8

spine by 7.5 mm SL. The full adult complement of IV, 26–29 is present by 7.0 mm SL. Pectoral rays develop last, dorsad to ventrad, from 5.9 mm SL on. The full adult complement of 17–18 rays forms by 15 mm SL.

Branchiostegals develop during flexion, at 3.0–6.0 mm (Fig. 2B–D; Table 4). All branchiostegals are formed at 10 mm SL. Scales are developing on one of the two 9.2 mm SL specimens and are completely formed on specimens 15 mm SL and longer.

Pigmentation. — Yolk-sac larvae have unpigmented eyes, and a distinct pattern of melanophores on the forebrain and midbrain, the anterior end of the oil globule, the end of the intestine above the anus, and around the notochord tip (Fig. 1A). As the yolk depletes, the eye becomes pigmented and melanophores appear on the pelvic anlage (Fig. 1B). The pigment on the oil globule becomes incorporated internally above the anterior intestine. This internal pigment eventually lies over the gas bladder (Figs. 1–3). At about 2.0 mm SL, the pigment on the forebrain is incorporated internally as a round spot on one side of the forebrain. This spot is occasionally absent but usually is present on the right side. In the illustrations, this spot is shown on the left side to indicate its presence, but in all illustrated specimens, it actually occurs on the right. By 3.0 mm SL, the pigment around the notochord tip becomes restricted to two small melanophores which disappear when flexion begins (Figs. 1, 2A). The internal pigment over the anterodorsal surface of the gas bladder is present throughout development, although it becomes fainter as the muscles thicken. Internal melanophores are present midway over the intestine only in very few small specimens. An internal pigment spot is present on preflexion and flexion larvae over the hindgut before the anus (Figs. 1D, 2). In postflexion *Beryx*, this spot is elevated as the gas bladder extends posteriorly over the hindgut (Fig. 3A) and is absent in specimens larger than 7.0 mm SL (Fig. 3B). An external melanophore over the posterior end of the hindgut is usually present (Figs. 1–3), although it is not seen in some pre- and early flexion specimens. This melanophore is absent or incorporated internally in larvae larger than 6.0 mm SL. Two internal melanophores appear in the otic capsule in larvae larger than 6.0 mm SL. Pigment on the pelvic fins is present in small preflexion larvae (Fig. 1B) and in postflexion specimens (Fig. 3). It is likely that the pelvic rays and membranes are pigmented at all sizes but that the fins were damaged during capture. Larvae larger than 7.0 mm have melanophores at the tip of the elongate dorsal ray. The only external body melanophores of postflexion larvae are on the frontals, over the forebrain.

Juvenile *Beryx* remain pale, with few melanophores (Fig. 4; Abe and Maruyama, 1971; Krefft, 1976), although erythrophores that disappear with preservation give the juveniles a red color (Abe, 1969). A photograph of a freshly caught juvenile *B. decadactylus* (MCZ 61484; 23.3 mm SL) from the Atlantic shows a transparent body, except for silver branchial, otic, and peritoneal regions. The body has a rosy tinge, particularly at the nasal area, along the vertebrae, and along the body margins. The fins are rosy, and the elongate fin rays are red. In overall appearance, the specimen resembles a reddish medusa. Resemblance to coelenterates has been suggested as an explanation for development of elongate fin rays in fish larvae (Govoni et al., 1984; Kendall et al., 1984).

Comparison of Young Beryx decadactylus and B. splendens. — Postflexion and juvenile *B. decadactylus* differ from *B. splendens* only in minor ways (Tables 1–4; Fig. 4). No differences were found in most morphometric features. Body depth, snout-to-eye distance, and snout-to-pelvic distance were greater in *B. decadactylus* than in *B. splendens* > 15 mm SL (Tables 1, 2). *Beryx decadactylus* are similar to

B. splendens in head spine development at sizes <15 mm SL. Juvenile *B. decadactylus* (>15 mm SL) have fewer spines on the interopercle, frontal, supraorbital ridge, and dentary. Only the anterolateral ridge of the preopercle has more spines in juvenile *B. decadactylus* than in *B. splendens*. Juvenile *B. splendens* have more accessory spines on the opercular and preopercular spines (Fig. 4).

All specimens of *B. decadactylus* are too large to determine whether the sequence of fin ray formation differs between the two species (Table 4). At present, the difference in dorsal ray count is the only character that allows specific identification of *Beryx* larvae and juveniles.

Pigment differences between the two species are subtle (Fig. 4). *Beryx decadactylus* have more pigment on the peritoneum and branchial region beneath the posterior edge of the gill cover. The latter pigment may prove valuable in distinguishing postflexion *B. decadactylus* from *B. splendens* prior to dorsal ray formation. More specimens of *B. decadactylus* are needed to determine whether this is specific, rather than individual, pigment variation.

Distribution at the Hancock Seamount.—*Beryx* larvae were found almost exclusively in the upper 50 m. They were approximately twice as abundant at 0–25 m than at 25–50 m. Most were captured at night, with no increase in numbers at greater depths during the day; therefore, net avoidance may account for the diel difference in catches.

Larval *Beryx* were found at the Hancock Seamount in July 1984 but not in February 1985 (NMFS, unpubl. data) even though the same collection methods were used. Based on collections of larvae, alfonsoin spawn during summer in this region.

SYSTEMATIC IMPLICATIONS

It has often been suggested that the order Beryciformes is not monophyletic (Zehren, 1979; Lauder and Liem, 1983; Keene and Tighe, 1984). For example, the Polymixiidae has been variously excluded from or included in the order, and the Holocentridae has been suggested to be more closely related to perciforms than to other beryciforms (Zehren, 1979). Larval characters may aid in determining the relationships of the beryciform families (Keene and Tighe, 1984).

Larval and juvenile *Beryx* have few character states that can be identified as synapomorphic with other beryciform families. The development of spinous, procurent caudal rays is one (Lauder and Liem, 1983), although the distribution of this state needs to be surveyed. The juvenile head spines of *Beryx* (Fig. 5) may be informative; recent studies of percomorphs have demonstrated the value of ontogenetic cranial characters in systematics (Johnson, 1984; Johnson and Washington, 1987). The bones of the opercular and pectoral series bear numerous spines, as is common for larval percomorphs (Johnson, 1984). As in many percomorph families (Leis and Rennis, 1983; Johnson, 1984), spines are found along the posterior margin and anterolateral flange of the preopercle. In the circumorbital series, the large spine of the first infraorbital, among the first to develop, persists as large and isolated in adults (Zehren, 1979).

Johnson (1984) has suggested that larval spines of the cranial bones may be among the most useful for elucidating relationships among percomorphs. The frontals of *Beryx* larvae are heavily ornamented. Large anteromedial spines are characteristic of flexion and larger larvae. In addition, the frontals are rugose at relatively small sizes (Table 3). The degree of head spine ornamentation of larval *Beryx* does not approach that seen in many beryciform larvae (Keene and Tighe, 1984). The large spines on the first infraorbital seem to be autapomorphic for the

genus. *Beryx* lack the enlarged, serrate supraoccipital crest of the holocentrids (Keene and Tighe, 1984). The holocentrids share this character with the perciform families Scombroptidae, Lethrinidae, Cepolidae, Priacanthidae, and Pentacerotidae (Johnson, 1984). *Beryx* larvae also lack the enlarged parietal spines that unite the Anoplogasteridae and Diretmidae (Keene and Tighe, 1984). Among the Melamphidae, only *Poromitra* has head spination similar to *Beryx*, including frontal spines in *P. capito* (Ebeling and Weed, 1973) and *P. crassiceps* (pers. observ.). The trachichthyids have a complex pattern of small head spines (Keene and Tighe, 1984). Use of larval head spination in the systematics of Beryciformes must await the exact description of those spines in the various families.

Other characters of interest include the shape and coiling of the intestine and the early development of the fins. Again, *Beryx* larvae are most similar to *Melamphaes* in these characters (Keene and Tighe, 1984). Beryciform families with early pelvic fin development include the Anomalopidae, Holocentridae, Melamphidae, Monocentrididae, and Gibberichthyidae (Keene and Tighe, 1984; Okuyama, 1988; Colin, in press). Larval *Beryx* share with the percoid family Pempheridae not only the early pelvic development, but also the form of the intestine and the persistence of a remnant of the dorsal finfold that resembles an adipose fin in larvae nearing transformation (Leis and Rennis, 1983).

Larval characters will only be useful in beryciform systematics when a thorough survey of character states exists. More importantly, the polarity of these states must be determined at the basal level of the Percomorpha, to avoid the persistent problem of defining groups such as the Beryciformes by plesiomorphic percomorph states. Many larval characters of *Beryx*, such as the spines on the gill cover and the intestine shape, may prove to be plesiomorphic for percomorphs and, therefore, uninformative about the relationships of beryciform families.

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MATERIAL EXAMINED

Beryx spp.: Uncatalogued. 130 (1.3–6.0 mm SL), Hancock Seamount, 29°46.9'–29°48.1'N, 179°02.7'–179°05.3'E, and vicinity, 29°45.0'–29°50.2'N, 178°46.5'–178°56.5'E, 1 m² Tucker trawl, 0–50 m, 9–28 July 1984.

Beryx splendens: Uncatalogued. 1 (3.0 mm SL), reared from strip-spawned adults collected at Hancock Seamount, 29°48'N, 179°04'N, handline, 30 July 1984. Uncatalogued. 3 (7.3–7.5 mm SL), vicinity of Hancock Seamount, 29°48.1'–29°54.8'E, 178°49.6'–178°54.8'E, 1 m² Tucker trawl, 0–50 m 9–10 July 1988. MCZ 055334. 1 (27.5 mm SL), North Atlantic, 41°31'N, 55°11'W, 10-foot Isaacs-Kidd midwater trawl (IKMT), 22–30 m, 5 September 1964. MCZ 59033. 1 (15.2 mm SL, cleared and stained with alcian blue), North Atlantic, 34°18'N, 75°08'W, 10 m² MOCNESS, 70–140 m, 16 August 1978. MCZ 064862. 3 (9.2–10.3 mm SL), North Atlantic, 31°57'N, 77°21'W, 10 m² MOCNESS, 0–70 m, 7 August 1978. MCZ 064864. 1 (21.7 mm SL), North Atlantic, 15°30'N, 25°12'W, 10-foot IKMT, 85–95 m, 24 November 1970. MCZ 064865. 1 (7.4 mm SL), North Atlantic, 14°38'N, 50°12'W, 10-foot IKMT, 0–515 m, 10 October 1973. MCZ 068672. 1 (15.0 mm SL), North Atlantic, 30°01'N, 80°10'W, 10m² MOCNESS, 0–250 m, 4 August 1978. MCZ 068673. 1 (10.0 mm SL), North Atlantic, 34°15'N, 75°00'W, 10 m² MOCNESS, 0–70 m, 14 August 1978.

Beryx decadactylus: ARC 8602986, 1 (11.5 mm SL), North Atlantic, 42°09'N, 63°27'W, pelagic juvenile gadoid trawl (IGYPT), 0–204 m, 27 October 1984. MCZ 061484, 1 (23.3 mm SL), North Atlantic, 40°20.5'N, 50°47.1'W, 10 m² rectangular midwater trawl, 60 m wire out, 16 August 1984. MCZ 064863, 1 (16.4 mm SL), North Atlantic, 31°41'N, 76°58'W, 10 m² MOCNESS, 0–50 m, 31 July 1978. MCZ 064866, 2 (8.5–10.1 mm SL), North Atlantic, 32°10'N, 77°03'W, 10 m² MOCNESS, 0–110 m, 1 August 1978. MCZ 064867, 1 (21.0 mm SL), North Atlantic, 37°37'N, 66°43'W, 10-foot IKMT, 36–36 m, 26 August 1967.

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