

Larval and osteological development of the mote sculpin (*Normanichthys crockeri*) (Pisces:Normanichthyidae) from the Independencia Bight, Pisco, Peru

J. A. VELEZ^{1*}, W. WATSON², E. M. SANDKNOP², W. ARNTZ¹ AND M. WOLFF³

¹ALFRED WEGENER INSTITUTE FOR POLAR AND MARINE RESEARCH, COLUMBUSSTRASSE, D-27568 BREMERHAVEN, GERMANY, ²NATIONAL MARINE FISHERIES SERVICE, SOUTHWEST FISHERIES SCIENCE CENTER 8604 LA JOLLA SHORES DRIVE, CA 92038, USA AND ³CENTER FOR TROPICAL MARINE ECOLOGY, FAHRENHEITSTRASSE 6, 28359 BREMEN, GERMANY

*CORRESPONDING AUTHOR: jvelez@awi-bremerhaven.de

Ontogeny of Normanichthys crockeri is described and illustrated based on 66 specimens (1.9–20.5 mm; including recently hatched larvae through to the transformation stage) collected in Bahia Independencia, Pisco, Peru. Larvae hatch at approximately 1.8 mm, undergo notochord flexion at ca. 6.2–9.0 mm, and transform to juveniles at ca. 20.0 mm. Larvae were identified by the series method, using a combination of meristic and developmental characters that permitted definitive identification. Diagnostic features of the larvae include early development of large, lightly pigmented pectoral fins; early dorsal midline pigment on the trunk and tail which decreases gradually to none by the beginning of the flexion stage and does not reappear until late postflexion stage; and pigment ventrally, on the midlines of the abdominal and postanal regions, on the preanal until late postflexion stage, at the angular, on the caudal region, and usually at the cleithrum. Larvae are moderately slender with preanal length roughly half of body length (ca. 40–53% body length). They have 1,5 pelvic-fin rays, 7+6 principal caudal-fin rays and 36–37 myomeres (11–13+24–26, usually 13+24). The cleithra and bones of the jaws and opercular series are among the first to begin ossifying. The anterior vertebrae begin to ossify at ca. 5.0 mm and addition is posteriorly. The pectoral fin is the first to begin ray formation, followed sequentially by the principal caudal-fin rays, second dorsal- and anal-fin rays (forming concurrently), spiny dorsal-fin rays, and pelvic-fin rays.

INTRODUCTION

Marine fish diversity in Peru is high and the larval stages of many taxa are poorly known. An abundant coastal species, *Normanichthys crockeri* Clark, 1937 is a small (maximum ca. 11.0 cm), schooling, pelagic fish endemic to the southeast Pacific from Chimbote, Peru to Isla Mocha, Chile. *Normanichthys* grazes on aquatic plants and feeds on small fish, zooplankton and phytoplankton; its mode of reproduction and eggs are unknown. This species, commonly known as mote sculpin or camotillo (Clark, 1937), is not commercially important, and thus has been the subject of relatively little research.

There has been considerable disagreement among authors concerning the taxonomic placement of the monospecific family Normanichthyidae. *Normanichthys* has been allied with the cottoid fish (Clark, 1937; Norman,

1938; Fowler, 1951; Berg, 1947; Greenwood *et al.*, 1966), placed in its own scorpaeniform suborder, Normanichthyoidei (Nelson, 1994; Eschmeyer, 1998), and considered ‘*incertae sedis*’ in the Scorpaeniformes (Balbontín and Pérez, 1980; Washington *et al.*, 1984b; Mandrytza, 1991; Vegas and Pequeño, 1993; Yabe and Uyeno, 1996). Here we follow Eschmeyer (Eschmeyer, 1998), in placing *N. crockeri* in the scorpaeniform suborder Normanichthyoidei, but we note that a feature of its skeletal development suggests the possibility that its phylogenetic relationships are outside the Scorpaeniformes.

Larval *N. crockeri* were described and illustrated by Balbontín and Pérez (Balbontín and Pérez, 1980), based on a series of 19 specimens (4.16–16.3 mm), and Washington *et al.* (Washington *et al.*, 1984a) provided an illustration and brief discussion of the larval features. Developmental osteology was not included in either of

these studies. Our decision to re-describe *N. crockeri* was based on a more complete ontogenetic series (1.9–21.7 mm) and larger number (5155) of specimens available to us than were available in the earlier studies. We provide here a re-description of development from just after hatching through transformation to the juvenile stage, including new information about hatching size, and larval morphology, pigmentation and some aspects of osteological development, to supplement the work of Balbontín and Pérez (Balbontín and Pérez, 1980) and to facilitate identification of this species in ichthyoplankton samples.

METHOD

Larval *Normanichthys crockeri* were collected during eight monthly surveys (January–March, May, August–November) in 2000 in Independencia Bight (14°06′–14°20′S; 76°00′–76°18′W), a shallow bight (average depth 20–25 m) in Pisco, Peru. Plankton was collected with a 60 cm, non-closing bongo net equipped with 0.333 mm and 0.505 mm nitex mesh nets and cod ends, towed at a depth of 10 m, and with a 0.5 m ring net (0.333 mm nitex mesh) towed at the surface; both nets were equipped with calibrated flow meters. All tows were taken at speeds of 3 km for 10 min and samples were preserved in 4% formalin immediately after collection. Totals of 56 horizontal tows were made at each depth at four stations (Figure 1). All sampling was carried out during daylight hours except during September, when samples were taken every 3 h during a 24 h period at two of the stations (Panteón and Tunga) (Figure 1).

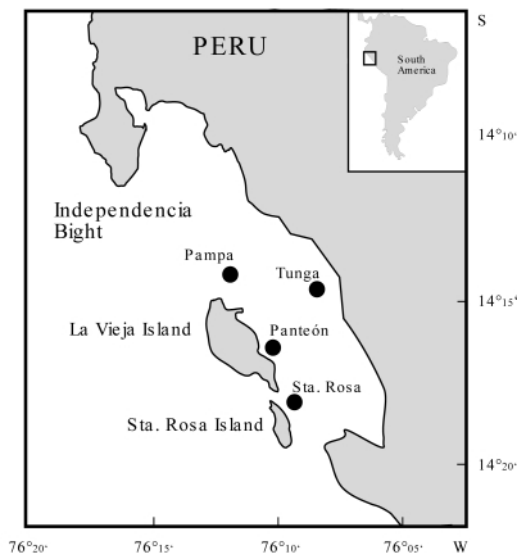


Fig. 1. Study area; Independencia Bight, Pisco Peru. Sampling locations are indicated by black circles. Average depth 20–25 m.

In the laboratory all fish larvae were sorted from the samples and identified to the lowest taxon possible. The larvae were stored in 4% formalin. A total of 5155 larval *N. crockeri* (1.9–21.6 mm body length) were identified, 66 were selected for description, of which forty-four larvae (2.7–20.6 mm) were deposited at the Zoological Institute and Zoological Museum, University of Hamburg (ZHM-9394 to ZHM-9397); nineteen larvae (7.3–14.0 mm) and five adult specimens ranging in size from 59.3 to 71.8 mm were obtained from the Marine Vertebrates Collection of SCRIPPS Institution of Oceanography (SIO 83-147 and SIO 01-75); these specimens had been collected from San Vicente Bight, Chile.

Larvae were identified by the series method, using a combination of meristic and developmental characters that permitted definitive identification. We used only specimens in good condition, which were measured to the nearest 0.02 mm with the ocular micrometer of a dissecting microscope. Measurements were completed within 1.5 years after collection. Methods of counting and landmarks for measurements are defined by Moser and by Leis and Carson-Ewart (Moser, 1996; Leis and Carson-Ewart, 2000). Body parts measured include: Body Length (BL), Snout–Anus Length (Sn-A), Body Depth (BD), Head Length (HL), Head Width (HW), Snout Length (SL), Eye Diameter (ED), Pectoral Fin Length (P_1L) and Pelvic Fin Length (P_2L). In the following description larval lengths always refer to body length. The morphometric series served as the basis for descriptions of the pigment pattern. Description of pigmentation refers solely to melanophores. Six specimens (ZHM-9394) were illustrated, to show pigmentation characters and morphological changes, and to provide identification of all stages of development of *N. crockeri*. Eight specimens (ZHM-9395) ranging from preflexion to late transformation stage were cleared with potassium hydroxide and stained with Alizarin red-S, to observe ossification of the jaws, suspensorium and opercular series bones, axial skeleton, appendicular skeleton, and fins. Staining procedures followed Potthoff (Potthoff, 1984). Skeletal structures were considered ossified upon uptake of Alizarin red-S stain. Twenty-four specimens ranging from postflexion to adult were selected for radiography to obtain more accurate meristic counts.

RESULTS

Morphology

Larvae hatch at a small size: our smallest specimen was 1.8 mm BL. Based on its relatively undifferentiated stage of development, this specimen appeared to have hatched recently, but it had no remaining yolk. Notochord flexion

begins between about 6.2 and 7.0 mm and ends at about 9.0 mm, and transformation to the juvenile stage begins at ca. 20.0 mm and is completed by about 22.0 mm.

Larvae elongate and slender (Figures 2, 3): BD averages 13% BL in the preflexion stage, increasing to 19% in the transformation stage, and decreasing to 17% in adults. Sn-A distance is 40–53% BL throughout larval development, increasing to 59% in adults (Table I). Head is relatively small, initially rounded but becomes more wedge-shaped as snout elongates (by ca. 3.0 mm). Head length is 17–31% BL through most of the larval period, increasing to 34% during transformation. Larvae become compressed: head width decreases from 60% HL in early larvae to 38% in transforming larvae through to adult. Eye diameter in preflexion stage is about 38% HL, decreases to ca. 27% and 22% HL in early flexion and postflexion larvae, respectively, and to 20% HL by transformation. Pectoral fin length increases from 2% BL early in preflexion stage (1.9 mm) to 14% BL late in stage (6.2 mm), to 20% and 29% BL in flexion and postflexion stages, respectively, and to 26% in transformation stage (Table I).

Pigmentation

Head pigment is usually absent in preflexion and flexion stages; we observed internal hindbrain pigment in two specimens (5.7 mm, 7.8 mm). Head pigment usually first appears internally at hindbrain during postflexion stage (ca. 9.2 mm) and externally over midbrain area (by ca. 16 mm); increases internally and externally (Figure 3B). During transformation much of the dorsal surface of the head becomes pigmented. Lower lip and snout pigment does not usually appear until near the end of postflexion stage (15.2 mm), although a single pigment spot was

observed at the lower lip in two specimens (10.3 mm, 10.5 mm). During transformation pigmentation forms and increases between the eyes, on the snout, and on the mandibular region (Figure 3B, C). The gular region has a single ventral pigment spot during preflexion stage (Figure 2A, C); one to three spots at angular during all stages. Ventral pigment appears in the branchiostegal region in late preflexion stage (ca. 5.7 mm). A single melanophore usually develops on or under the gill cover during the flexion stage (Figure 2C–E) and more are added during transformation (Figure 3B, C).

The most conspicuous pigment in early larvae is a single dorsal midline row of 3–13 melanophores on the trunk and tail. The number of dorsal melanophores gradually decreases during preflexion stage: a 3.3 mm larva had 13 melanophores and a 6.1 mm larva had only three. Dorsal pigment is absent by the beginning of the flexion stage (ca. 7.0 mm), and the dorsum of trunk and tail remain unpigmented until late in postflexion stage when melanophores form on the bases of the second dorsal fin-rays 6–9 (by 12.5–15.5 mm). During transformation a total of eight pigment saddles form below the dorsal fins and on the caudal peduncle (Figure 3B, C).

Minute melanophores are present on the isthmus by the end of the preflexion stage and increase in number during postflexion stage. Ventral midline pigment is always present, extending from near the cleithral symphysis to near the notochord tip (Figures 2, 3). During the postflexion stage a row of melanophores forms along each side of the anal fin (by 9.2 mm) and a single row continues posteriorly from the end of the anal fin to the caudal fin. There are one to three melanophores ventrally and dorsally at the notochord tip in the preflexion stage; the

Table I: Morphometric data of Normanichthys crockeri larvae from Independencia Bight, Peru (range and mean values). Data on adult specimens obtained from the Marine Vertebrate Collection of SCRIPPS (SIO 83–147)

Morphometric data	Preflexion (1.9–6.2 mm)		Flexion (7.1–11.0 mm)		Postflexion (12.5–15.5 mm)		Transformation (20.5–21.6 mm)		Adults (59.3–71.8 mm)	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Sn-A/BL	0.37–0.41	0.40	0.39–0.49	0.45	0.46–0.56	0.52	0.49–0.55	0.53	0.58–0.60	0.59
BD/BL	0.11–0.14	0.13	0.15–0.17	0.16	0.17–0.19	0.18	0.18–0.19	0.19	0.16–0.18	0.17
HL/BL	0.12–0.23	0.17	0.21–0.29	0.25	0.26–0.34	0.31	0.33–0.35	0.34	0.34–0.36	0.35
HW/HL	0.37–0.82	0.60	0.54–0.72	0.59	0.32–0.51	0.46	0.29–0.41	0.38	0.35–0.42	0.38
SnL/HL	0.18–0.36	0.23	0.20–0.28	0.24	0.22–0.31	0.24	0.24–0.24	0.24	0.20–0.23	0.22
ED/HL	0.28–0.54	0.38	0.24–0.29	0.27	0.19–0.28	0.22	0.18–0.22	0.20	0.23–0.24	0.24
P1L/BL	0.02–0.14	0.07	0.14–0.26	0.20	0.24–0.30	0.29	0.23–0.29	0.26	0.23–0.25	0.24
P2L/BL	–	–	–	–	0.05–0.25	0.20	0.16–0.18	0.17	0.16–0.18	0.17

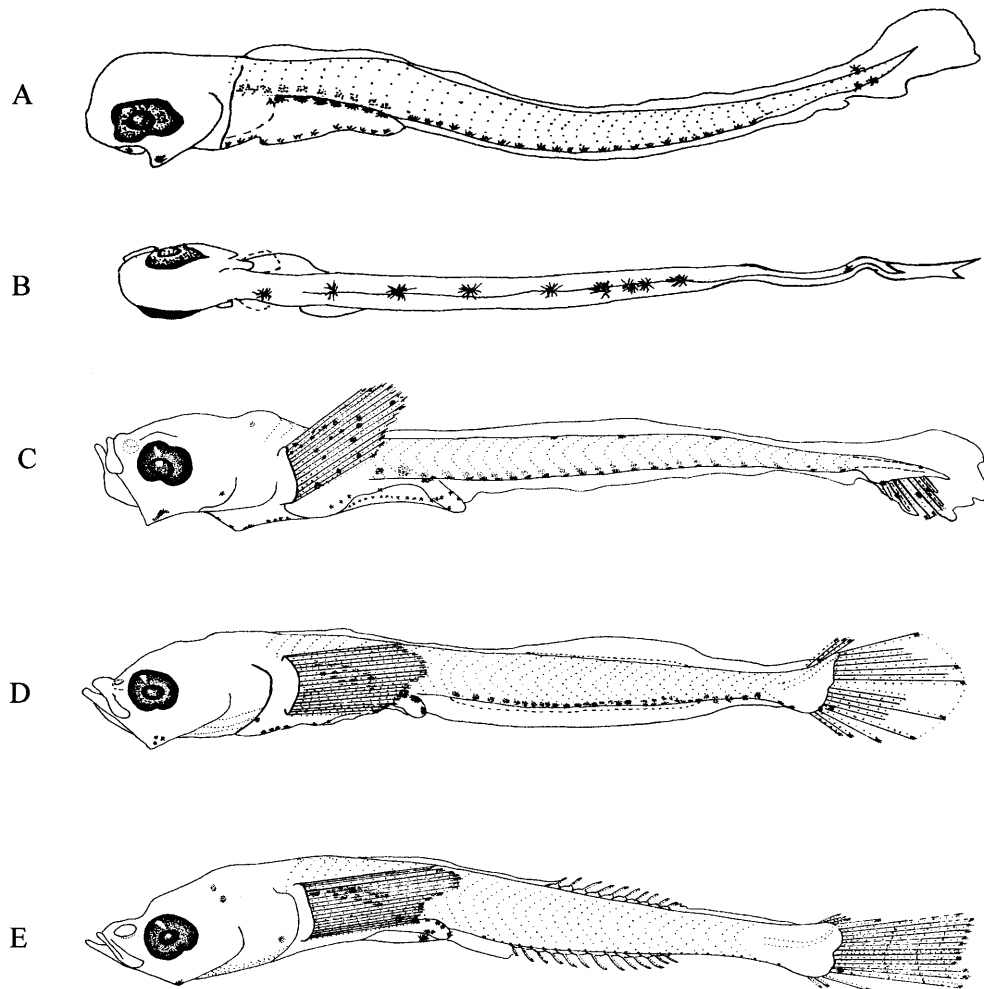


Fig. 2. Larvae of *Normanichthys crockeri*. (A) and (B) 2.7 mm (early preflexion stage, lateral and dorsal views, respectively); (C) 4.9 mm (middle preflexion stage); (D) 7.7 mm (flexion stage); and (E) 9.2 mm (early postflexion stage).

dorsal melanophore disappears and ventral melanophores become situated on the lower principal caudal-fin rays during the flexion stage. Preanal finfold pigment present during preflexion, flexion stages, but commonly is not visible in field-collected specimens because the delicate finfold is usually damaged. Ventral pigment in the transformation stage is mostly confined to the base of the anal fin, leaving the lower parts of the body and belly pale (Figure 3B).

Lateral pigment is absent through the postflexion stage. During transformation, eight pigment saddles extend ventrally to just below the lateral line (Figure 3B, C). Six lateral pigment patches between the saddles also extend to just below the lateral line. Dorsal, dorsolateral and mid-lateral pigment patches seem to merge into minutely punctate dots.

Three or four internal pigment patches are located dorsally over the gas bladder and gut, and ventrally on the gut. Dorsal gut pigment becomes embedded at about 7.0 mm. Large, lateral, external melanophores (three to seven) appear on the abdomen at about 7.2 mm, spread ventrolaterally during the flexion stage (Figure 2D) until about 13.0 mm, then decrease at about 15.7 mm. Ventral gut pigment is present from preflexion to postflexion stages, increases anteriorly until about the mid-postflexion stage, and usually is absent by end of stage.

Pectoral-fin pigment is sparse and minute, but present along the fin-rays in all stages. Pigment develops on the bases of anal- and of some segmented dorsal-fin rays during the postflexion stage, as noted above, but pelvic- and first dorsal-fin pigment is absent until transformation. Pigment develops on the caudal-fin margin and caudal

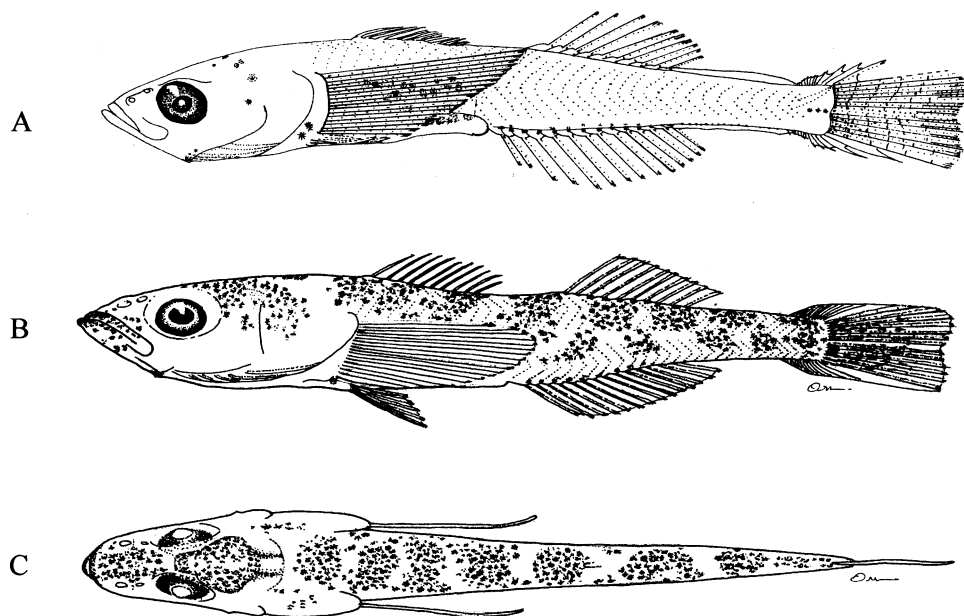


Fig. 3. Larvae of *Normanichthys crockeri*. (A) 16.2 mm (late postflexion stage); (B) and (C) 20.5 mm (transformation stage; lateral and dorsal views, respectively).

peduncle in postflexion stage. A melanophore or two appears on the caudal peduncle at about 11.0 mm (mid-postflexion), increases to three to five melanophores (usually three; Figure 3A). Pigment increases on the bases of the principal caudal-fin rays, usually only on the lower rays until late postflexion stage when it is also found on the upper rays (Figure 3A). In transforming larvae, pigment increases noticeably on the bases of the principal caudal-fin rays to form a solid bar, with sparser pigment extending distally, usually confined to the lower rays.

Osteological development

Ossification of the selected skeletal elements is summarized in Table II. Precision is limited by the small number of cleared and stained specimens. Nevertheless, Table II provides a general picture of the sequence of ossification of the selected elements during the larval stage.

Mandibular arch

Ossification of the maxillary and dentary is well underway and the premaxillary is just beginning to ossify in smallest cleared and stained larva (3.2 mm). By 10.3 mm both jaws are well ossified and the first two teeth are visible anteriorly on the lower jaw (one on each dentary). The 14.2 mm specimen had seven teeth on each dentary but lacked teeth on the upper jaw. The transforming specimen (20.3 mm) had 14 teeth on each dentary and 19 on each premaxillary. The articular and angular begin

ossifying at ca. 5.0 mm, and approach the adult shape by ca. 6.0 mm.

Suspensorium

Elements of the suspensorium, particularly the palatine series, ossify later. The symplectic begins to ossify around the lower end of the hyomandibulosymplectic cartilage at ca. 5.4 mm, and is mostly ossified (except at its proximal and distal ends) by 10.3 mm. The hyomandibular is entirely cartilaginous at ca. 5.9 mm, but ossification is well underway by 10.3 mm. By 14.2 mm, the foramen for passage of the trigeminofascialis nerve is apparent and the hyomandibular approaches its adult form. By 20.3 mm the foramen is becoming enclosed in a ventrally directed tube. The quadrate begins to ossify by 10.3 mm, but was not well ossified in the largest specimen (transforming, 20.3 mm). The palatine begins to ossify along its lower margin at ca. 10.5 mm, reaching more or less adult shape but remaining only partially ossified by 20.3 mm. The ectopterygoid begins ossifying along its ventral margin by 14.2 mm and both the metapterygoid and entopterygoid start ossifying after 14.2 mm, but before 20.3 mm; all three were only partly ossified in the largest specimen.

Opercular series

The opercle is the first bone in the opercular series to start ossification, by 5.0 mm; by 10.5 mm it is well ossified. The subopercle and interopercle apparently begin forming

*Table II: Sequence of ossification in larvae of *Normanichthys crockeri*. The initial ossification of an element is indicated by the black point. The arrow indicates the larval size at which the element achieves the general shape it will have in the juvenile and adult. When a bone is still not complete in the 20.3 mm specimen, no arrowhead is drawn on the line*

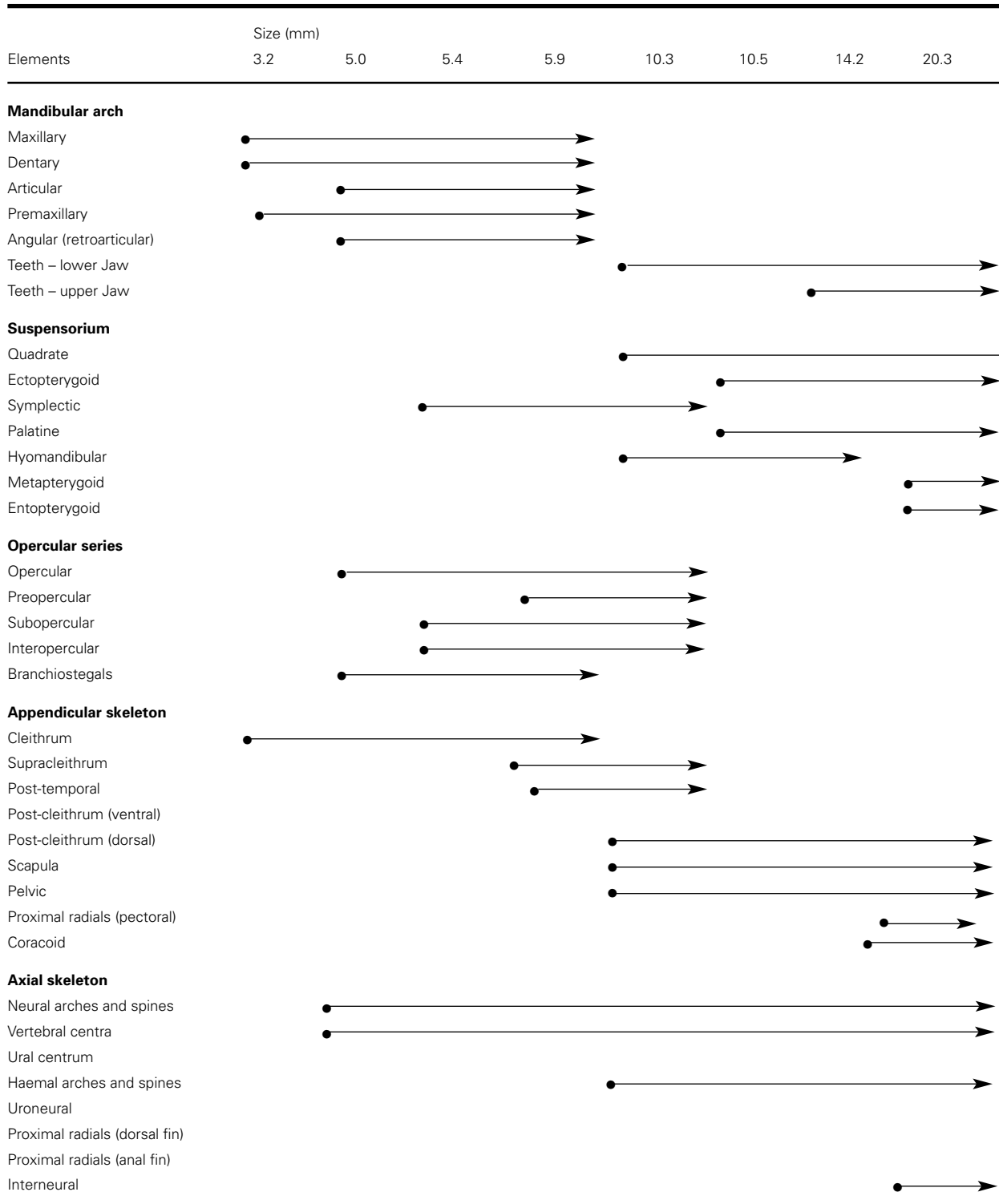


Table II: Continued

Elements	Size (mm)							
	3.2	5.0	5.4	5.9	10.3	10.5	14.2	20.3
Caudal skeleton								
Parhypural		●	→					
Hypural 1+2 (fused)		●	→					
Hypural 3		●	→					
Hypural 4		●	→					
Hypural 5					●	→		
Epural (3)							●	→

simultaneously at ca. 5.4 mm. Both bones approach their adult shapes by ca. 10.3 mm. The last opercular series bone to begin ossifying is the preopercle, at 5.9 mm. Opercular series bones do not develop spines.

Appendicular skeleton

The cleithrum was slender and ossified in the smallest specimen examined (3.2 mm). The supracleithrum begins to ossify by 5.9 mm and the posttemporal starts after 5.9 mm but before 10.3 mm. Both were well ossified with more or less adult form in the 10.3 mm specimen. A small dorsal postcleithrum begins to ossify at ca. 10.3 mm and is well ossified by 20.3 mm. The ventral postcleithrum apparently does not form during the larval stage. The scapula was ossifying in its central region in the 10.3 mm specimen, but was apparently not ossifying in the 10.5 mm specimen. By 14.2 mm all but the distal third of the scapula is ossifying and by 20.3 mm it is almost completely ossified. Ossification of the coracoid commences at ca. 14.2 mm and is nearly complete by 20.3 mm. The pectoral proximal radials are not ossifying at 14.2 mm, but the 20.3 mm specimen had all four radials ossifying in the centre, with the upper two supported by the scapula and the lower two by the coracoid. Pelvic basiptyrgia were ossifying near their distal ends in the 10.3 and 14.2 mm specimens, but were apparently not ossifying in the 10.5 mm specimen. By 20.3 mm they are well ossified with essentially adult form.

Axial skeleton

Neural arches are the first bones of the axial skeleton to ossify. The first six neural arches ossify by 5.0 mm, nine arches ossify at 5.4 mm, and the first 33 ossify at 10.3 mm (32 in the 10.5 mm specimen). The arches ossify upward from their bases and addition is caudal. The 14.2 mm

specimen had 35 neural arches, the last four ossified only at their bases and the first two lacking neural spines and open dorsally, but the next 25 being closed and bearing ossifying neural spines. In the 20.3 mm specimen all 36 neural arches were closed, well ossified, and each, except the last, bore an ossifying neural spine. The next elements of the axial skeleton to begin ossifying are the vertebral centra. The anterior six centra ossify at 5.4 mm and by 10.3 mm all 36 (including urostyle) are well ossified (only the first 31 centra plus the urostyle in the 10.5 mm specimen). Addition of the centra is apparently caudal, except the urostyle begins to ossify (by 5.9 mm) before the most caudal centra. There are 12–15 abdominal and 22–24 caudal vertebrae (12–13+24 in cleared and stained larvae). Neither haemal arches nor haemal spines are ossified in the 5.9 mm specimen, but in the 10.3 mm specimen all haemal arches and spines are ossifying. First five haemapophyses, at vertebral centra 8–12, are ossifying at 10.3 mm and by 14.2 mm seven are present on centra 7–13. Epipleurals begin to ossify at the end of the larval stage: first nine (of 16) being present on centra 7–13.

Other bones of the head

Although ossification of the neurocranium and the hyoid and branchial arches was not specifically examined, development of a few of these bones was noted. In the neurocranium, the first bones to begin ossifying are parasphenotic, after 3.2 mm but before 5.0 mm, and basioccipital at about 5.4 mm. In the 10.3 mm specimen most bones in the brain case were ossifying. In the branchial arch two pairs of pharyngobranchial teeth (one pair large) are present by 5.0 mm and three pairs (one large) are present by 5.4 mm. In the hyoid arch the first four branchiostegal rays are ossifying by 5.4 mm and the fifth is added by 5.9 mm.

Table III: Development of fin rays of Normanichthys crockeri from Independencia Bight, Peru. Notochord flexion begins at about 6.2 mm and ends at ca. 9.0 mm. Transformation begins at ca. 20.0 mm body length. Specimens 59.3–71.8 mm are adults

Length (mm)	First dorsal	Second dorsal	Anal	Caudal Principal	Procurrent	Pectoral	Pelvic
1.9–2.9	–	–	–	–	–	Bud	–
3.3–3.5	–	–	–	–	–	Beg. rays	–
3.6	–	–	–	–	–	5	–
3.9–4.1	–	–	–	–	–	7–8	–
4.6	–	–	–	Hypurals forming	–	8–9	–
5.0	–	–	–	2+2	–	10–11	–
5.5–5.8	–	–	–	4–5+5	–	13–14	–
5.9	–	–	–	5+5	–	13–15	–
6.1	–	–	–	6+6	–	18	–
6.2	–	–	–	6+6	–	18	–
7.1	–	–	–	7+6	1+1	18	–
7.3	–	Anlage	Anlage	7+6	3+2	18	–
7.7	–	Anlage	Anlage	7+6	3+3	18	–
7.9–8.1	–	Anlage	Anlage	7+6	0–3+1–3	18	–
8.5	–	8	9–10	7+6	1+1	18	–
9.2–9.4	Anlage	10	13–14	7+6	4+3	17–18	Bud
10.0	V	11	14	7+6	4+4	18	Bud
10.3–10.5	X	11	15	7+6	7–13+8–12	18	Bud
12.5–13.2	X	11	14–15	7+6	12+12	18	1,5
14.3	X	11	13	7+6	12+12	17	1,5
14.7	X	10	14	7+6	12+12	18	1,5
15.2	IX–X	10	13	7+6	13+12	18	1,5
15.5	X	10	14	7+6	12+10	18	1,4
20.1	X	10	14	7+6	13+12	19	1,5
20.5	X	10	14	7+6	13+13	18	1,5
21.6	X	11	14	7+6	13+12	18	1,5
21.7	X	10	13	7+6	14+13	19	1,5
59.3–71.8	X–XI	11	14–15	7+6	12–14+12–13	17–19	1,5

Caudal skeleton

Development of the caudal complex starts at about 4.6 mm (Table III). Cartilaginous parhypural and hypurals 1–4 (hypurals 1 and 2 fused) are observed in the 5.0 mm specimen; by 5.9 mm the lower hypural (1+2) and hypural 3 begin to ossify in their central regions and hypural 4 along the lower edge. Parhypural begins to ossify after 5.9 mm; by 10.3 mm both the parhypural and hypurals 1–4 are fully ossified except at their distal ends. Hypural five begins to ossify between 10.3 and 14.2 mm. The three cartilaginous epurals visible at 10.5 mm and epurals 2 and 3 begin ossifying around their centres by 14.2 mm. All

elements of the caudal skeleton are largely ossified by the transformation stage (20.3 mm).

Fin development

The sequence of initial fin-ray development is: pectoral, caudal, second dorsal and anal, first dorsal, pelvic (Table III). Pectoral fins, lacking rays, are present at hatching. Developing pectoral-fin rays first become apparent at 3.3 mm, and the full adult complement of 18 (17–19) rays is present by ca. 6.0 mm. Addition of rays is ventral. Uppermost three rays are supported by scapula, the next three by the first pectoral radial, and four each by radials 2–4.

The caudal fin is the second fin to begin formation. Hypurals first appear at about 4.6 mm and principal caudal-fin rays begin to form at about 5.0 mm (Figure 2C), with the full complement of 7+6 principal rays being present by about 7.0 mm (Figure 2D). Posterior procurrent caudal-fin rays begin to form during the flexion stage (Table III; Figure 2D), are gradually added anteriorly until transformation stage (Figure 3B, C), when the full complement of 12–14+12–13 rays is present (Table III; Figure 3B, C). Dorsally, the posteriormost procurrent ray is partially supported by the fifth hypural and the next ray by the third epural; no other dorsal procurrent rays appear to be directly supported by bony or cartilaginous structures during the larval stage. Ventrally, the posteriormost two procurrent rays are supported by the haemal spine of preural centrum two, the next four by a radial cartilage, and the next two by the haemal spine of preural centrum three. The remaining ventral procurrent rays are apparently not directly supported by bony or cartilaginous structures in larvae. The second dorsal fin and anal fin begin to develop simultaneously about mid-way through flexion stage: anlage of each are first visible by ca. 7.3 mm (e.g. Figure 2D), and between 9.2 and 9.4 mm (early postflexion stage, Figure 2E) full complements of 10–11 segmented dorsal fin-rays and 13–15 segmented anal-fin rays are present (Table III). The middle soft rays apparently form first in each fin, and addition is both cephalad and caudad. Dorsal- and anal-fin pterygiophores supporting the soft rays begin to ossify after the rays have formed, between 10.3 and 14.2 mm. Ossification begins simultaneously on each proximal and distal radial near their junction and is nearly complete by 20.3 mm. The spinous dorsal fin begins to develop early in postflexion stage (ca. 9.2 mm), just after dorsal soft-rays and anal rays are completed. Five anterior spines are present by 10.0 mm and the full complement of X–XI spines is completed between 10.3 and 10.5 mm (Table III). Ossification of the pterygiophores supporting the dorsal spines, and of the four interneurals that precede the dorsal fin, begins some time after 14.2 mm but before 20.3 mm. There are no anal-fin spines. Pelvic fin buds form early in the postflexion stage (by 9.2 mm), directly below the pectoral fins. The full complement of one spine and five rays is present by 12.5 mm (Table III, Figure 3A).

Abundance and distribution

Normanichthys crockeri is a pelagic fish endemic to the coastal waters of the southeast Pacific from Peru and Chile; it is abundant in Independencia Bight. There are no published data on the distribution of larval *N. crockeri*. In our surveys *N. crockeri* accounted for 37.5% of the total fish larvae taken in Independencia Bight during 2000. Larval *N. crockeri* were found at all stations, but were most

abundant in the vicinities of Santa Rosa and La Vieja Islands: 80.3% were collected at Santa Rosa, followed by Pampa (8.8%), Panteon (7.7%) and Tunga (3.2%) (Figure 1). Larval *N. crockeri* were found only in the samples collected at 10 m depth, at temperatures ranging from 13.4°C to 17.7°C. Over 78% of the larvae occurred at mean temperatures of 13.5°C to 14.2°C. Recently hatched larvae were caught throughout the year, but abundances were highest in spring (October–November), and approximately 97.7% of all the larvae were taken during October and November.

DISCUSSION

This description of *Normanichthys crockeri* from recently hatched larvae through to transformation supplements the description by Balbontín and Pérez (Balbontín and Pérez, 1980). Results of the two studies were generally concordant; there appeared to be no significant differences between Peruvian and Chilean specimens. However, we found small differences in the sizes at which larval stages began and ended and in the sizes at which the fins formed, with these events typically occurring at somewhat smaller larval lengths in our specimens (Table IV). There were also some slight differences in the sequence of fin formation, in fin-ray counts, and in fin positions (Table IV). These differences were primarily a result of the larger number of specimens and more complete size series available to us.

Diagnostic features

The distinguishing characters of the larvae are: an elongate, moderately slender body; preanal length about half of body length; large, pigmented pectoral fins; a distinct dorsal midline melanophore series on the trunk and tail, which gradually decreases from as many as 13 melanophores early in the preflexion stage to none by the beginning of the flexion stage; pigment ventrally on the gut and tail, at the angular, on the cleithra, and on the caudal region, it has 7+6 principal caudal-fin rays and 36–37 myomeres.

Early larvae of *N. crockeri* resemble those of some cheilodactylids, and to a lesser extent, some aplodactylids and kyphosids. Many species of the last family have similar pigment patterns in the preflexion stage and similar gut length compared with *N. crockeri*, but far fewer vertebrae (usually 25–27, except *Graus nigra*, a girelline with 34 vertebrae). Larval *G. nigra* are unknown and might be confused with *N. crockeri* because of their similar myomere count and potentially similar pigmentation, but, based on other girelline larvae, they may be more heavily pigmented and probably have smaller pectoral fins than *N. crockeri* (Watson, 1996; Konishi, 1988). Larval

*Table IV: Comparison of some characters in larval *Normanichthys crockeri* emphasizing differences between this study and that of Balbontín and Pérez (Balbontín and Pérez, 1980) study*

Character	Present study	Balbontín and Pérez, 1980
Collection location	Independencia Bight, Peru*	Valparaiso Bay, Chile
Number of specimens examined	66	19
Size range (mm)	1.9–21.6	4.6–16.3
Total myomeres	36–37	35–37
Fin developmental sequence	1P, Caudal, 2D&Anal, 1D, 2P	1P, Caudal, 2D, Anal, 2P, 1D
Approximate size (mm) at:		
preflexion	1.9–6.2	4.6–<7.2
flexion	6.2–8.5	7.2–<10.6
postflexion	9.2–≤15.5	≥9.8–16.2
transformation	≥15.5–21.6	–
beginning of hypural formation	4.6	6.0–6.1
First appearance of fin anlage		
first dorsal	9.2	16.3
second dorsal	7.3	8.8–9.4
anal	7.3	8.8–9.4
pelvic	9.2	8.6–8.8
First appearance of fin-rays		
pectoral	3.3–3.6	4.6
first dorsal	10.0	16.3
second dorsal	8.5	>9.4–≤10.6
anal	8.5	>9.4–≤10.6
principal caudal rays	5.0	6.9
procurrent caudal rays	6.1	16.3
pelvic	12.5	–
Completion of fin-rays		
pectoral	6.1	10.6
first dorsal	10.3	–
second dorsal	9.2	10.6
anal	9.2	16.3
principal caudal rays	6.1	10.6
procurrent caudal rays	>15.2	–
pelvic	12.5	–
Position of fins (Myomere)		
first dorsal	4 th –13 th	–
second dorsal	17 th –18 th –26 th –27 th	17 th –28 th
anal	14 th –27 th	17 th –28 th
Total number of fin-rays		
pectoral	18–19	17–19
first dorsal	10	–
second dorsal	10–11	10–12
anal	13–14	13–15
principal caudal	7+6	6+6
procurrent caudal	12–14+12–13	–
pelvic	1,5	–

1P, Pectoral; 1D, first dorsal; 2D, second dorsal; 2P, pelvic.

*Included specimens from Chile (SIO 83–147 and SIO 01–75).

Cheilodactylidae and Aplodactylidae have myomere counts (34–36) similar to *N. crockeri*, and some cheilodactylids are pigmented much like *N. crockeri*. However, the following characters should distinguish the larvae of both families from *N. crockeri*: aplodactylids are more heavily pigmented than *N. crockeri* in the preflexion stage, both aplodactylids and cheilodactylids have pigmented but smaller pectoral fins than *N. crockeri*, and both have a single dorsal fin, in contrast to the two separate fins of *N. crockeri* (B. Watson, personal communication).

Osteology

Aspects of skeletal development are described here for the first time. Since bone formation is a gradual process that continues throughout the life of the fish, selection of the point at which an element achieves an essentially adult form (as shown in Table II) is subjective (Moser, 1972). For the most part skeletal development is much like development in a variety of scorpaeniform and other fish (Moser, 1972; Peters, 1983; Potthoff *et al.*, 1984; Yuschak and Lund, 1984; Watson, 1987). Skeletal configuration in the largest cleared and stained *N. crockeri* was consistent with the description by Yabe and Uyeno (Yabe and Uyeno, 1996). A perhaps somewhat unusual feature in *N. crockeri* development is the formation of neural arches and vertebral centra before the haemal arches. This differs from the apparently usual scorpaeniform sequence in which both neural and haemal arches form before the vertebral centra (Matarese and Marliave, 1982; Washington *et al.*, 1984a; Yuschak and Lund, 1984; Matarese and Vinter, 1985), although a *Normanichthys*-like pattern has been reported in Sebastidae (Moser, 1972). A more striking feature of skeletal development in *N. crockeri* is the sequence of initial ossification of the opercular series bones, with the preopercle commencing ossification last, after the interopercle and subopercle. In contrast, the apparently usual condition in scorpaeniform fish is for the preopercle to begin ossifying before (or in some cases simultaneously with) the subopercular and interopercular bones (Moser, 1972; Kendall and Vinter, 1984; Yuschak and Lund, 1984). This difference, perhaps supported by the difference in axial skeleton ossification, suggests the possibility that *Normanichthys* phylogenetic relationships might be elsewhere than with the Scorpaeniformes.

ACKNOWLEDGEMENTS

This study was supported by the German Academic Exchange Service (DAAD), the Alfred Wegener Institute for Polar and Marine Research (AWI) in Bremerhaven, Germany and the Volkswagen Foundation. Our thanks are due to two anonymous reviewers for their helpful comments. The first author is grateful to Dr H. G. Moser

for revision and critical reading of an earlier draft, to S. Thatje, Dr J. Laudien, J. Raguá-Gil, and R. Krockner for their constructive comments and help, and to Dr S. Schiel, AWI, for advice and support. This study could not have been accomplished without the generous co-operation of many people, particularly Professor Dr Jaime Mendo and his group of students for their assistance in the sampling operations in Peru. I am indebted to the ichthyoplankton groups of IMARPE, Peru; CICIMAR, Mexico and the SWFSC, La Jolla, CA for providing support and also providing space and equipment in their laboratories. I also thank H. J. Walker and C. Klepadlo (SCRIPPS, Institution of Oceanography) who provided specimens, H. Orr who drew Figures 3B and C, and V. Growney who helped with the photographs. Special thanks go to H. Prieto, R. Jordan and Dr E. Brinton for their hospitality in San Diego, CA.

REFERENCES

- Ahlstrom, B. H. and Moser, H. G. (1976) Eggs and larvae of fishes and their role in systematic investigations and in fisheries. *Rev. Trav. Inst. Peches Marit.*, **40**, 379–398.
- Balbontin, F. and Pérez, R. (1980) Descripción de los estados larvales de *Normanichthys crockeri* Clark (Perciformes: Normanichthyidae) del área de Valparaíso, Chile. *Rev. Biol. Mar. Dep. Oce. Univ. Chile, Valparaíso*, **17**, 81–95.
- Berg, L. S. (1947) *Classification of Fishes, Both Recent and Fossil*. Document reproduction unit, Thai National Documentation Center, Bangkok-1965. J. W. Edwards Eds, Ann Arbor, MI, 346–517pp.
- Chirichigno, N. F. (1998) *Clave Para Identificar los Peces Marinos del Perú*. Inf. Inst. Mar Perú, publicación especial. 2nd edn. Callao, Perú, 496 pp.
- Clark, H. W. (1937) New fishes from the Templeton Crocker Expedition of 1934–35. *Copeia*, **2**, 88–91.
- Eschmeyer, W. N. (1998) *Catalog of Fishes*. California Academy of Sciences, San Francisco.
- Fowler, H. W. (1951) Analysis of the fishes of Chile. *Rev. Chilena Hist. Nat.*, **51–53**, 263–326.
- Greenwood, P. H., Rosen, D. E., Weitzman, S. H. and Myers, G. S. (1966) Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. Nat. Hist.*, **1341**, 339–456.
- Kendall, A. W., Jr. and Vinter, B. (1984) *Development of Hexagrammids (Pisces: Scorpaeniformes) in the Northeastern Pacific Ocean*. U. S. Dep. Commer., NOAA Tech. Rep. NMFS 2, 44 pp.
- Konishi, Y. (1988) Girellidae. Pages 509–511 In Okiyama, M. (ed.), *An Atlas of the Early Stage Fishes in Japan*. Tokai University Press, Tokyo, pp. 509–511.
- Leis, J. M. and Carson-Ewart B. M. (2000) *The Larvae of Indo-Pacific Coastal Fishes: An Identification Guide to Marine Fish Larvae. Fauna Malesiana Handbooks*. Brill, Leiden.
- Mandrytza, S. A. (1991) The peculiarities of the seismosensory system of *Normanichthys crockeri* Clark (Scorpaeniformes, Normanichthyidae). *Proc. Zool. Inst., Leningrad*, **235**, 9–21.
- Matarese, A. C. and Marliave, J. B. (1982) Larval development of laboratory-reared rosy lip sculpin, *Ascelichthys rhodorus* (Cottidae). *Fish. Bull.*, **80**, 345–355.

- Matarese, A. C. and Vinter, B. M. (1985) The development and occurrence of larvae of the longfin Irish lord, *Hemilepidotus zapus* (Cottidae). *Fish. Bull.*, **83**, 447–457.
- Moser, H. G. (1972) Development and geographic distribution of the rockfish *Sebastes macdonaldi* (Eigenmann and Beeson, 1893), family Scorpaenidae, off Southern California and Baja California. *Fish. Bull.*, **70**, 941–958.
- Moser, H. G. (1996) *The Early Stages of Fishes in the California Current region*, CALCOFI Atlas No. 33. Allen Press, Inc., Lawrence KA, 1503 pp.
- Nelson, J. S. (1994) *Fishes of the World*. 3rd edn. John Wiley and Sons, Inc., New York, 600 pp.
- Norman, J. R. (1938) On the affinities of the Chilean fish, *Normanichthys crockeri* Clark. *Copeia*, **1938**, 29–32.
- Peters, K. M. (1983) Larvae and early juvenile development of the frillfin goby, *Bathygobius soporator* (Perciformes: Gobiidae). *Northeast Gulf Sci.*, **6**, 137–153.
- Potthoff, T. (1984) Clearing and staining techniques. In Moser H. G., Richards W. J., Cohen D. M., Fahay M. P., Kendall A. W. Jr. and Richardson S. L. (eds), *Ontogeny and Systematics of Fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. No. 1.*, Allen Press, Lawrence, KS, pp. 35–37.
- Potthoff, T., Kelley, S., Moe, M. and Young, F. (1984) Description of porkfish larvae (*Anisotremus virginicus*, Haemulidae) and their osteological development. *Bull. Mar. Sci.*, **34**, 21–59.
- Vegas, G. E. and Pequeño R. G. (1993) Contribución al conocimiento biológico de *Normanichthys crockeri* Clark, 1937 (Osteichthyes, Scorpaeniformes). *Rev. Biol. Mar. Valparaíso*, **28**, 1–36.
- Watson, W. (1987) Larval development of the endemic Hawaiian blennioid, *Enchebyurus brunneolus* (Pisces: Blenniidae: Omobranchini). *Bull. Mar. Sci.*, **41**, 856–888.
- Watson, W. (1996) Kyphosidae: sea chubs. In Moser, H. G. (ed.), *The Early Stages of Fishes in the California Current region*, CALCOFI Atlas No. 33. Allen Press, Lawrence, KS, pp. 1038–1045.
- Washington, B. B., Moser, H. G., Laroche, W. A. and Richards, W. J. (1984a) Scorpaeniformes: development. In Moser H. G., Richards W. J., Cohen D. M., Fahay M. P., Kendall A. W. Jr. and Richardson S. L. (eds), *Ontogeny and Systematics of Fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. No. 1.*, Allen Press, Lawrence, KS, pp. 405–428.
- Washington, B. B., Eschmeyer, W. N. and Howe, K. M. (1984b) Scorpaeniformes: relationships. In Moser H. G., Richards W. J., Cohen D. M., Fahay M. P., Kendall A. W. Jr. and Richardson S. L. (eds), *Ontogeny and Systematics of Fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. No. 1.* Allen Press, Lawrence, KS, pp. 438–447.
- Yabe, M. and Uyeno, T. (1996) Anatomical description of *Normanichthys crockeri* (Scorpaeniformes, incertae sedis: Family Normanichthyidae). *Bull. Mar. Sci.*, **58**, 494–510.
- Yuschak, P. and Lund, W. A. (1984) Eggs, larvae and osteological development of the northern searobin, *Prionotus carolinus* (Pisces, Triglidae). *J. Northw. Atl. Fish. Sci.*, **5**, 1–15.

Received on September 23, 2002; accepted on December 4, 2002