Early life history stages of the whitetip flyingfish, *Cheilopogon xenopterus* (Gilbert, 1890) (Pisces: Exocoetidae)

William Watson
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038-0271
E-mail address: billwatson@ucsd.edu

Abstract.–The whitetip flyingfish, *Cheilopogon xenopterus*, is an epipelagic resident of tropical and subtropical eastern Pacific waters. Its eggs are spherical, average 1.8 mm in diameter, and have an homogeneous yolk and no oil globule. About 53 filaments averaging 1 mm in length are evenly distributed on the chorion. The notochord flexes, fin-ray formation is nearly complete, and the characteristic larval pigmentation pattern is established prior to hatching at a larval length of about 2.8–3.3 mm. Larvae hatch with pigmented eyes, functional mouth, and little remaining yolk. Pectoral- and pelvic-fin rays initially are short but elongate rapidly to ca. 25–50% and 20–40% of body length, respectively. A pair of mandibular barbels form at about 4 mm and fuse mesially at about 8 mm. Scales begin to form along the lateral line at about 13–14 mm and cover the body by 26 mm.

The characteristic pigment pattern, visible through the early juvenile stage, consists of the following: melanophores scattered over the mid- and hindbrain, continuing posteriorly as two rows (increasing to four or more rows) along the dorsal margin; a row of melanophores on the horizontal septum of the tail (after hatching); a patch on each side over the hypural area; and two rows along the anal-fin base. Internal pigment is present on the mid- and hindbrain, over the gut, and over the notochord. The pectoral and pelvic fins are sparsely pigmented at hatching and become increasingly pigmented with growth. A barred pigment pattern begins to develop on the body at about 8 mm and by the juvenile stage about six bars are present.

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Flyingfishes, surface-oriented residents of all warm oceans, are well known for their ability to leap from the water and glide over long distances. Flyingfishes can be abundant locally, many are attracted to light, and the gustatory quality of their flesh is generally good (Heemstra and Parin, 1986; Gillett and Ianelli, 1991; Parin, 1995). Directed fisheries for flyingfish currently exist, primarily in parts of the Indo-West Pacific and Caribbean; few such fisheries exist elsewhere (Gillett and Ianelli, 1991; Oxenford et al., 1995; Parin, 1995).

The family contains eight or nine genera and about 50–60 species (Nelson, 1994; Dasilao et al., 1996); nearly half the species are in the genus *Cheilopogon* (Heemstra and Parin, 1986). Eggs have been described for nine *Cheilopogon* species (Barnhart, 1932; Hubbs and Kampa, 1946; Miller, 1952; Imai, 1959; Gorbunova and Parin, 1963; Parin and Gorbunova, 1964; Kovalevskaya, 1965; Gibbs and Staiger, 1970; Vijayaraghavan, 1975; Shigonova and Kovalevskaya, 1991; Watson, 1996), and at least some larval stages are known for 16 species (Hildebrand and Cable, 1930; Barnhart, 1932; Breder, 1938; Hubbs and Kampa, 1946; Imai, 1959, 1960; Gorbunova and Parin, 1963; Kovalevskaya, 1965, 1975, 1977, 1982; Vijayarhagavan, 1975; Chen, 1987, 1988; Shigonova and Kovalevskaya, 1991; Belyanina, 1993; Parin and Belyanina, 1996; Watson, 1996). The purposes of this paper are to provide a description of the egg, larval, and early juvenile stages of the endemic eastern Pacific species *Cheilopogon xenopterus* (Gilbert, 1890) and to compare these briefly with the early stages described for other *Cheilopogon* species in the eastern Pacific.

Materials and methods

Descriptions are based on 20 eggs and a size series of 45 larvae (2.8–22.8 mm) and 8 juveniles (25.9–44.8 mm). Neustonic eggs and larvae and three of the juveniles were collected with Manta nets (Brown and Cheng, 1981) during Marine Mammals Division (Southwest Fisheries Science Center) dolphin surveys in the eastern tropical Pacific (Thayer et al., 1988a, 1988b; Lierheimer et al., 1989, 1990; Philbrick et al., 1991, 1993). The Manta samples were taken nightly from late July through early November or December, 1987–90, and 1992, between about 2–16°N and east of about 115°W. A few juvenile and adult specimens of *C. atrisignis*, *C. dorsomaculata*, *C. furcatus*, *C. papilio*, *C. spilonotopterus*, and *C. xenopterus*, radiographed to make fin-ray and vertebral counts for comparison with counts from series specimens, were obtained from the Scripps Institution of Oceanography Marine Vertebrates Collection (SIO).

Eggs, larvae, and juveniles (except those used exclusively for radiography) were measured to the nearest 0.04 mm by using a Wild M-5 binocular microscope equipped with an ocular micrometer. Dimensions measured for eggs included chorion diameter, maximum yolk diameter, and lengths of the shortest and longest intact chorionic filaments, and for larvae and juveniles, body length (BL), preanal length (PAL), head length (HL), snout length (SnL), barbel length (BbL), eye diameter (ED), head width (HW), body depth (BD), and lengths of the pectoral (P_1L) and pelvic (P_2L) fins. All these dimensions, except chorionic filament length (measured along the axis of the filament from its point of attachment on the chorion to its free tip), are defined by Moser (1996). Larval lengths refer to formalin-preserved body length. All descriptions of pigmentation refer solely to melanistic pigment.

One late embryo (3.3 mm) dissected from the egg and eight larvae (2.9–16.8 mm) were cleared and stained with alcian blue and alizarin red S according to the method of Taylor and VanDyke (1985) to elucidate the development of the axial skeleton and fins and to aid in making counts. Illustrations were made with a Wild M-5 microscope equipped with a camera lucida.

Identification

Specimens were identified by the series method. A size series of larvae and juveniles, linked by shared morphological, meristic, and pigmentation characters, was traced down to recently hatched larvae from juveniles that could be identified by using known juvenile and adult characters. The smallest larvae shared a pigmentation pattern with late-stage embryos that allowed identification of the eggs.

Of the eight flyingfish genera in the eastern tropical Pacific (Parin, 1995; Dasilao et al., 1996), only *Cheilopogon* has paired mandibular barbels during at least part of the larval and juvenile stages (Parin, 1961a, 1961b; Collette et al., 1984). (*Parexocoetus brachypterus* develops a pair of mandibular barbels, and a small beak as well, during the juvenile stage: Collette et al., 1984.) Of the nine *Cheilopogon* species in and near the area (Table 1; Parin, 1995), larvae are known for five: (*C. atrisignis*: Chen, 1987, 1988; *C. furcatus*: Hildebrand and Cable, 1930; *C. heterurus hubbsi*: Barnhart, 1932; Watson, 1996; *C. pinnatibarbatus californicus*: Hubbs and Kampa, 1946; Watson, 1996; and *C. spilonotopterus*: Kovalevskaya, 1977; Chen, 1987, 1988). All five differ from the series treated here. *Cheilopogon rapanouiensis* was eliminated from consideration by its higher vertebral, pectoral-fin ray, and predorsal scale counts (45–46 vs. 43, 16–17 vs. 13–15, and 31–33 vs. 27–28, respectively). *Cheilopogon papilio* was eliminated because of its lower dorsal-fin ray count (9–10 vs. 12–13), usually lower pectoral-fin ray count (12–13 vs. 13–15), because of separate rather than fused barbels and much heavier pectoral- and pelvic-fin pigmentation in the juvenile stage, and because of restricted distribution in coastal waters and the lower Gulf of California (Parin, 1995). The remaining two species, *C. dorsomaculata* and *C. xenopterus*, are widely distributed in the eastern tropical Pacific (Parin, 1995), are quite similar in appearance as small (<ca. 40 mm) juveniles, and both were considered as possible identifications for the present series. Predorsal scale counts from the largest series juveniles (27–28 scales) are consistent with *C. xenopterus* and slightly high for *C. dorsomaculata* (Table 1). Pectoral-fin ray counts for series specimens having full complements of rays (>9 mm; 13–15 rays) match the range for *C. xenopterus* and fall below to within the lower half of the range for *C. dorsomaculata* (Table 1). Juvenile *C. dorsomaculata* typically have less pelvic-fin pigment than *C. xenopterus*, and in this character the larger series specimens are consistent with *C. xenopterus*. Thus, I concluded that the series is *C. xenopterus*.

Specimens examined

Listings are given as cruise and station number or SIO catalogue number, and in parentheses number of specimens and size range. Specimens listed with cruise numbers are housed at the National Marine Fisheries Service Southwest Fisheries Science Center; specimens with SIO numbers are housed at the Scripps Institution of Oceanography Marine Vertebrates Collection.

Cheilopogon xenopterus (Gilbert, 1890).

Eggs: 8910JD: 3-100 (3: 1.8–1.9 mm), 3-102 (7: 1.8–1.9 mm), 4-107 (1: 1.7 mm); 9210JD: 1-001 (4: 1.8–1.9 mm), 1-008 (4: 1.8–1.9 mm), 3-047 (1: 1.8 mm).

Larvae: 8710JD: 1-009 (1: 15.2 mm), 2-016A (1: 2.8 mm), 3-046 (6: 3.4–4.8 mm), 3-054 (1: 2.9 mm), 3-056 (1: 4.9 mm), 3-075 (1: 2.9 mm), 3-078 (2: 5.3, 14.3 mm); 8710M4: 1-003 (1: 4.1 mm); 8810JD: 2-049 (1: 8.0 mm), 3-086 (1: 7.5 mm), 3-118 (5: 8.7-13.6 mm), 4-153 (1: 8.3 mm); 8910JD: 1-015 (1: 2.9 mm), 1-019 (1: 6.4 mm), 1-021 (1: 13.7 mm), 2-056 (1: 6.8 mm), 3-104 (1: 4.8 mm); 8910M4: 1-010 (1: 12.5 mm), 1-012 (1: 3.4 mm), 4-143 (2: 9.8, 13.9 mm); 9010JD: Manta 54 (1: 13.4 mm), Manta 65 (1: 6.4 mm), Manta 74 (1: 22.8 mm); 9210JD: Manta 2 (1: 8.1 mm), Manta 9

Table 1

Selected meristic characters for the *Cheilopogon* species that occur in and near the eastern tropical Pacific Ocean. The pectoral-fin ray count includes the small, spine-like first pectoral-fin ray. Data are from Parin (1960, 1961a), Watson (1996), and counts made during this study. D = dorsal; A = anal; P_1 = pectoral; Proc.C = procurrent caudal-fin rays.

	Vertebrae			Fin rays				
Species	Abdominal	Caudal	Total	D	A	P_1	Proc. C	Predorsal scales
atrisignis	28–30	15–16	43–45	13–15	9–10	13–15	6+8	31–40
dorsomaculata	28–29	14–15	42–44	11–14	9–10	14–17	5–6+6–7	23–25
furcatus	29–31	14–15	43–46	12–14	9–11	14–18	7+6–8	27–35
heterurus hubbsi	31–33	15–17	47–49	12–14	8–11	14–16	6–7+7	28–36
papilio	28–29	14–15	42–44	9–10	9–10	12–13	4–5+6	29–33
pinnatibarbatus californicus	31–35	16–17	48–51	9–13	9–12	14–15	5–6+6–8	40–43
rapanouiensis	30–31	15–16	45–46	11–12	10–11	16–17		31–33
spilonotopterus	29	14	43	13–14	10–11	13–15	6+7	29–34
xenopterus	27–30	13–15	42–44	10–13	9–10	13–15	5–6+6–8	27–30

(1: 6.3 mm), Manta 11 (2: 4.7, 5.3 mm), Manta 19(?) (1: 8.1 mm), Manta 34 (2: 5.3, 5.6 mm), Manta 37 (1: 16.5 mm), Manta 47 (1: 6.5 mm), Manta 51 (1: 6.8 mm); SIO 63-54 (1: 18 mm).

Juveniles: 8710JD: 1-006 (1: 25.9 mm); 8810JD: 3-108 (1: 44.8 mm); 8910JD: 1-039 (1: 36.4 mm); SIO 63-31 (1: 116 mm); SIO 63-96 (1: 38.5 mm); SIO 63-105 (7: 34.5–57.0 mm); SIO 63-608 (3: 64–92 mm); SIO 64-539 (1: 62 mm); SIO 72-121 (2: 42, 45 mm); SIO 73-400 (3: 63–76 mm).

Cheilopogon atrisignis (Jenkins, 1903). SIO 79-29 (1: 52 mm).

Cheilopogon dorsomaculata (Fowler, 1944). SIO 52-399 (1: 46 mm); SIO 52-416 (6: 147–214 mm); SIO 58-318 (1: 179 mm); SIO 78-214 (1: 36.5 mm).

Cheilopogon furcatus (Mitchill, 1815). SIO 76-246 (1: 52 mm); SIO 93-89 (1: 183.5 mm FL).

Cheilopogon papilio (Clarke, 1936). SIO 58-395 (2: 65–75 mm); SIO 69-387 (2: 20, 21 mm); SIO 93-95 (2: 109, 115.5 mm).

Cheilopogon spilonotopterus (Bleeker, 1866). SIO 60-265 (1: 103 mm); SIO 69-405 (1: 39 mm).

Description of eggs

Morphology

Eggs spherical, average 1.8 mm in diameter (range 1.7–1.9 mm), have narrow perivitelline space (mean yolk diameter 1.7 mm, range 1.5–1.8 mm), homogeneous yolk, and lack oil globules (Fig. 1). Between about 42 and 64 slender filaments (mean 53) evenly distributed over smooth, transparent chorion; each attached to chorion at one end and all of similar length (mean 1.2 mm, range 0.7–1.4 mm).

Pigmentation

Chorion unpigmented, yolk colorless to pale yellow. Embryonic pigmentation first appears about midway through development (stage VIII; embryonic tail length increases from 50% to 100% HL during this stage; e.g. Moser and Ahlstrom, 1985) as one to few small melanophores dorsolaterally on midbrain area and small cluster just anterior to each pectoral-fin bud (Fig. 1B). Pigmentation increases dorsolaterally on head, forms around margins of eyes and ventrally on head in stage IX (tail > HL but < 50% yolksac length). During this stage melanophores spread posteriorly and dorsally from prepectoral clusters, forming two rows on dorsum to midway along embryonic axis, and melanophores form dorsally on developing gut, beginning posteriorly early in stage. By stage X (tail extends 50–75% of yolksac length) characteristic larval pigment pattern clearly visible, with dorsal rows extending to near end of tail, a few melanophores around margin of caudal peduncle, and two rows along base of anal fin (Fig. 1C). Near end of embryonic development (stage XI: tail extends >75% of yolksac length) melanophores fill in over central axis of head, form near distal margins of pectoral fins and proximally on caudal fin, may form near distal margins of pelvic fins (present in one of three stage-XI specimens examined), form in internal series over notochord and posteriorly under notochord, and become increasingly dense on dorsal and ventral margins near midtail. Eyes become fully pigmented during stage XI.

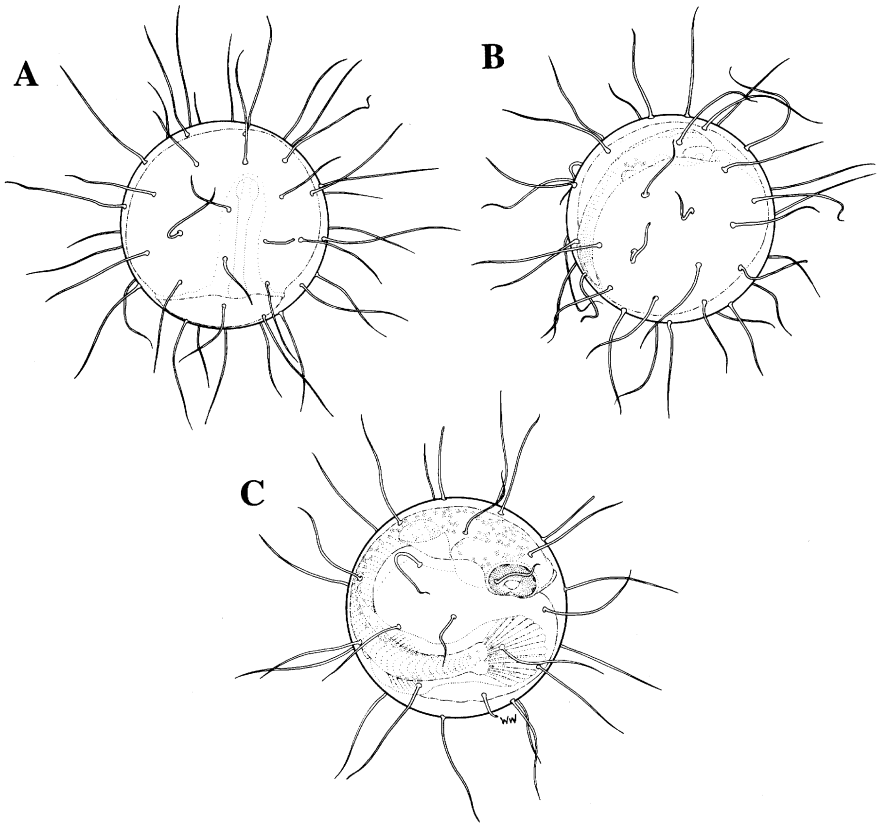

Figure 1

Eggs of *Cheilopogon xenopterus*. (**A**) stage VI, 1.8 mm (8910JD, station 3-102); (**B**) stage VIII, 1.8 mm (9210JD, station 1-008); (**C**) stage X, 1.9 mm (8910JD, station 3-100).

Description of larvae

Morphology

Larvae hatch at about 2.9–3.3 mm length and have little remaining yolk, functional mouth, fully flexed notochord, and rays forming in all fins (Fig. 2). Larvae moderately elongate, with preanal length near 80% BL at hatching, become increasingly elongate with preanal length decreasing to near 70% BL by ca. 8 mm (Table 2). Eyes initially oval (vertical axis about 70% horizontal axis), gradually becoming nearly round. Pectoral- and pelvic-fin rays initially short (near 10% BL), rapidly elongate to ca. 25–50% and 20–40% BL, respectively. Height of dorsal fin increases from about 15% BL in large larvae (15–18 mm) to about 28% BL in small juveniles (by ca. 36 mm). A pair of mandibular barbels forms at about 4 mm. Barbels originate as low, anteroventral thickening that elongates into a slender, flattened flap on each side of lower jaw. Barbels broaden, develop frilled margins, and fuse mesially at their bases by about 8.3 mm (Figs. 2–4). Scales form along lateral line beginning at about 13–14 mm and cover body by 26 mm. There are 27–30 predorsal scales and seven scale rows between dorsal-fin origin and lateral line.

Vertebral column and fin development

Notochord flexion begins during embryonic stage VIII (dorsal, anal, caudal finfolds first visible in this stage) and is completed early in stage IX. Vertebral column ossification begins soon after hatching. Neural and haemal arches and spines apparently form first, before corresponding vertebral centra. Ossification of arches apparently anterior to posterior: in 3.8-mm specimen all arches ossifying except last three neural arches, last haemal arch, and last three or four neural and haemal spines (all present as cartilage). Direction of ossification of individual arches apparently distad from base: in 3.8-mm specimen haemal arches 11–13 appear to be ossifying from near base

Table 2

Summary of measurements of *Cheilopogon xenopterus*, expressed as percentage of body length (BL) or head length (HL). For each measurement the mean is given above and the range is given below. For eye diameter (ED), eye length is given first and eye height second; *n* = number of specimens. Specimens 24.1 mm and larger were considered juveniles. PAL= preanal length; P_1L = pectoral-fin length; P_2L = pelvic-fin length HW = head width; SnL = snout length; BbL = barbel length.

BL (mm)	*n*	PAL/BL	BD/BL	HL/BL	P_1L/BL	P_2L/BL	HW/HL	SnL/HL	ED/HL	BbL/HL
2.8–4.0	9	76	24	33	28 (*n*=6)	28 (*n*=5)	69	14	42,31	0.3
		71–88	22–28	30–39	12–35	18–32	67–74	12–17	39–47, 28–34	0–3
4.1–6.0	10	72	21	30	38 (*n*=8)	38 (*n*=9)	69	17	41,33	4 (*n*=9)
		68–75	19–24	29–33	27–50	34–44	66–75	13–23	38–45, 29–35	2–10
6.1–8.0	8	70	18	26	37 (*n*=5)	30	67	17	41,34	17 (*n*=7)
		68–73	17–20	24–28	35–40	28–33	63–73	14–20	38–42, 31–37	10–24
8.1–10.0	6	69	17	24	39 (*n*=5)	35 (*n*=5)	66	17	43,36	36
		66–71	16–18	23–25	35–43	30–39	61–72	16–19	40–46, 33–42	24–48
10.1–12.0	2	68	17	22	40(*n*=1)	31	67	16	44,37	46
		68–68	16–17	22–22		30–32	67–67	16–17	43–44	39–53
12.1–14.0	5	68	15	20	42	35	71	18	46,42	49
		66–68	14–16	19–20	39–46	34–37	68–73	16–19	43–48, 39–45	39–57
14.1–16.0	2	73	16	21	48	39	73	15	47,43	65
		72–75	16–17	20–21	46–49	37–41	70–76	13–17	44–50, 42–43	59–72
16.1–18.0	2	68	16	20	50	41	74	20	45,43	71
		68–68	15–18	19–20	49–52	41–41	73–75	17–22	44–47, 41–45	59–83
22.1–24.0	1	68	15	20	58	39	71	20	46,45	61
24.1–26.0	1	69	15	19	56	39	76	18	48,47	55
34.1–36.0	1	71	16	21	65	43	70	24	38,37	43
36.1–38.0	1	72	16	20	68	44	73	17	42,44	44
38.1–40.0	1	74	15	22	72	43	67	18	36,36	43
40.1–42.0	2	72	16	22	67	42	67	21	39,40	46
		71–73	15–16	22–22	67–68	41–42	66–68	20–23	36–41, 38–42	39–53
42.1–44.0	1	71	16	22	69	43	66	20	38,37	39
44.1–46.0	1	77	19	21	72	42	79	19	43,44	53

of each haemapophysis. In 6.3-mm specimen last four neural arches and spines broadening and by 8.2 mm last six much broader than more anterior neural arches and spines. These broad posterior neural arches and spines provide the necessary attachment surfaces for the large supracarinalis posterior, flexor dorsalis, and flexor ventralis muscles (Winterbottom, 1974; Dasilao et al., 1996) which are involved in generating the strong caudal thrust required for gliding.

Ossification of each vertebra begins ventrally. As bone spreads dorsad from ventrum, ossifications also form at bases of the two neurapophyses and spread mesially and ventrad to complete centrum. Centra apparently added from anterior to posterior, but urostyle and penultimate centrum ossify before other caudal vertebrae. All vertebrae ossified by 5.2 mm (Table 3). There are 42–44 vertebrae: 27–30 abdominal and 13–15 caudal (modally 29 + 14 = 43).

Pleural ribs first visible in 6.3-mm specimen (Table 3). These ossify adjacent to parapophyses beginning at third vertebra (at second vertebra on one side in one specimen) and are added posteriorly. Epineural intermuscular bones begin ossifying in myosepta anteriorly, initially remote from vertebrae, by 8.2 mm (Table 3), and pairs added posteriorly. Ossification of each rib and epineural intermuscular bone is both mesial toward adjacent parapophysis, and distal. Full complements of both series not yet formed in largest cleared and stained specimen.

Caudal and pectoral are first fins to begin forming. Hypural elements first visible in late stage-VIII embryos, begin ossifying soon after hatching (by 2.9 mm). Retrorse basal spur forms on hypural 1 by 6.3 mm. Uroneural ossifying by 5.2 mm and epurals 1 and 2 by 6.3 mm. Epural 3 not clearly ossifying until 8.2 mm. Principal caudal-fin rays begin to form

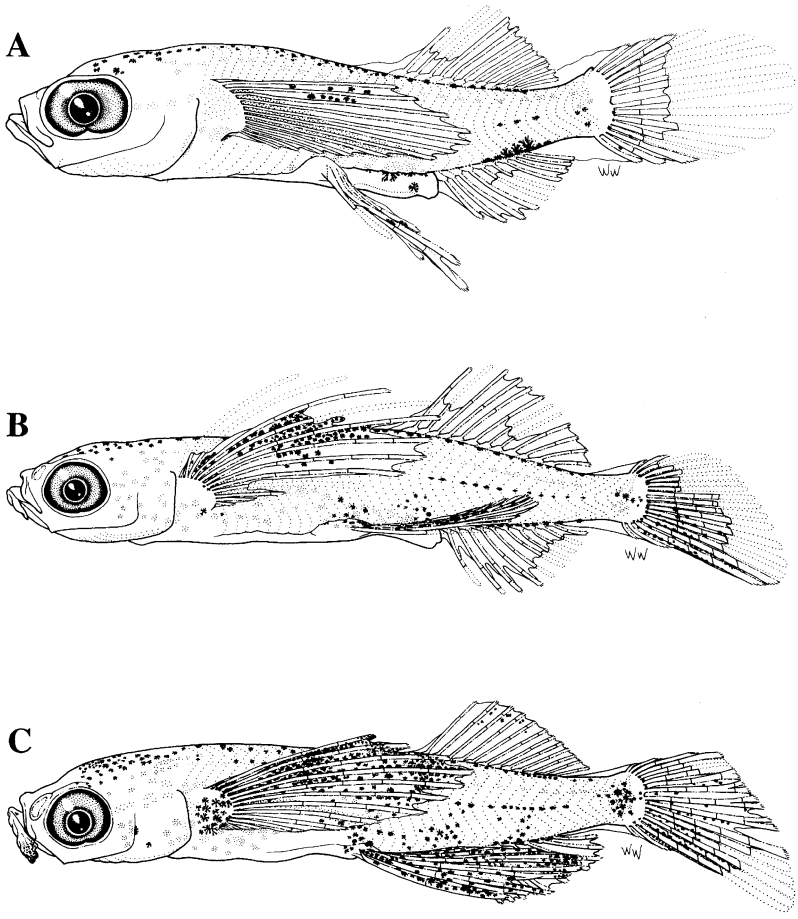

Figure 2

Larval *Cheilopogon xenopterus*, lateral view. (**A**) 3.5 mm (8710JD, station 3-046); (**B**) 8.0 mm (8810JD, station 2-049); (**C**) 8.1 mm (9210JD, station Manta 2). Fin rays shown in dotted lines are based on fins of other specimens of similar size.

during embryonic stage X (Table 3) and all 7+8 rays present at hatching. All principal rays supported by hypurals through at least 8.2 mm but by 10.5 mm lowermost principal ray partially supported by haemal spine associated with preural centrum 1. By 13.4 mm lowermost principal ray fully supported and adjacent principal ray partially supported by haemal spine, and by 16.8 mm both rays fully supported by haemal spine. Procurrent caudal-fin rays begin to form shortly after hatching (by 3.8 mm) but full complement of 5–6 dorsal and 6–8 ventral rays not attained until near end of larval development (by 16.8 mm). Caudal fin initially rounded, becomes assymetrical as lower principal rays elongate, beginning at about 5 mm.

Pectoral-fin buds form in stage-VIII embryos, almost simultaneously with beginning of notochord flexion, and upper rays form during embryonic stage X. Addition of rays is ventrad, with full complement of 13–15 rays (including uppermost small, spine-like ray) attained by 9.3 mm (Table 3). Lowermost ray quite small and nearly completely covered by scales in juveniles larger than

Table 3

Counts for cleared and stained *Cheilopogon xenopterus*. In cases where two counts are given for one category, the first value is the count from the left side, the second is from the right side. Pectoral fin-ray counts include the first small, spine-like ray. D = dorsal; A = anal; P_1 = pectoral; P_2 = pelvic; C = caudal.

	Vertebrae					Fin rays				
BL (mm)	Abdominal	Caudal	Pleural ribs	Epineural inter-muscular	Branchiostegal rays	D	A	P_1	P_2	C
3.3 (embryo)	0	0	0	0	2	0	0	3	5	0+5+5+0
2.9	0	0	0	0	2	11	10	6	6	0+7+8+0
3.8	23	2	0	0	6	12	10	13	6	1+7+8+1
5.2	28	15	0	0	7	12	10	11	6	2+7+8+2
6.3	29	14	12	0	7,8	13	10	12	6	2+7+8+2
8.2	29	14	15	8	9	12	9	12	6	3+7+8+3
10.5	29	14	17	14	9	12	11	13	6	3+7+8+4
13.4	28	15	20,21	26	9	12	9	15,14	6	4+7+8+6
16.8	28	15	22	29	11	13	9	15	6	6+7+8+7

about 38 mm. Pelvic-fin buds form during embryonic stage IX, at about completion of notochord flexion. All six pelvic-fin rays apparently present at hatching.

Cartilaginous dorsal- and anal-fin pterygiophores form late during embryonic development: cleared and stained late stage-X embryo had six dorsal, five anal-fin pterygiophores. Addition and ossification of pterygiophores apparently anterior to posterior. Each pterygiophore initially is single cartilage which begins to ossify near middle of lower portion (forming proximal radial). Although pterygiophores did not stain well in smaller larvae, at least first three or four anal-fin pterygiophores beginning to ossify in 3.8-mm specimen and first five or six dorsal- and anal-fin pterygiophores in 5.2-mm specimen. By 6.3 mm all but posterior three or four dorsal proximal radials ossifying, and distal radials appear to be ossifying adjacent to fin-ray bases. About 8.2–13.4 mm separate ossifications, probably representing middle radials, form on cartilage between proximal and distal radials, but by 16.8 mm each proximal + middle radial appears to be a single ossified unit. Dorsal- and anal-fin rays begin to form in stage-XI embryos; all anal- and most dorsal-fin rays present at hatching.

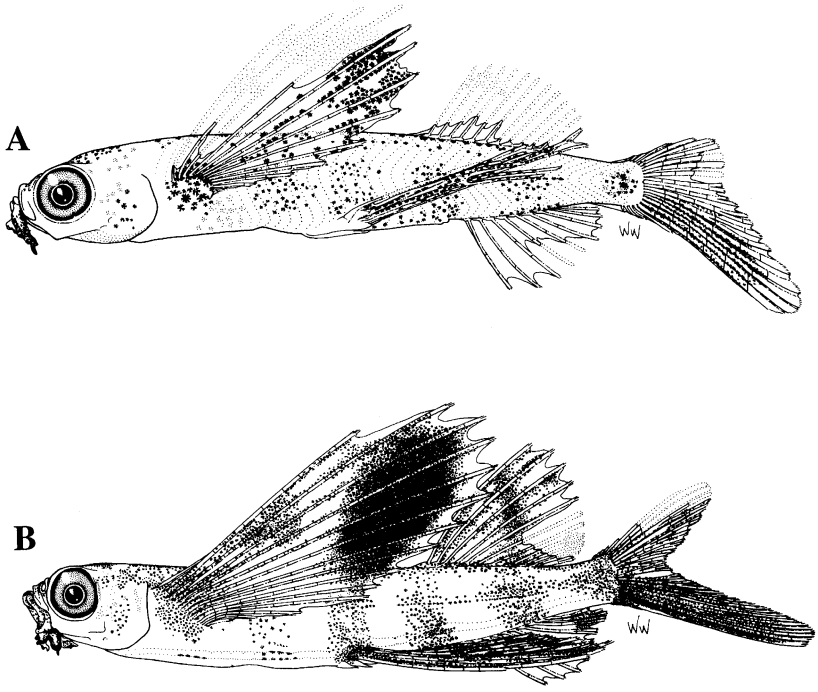

Figure 3

Cheilopogon xenopterus, lateral view. (**A**) larva, 12.5 mm (8910M4, station 1-010); (**B**) juvenile, 36.4 mm (8910JD, station 1-039). Fin rays (and fin pigment in A) shown in dotted lines are based on fins of other specimens of similar size.

Pigmentation

Most elements of basic pattern established during late embryonic development are visible throughout larval period. Principal internal elements of pattern are 1) melanophores under mid- and hindbrain (difficult to see after about 6 mm); 2) row over notochord (difficult to see after about 6 mm); 3) melanophores present around urostyle and proximally on hypurals; 4) melanophores present dorsally, dorsolaterally on gut. Principal external elements are: 1) dorsal melanophores covering mid- and hindbrain areas; 2) two somewhat irregular rows along dorsal margin of trunk and tail (increasing to four rows after about 9 mm), and melanophores in each row usually more closely spaced along posterior half of dorsal-fin base; 3) two rows along anal-fin base, commonly expanded along posterior half of fin base; 4) patch on each side over urostyle and hypural area; 5) scattered melanophores on pectoral, pelvic, and caudal fins.

Subsequent additions to internal pigmentation include melanophores spreading around sides of mid- and hindbrain and increasing in number anteriorly over notochord, forming internally on opercular area beginning at about 6–6.5 mm, and spreading ventrolaterally on gut (primarily anteriorly), surrounding gut at level of pectoral-fin bases between 12 and 18 mm. Pigmentation on urostyle and hypural area usually increases somewhat. External dorsal pigmentation on head slowly increases, spreading forward onto snout after about 13 mm. Melanophores form on upper jaw by about 10 mm. In early juveniles, melanophores over mid- and hindbrain spread ventolaterally, reaching level of pectoral-fin origin by about 36 mm. External melanophores present on central opercular area by about 8 mm (Fig. 2C), form indistinct bar across cheek by about 12–15 mm (Fig. 3A). Barbels initially unpigmented, become densely pigmented distally, usually beginning between 6 and 7 mm. As barbels broaden, melanophores become more concentrated along distal margins and after barbel fusion, connecting membrane becomes intensely pigmented along distal margin (by 12–13 mm:

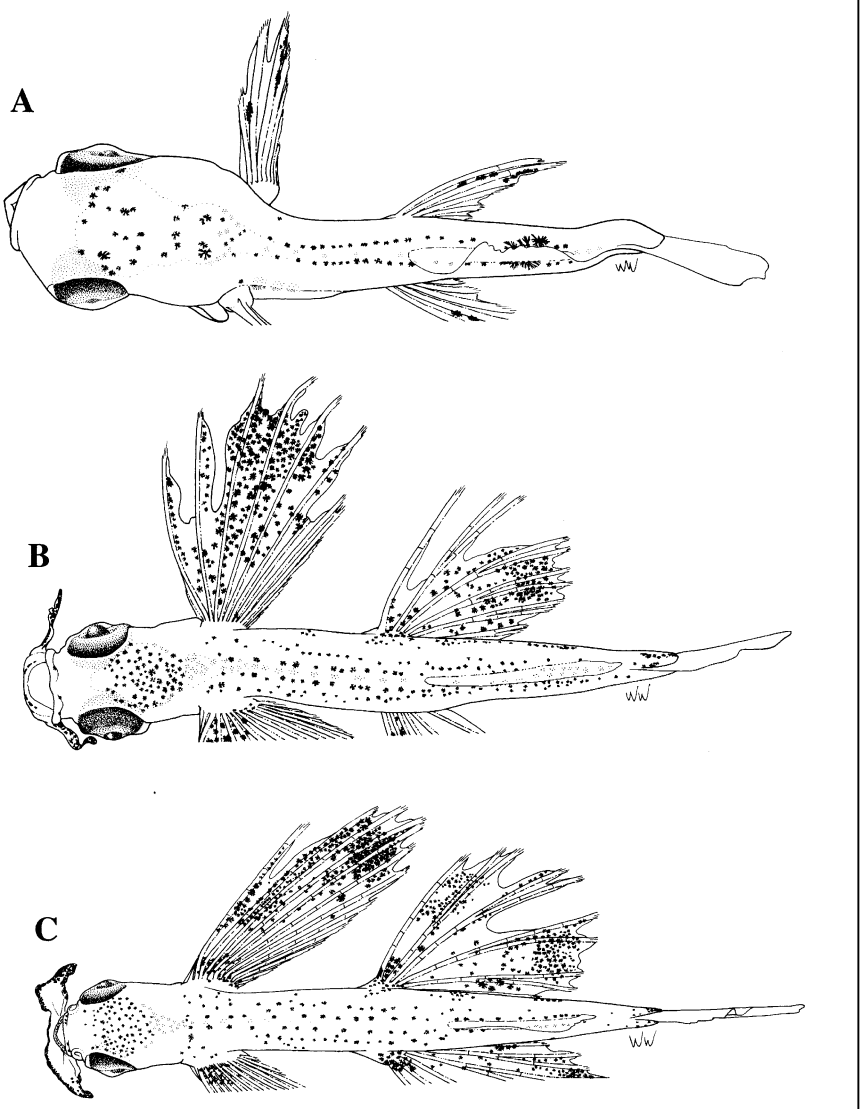

Figure 4

Larval *Cheilopogon xenopterus*, dorsal view. (**A**) 2.9 mm (8910JD, station 1-015); (**B**) 10.5 mm (8810JD, station 3-118); (**C**) 13.4 mm (9010JD, station Manta 54).

Fig. 4C). Few melanophores usually form along lower jaw after about 7 mm.

Soon after hatching, a row of melanophores forms along horizontal septum, originating just behind midtail and spreading cephalad and caudad (primarily cephalad) along tail (Fig. 2, A and B). Barred pattern begins to develop at about 6 mm as melanophores spread upward from pelvic-fin bases and from ventral margins of last three or four preanal myomeres (Fig. 2B). Two more bars begin to spread upward from vicinity of anal-fin rays 5–8 and from midway between pectoral- and pelvic-fin bases (Figs. 2C, 3A) between about 8 and 9 mm. Bars usually do not reach dorsal margin in larvae. Pigmentation on pectoral-fin base sparse until about 8 mm then increases, spreads onto adjacent myomeres, and in juveniles merges with melanophores spreading downward from dorsum to form saddle (Figs. 2C; 3, A and B). Melanophore cluster on hypural area expands to cover almost entire area by about 13 mm. Juveniles thus display six or seven bars (including pectoral saddle); in juveniles >30–40 mm posterior three or four bars most prominent (Fig. 3B).

Pectoral-fin pigmentation initially sparse. After hatching, melanophores gradually spread over membranes between upper 5–6 rays, a few scattered between all but lowermost 3–4 rays, by about 8 mm (Fig. 2, A–C). Pigment patterns variable in larvae

<10–12 mm, except that melanophores tend to be more concentrated near distal margin between upper 5–7 rays and in patch about midway along upper rays. After about 12 mm concentration midway along upper rays commonly persists, but may diminish or disappear, and distal patch expands to form distinct blotch along upper 6–8 rays, bordered by unpigmented (or sparsely pigmented) margin (Fig. 4C). Distal blotch expands into elongate oval band over much of width of pectoral fin in juveniles (Fig. 3B). Upper 4–6 pectoral rays also may remain sparsely to moderately pigmented, especially proximally and in the blotch midway along upper rays, in larger larvae and juveniles. Apart from upper rays and distal blotch or band, remainder of fin has little pigment after ca. 15 mm.

Pelvic-fin pigment may form before hatching; always present after hatching. Sparse initially, commonly sparse to moderate throughout larval development (Fig. 4). Pattern variable: melanophores tend to be more concentrated near distal margin of most or all of fin, in distal patch at innermost ray or between two or three middle rays, or in two distal patches at innermost and outermost rays. Occasionally melanophores more concentrated distally and midway along rays. Distal patch near middle of fin is most common pattern in larger larvae and juveniles.

Caudal-fin pigmentation forms in late embryos, initially proximally, mostly or entirely on lower rays. Pigment increases and spreads to about three-quarters of length of lower principal rays by ca. 8 mm. Melanophores consistently present on upper part of fin by about 8 mm but pigment here is sparse in larvae and sparse to moderate in juveniles.

Diagonal band forms on dorsal fin, originating distally between anterior 2–3 rays just after 8 mm (Fig. 2C) and reaching base of rays 6–7 between 18 and 22 mm. Pigmentation may be sparse in lower (=posterior) part of band and in larger juveniles band appears more like elongate oval patch along first 5–6 rays. Distal blotch forms at last 2–3 rays beginning at about 12–13 mm. Melanophores form on membranes between (primarily adjacent to) first 5–6 rays after 18 mm. Anal fin unpigmented in larvae, but distal blotch forms at last 2–3 rays in juveniles (Fig. 3B).

Comparisons

Eggs

Most exocoetids have spherical eggs that are about 1.5–3 mm in diameter, lack oil globules, and have filaments on the chorion (Collette et al., 1984). *Cheilopogon* eggs are typical exocoetids in these characters. For most of the *Cheilopogon* species the filaments are evenly distributed as in *C. xenopterus*. Only *C. heterurus* and *C. unicolor* have been described as having a different arrangement, with filaments grouped in bipolar clusters (Barnhart, 1932; Miller, 1952; Imai, 1959; Gorbunova and Parin, 1963; Watson, 1996). Among the species with uniform filament distribution, the number of filaments ranges from about 10 to 90; the range in *C. xenopterus* (about 40–60) apparently is typical (e.g. Collette et al., 1984). Filament length in these species ranges from less than 1 mm to just over 10 mm; most commonly the filaments are long, a character shared with *Cypselurus* (e.g. Collette et al., 1984). The short filaments of *Cheilopogon xenopterus* (about 1 mm) are a character shared with *Prognichthys* (Kovalevskaya, 1982) and with at least some of the members of the *C. nigricans* species group (Parin and Belyanina, 1996), which includes *C. dorsomaculata* and *C. xenopterus* in the eastern tropical Pacific. Eggs have not been described for *C. dorsomaculata* or the two *Prognichthys* species in the eastern tropical Pacific (Parin, 1995) and it is unknown how they might be distinguished from the eggs of *C. xenopterus* except that late stage *Prognichthys* embryos should be more densely pigmented. An unidentified type of exocoetid egg (2.2 mm diameter with ca. 150 short filaments) occasionally co-occurs with *C. xenopterus* in plankton samples; it might be one of these species (larval *Prognichthys* are relatively common in the samples).

Collette et al. (1984) noted that some flyingfishes apparently have a preanal finfold during early development and suggested that it is an embryonic feature that is lost soon after hatching. There is no preanal finfold in *C. xenopterus*.

Larvae and juveniles

Larval *Cheilopogon* range between about 4 and 6 mm (e.g. Collette et al., 1984) and are well developed at hatching. *Cheilopogon xenopterus* may be a bit smaller than usual, but otherwise is typical of the genus at hatching. *Cheilopogon* larvae develop a pair of mandibular barbels that persist into the juvenile stage and remain separate or fuse mesially—the membrane joining the barbels either remaining low and simple or becoming broad and fimbriate. Among the *Cheilopogon* species in the eastern Pacific, *C. furcatus*, *C. heterurus hubbsi*, and *C. papilio* retain separate barbels in the juvenile stage. The barbels become fused basally by means of a low, sparsely pigmented or unpigmented membrane in *C. atrisignis* and *C. spilonotopterus*, whereas in *C. dorsomaculata* and *C. xenopterus* the basal membrane is somewhat broader and densely pigmented along its margin.

Only one species, *C. pinnatibarbatus*, is known to have a broad, fimbriate membrane that unites the barbels (Hubbs and Kampa, 1946; Imai, 1959). The barbels become moderately long (Bbl > HL) in *C. atrisignis* and *C. spilonotopterus*, whereas the other species retain relatively short barbels (Bbl < HL). The size and condition of the barbels in *C. rapanouiensis* are unknown, but in the closely related species *C. agoo* they are short (Chen, 1987, 1988).

Larval pigmentation in *Cheilopogon* initially ranges from sparse to dense and typically increases gradually during development. The sparsely pigmented larvae, including *C. xenopterus*, probably *C. atrisignis* and *C. dorsomaculata*, and possibly *C. spilonotopterus* and *C. papilio*, display a pattern primarily of melanophore rows on the dorsum, on the horizontal septum, and on the ventral margin of the tail, and usually bars form in the latter part of the larval stage (Kovalevskaya, 1965, 1977; Chen, 1987, 1988). The more heavily pigmented species, including *C. furcatus*, *C. heterurus hubbsi*, and *C. pinnatibarbatus californicus*, display a pattern similar to that of larval *Cypselurus*, with melanophores more evenly distributed over the trunk and at least anteriorly on the tail (sometimes diminishing to dorsal, midlateral, and ventral rows on the posterior half of the tail) (Hildebrand and Cable, 1930; Hubbs and Kampa, 1946; Watson, 1996). *Cheilopogon rapanouiensis* might belong to this latter group as well, if its larvae resemble the moderately pigmented larvae of *C. agoo* (Chen, 1987, 1988). Juveniles of most species are barred; about six bars (as in *C. xenopterus*) is common.

Larvae and juveniles of *C. xenopterus* usually can be distinguished without great difficulty from the other flyingfish species in the eastern Pacific, except perhaps from *C. dorsomaculata*. The position of the anal-fin origin below dorsal rays 4–7 distinguishes *C. xenopterus* from *Exocoetus*, *Fodiator*, *Hirundichthys*, and *Oxyporhamphus*, in which the anal-fin origin ranges from just ahead of the dorsal-fin origin to under dorsal rays 1–3, depending on species (e.g. Imai, 1954; Kovalevskaya, 1964, 1980; Chen, 1988; Watson, 1996). Larger larvae and juveniles of all four genera are further distinguished from *C. xenopterus* (and all the other *Cheilopogon* species) by their lack of paired mandibular barbels. *Cheilopogon xenopterus* (and all the other flyingfishes) are also distinguished from *Exocoetus* by having much more posteriorly placed pelvic fins. Larval *Fodiator* and *Oxyporhamphus* are unique in developing a beak beginning at about 6 mm and 8 mm, respectively, whereas *Parexocoetus* acquires a much smaller beak in the juvenile stage, by about 18 mm (e.g. Collette et al., 1984; Watson, 1996). *Cheilopogon xenopterus* is rather sparsely pigmented, in contrast to the more general, denser pigmentation of larval *Cypselurus*, *Exocoetus*, *Fodiator*, *Parexocoetus*, *Prognichthys*, and the three or four *Cheilopogon* species noted above (e.g., Hildebrand and Cable, 1930; Imai, 1959, 1960; Kovalevskaya, 1980; Chen, 1988; Watson, 1996). Among the more sparsely pigmented flyingfish larvae, *Hirundichthys* (which may be moderately pigmented initially, but become more sparsely pigmented on at least the prepelvic part of the trunk; e.g. Kovalevskaya, 1980) and *Oxyporhamphus* are easily distinguished from *C. xenopterus* by the characters noted above. In addition, larval *Oxyporhamphus* are more elongate, with much shorter pectoral and pelvic fins, and they lack a row of melanophores along the horizontal septum before about 9 mm (e.g. Khrapkova-Kovalevskaya, 1963; Watson, 1996) in contrast to before 4 mm in *C. xenopterus*. Among the five *Cheilopogon* species in the eastern Pacific with sparsely pigmented (or assumed to be sparsely pigmented) larvae, it usually should be possible to distinguish *C. atrisignis* and *C. papilio* from *C. xenopterus* by a combination of myomere and dorsal, anal, and (in larger larvae) pectoral-fin ray counts (e.g. Table 1). At larger sizes (small larvae have not been described) larval *C. atrisignis* and *C. spilonotopterus* can be distinguished from *C. xenopterus* by barbel structure and pigmentation, and *C. papilio* can be distinguished by barbel structure and fin pigmentation, as noted above. Large larval and juvenile *C. spilonotopterus* are more fully and evenly pigmented on the trunk (by about 14 mm) and lack the barred pattern displayed by larger larval and juvenile *C. xenopterus* (e.g. Kovalevskaya, 1977; Chen, 1987, 1988). *Cheilopogon papilio* likewise become more generally pigmented than *C. xenopterus*, although four or five bars remain visible through at least 21 mm. Juvenile *C. dorsomaculata* smaller than about 40 mm bear a striking resemblance to *C. xenopterus* but can be distinguished by small differences in meristic characters (Table 1) and have more sparsely pigmented (nearly unpigmented) pelvic fins than do *C. xenopterus*. Larvae of *C. dorsomaculata* have not been described, but the similarity of the small juveniles to *C. xenopterus* suggests that it may be difficult to distinguish the larvae of the two species.

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