Abstract—Larvae of the genus *Icelinus* are collected more frequently than any other sculpin larvae in ichthyoplankton surveys in the Gulf of Alaska and Bering Sea, and larvae of the northern sculpin (*Icelinus borealis*) are commonly found in the ichthyofauna in both regions. Northern sculpin are geographically isolated north of the Aleutian Islands, Alaska, which allows for a definitive description of its early life history development in the Bering Sea. A combination of morphological characters, pigmentation, preopercular spine pattern, meristic counts, and squamation in later developmental stages is essential to identify *Icelinus* to the species level. Larvae of northern sculpin have 35–36 myomeres, pelvic fins with one spine and two rays, a bony preopercular shelf, four preopercular spines, 3–14 irregular postanal ventral melanophores, few, if any, melanophores ventrally on the gut, and in larger specimens, two rows of ctenoid scales directly beneath the dorsal fins extending onto the caudal peduncle. The taxonomic characters of the larvae of northern sculpin in this study may help differentiate northern sculpin larvae from its congeners, and other sympatric sculpin larvae, and further aid in solving complex systematic relationships within the family Cottidae.

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Description of early life history stages of the northern sculpin (*Icelinus borealis* Gilbert) (Teleostei: Cottidae)

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The sculpin family, Cottidae, is a speciose, morphologically diverse group of fishes with a worldwide distribution comprising as many as 275 species in about 70 genera (Nelson, 2006). Greatest diversity occurs in the Northeast Pacific Ocean and Bering Sea with 96 species in 34 genera where they are found in almost every benthic habitat from the intertidal to the upper continental slope (Mecklenburg et al., 2002; Nelson, 2006; Pietsch and Orr, 2006). Cottids are primarily predators of smaller fish and crustaceans, and many species are preyed upon by larger fishes and marine mammals, particularly pinnipeds (Browne et al., 2002; Pietsch and Orr, 2006). Cottids are one of several prey species exploited by the harbor seal (*Phoca vitulina*). Cottid species, including the northern sculpin (*Icelinus borealis*), are abundant in waters surrounding rookeries of Steller sea lions (*Eumetopias jubatus*) where they contribute to the diversity of available prey species (Mueter and Norcross, 2000; Browne et al., 2002; Fritz and Hinckley, 2005). New cottid species continue to be described; however, the systematics and life histories of most species are poorly known. A more complete understanding of the diversity of the family is necessary to fully understand their role in the dynamics of North Pacific ecosystems (Hoff, 2006; Pietsch and Orr, 2006).

Icelinus borealis is the most common species of *Icelinus* in the Gulf of Alaska and the only species of *Icelinus* known from the Bering Sea. It is reported to be an important component of the ichthyofauna in both regions (Mueter and Norcross, 2000; Mecklenburg et al., 2002). Adults are distributed from Attu Island in the Aleutian Islands and Bristol Bay in the eastern Bering Sea to southern Puget Sound, Washington, at depths of 4–247 m, on nearly all types of substrate (Mecklenburg et al., 2002). Larvae of *Icelinus* are the most frequently collected larval cottids in the Northeast Pacific Ocean and Bering Sea, occurring in 9.3% (ranked 12th of all taxa collected) of ichthyoplankton samples collected by the Alaska Fisheries Science Center (AFSC).

Larvae of *Icelinus* have primarily been collected in continental shelf and slope waters of the Bering Sea, through Unimak Pass to the Gulf of Alaska and Shelikof Sea Valley, around Kodiak Island, and southward to the west coast of the United States. In the Shelikof Sea Valley, they are most often collected along the northern side, closest to the Alaska Peninsula (Matarese et al., 2003). *Icelinus* comprises 11 species that are diagnosed by pelvic fins having one spine and two rays, four preopercular spines (the dorsalmost is longest and bifid or trifid), two rows of ctenoid scales directly beneath the dorsal fins, and gill membranes that are united and free from the isthmus (Bolin, 1936; Yabe et al., 1983; Yabe et al., 2001; Nelson et al., 2004; Rosenblatt and Smith, 2004). Adult *I. borealis* reach 10 cm standard length and lack distinct postocular spines, possess a long cirrus at the base of the nasal spine, the first or second dorsal-fin spines are not longer than the third or fourth, and the two rows of ctenoid scales below the dorsal fins extend onto the caudal peduncle (Bolin, 1936; Mecklenburg et al., 2002).

This study is the first to identify and describe the larval and juvenile stages of *I. borealis*. Previous descriptions were based on misidentified specimens or were made at a more conservative generic level because of difficulty distinguishing among species of *Icelinus* and between *Icelinus* and other sympatric cottid larvae. Larvae of *Icelinus quadriseriatus* from the coast of California are currently the only *Icelinus* larvae described (Feeney, 1987). Larvae tentatively identified as *I. borealis* in early literature were misidentified as *Ruscarius meanyi* based on a pelvic-fin ray count of 1, 2—a count diagnostic of *Icelinus* but also occurring rarely in *R. meanyi* (Blackburn, 1973; Richardson, 1977; Richardson and Pearcy, 1977; Richardson and Washington, 1980; Washington, 1981; Begle, 1989). Current literature has continued to identify larvae of *Icelinus* at the generic level; however, Matarese et al. (1989, 2003) have cautiously identified illustrations as *I. borealis*. *Icelinus borealis* has cautiously been identified at the species level because three other species of *Icelinus* with unidentified larvae (*I. burchami*, *I. filamentosus*, and *I. tenuis*), and other unidentified cottid larvae (e.g., *Icelus*) are also found in the Gulf of Alaska.

Uniformity between larval *Icelinus* and other cottid larvae is noted in the assignment of phenetic groups based on shared larval characters (e.g., preopercular spine pattern, body shape, and pigmentation) (Richardson, 1981). *Icelinus* is included in phenetic group 2, which includes *Paricelinus*, *Triglops*, *Icelus* (tentatively), and *Chitonotus*, and is characterized by a slender body shape, pointed snout, and four prominent preopercular spines (Richardson, 1981). Further study of phenetic groups has increased the size of group 2, the "*Myoxocephalus* group," to include a total of 13 genera (Matarese et al., 1989; Moser et al., 1996). The *Myoxocephalus* group includes the genera previously included in group 2 as well as the genera *Myoxocephalus*, *Ruscarius*, *Ascelichthys*, *Orthonopias*, *Enophrys*, *Radulinus*, *Gymnocanthus*, and *Synchirus* (Matarese et al., 1989; Moser et al., 1996). Members of the *Myoxocephalus* group have four preopercular spines and are defined by a unique larval character, namely a bony preopercular shelf (Moser et al., 1996).

Larvae of *Icelinus* are reported to be the most frequently collected larval cottids in the Northeast Pacific Ocean and Bering Sea. Although collected in large numbers, the size range of specimens is limited, which has hindered compiling the developmental series necessary for description. Increased ichthyoplankton sampling conducted in the Bering Sea in the 1990s has provided the specimens necessary to describe larvae of *I. borealis* using meristic counts and morphological characters, including pigmentation and preopercular spination. This study presents an illustrated developmental series and general aspects of osteological development for *I. borealis*.

Methods

A total of 53 specimens (7.4–51.7 mm standard length [SL]) collected during AFSC research cruises in the Bering Sea and Gulf of Alaska between 1979 and 2002 were examined (Fig. 1). Specimens were collected at depths to 400 m, primarily using 60-cm bongo nets and Methot trawls. Specimens were initially preserved in 5% formalin buffered with sodium borate, then later transferred to 70% ethanol. Nineteen specimens were cleared and stained using the method of Potthoff (1984). Twenty-two adult *Icelinus borealis* specimens were radiographed to verify the vertebral count of 35–36 recorded in literature.

Specimens were grouped using the series method, by positively identifying juveniles using known adult characteristics then linking those specimens to progressively smaller specimens using shared characteristics (Neira et al., 1998). Larvae were identified using reported generic characters for *Icelinus* including 35–36 vertebrae (myomeres) and four distinct preopercular spines, if developed. Illustrated *Icelinus* (tentatively identified as *I. borealis*) from Matarese et al. (1989) were also used to compare general morphological and pigment characters.

Meristic counts are reported for ossified elements using cleared and stained or radiographed material. Morphometric measurements were taken following Richardson and Washington (1980) using a digital image analysis system with Image Pro Plus, vers. 4.5 software (Media Cybernetics, Inc., Silver Spring, MD). Both body length and proportional measurements are in SL unless otherwise noted. Developmental terminology follows Kendall et al. (1984). Nomenclature describing caudal-fin development follows Matarese and Marliave (1982).

Only melanistic pigmentation is described. Nomenclature describing pigment pattern follows Busby and Ambrose (1993). The term "band" refers to an aggregation of melanophores oriented vertically; "bar" refers to an aggregation that is oriented horizontally. Illustrations were rendered using a camera lucida attached to a dissecting stereomicroscope.

Material examined

Larvae: 53 specimens examined, 7.4–51.7 mm. UW 105110, 1 (16.7 mm), Bering Sea, 52°35.9′N, 173°25.6′W, 137 m depth, 2 August 1997, FV *Vesteraalen*; UW 105111, 1 (13.4 mm), Bering Sea, 56°31.9′N, 166°25.4′W, 88 m depth, 16 July 1994, RV *Miller Freeman*; UW 105113, 2 (14.4–15.1 mm), Bering Sea, 56°30.6′N, 168°60.0′W, 95 m depth, 23 July 2001, TS *Oshoro maru*; UW 105114, 1 (12.1 mm), Bering Sea, 54°59.7′N, 166°58.9′W, 100 m depth, 19 July 1995, TS *Oshoro maru*; UW 105116, 1 (14.5 mm), Bering Sea, 56°59.6′N, 170°00.4′W, 62 m depth, 25 July 1996, TS *Oshoro maru*; UW 105117, 2 (13.4–14.3 mm), Bering Sea, 57°01.1′N, 171°00.2′W, 94 m depth, 25 July 1996, TS *Oshoro maru*; UW 105119, 2 (14.3–16.3 mm), Bering Sea, 55°00.9′N, 166°01.4′W,

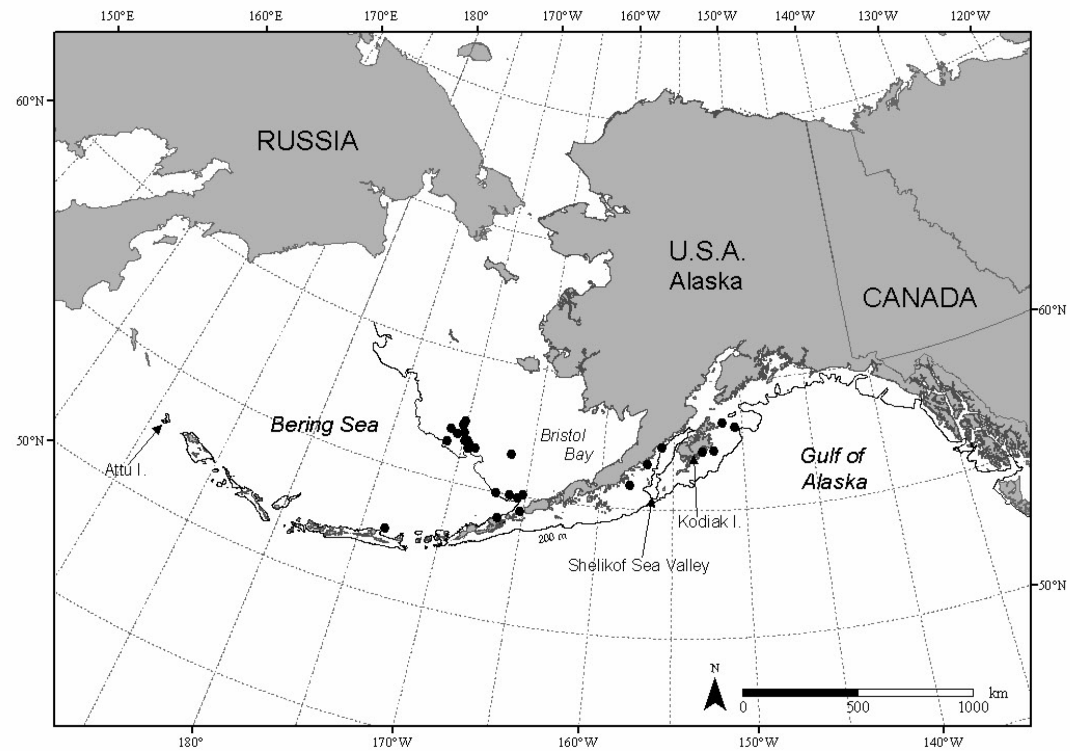

Figure 1

Station locations (•) in the Bering Sea and Gulf of Alaska where larval and juvenile northern sculpin (*Icelinus borealis*) were collected by the Alaska Fisheries Science Center, National Marine Fisheries Service (1979–2002).

100 m depth, 21 July 1997, TS *Oshoro maru*; UW 105121, 1 (32.1 mm), Gulf of Alaska, 58°12.1′N, 150°27.0′W, 115 m depth, 16 May 1985, RV *Poseidon*; UW 105122, 1 (7.9 mm), Bering Sea, 54°01.3′N, 166°33.9′W, 100 m depth, 25 April 1993, RV *Miller Freeman*; UW 105124, 1 (51.7 mm), Gulf of Alaska, 55°55.5′N, 157°56.0′W, 94 m depth, 23 June 1998, RV *Wecoma*; UW 105125, 2 (10.7–15.2 mm), Gulf of Alaska, 58°22.1′N, 151°22.2′W, 100 m depth, 1 June 2002, RV *Miller Freeman*; UW 105127, 1 (8.3 mm), Bering Sea, 54°55.5′N, 165°29.1′W, 119 m depth, 23 May 2003, RV *Miller Freeman*; UW 105129, 2 (9.2–9.3 mm), Bering Sea, 56°27.3′N, 169°28.3′W, 94 m depth, 12 July 1997, RV *Wecoma*; UW 105131, 1 (8.8 mm), Bering Sea, 56°27.3′N, 169°28.3′W, 30 m depth, 12 July 1997, RV *Wecoma*; UW 105133, 2 (8.5–12.5 mm), Bering Sea, 56°30.2′N, 169°28.5′W, 78 m depth, 10 July 1997, RV *Wecoma*; UW 105134, 1 (14.9 mm), Bering Sea, 56°41.4′N, 169°48.5′W, 74 m depth, 8 July 1997, RV *Wecoma*; UW 105136, 2 (8.0–9.2 mm), Bering Sea, 56°42.6′N, 169°35.9′W, 64 m depth, 10 July 1997, RV *Wecoma*; UW 105138, 1 (13.2 mm), Bering Sea, 56°42.6′N, 169°35.9′W, 25 m depth, 10 July 1997, RV *Wecoma*; UW 105140, 2 (10.0–14.1 mm), Bering Sea, 56°42.6′N, 169°36.1′W, 70 m depth, 9 July 1997, RV *Wecoma*; UW 105142, 1 (14.9 mm), Bering Sea, 56°42.7′N, 169°36.5′W, 72 m depth, 9 July 1997, RV *Wecoma*; UW 105144, 1 (10.2 mm), Bering Sea, 56°53.2′N, 170°26.7′W, 87 m depth, 6 July 1997, RV *Wecoma*; UW 105146, 2 (15.4–16.5 mm), Bering Sea, 57°17.3′N, 170°10.1′W, 30 m depth, 6 July 1997, RV *Wecoma*; UW 105148, 1 (14.5 mm), Bering Sea, 57°21.2′N, 170°08.3′W, 50 m depth, 13 July 1997, RV *Wecoma*; UW 105149, 1 (7.4 mm), Bering Sea, 54°24.9′N, 165°09.0′W, 140 m depth, 25 April 1997, RV *Miller Freeman*; UW 105151, 3 (43.2–45.9 mm), Gulf of Alaska, 57°18.5′N, 152°02.8′W, 74 m depth, 13 September 1993, RV *Miller Freeman*; UW 105152, 1 (41.7 mm), Gulf of Alaska, 57°15.7′N, 152°53.7′W, 87 m depth, 16 September 1993, RV *Miller Freeman*; UW 105154, 1 (14.1 mm), Bering Sea, 56°32.0′N, 166°25.4′W, 88 m depth, 16 July 1994, RV *Miller Freeman*; UW 105156, 1 (19.6 mm), Bering Sea, 57°24.9′N, 170°05.6′W, 52 m depth, 13 September 1999, RV *Miller Freeman*; UW 105157, 1 (11.6 mm), Gulf of Alaska, 56°46.2′N, 156°46.7′W, 101 m depth, 27 May 1995, RV *Miller Freeman*; UW 105159, 1 (9.4 mm), Gulf of Alaska, 57°24.5′N, 155°48.6′W, 100 m depth, 28 May 1995, RV *Miller Freeman*; UW 105160, 1 (17.9 mm), Bering Sea, 55°04.4′N, 165°08.0′W, 108 m depth, 26 July 1996, RV *Miller Freeman*; UW 105162, 2 (13.4–15.8 mm), Bering Sea, 56°28.3′N, 169°26.9′W, 87 m depth, 1 August 1996, RV *Miller Freeman*; UW 105164, 2 (11.1–12.9 mm), Bering Sea, 56°30.3′N, 171°02.5′W, 119 m depth, 4 August 1996, RV *Miller Freeman*; UW 105165, 3 (14.8–16.0 mm), Bering Sea, 56°32.7′N, 169°27.4′W, 63 m depth, 2 August 1996, RV *Miller Freeman*; UW 105167, 1 (13.8 mm), Bering Sea, 56°34.6′N, 169°24.3′W, 44 m depth, 2 August 1996, RV

Table 1

Body proportions of larvae and juveniles of northern sculpin (*Icelinus borealis*). Values for each body proportion are expressed as percentage of standard length (SL) or head length (HL): mean, standard deviation, and range.

Body proportion	Flexion	Postflexion	Juvenile
Sample size	9	27	8
Standard length	9.1 ±0.74 (8.0–10.2)	14.9 ±2.40 (11.1–22.7)	38.6 ±10.3 (24.1–51.7)
Head length/SL	25.2 ±0.02 (22.2–28.4)	34.3 ±0.04 (26.2–41.5)	37.9 ±0.02 (35.2–39.8)
Snout length/HL	27.9 ±0.04 (24.8–37.9)	26.8 ±0.03 (20.0–32.4)	27.9 ±0.05 (21.8–39.0)
Eye diameter/HL	31.0 ±0.03 (25.3–33.7)	24.3 ±0.02 (20.2–30.3)	27.8 ±0.01 (26.1–30.6)
Snout-to-anus length/SL	44.6 ±0.03 (38.7–48.6)	47.2 ±0.03 (42.3–54.0)	50.6 ±0.04 (46.4–57.7)
Body depth/SL	20.3 ±0.02 (17.6–23.2)	21.9 ±0.02 (17.6–27.1)	20.5 ±0.02 (17.4–22.7)
Pectoral-fin length/SL	10.1 ±0.02 (6.6–13.4)	24.2 ±4.30 (13.8–32.4)	24.5 ±2.80 (19.6–28.8)

Miller Freeman; UW 105169, 1 (24.9 mm), Bering Sea, 56°31.2′N, 169°28.8′W, 68 m depth, 11 September 1997, RV *Miller Freeman*; UW 105172, 1 (24.1 mm), Bering Sea, 57°17.3′N, 170°09.3′W, 39 m depth, 16 September 1997, RV *Miller Freeman*; UW 105174, 1 (22.7 mm), Bering Sea, 57°16.3′N, 170°11.0′W, 16 September 1997, RV *Miller Freeman*.

Adults: 22 specimens examined, 32.0–77.0 mm. UW 027383, 4 (41.0–50.0 mm), eastern North Pacific, 60°12.0′N, 147°45.0′W, 30 m depth, 1 August 1989, RV *Discovery*, J. W. Orr; UW 029499, 5 (32.0–55.0 mm), eastern North Pacific, 60°21.0′N, 147°49.0′W, 40 m depth, 6 August 1989, RV *Discovery*, J. W. Orr; UW 040432, 3 (45.0–64.0 mm), eastern North Pacific, 60°18.0′N, 147°50.0′W, 142 m depth, 31 July 1989, RV *Discovery*, C. Eaton; UW 111416, 2 (55.0–62.0 mm), eastern North Pacific, 52°39.8′N, 169°21.6′W, 114 m depth, 24 May 2003, FV *Northwest Explorer*, J. W. Orr; UW 040955, 4 (44.0–45.0 mm), eastern North Pacific, 60°33.2′N, 147°35.0′W, 40 m depth, 1 October 1989, A. M. Shedlock; UW 027174, 4 (60.0–77.0 mm), eastern North Pacific, Gulf of Alaska, Yakutat Bay, FV *Resolution*.

Results

Morphology

The smallest larva examined in this study was 7.4 mm notochord length (NL) and in preflexion (Fig. 2A). Notochord flexion began at approximately 8.0 mm and was complete around 11.0 mm (Fig. 2B). Postflexion larvae were 11.0–16.0 mm (Fig. 2C). Transformation to the juvenile stage occurred between 16.0 mm and 24.0 mm (Fig. 2D). Specimens larger than 24.0 mm were considered juveniles and identified using adult characters (Fig. 2E).

During preflexion, the head was small and round, measuring 18% SL, increasing to 38% SL by the juvenile stage (Table 1). The snout was initially rounded, but became notably pointed by flexion; snout length was 24% head length (HL) during preflexion, increasing to approximately 28% HL during flexion through the juvenile stage. Snout-to-anus length steadily increased from 39% SL during preflexion to 51% SL in juveniles. Body depth was initially 17% SL during preflexion, but increased to approximately 20% SL in later stages.

Pigmentation

Two preflexion specimens were available for study: one 7.4 mm NL and one 7.9 mm NL. Both specimens were lightly pigmented (Fig. 2A). A single melanophore was present on the lower jaw angle. Pigment on the gut consisted of one to three individual melanophores anteriorly, and moderate pigmentation on the anus. A single row of nine postanal ventral melanophores (PVMs) was present on both specimens. Pigmentation on the caudal finfold was present on the 7.4 mm NL specimen. Pigment on the head, gut, and anus steadily increased during flexion (Fig. 2B).

Twenty-six postflexion and transforming specimens were examined. Melanophores were present dorsally over the mid- and hind-brain (Fig. 2C). Minute melanophores were present on the orbital rim. Loosely grouped melanophores were present in postorbital and suborbital regions, upper and lower jaws, on the cheek, operculum, chin, and isthmus. Pigment was present on the nape. The gut was pigmented along the anterodorsal surface and extended dorsolaterally toward the anus. Three to 14 PVMs were present on specimens between preflexion and postflexion stages; nine was the modal value (Table 2). The size, shape, and location of PVMs were variable among specimens. Lateral body pigment developed as vertical (dorsal to ventral) bands that were composed of densely aggregated small melanophores. The anterior (first) lateral band was located directly under the first dorsal fin and extended ventrally to the gut. The second band developed as a small aggregation of melanophores located mediolaterally on the body. When fully developed, the second band extended from the anterior portion of the second dorsal fin to the mediolateral part of the body. Pigment developed on the first dorsal fin, particularly on the membrane between

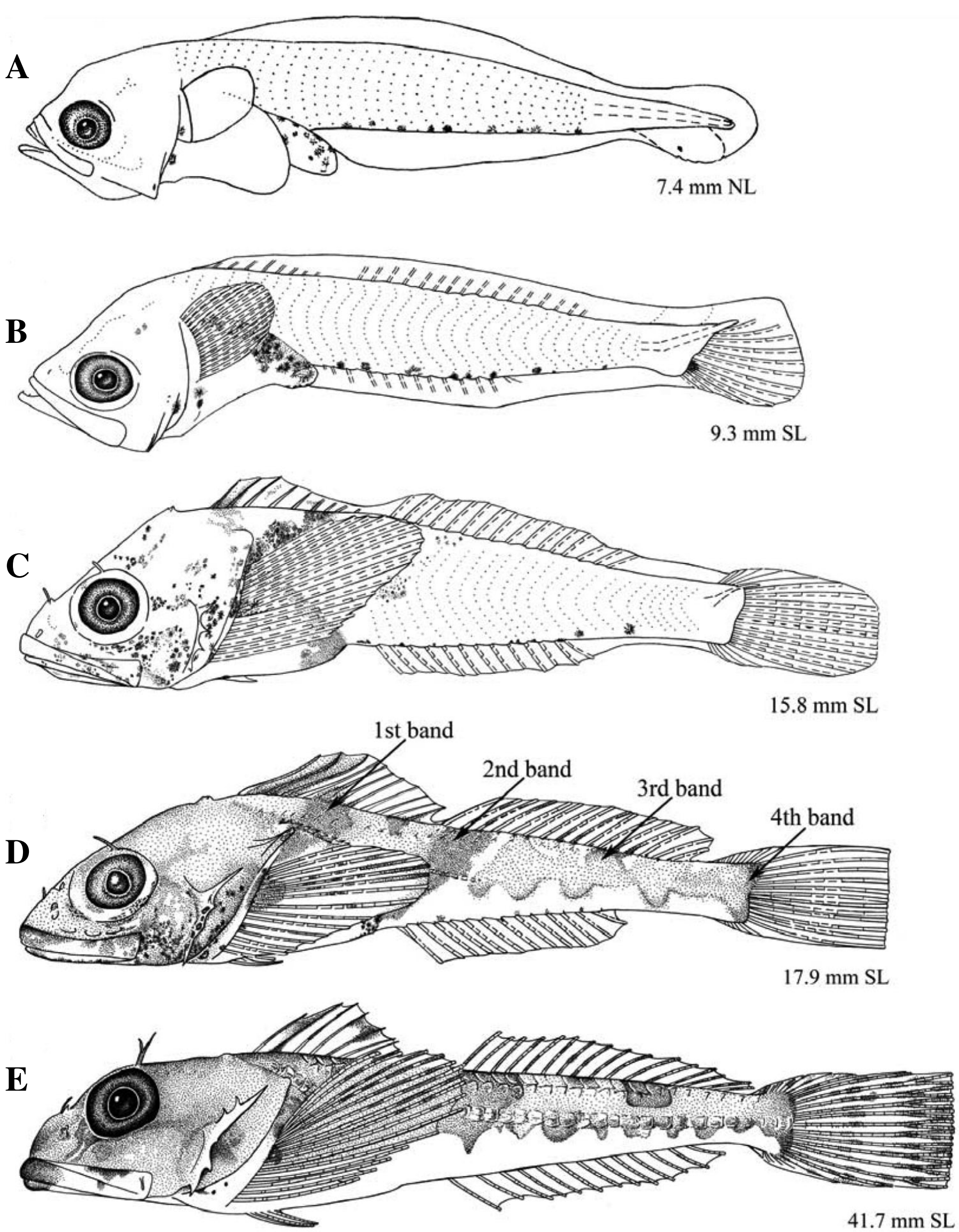

Figure 2

Developmental series of northern sculpin (*Icelinus borealis*): (**A**) preflexion larva, 7.4 mm NL, UW 105149, Bering Sea, 54°24.9′N, 165°09.0′W, 140 m depth, 25 April 1997; (**B**) flexion larva, 9.3 mm SL, UW 105129, Bering Sea, 56°27.3′N, 169°28.3′W, 94 m depth, 12 July 1997; (**C**) postflexion larva, 15.8 mm SL, UW 105162, Bering Sea, 56°28.3′N, 169°26.9′W, 87 m depth, 1 August 1996; (**D**) transformation larva, 17.9 mm SL, UW 105160, Bering Sea, 55°04.4′N, 165°08.0′W, 108 m depth, 26 July 1996; (**E**) juvenile, 41.7 mm SL, UW 105152, Gulf of Alaska, 57°15.7′N, 152°53.7′W, 87 m depth, 16 September 1993. Abbreviations: NL=notochord length; SL=standard length. Illustrations by R. L. Cartwright.

the first two or three spines. Rays of the second dorsal fin were also pigmented in some specimens. Large, dark melanophores were present on the pectoral-fin base, and some pigmentation developed on the rays near the base. One or two melanophores were present on or near the pelvic-fin base.

Throughout transformation of larvae of *I. borealis* into the juvenile stage, pigmentation continued to increase on the head until the entire area was nearly covered with small melanophores (Fig. 2D). Gut pigment was less visible. The first and second lateral pigment bands were fully developed. The third lateral pigment band developed directly beneath the posterior portion of the second dorsal fin approximately between fin rays 11 and 13. Pigment in the fourth band was located on the caudal peduncle and extended posteriorly onto the caudal fin. Pigment was also scattered mediolaterally, giving the appearance of a horizontal bar posterior to the second band. Pigment developed on the caudal-fin rays.

At the beginning of the juvenile stage, lateral bands were well defined by dark pigment (Fig. 2E). Larval pigmentation (e.g., PVMs) was still present until at least 24.9 mm, but by 33.0 mm no residual larval pigment remained. Scattered melanophores on the mediolateral part of the body between the second and fourth bands were retained and looked like small pigment blotches.

Table 2

Total postanal ventral melanophores (PVMs) of larvae and juveniles of northern sculpin (*Icelinus borealis*). Specimens between dotted lines (-----) are undergoing notochord flexion; specimens between lines (– — –) are in transformation stage. Abbreviation: SL = standard length.

Body length (mm SL)	Postanal ventral melanophores
7.4	—
7.9	9
8.8	9
10.2	4
11.6	9
13.4	14
14.3	9
14.8	9
14.9	7
15.1	11
15.8	9
16.0	8
16.3	10
17.9	7
19.6	5
22.7	3
24.1	3
24.9	7
32.1	0
41.7	0
43.2	0
45.1	0
45.9	0
51.7	0

Cirri

Cirri developed during the postflexion stage. Supraocular cirri were first to develop. Supraocular cirri are typically bifid or trifid, but occasionally have more than three terminal filaments. The development of nasal and postorbital cirri followed supraocular cirri. During transformation into the juvenile stage, cirri developed posterodorsally on the maxilla. By 25.0 mm, one small cirrus was present both anteriorly and posteriorly of the parietal and nuchal spines, and more than one opercular cirrus may develop per side (two cirri were present dorsally on each opercle of a 46.0-mm specimen). A full complement of supraocular, nasal, postorbital, maxillary, occipital, and opercular cirri was present in juveniles.

Meristic features

Except for the dorsal-fin spines and rays and the superior procurrent caudal-fin rays, fins ossified by 14.3 mm (Table 3). Dorsal-fin spines and rays were completely ossified at 15.8 mm, as were the superior procurrent caudal-fin rays. Vertebral centra (9–11 abdominal + 24–27 caudal) ossified at 14.3–15.8 mm. By 15.0 mm, lateral line scales began to develop; by 15.8 mm, two dorsal scale rows began to develop immediately beneath the dorsal fins. Lateral line scales and the two dorsal scale rows were ossified by 24.0 mm. Pterygiophores of the dorsal and anal fins ossified by 24.1 mm. Adult radiographs resulted in vertebral counts of 35–36.

Spination

Head spines developed during flexion. At 8.8 mm, parietal spines were minute but ossified. Four preopercular spines were present; the dorsalmost spine was most pronounced. At 11.6 mm, small nuchal spines, approximately half the size of the parietals, were present. By 14.3 mm, nasal spines were ossified. Parietal and nuchal spines fused together at their tips to form parietal sensory canals. By 16.0 mm, the dorsalmost preopercular spine was bent upward and the ventralmost spine downward and forward. The fused parietal and nuchal spines were less prominent. Nasal spines were well developed and slightly curved posteriorly by 22.7 mm. At approximately 24.0 mm, the dorsalmost preopercular spine was very large and bifurcate; the dorsalmost spine may become trifurcate by the juvenile stage.

Caudal skeleton

The caudal skeleton consisted of one ural centrum, preural centra, neural and haemal spines, three epurals, two uroneurals, one superior hypural ($HY_{4\text{-}5}$), one inferior hypural ($HY_{1\text{-}3}$), and 25–31 caudal-fin rays (7–11, 6 + 6, 4–8) (Fig. 3). At 8.8 mm, $HY_{1–3}$ and $HY_{4–5}$ were fused and all 12 principal caudal-fin rays (6 + 6) were present (Fig. 3A). Three epurals formed by 12.0 mm. Each preural centrum had one neural and one haemal spine; however, in some specimens the first preural centrum had

Table 3

Meristic counts of larvae and juveniles of northern sculpin (*Icelinus borealis*). Specimens between dotted lines (- - - - -) are undergoing notochord flexion; specimens between dashed lines (– — –) are undergoing transformation. Abbreviation: SL = standard length.

Body length (mm SL)	Dorsal-fin		Anal-fin rays	Pectoral-fin rays		Pelvic-fin spine & rays		Caudal-fin rays: Superior		Caudal-fin rays: Inferior		Vertebrae			Branchio-stegal rays
	Spines	Rays		Left	Right	Left	Right	Procurrent	Principal	Principal	Procurrent	Abdominal	Caudal	Total	
7.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
*8.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
*10.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
*11.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
*13.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
*14.3	—	—	13	16	16	I, 2	I, 2	—	6	6	7	9	26	35	6
*14.8	—	—	—	—	—	—	—	—	6	6	—	—	—	—	—
*14.9	—	—	—	16	16	—	—	—	—	—	—	—	—	—	6
*15.1	—	—	—	16	16	—	—	—	—	—	—	—	—	—	6
*15.8	X	17	14	16	17	I, 2	I, 2	9	6	6	7	10	25	35	6
*16.0	—	—	—	16	16	I, 2	I, 2	—	6	6	—	—	—	—	6
*16.3	X	16	13	16	16	I, 2	I, 2	10	6	6	8	11	25	36	6
+17.9	X	16	#	15	15	I, 2	I, 2	11	6	6	8	11	25	36	6
*19.6	XI	16	12	16	16	I, 2	I, 2	10	6	6	7	10	25	35	6
*22.7	XI	16	13	16	15	I, 2	I, 2	10	6	6	4	10	25	35	6
*24.1	X	16	13	16	16	I, 2	I, 2	10	6	6	8	#	#	36	6
+24.9	IX	16	13	16	16	I, 2	I, 2	9	6	6	8	10	26	36	6
+32.1	X	16	13	16	16	I, 2	I, 2	10	6	6	7	10	26	36	6
+41.7	IX	16	13	16	16	I, 2	I, 2	10	6	6	7	11	25	36	6
+43.2	X	16	13	16	16	I, 2	I, 2	8	6	6	6	11	25	36	6
+45.1	X	15	12	16	16	I, 2	I, 2	9	6	6	8	#	#	36	6
+45.9	#	15	12	15	15	I, 2	I, 2	9	6	6	8	11	25	36	6
+51.7	IX	14	12	16	16	I, 2	I, 2	9	6	6	8	11	25	36	6

* Cleared and stained specimens.
\+ Radiographed specimens.
\# Could not obtain accurate count.

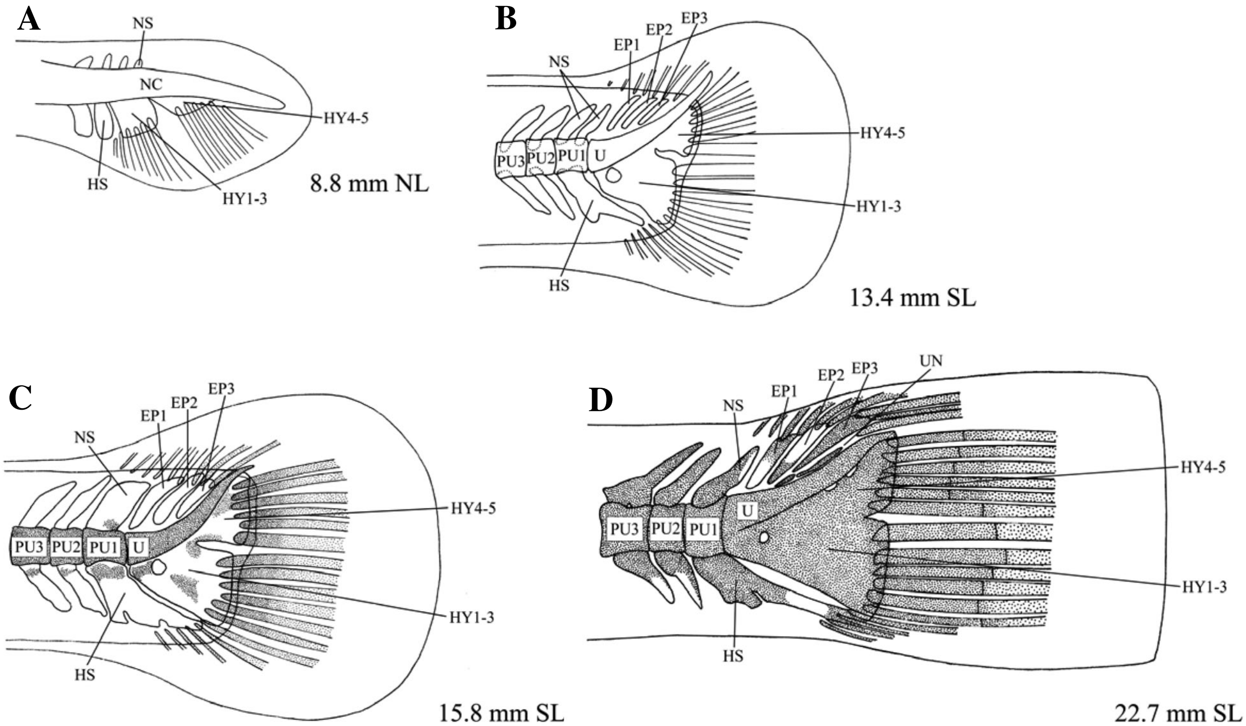

Figure 3

Development of caudal skeleton of northern sculpin (*Icelinus borealis*). (**A**) Flexion larva, 8.8 mm NL, UW 105131, Bering Sea, 56°27.3′N, 169°28.3′W, 30 m depth, 12 July 1997; (**B**) postflexion larva, 13.4 mm SL, UW 105111, Bering Sea, 56°31.9′N, 166°25.4′W, 88 m depth, 16 July 1994; (**C**) postflexion larva, 15.8 mm SL, UW 105162, Bering Sea, 56°28.3′N, 169°26.9′W, 87 m depth, 1 August 1996; (**D**) juvenile, 22.7 mm SL, UW 105174, Bering Sea, 57°16.3′N, 170°11.0′W, 16 September 1997. Abbreviations: NL=notochord length; SL=standard length; $HY_{1\text{-}3}$=hypurals 1–3; $HY_{4\text{-}5}$=hypurals 4–5; EP (1, 2, 3)=epural(s) (1, 2, 3); NS=neural spine; HS=haemal spine; NC=notochord; U=ural centrum; PU (1, 2, 3)=preural centra (1, 2, 3); UN=uroneural. Illustrations by R. L. Cartwright.

two neural spines (Fig. 3B). All five hypurals ($HY_{1–5}$) fused by 13.4 mm. By 15.8 mm, the ural centrum, preural centra, and principal caudal-fin rays ossified (Fig. 3C). Hypurals ossified by 16.0 mm. Two uroneurals were present and ossified by 20.0 mm; neural and haemal spines on the first preural centrum and procurrent caudal-fin rays were ossified. Epurals ossified by 22.7 mm (Fig. 3D). By the juvenile stage at approximately 24.0 mm, development of the caudal skeleton was complete.

Discussion

Information about the early life history of *Icelinus* is conspicuously sparse in literature. This study presents the first description of larval and juvenile *Icelinus borealis*. *Icelinus borealis* larvae exhibit a unique geographic distribution in the Bering Sea and are geographically isolated north of the Aleutian Islands—which provides for a definitive description of its development. A combination of morphological characters, pigmentation, preopercular spine pattern, meristic counts, and squamation in later developmental stages is essential to identify *Icelinus* at the species level. Larvae of *I. borealis* have 35–36 myomeres. The body is lightly pigmented, and the most useful character is the presence of 3–14 (mode=9) irregular PVMs that persist through transformation into the juvenile stage. Four prominent preopercular spines and three rows of spiny ctenoid scales develop during transformation into the juvenile stage; one row is along the lateral line and two are directly beneath the dorsal fins. Identification of *I. borealis* larvae in other geographic areas, such as the Gulf of Alaska, is complicated by the co-occurrence of other species of *Icelinus*.

Icelinus filamentosus is found with *I. borealis* throughout the Gulf of Alaska but, if collected, has not been identified in ichthyoplankton samples (Matarese et al., 1989; Mecklenburg et al., 2002). Larvae of *I. borealis* differ from *I. filamentosus* primarily by having an anal-fin ray count of 11–14 (vs. 13–16) and a vertebral count of 35–36 (vs. 34–37) (Table 4). *Icelinus burchami* and *I. tenuis* also are found with *I. borealis*; however, the northernmost extent of their geographic ranges is

Southeast Alaska and do not extend farther north into the Gulf of Alaska or into the Bering Sea (Matarese et al., 1989; Mecklenburg et al., 2002). Larvae of *I. burchami* and *I. tenuis* have not been identified, but there are subtle differences in meristic counts of juveniles and adults between these species and *I. borealis* (Table 4). Juvenile *Icelinus* may be distinguished by using adult characters in any geographic location (e.g., by the presence of elongated, threadlike first two dorsal spines in *I. filamentosus*).

Icelinus quadriseriatus is the only species of *Icelinus* with currently identifiable and described early life history stages. *Icelinus quadriseriatus* is distributed from Sonoma County, California, south to Cabo San Lucas, Baja California, Mexico (Feeney, 1987). Although *I. borealis* and *I. quadriseriatus* are geographically separated and their distributions do not overlap, it is important to compare the larvae of these species. Larvae of *I. borealis* and *I. quadriseriatus* are similarly pigmented; however they differ primarily in number of PVMs and ventral gut pigment. *Icelinus borealis* PVMs number from three to 14 (vs. 25–63). *Icelinus borealis* may have a few, individual melanophores present on the ventral gut during preflexion, whereas *I. quadriseriatus* has ventral gut pigment consisting of one to six rows of melanophores aligned anteroposteriorly in early development. *Icelinus quadriseriatus* retains ventral gut pigment throughout its larval development (Feeney, 1987). *Icelinus borealis* differs from *I. quadriseriatus* by having an anal-fin ray count of 11–14 (vs. 10–15), and a vertebral count of 35–36 (vs. 33–35) (Table 4). *Icelinus borealis* and *I. quadriseriatus* also undergo flexion at different times (8.0–11.0 mm vs. 5.2–7.6 mm, respectively) (Feeney, 1987).

After examining all available putative larval specimens of *Icelinus* from the Bering Sea, it was found that the majority of larvae at AFSC were not *I. borealis* but probably members of the closely

Table 4

Comparison of meristic counts of *Icelinus* and *Icelus* (Yabe et al., 1980; Matarese et al., 1989; Moser et al., 1996; Yabe et al., 2001; Mecklenburg et al., 2002; Rosenblatt and Smith, 2004; Tsuruoka et al., 2006). Counts in parentheses (*I. borealis*) indicate the mode. Abbreviations: C=central; S=southern; SE=southeast; SS=south of southern.

			Fins				
Species	Common name	Distribution	Dorsal	Anal	Pectoral	Pelvic	Vertebrae
Icelinus borealis	northern sculpin	Washington–Bering Sea	IX–XI + 14–17 (X + 16)	11–14 (13)	14–17 (16)	I,2	35–36*
I. burchami	dusky sculpin	S California–SE Alaska	VIII–XI + 15–18	10–14	16–19	I,2	33–37
I. cavifrons	pit-head sculpin	SS California–C California	IX–XII + 12–15	11–13	14–16	I,2	35–37
I. filamentosus	threadfin sculpin	S California–Gulf of Alaska	IX–XII + 15–18	13–16	16–18	I,2	34–37
I. fimbriatus	fringed sculpin	S California–British Columbia	X–XI + 12–14	12–14	16–18	I,2	35–37
I. japonicus	Futasuji-kajika	Japan	IX–X + 12–13	10–11	15–17	I,2	33
I. limbaughi	canyon sculpin	S California	IX–X + 13–15	8–12	15–17	I,2	31–36
I. oculatus	frogmouth sculpin	S California–British Columbia	X–XI + 15–17	13–14	17	I,2	37
I. pietschi	Hime-futasuji-kajika	Onagawa, Japan–Iturup I., Kuril Is.	X + 13–14	11–12	16	I,2	32–34
I. quadriseriatus	yellowchin sculpin	SS California–C California	VII–X + 12–16	10–15	15–17	I,2	33–35
I. tenuis	spotfin sculpin	SS California–SE Alaska	IX–XI + 16–19	13–17	15–17	I,2	37–39
Icelus canaliculatus	blacknose sculpin	Gulf of Alaska–Bering Sea	VII–VIII + 22–25	18–20	15–19	I,3	37–39
I. euryops	wide-eye sculpin	Gulf of Alaska–Bering Sea	VIII–X + 20–23	15–19	16–18	I,3	41–42**
I. spatula	spatulate sculpin	Gulf of Alaska–Arctic	VII–XI + 18–22	13–18	16–20	I,3	39–41
I. spiniger	thorny sculpin	British Columbia–Bering Sea	VIII–X + 19–23	15–19	17–20	I,3	40–42
I. uncinalis	uncinate sculpin	Bering Sea	IX + 19–20	14–16	17–18	I,3	37–40

* Counts obtained from literature and radiographs of adult specimens.
** Counts obtained from radiographs of adult specimens.

related genus, *Icelus*. The majority of larvae had higher myomere counts (37–42) than *Icelus* (35–36) and a different pelvic-fin count (1, 3) than *I. borealis* (1, 2) (Table 4). Larvae of *I. borealis* and *Icelus* had the same general body shape, presence of irregular PVMs (size, shape, location), similar pigmentation on the head, gut, and anus, four prominent preopercular spines, and a distinctive bony shelf on the anterior portion of the preopercle. *Icelinus* and *Icelus* were also placed in the same phenetic group by Richardson (1981) based on shared larval characters. There are five species of *Icelus* in the Bering Sea; however, *Icelus spatula* and *I. spiniger* are most abundant in the geographic area where *Icelinus borealis* is found (Matarese et al., 1989).

This study provides a sound method for identifying larval *I. borealis* in the Bering Sea and is applicable to juvenile specimens as far south as southern Puget Sound, Washington. Although only two preflexion specimens were available for study, morphological characters and patterns of pigmentation at this stage of development are an important contribution. Taxonomic characters presented here could elucidate distinctiveness or similarity of *Icelinus* among other cottid genera (e.g., *Ruscarius*, *Icelus*) and co-occurring species (e.g., *Icelinus filamentosus*)—an important beginning to solving the complicated systematic relationships within the family Cottidae (Richardson, 1981). Although *I. borealis* larvae were identified in this study from the Bering Sea, definitive identification of larval *I. borealis* in other geographic areas will depend on the comparison of *I. borealis* with its congeners and other sympatric cottid larvae.

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