Redescription of *Paraliparis holomelas* Gilbert, 1896 (Teleostei: Liparidae), with a description of early life history stages

Morgan S. Busby✉ and Rachael L. Cartwright

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering Division, 7600 Sand Point Way NE, Building 4, Seattle, WA 98115, USA (e-mail: Morgan.Busby@noaa.gov)

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Abstract The poorly known liparid fish *Paraliparis holomelas* Gilbert, 1896 is redescribed primarily based on specimens from the Gulf of Alaska, and the first illustration of this species is presented. Originally described from the southeastern Bering Sea and later reported from the Sea of Okhotsk, this material also represents an eastward extension of the species range. *Paraliparis holomelas* is distinguished from other North Pacific *Paraliparis* by morphological features and meristic counts. A complete description of the early life history stages of *P. holomelas* is also presented, which includes the first account and illustration of a yolk-sac larva in the genus *Paraliparis*.

Key words Liparidae · *Paraliparis holomelas* · Redescription · Larval development

The liparid genus *Paraliparis* Collett, 1878 comprises 106 species known from oceans of the Northern and Southern Hemispheres (Chernova et al., 2004). The poorly known species *Paraliparis holomelas* (Fig. 1) was originally described by Gilbert (1896) from two specimens, one collected in the Aleutian Islands near Unalaska Island (depth, 742 m) and the other from the southeastern Bering Sea west of the Pribilof Islands (depth, 2972 m) (Fig. 2A). Jordan and Evermann (1898) designated these two specimens as lectotype and paralectotype. Two additional specimens were reported by Schmidt (1950) from the Sea of Okhotsk at depths of 128 and 3350 m. The original description and reported meristic counts for several eastern North Pacific species of *Paraliparis*, including *P. holomelas*, are incomplete and based on observations of very few specimens (Gilbert, 1896). In addition, the lectotype and paralectotype of *P. holomelas* have deteriorated to the point where they are of little use for comparative studies (Fig. 3). After a preliminary examination of material, we found it necessary to redescribe *P. holomelas.*

Very little is known about reproduction and development of eggs and larvae of deep-water liparid fishes, and this is particularly true of the genus *Paraliparis*. Wenner (1979) reported spawning periods, fecundities, and ovarian egg diameters of *Paraliparis calidus* Cohen, 1968, *Paraliparis copei* Goode and Bean, 1896, and *Paraliparis garmani*, Burke, 1912 from the western Atlantic. Stein (1980) provided data on spawning period, fecundity, and ovarian egg diameters for *Paraliparis cephalus* Gilbert, 1892, *Paraliparis latifrons* Garman, 1899, *Paraliparis megalopus* Stein, 1978, and *Paraliparis mento* Gilbert, 1892 from the northeast Pacific. He also hypothesized that male *Paraliparis* guard nests. Able et al. (1984) summarized available information on early life history of *Paraliparis* (mostly from Stein, 1980) and presented illustrations of *P. calidus* and *P. copei* from the St. Lawrence River estuary, Canada. Able et al. (1986) updated information on larvae of *P. calidus* and *P. copei*. Matarese et al. (1989) provided an illustration of a 28.5 mm unidentified juvenile *Paraliparis* from the eastern North Pacific Ocean. More recently, Ambrose (1996) presented preliminary data and an illustration of larval *P. cephalus*.

In this study, we redescribe adults of *P. holomelas* based on our examination of 27 adult specimens collected in the Gulf of Alaska and Bering Sea, the two type specimens from the Bering Sea, and one specimen from the Sea of Okhotsk [reported in Schmidt (1950)]. We also provide the first illustrations of this species and characters to distinguish adult *P. holomelas* from other *Paraliparis* species reported from Alaskan and adjacent waters (Mecklenburg et al., 2002). Additionally, we present a developmental series of the larvae and early juveniles of *P. holomelas*; this is the first complete developmental series reported for the genus *Paraliparis* and includes the first account and illustration of a yolk-sac stage larva of *Paraliparis*. Finally, we present information on the geographic and depth distributions of *P. holomelas* larvae and adults.

Materials and Methods

Material was collected from the Gulf of Alaska and Bering Sea with a variety of gear including 60-cm bongo nets, epibenthic sleds, midwater trawls, bottom trawls, and 1-m^2 Tucker trawls. Additional material was obtained from or examined in museum collections. Depths, when not provided in collection data, were determined from navigation

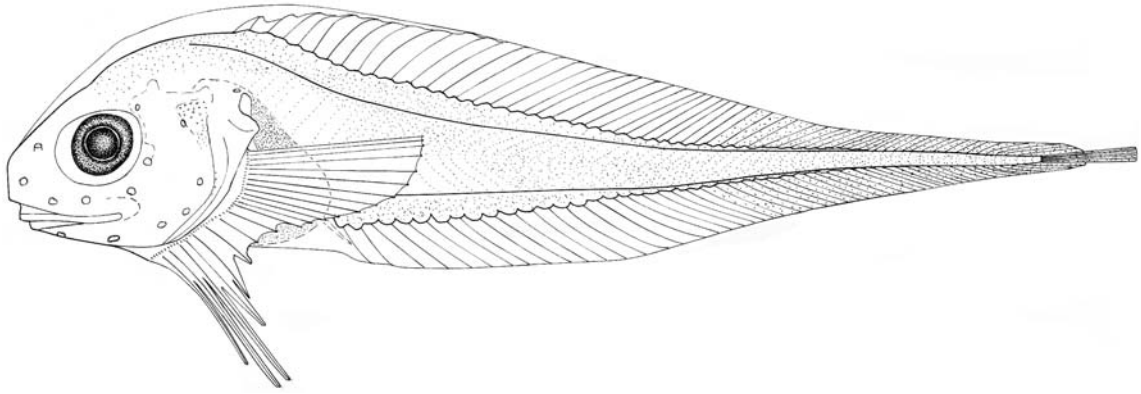

Fig. 1. *Paraliparis holomelas*, UW 046118, 69.0 mm SL, lateral view

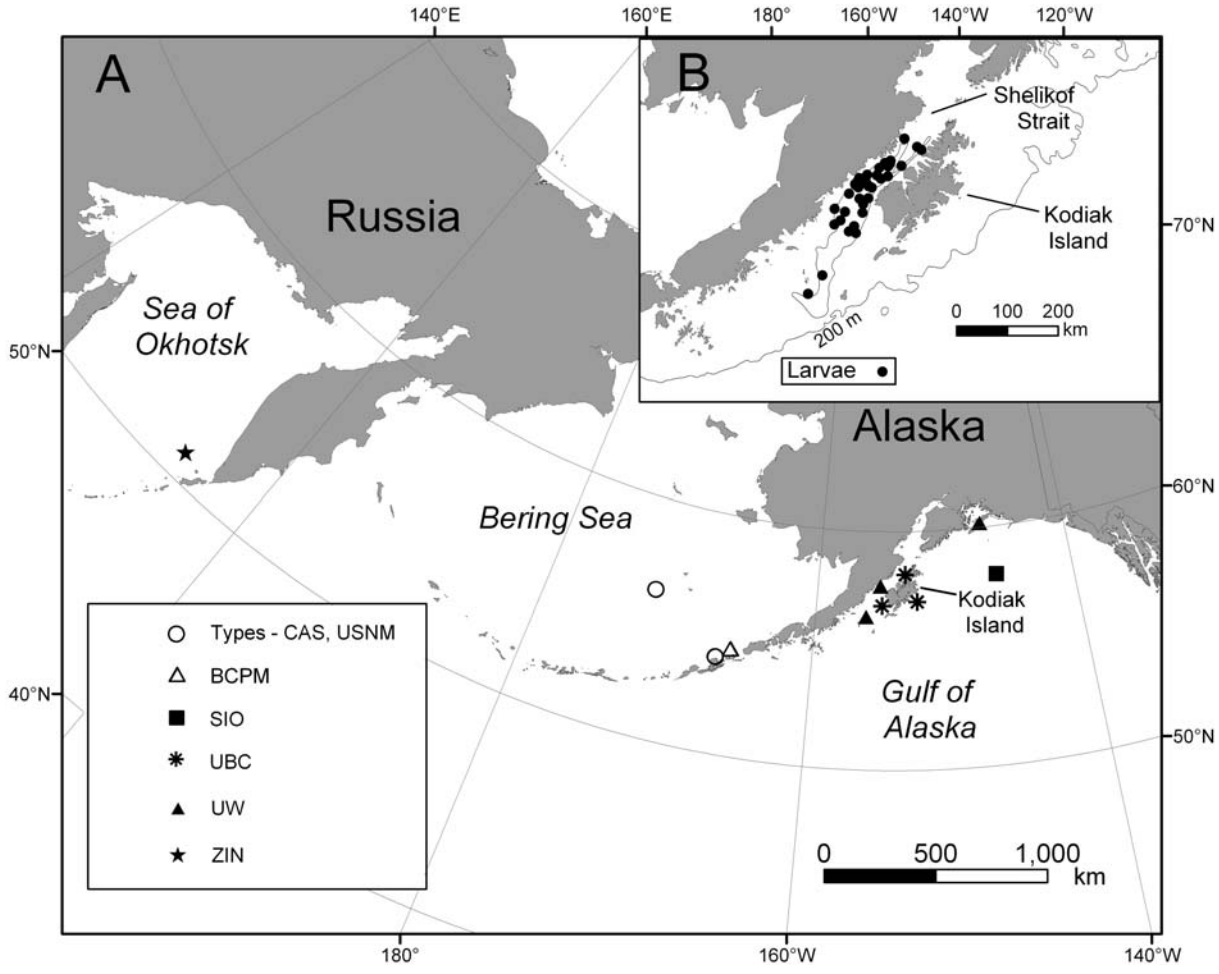

Fig. 2. **A** Collection localities of adult *Paraliparis holomelas* based on material examined in this study. **B** (*Inset*) Distribution of *Paraliparis holomelas* larvae based on material examined in this study

charts. Adult counts, measurements, abbreviations, and other terminology follow Andriashev and Stein (1998) as amended in Stein et al. (2001) with the addition of the following: caudal fin length, dorsal fin overlap on caudal fin, and anal fin overlap on caudal fin. Proportions are expressed in percent standard length (SL) or head length (HL) unless otherwise specified. Adults were measured with dial calipers to the nearest 0.1 mm. A dissecting microscope interfaced with a computer digital image analysis system and a video camera were used to collect measurements of larvae and juveniles to the nearest 0.1 mm. Larvae of *P. holomelas* were identified using a serial approach working backward from juveniles of known identity. Measurements were taken from the left side of the fish except when a

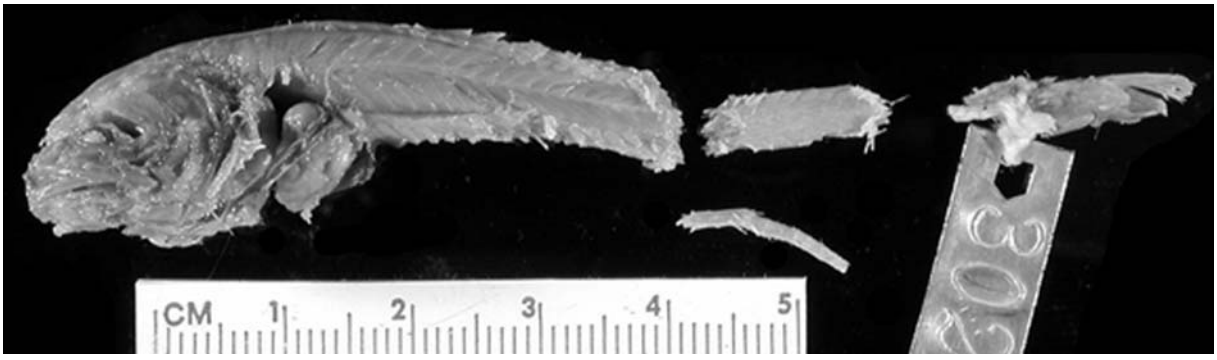

Fig. 3. Photograph of *Paraliparis holomelas* paralectotype, CAS 103026

character was damaged, then the right side was measured. Certain measurements could not be obtained from damaged specimens. Description of caudal-fin morphology and adult counts of dorsal- and anal-fin rays, pleural ribs, and vertebrae were obtained from radiographs.

Development of skeletal features in larvae and morphology of pectoral girdles dissected from adults were examined in specimens cleared and stained using the method of Potthoff (1984). Specimens were initially preserved in 5%–10% formalin. Therefore, only melanistic pigmentation is described. Institutional abbreviations follow Leviton et al. (1985).

Paraliparis holomelas Gilbert, 1896

(English name: Ebony snailfish)
(Figs. 1–5)

Paraliparis holomelas Gilbert, 1896: 441 [original description of two specimens 95 and 100 mm, sex unknown, southeastern Bering Sea, north of Unalaska Island, *Albatross* stations 3308 and 3332, depths 742 and 2972 m (406 and 1652 fathoms)]; Jordan and Evermann, 1898: 2140 (description, type designation); Evermann and Goldsborough, 1907: 334 (in part; additional records from Alaskan waters later described as *Paraliparis deani* new species by Burke, 1912: 571–572); Burke, 1930: 175–176 (in key; description); Jordan et al., 1930: 404 (list); Taranetz, 1937: 138 (list); Schmidt, 1950: 214 (description, first records from Sea of Okhotsk); Wilimovsky, 1954: 287 (list); Wilimovsky, 1958: 80 (in key); Quast and Hall, 1972: 31 (list, references); Stein, 1978: 45–46 (comparison with *Paraliparis latifrons*); Pitruk, 1990: 41 (list); Dudnik and Dolganov, 1992: 63 (list); Sheiko and Fedorov, 2000: 33 (list); Mecklenburg et al., 2002: 582, 638 (in key, distribution in Alaskan waters, references); Chernova et al., 2004: 39 (checklist).

Material examined. Adults: 30 specimens including the lectotype and a photograph and radiograph of the paralectotype. USNM 48637 (lectotype), female with eggs (according to Burke, 1930), 95.0 mm (from original description, unclear if SL or TL, specimen now too damaged to remeasure), *Albatross* Station 3332, southeastern Bering Sea, north of Unalaska Island, 54°02′50″ N, 166°45′00″ W, 21 Aug. 1890, depth 742 m. CAS 103026 (paralectotype, photograph and radiograph only), sex unknown, 100.0 mm (from original description, unclear if SL or TL, specimen now too damaged to remeasure), *Albatross* Station 3308, southeastern Bering Sea, west of Pribilof Islands, 56°12′00″ N, 172°07′00″ W, 04 Aug. 1890, depth 2972 m. SIO 63-536-56A, 68.0 mm SL, sex unknown, northern Gulf of Alaska, 58°00′00″ N, 146°00′00″ W, 1961 (exact date unknown), depth 2723 m. UBC 62-517, 4 females, 1 sex unknown, 49.0–75.0 mm SL, Raspberry Strait off Afognak Island, 58°12′00″ N, 153°12′00″ W, 25 Oct. 1961, depth 209 m, coll. R. Chang. UBC 62-526, 2 females, 66.0–75.0 mm SL, off Cape Alitak, southwest Kodiak Island, Alaska, 56°54′00″ N, 155°00′00″ W, 6 Oct. 1961, depth 55 m, coll. R. Chang. UBC 62-677, 1 female, 3 males, 56.0–62.0 mm SL, off Sitkalidak Island, Alaska, 57°06′00″ N, 152°30′00″ W, M/V *Arthur H.*, 23 Aug. 1961, 154 m. UW 044363, male, 65 mm SL, northeast of Semidi Islands, Alaska, 56°25′61″ N, 156°11′68″ W, R/V *Miller Freeman*, 18 Sept. 2000, depth 255 m. UW 046118, male, 70 mm SL, Shelikof Strait, Alaska, 57°43′41″ N, 155°08′10″ W, R/V *Miller Freeman*, 7 Apr. 1992, depth 295 m. UW 047281, mature female, 87 mm SL, off Hinchinbrook Island, Alaska, 60°11′04″ N, 146°54′43″W, F/V *Vesteraalen*, 5 July 1999, depth 231 m. ZIN 29089, sex unknown, 53 mm TL, northern Sea of Okhotsk off Pt. Elizaveta, 51°09′00″ N, 154°11′00″ E, R/V *Gagara*, 10 July 1932, depth 128 m. BCPM 980–595, 1 female, 1 male, 10 sex unknown, 60.0–78.0 mm SL, Bering Sea, 54°31′38″ N, 165°49′30″ W, M/V *Ocean Harvester*, 18 Aug. 1980, coll. A. Peden.

Larvae and juveniles: 93 specimens from the Gulf of Alaska. UW 95656, 2 specimens, 6.0–16.1 mm SL, 57°22′12″ N, 155°14′06″ W, R/V *Miller Freeman*, 12 Apr. 1986, depth 238 m. UW 95657, 1 specimen, 12.0 mm SL, 57°40′41″ N, 155°10′15″ W, R/V *Miller Freeman*, 4 May 1996, depth 279 m. UW 95658, 2 specimens, 11.5–31.8 mm SL, 57°44′00″ N, 154°24′30″ W, R/V *Miller Freeman*, 15 Mar. 1981, depth 200 m. UW 95659, 1 specimen, 16.2 mm SL, 57°53′54″ N, 154°00′00″ W, R/V *Poseydon*, 31 Mar. 1985, depth 196 m. UW 95660: 33 specimens (10.5–40.0 mm SL), 57°34′24″ N, 154°58′42″ W, R/V *Miller Freeman*, 19 Apr. 1991, depth 236 m. UW 95662, 2 specimens, 18.0–20.0 mm SL, 57°34′24″ N, 154°58′42″ W, R/V *Miller Freeman*, 19 Apr. 1991, depth 234 m. UW 95663, 1 specimen, 10.8 mm SL, 57°41′48″ N, 155°15′18″ W, R/V *Miller Freeman*, 7 Apr. 1989, depth 292 m. UW 95664, 3 specimens, 9.3–12.8 mm SL, 57°38′36″ N, 155°04′06″ W, R/V *Miller Freeman*, 12 May 1993, depth 243 m. UW 95665, 1 specimen, 10.2 mm SL, 56°50′48″ N, 155°31′36″ W, R/V *Miller Freeman*, 1 May 1989, depth 268 m. UW 95666, 1 specimen, 23.0 mm SL, 58°09′00″ N, 153°24′18″ W, R/V *Miller Freeman*, 20 May 1981, depth 208 m. UW 95667, 1 specimen, 12.0 mm SL, 57°56′06″ N, 154°20′30″ W, R/V *Miller Freeman*, 28 Apr. 1989, depth 228 m. UW 95668, 3 specimens, 10.9–13.7 mm SL, 58°19′48″ N, 153°54′48″ W, R/V *Miller Freeman*, 27 Apr. 1981, depth 269 m. UW 95669, 1 specimen, 10.0 mm SL, 55°50′06″ N, 156°38′00″ W, R/V *Mys Dalnyi*, 10 Apr. 1982, depth 209 m. UW 95670, 1 specimen, 29.0 mm SL, 57°44′36″ N, 154°43′48″ W, R/V *Miller Freeman*, 21 May 1981, depth 208 m. UW 95671, 1 specimen, 17.6 mm SL, 57°26′48″ N, 155°33′00″ W, R/V *Miller Freeman*, 8 Apr. 1987, depth 278 m. UW 95672, 1 specimen,

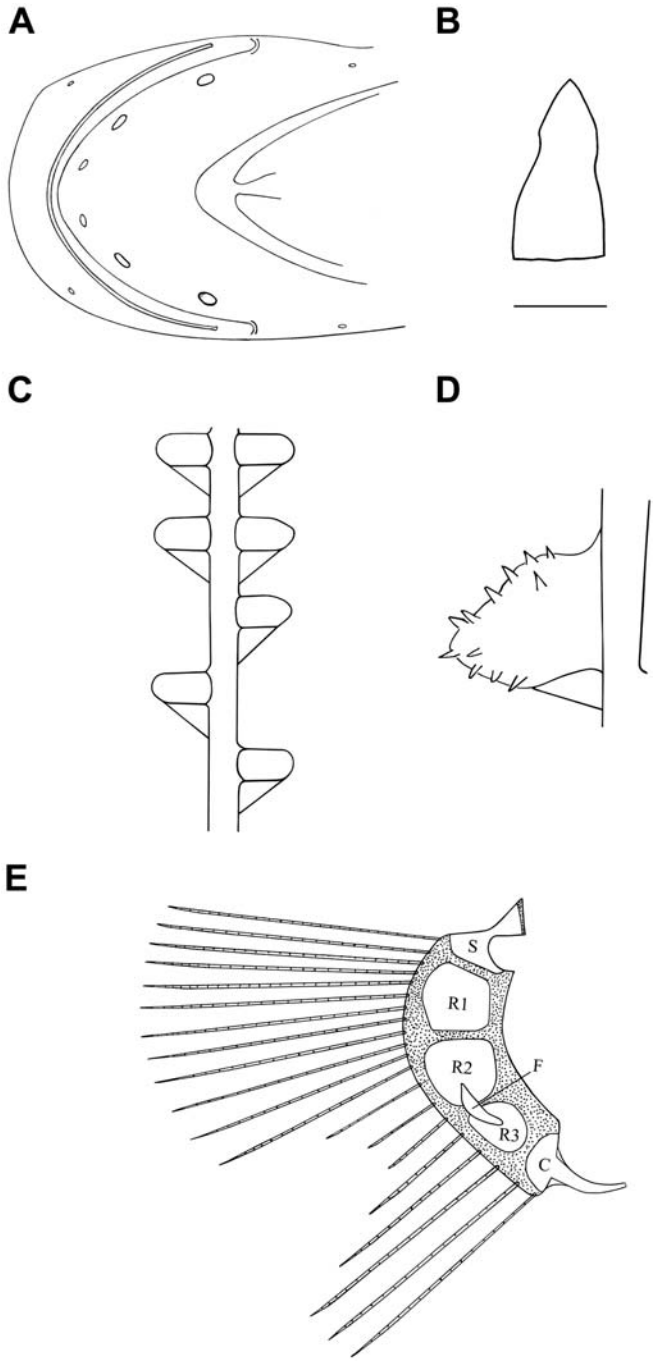

Fig. 4. **A** *Paraliparis holomelas*, UW 046118, 69.0 mm SL, ventral view of head showing chin pores. **B** Tooth of *Paraliparis holomelas*, UW 046118. *Bar* 0.05 mm. **C** Schematic diagram of dorsal half of gill rakers from first arch of right side of *Paraliparis holomelas*, UW 047281. **D** Spinule plate of gill raker from right gill arch of *Paraliparis holomelas*, UW 047281. **E** Right pectoral girdle of *Paraliparis holomelas*, UW 047281. *S*, scapula; *R1*, first radial; *R2*, second radial; *F*, fenestra; *R3*, third radial; *C*, coracoid

35.2 mm SL, 55°01′12″ N, 155°47′00″ W, R/V *Miller Freeman*, 9 Apr. 1987, depth 265 m. UW 95673, 1 specimen, 8.0 mm SL, 57°17′06″ N, 155°07′54″ W, R/V *Miller Freeman*, 25 Apr. 1991, depth 230 m. UW 95674, 1 specimen, 14.0 mm SL, 57°35′00″ N, 155°21′00″ W, R/V *Miller Freeman*, 7 Apr. 1989, depth 307 m. UW 95675, 1 specimen, 3.2 mm SL, 58°40′00″ N, 149°00′00″ W, R/V *Darwin*, 23 Mar. 1988, depth 127 m. UW 95676, 1 specimen, 18.0 mm SL, 57°58′42″ N, 154°19′36″ W, R/V *Miller Freeman*, 6 Apr. 1989, depth 268 m. UW 95677, 1 specimen, 40.0 mm SL, 57°41′12″ N, 155°10′18″ W, R/V *Miller Freeman*, 3 Apr. 1988, depth 244 m. UW 95678, 1 specimen, 18.6 mm SL, 57°28′48″ N, 155°23′36″ W, R/V *Miller Freeman*, 2 Apr. 1988, depth 281 m. UW 95679, 1 specimen, 14.0 mm SL, 56°57′12″ N, 155°57′00″ W, R/V *Miller Freeman*, 9 Apr. 1987, depth 253 m. UW 95680, 2 specimens, 13.5–47.0 mm SL, 57°38′30″ N, 155°18′36″ W, R/V *Miller Freeman*, 15 Apr. 1989, depth 346 m. UW 95681, 1 specimen, 13.0 mm SL, 57°08′54″ N, 155°08′30″ W, R/V *Miller Freeman*, 12 Mar. 1981, depth 220 m. UW 95682: 1 specimen, 27.0 mm SL, 57°58′12″ N, 154°20′24″ W, R/V *Miller Freeman*, 6 Apr. 1988, depth 262 m. UW 95683, 1 specimen, 57.0 mm SL, 57°59′12″ N, 154°15′00″ W, R/V *Miller Freeman*, 6 Apr. 1992, depth 279 m. UW 95684, 1 specimen, 16.5 mm SL, 56°49′30″ N, 155°19′24″ W, R/V *Miller Freeman*, 22 May 1981, depth 208 m. UW 95685, 2 specimens, 15.0–25.0 mm SL, 56°56′00″ N, 155°23′00″ W, R/V *Miller Freeman*, 14 Apr. 1989, depth 256 m. UW 95686, 1 specimen, 40.0 mm SL, 56°08′24″ N, 156°14′48″ W, R/V *Miller Freeman*, 22 May 1987, depth 227 m. UW 95687, 1 specimen, 14.6 mm SL, 57°45′12″ N, 155°01′18″ W, R/V *Miller Freeman*, 12 Apr. 1989, depth 302 m. UW 95688, 1 specimen, 28.0 mm SL, 57°22′54″ N, 154°58′48″ W, R/V *Miller Freeman*, 16 Mar. 1981, depth 229 m. UW 95689, 1 specimen, 18.0 mm SL, 57°39′30″ N, 155°15′48″ W, R/V *Miller Freeman*, 10 Apr. 1993, depth 300 m. UW 95690, 1 specimen, 38.0 mm SL, 57°53′18″ N, 154°24′00″ W, R/V *Miller Freeman*, 27 Apr. 1981, depth 207 m. UW 95691, 1 specimen, 11.2 mm SL, 57°56′42″ N, 154°29′54″ W, R/V *Miller Freeman*, 25 Mar. 1994, depth 268 m. UW 95692, 1 specimen, 14.0 mm SL, 57°38′42″ N, 155°16′48″ W, R/V *Miller Freeman*, 10 Apr. 1993, depth 302 m. UW 95693, 1 specimen, 13.0 mm SL, 57°33′06″ N, 154°53′06″ W, R/V *Miller Freeman*, 7 Apr. 1988, depth 228 m. UW 95694, 1 specimen, 10.7 mm SL, 57°12′06″ N, 155°57′36″ W, R/V *Miller Freeman*, 8 Apr. 1987, depth 240 m. UW 95695, 1 specimen, 45.2 mm SL, 55°33′06″ N, 155°16′36″ W, R/V *Miller Freeman*, 6 Apr. 1987, depth 259 m. UW 95696, 1 specimen, 18.0 mm SL, 58°11′54″ N, 153°31′54″ W, R/V *Miller Freeman*, 26 Apr. 1981, depth 176 m. UW 95697, 2 specimens, 14.8–22.8 mm SL, 57°38′39″ N, 155°04′03″ W, R/V *Miller Freeman*, 3 May 1996, depth 247 m. UW 104820, 38 specimens, 11.4–37.0 mm SL, 57°36′54″ N, 155°19′48″ W, R/V *Miller Freeman*, 4 Apr. 1993, depth 325 m. UW 104831, 18 specimens, 12.0–65.0 mm SL, 57°36′00″ N, 155°22′30″ W, R/V *Miller Freeman*, 10 Apr. 1993, depth 322 m. UW 104841, 18 specimens, 11.3–32.5 mm SL, 57°38′31″ N, 155°16′23″ W, R/V *Miller Freeman*, 4 Apr. 1993, depth 303 m.

Diagnosis. The following combination of characters distinguishes adult *Paraliparis holomelas* from other *Paraliparis*: 57–61 dorsal fin rays; 52–55 anal fin rays; 19–23 pectoral fin rays; 6–7 caudal fin rays; 60–65 total vertebrae; snout short, nearly equal to eye diameter with squared, blunt tip, projecting past upper jaw; eye with dorsal margin well below top of gill opening; mouth large, horizontal, slightly inferior, with cleft reaching to nearly vertical below posterior margin of eye; gill opening large and elongate with ventral margin well below level with ventral edge of eye and extending ventrally in front of 8–15 pectoral fin rays; opercular flap small, pointed, slightly hooked dorsally; pectoral fin with 13–16 rays in upper lobe, 4 or 5 in lower lobe, and 2 in a deep notch, both upper and lower lobes extending beyond anal fin origin; peritoneum and stomach dark; 7–10 pyloric caeca.

Description of adults. Body proportions and meristic counts are presented in Table 1. Head large, 4–5 times in SL,

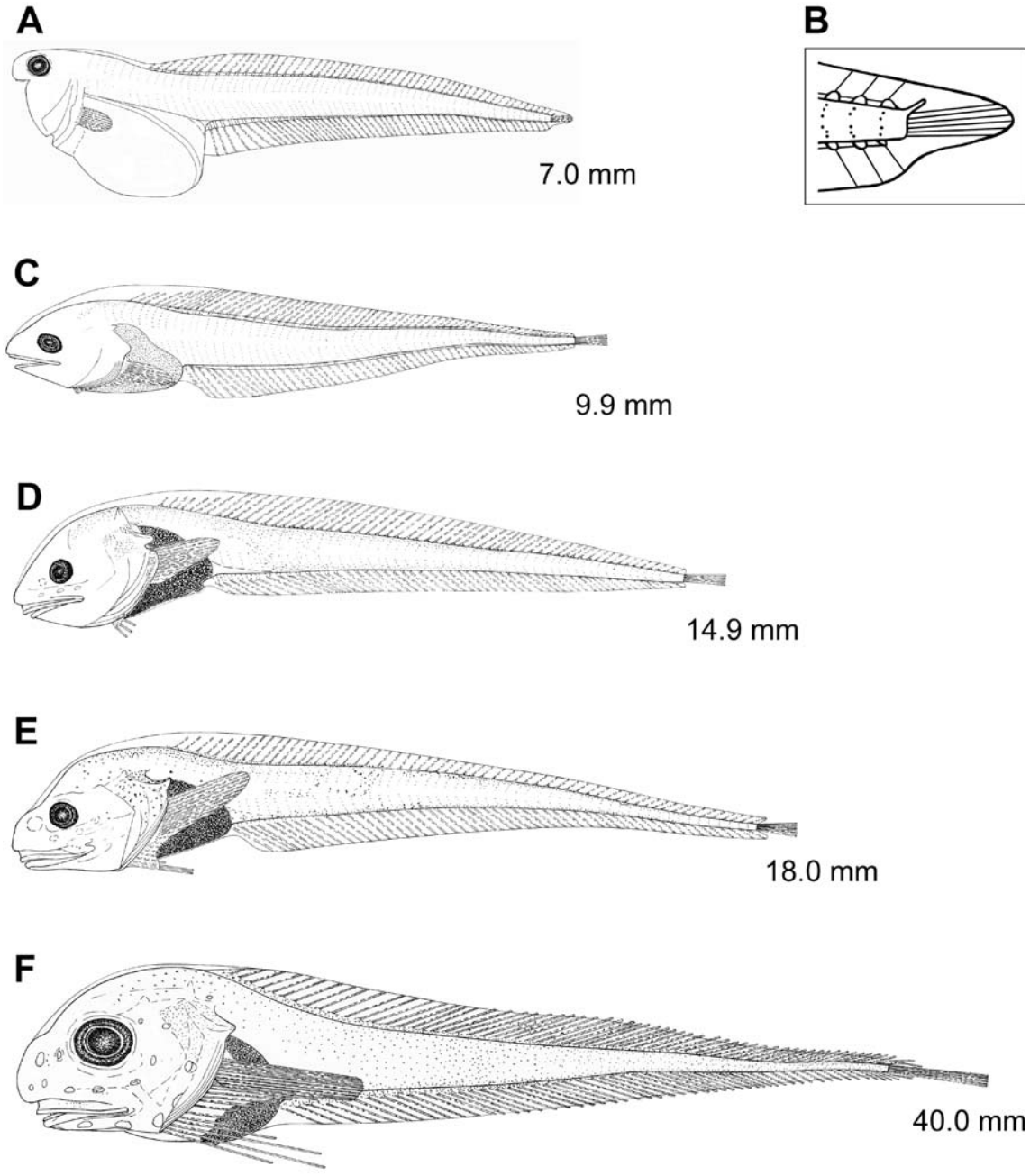

Fig. 5. Developmental series of *Paraliparis holomelas*. **A** Yolk-sac (flexion) larva 7.0 mm SL, UW 095661. **B** Caudal fin of yolk-sac (flexion) larva 7.0 mm SL, UW 095661. **C** Late flexion larva 9.9 mm SL, UW 095661. **D** Postflexion larva 14.9 mm SL, UW 095661. **E** Early juvenile 18.0 mm SL, UW 095661. **F** Juvenile 40.0 mm SL, UW 104579

deep and wide; its length 1.3 times depth and depth 1.3 times width. Dorsal contour slightly concave to snout, covered with gelatinous tissue. Snout short, nearly equal to eye diameter, with squared blunt tip, projecting past upper jaw; appearing wide and blunt from anterior view, texture very gelatinous. Rostral fold deep, but not covering upper lip. Nostril small, about 7–9 times in eye diameter, tube-like with raised rim, base of tube level with center of eye. Eye large, its upper margin well below the dorsal contour of head and dorsal margin clearly below top of gill opening. Interorbital space about 3/4 eye diameter. Suborbital space (distance from end of mouth cleft to eye) about 2/3 eye diameter. Mouth slightly inferior, horizontal, and large, with cleft reaching nearly to vertical below posterior margin of eye. Upper and lower lip folds wide but not covered by gelatinous folds of tissue. Lower jaw shorter than upper jaw and included in upper lip. In ventral view, chin moderately wide, with curved anterior contour, upper lip visible in its entirety, ventral margin of snout also visible (Fig. 4A). Teeth simple, short, and broad with a slight constriction near the

Table 1. Morphometric measurements and meristic counts of adult *Paraliparis holomelas*

Measurements	*n*	Mean %SL, range
SL	15	64.8, 53.0–87.0
HL	15	23.4, 20.9–24.6
Postorbital head length	14	11.9, 10.0–14.1
Suborbital length	14	3.8, 2.6–4.4
Snout length	14	5.2, 3.9–6.3
Maxilla length	14	9.9, 8.0–11.7
Mandible length	14	8.8, 6.7–9.8
Interorbital width	15	4.7, 3.8–6.3
Eye diameter	15	6.0, 5.1–7.0
Gill opening length	11	10.8, 7.0–16.4
Predorsal length	15	25.5, 22.1–29.8
Preanal length	14	34.3, 25.5–42.3
Mandible-to-anus length	12	21.3, 18.9–25.9
Anus-to-anal fin origin length	11	15.9, 11.4–19.3
Body depth at pectoral fin origin	14	18.4, 15.3–25.7
Body depth at anal fin origin	15	12.0, 7.9–14.7
Upper pectoral fin length	15	16.1, 13.8–18.3
Pectoral fin notch length	9	5.3, 4.6–6.0
Lower pectoral fin length	12	17.5, 14.3–19.7
Caudal fin length	6	10.6, 9.3–11.9
Dorsal fin over caudal fin length	6	3.8, 1.7–4.7
Anal fin over caudal fin length	5	3.7, 3.2–4.2
Counts		Mode, range
Dorsal fin rays	11	59, 57–61
Anal fin rays	11	54, 52–55
Pectoral fin rays, upper lobe	15	14, 13–16
Pectoral fin rays, notch	13	2, 2
Pectoral fin rays, lower lobe	13	5, 4–5
Pectoral fin rays, total	13	21, 19–23
Caudal fin rays	6	7, 6–7
Vertebrae, abdominal	16	9, 9–10
Vertebrae, caudal	11	55, 50–55
Vertebrae, total	12	64, 60–65
Number of gill rakers	5	10, 10–12
Branchiostegal rays	15	6, 6
Pyloric caeca	9	8, 7–10
Gill opening to pectoral fin ray number	12	14, 8–15
Cephalic sensory pores	15	2–6–7–1

middle (Fig. 4B). About 25 rows of 4–5 teeth on each side of upper and lower jaws. Outer rows of teeth widely spaced, inner rows narrowly spaced, particularly those near symphyses. Outer and inner teeth of approximately equal size.

Gill opening large, about 1.5 times eye diameter, ventral margin well below level with ventral edge of eye. Opercular flap small, pointed, slightly hooked dorsally in most individuals, covering upper half of gill opening. Gill rakers distally compressed, paired dorsally and ventrally, alternating in middle of arch (Fig. 4C). Rakers with slightly domed spinule plate, with up to 12 irregularly-positioned spinules (Fig. 4D).

Cephalic pores 2-6-7-1, mostly large, slightly larger than or equal to nostril diameter. Nasal pore interspace narrow, about 2/3 eye diameter. Nasal pores, second and third infraorbital pores, and all preoperculomandibular pores partially embedded in gelatinous tissue; fifth and sixth infraorbital pores, postorbital, and suprabranchial pores embedded to a lesser extent. Suprabranchial pore small, equal to or smaller in diameter than nostril, close to dorsal end of gill opening. Chin pores widely set, interspace about equal to distance between first and second preoperculomandibular pores (see Fig. 4A).

Interneural of first dorsal ray inserted between third and fourth neural spines, sometimes directly above fourth neural spine. Dorsal and anal fin rays united by fin membranes at tips. Gelatinous tissue surrounding dorsal- and anal-fin rays not well developed. Pectoral fin with narrow but evenly spaced rays in upper lobe, more widely spaced in deep notch and lower lobe, and encased in gelatinous tissue. Uppermost pectoral fin ray inserted on vertical through center margin of gill opening nearly level with center of eye. Lowermost ray inserted on vertical beyond posterior margin of eye. Upper and lower lobes both reaching beyond anal-fin origin. Three radials, large, closely and evenly spaced, a fenestra between second and third (Fig. 4E). Scapula with a very strong helve, coracoid sickle-shaped. Caudal fin base very narrow, about 9 times in eye diameter, and long with 6 or 7 rays (3 + 3 or 4 + 3). Dorsal fin overlapping caudal fin 1/3 to 1/2 of its length; anal fin overlapping caudal fin 1/3 of its length. Six or seven pleural ribs. Epipleural ribs not discernible on radiographs. Skin thin, gelatinous, naked.

Color in alcohol.—Generally lightly colored. Punctate melanophores present on head dorsally over midbrain, hindbrain, and nape. Small patch of melanophores present dorsally on preopercle. Small melanophores uniformly scattered over the entire body, including skin covering the dorsal and anal pterygiophores, posterior one-third of the dorsal, anal, and caudal fins. Orobranchial cavity light with a covering of small melanophores. Peritoneum and stomach dark. Pyloric caeca lightly pigmented near bases, with long, pale, pointed tips.

Maturity and reproduction. Sex was determined in 14 individuals; 9 were females and 5 males. The smallest sexually mature female was 56 mm SL. Ovaries of this individual and 6 others contained immature oocytes 0.25–0.90 mm diameter. Two females contained both immature and mature oocytes. The larger (87.0 mm SL) was ripe, with both ovaries measuring 11.4 mm in length and 7.6 mm in width and together containing 75 mature oocytes 1.6–2.5 mm diameter. Oocytes were irregularly shaped, opaque, and pale in coloration. Late-stage oocytes 1.2–1.6 mm were found in a smaller female (75.0 mm SL). Of five males identified, 2 (60.0 and 70.0 mm SL) appeared mature with enlarged, white testes.

Description of larvae and juveniles. *Morphology.*—Body proportions are presented in Table 2. Yolk-sac larvae 7.0 mm SL at hatching in flexion stage (Fig. 5A,B). Yolk large, 20% SL. Mouth open and functional. Flexion complete by 11.5 mm SL; postflexion stage 11.5–19.0 mm SL. Juvenile stage beginning around 19.0 mm SL.

Body slender, depth constant throughout development (Table 2). Head large, length increasing with development. Snout length constant throughout development. Upper jaw length increasing sharply after flexion; lower jaw length

Table 2. Morphometric measurements for *Paraliparis* larvae and juveniles

Body proportion	*n* = F, PF, J	Flexion	Postflexion	Juvenile
SL	19, 97, 32	10.0 ± 1.25 (6.7–11.5)	14.6 ± 2.18 (11.5–19.0)	28.3 ± 7.89 (19.1–46.5)
HL/SL	19, 97, 31	20.0 ± 0.02 (15.0–24.0)	21.0 ± 0.03 (15.0–32.0)	23.0 ± 0.02 (17.0–26.0)
Snout length/HL	19, 97, 31	28.0 ± 0.04 (22.0–35.0)	30.0 ± 0.04 (22.0–44.0)	28.0 ± 0.04 (17.0–40.0)
Upper jaw length/HL	19, 92, 31	33.0 ± 0.10 (15.0–54.0)	41.0 ± 0.08 (27.0–66.0)	44.0 ± 0.05 (36.0–54.0)
Lower jaw length/HL	18, 91, 31	26.0 ± 0.09 (14.0–42.0)	33.0 ± 0.08 (18.0–66.0)	34.0 ± 0.05 (20.0–46.0)
Eye diameter/HL	19, 97, 31	20.0 ± 0.04 (16.0–31.0)	18.0 ± 0.02 (13.0–28.0)	24.0 ± 0.04 (16.0–31.0)
Interorbital width/HL	19, 96, 29	24.0 ± 0.07 (14.0–39.0)	17.0 ± 0.04 (9.0–28.0)	20.0 ± 0.05 (10.0–29.0)
Postorbital head length/HL	18, 95, 31	52.0 ± 0.03 (48.0–57.0)	53.0 ± 0.06 (38.0–75.0)	50.0 ± 0.05 (42.0–58.0)
Suborbital distance/HL	19, 93, 31	17.0 ± 0.05 (6.0–26.0)	14.0 ± 0.04 (6.0–24.0)	17.0 ± 0.05 (8.0–33.0)
Gill opening/HL	15, 53, 24	25.0 ± 0.10 (18.0–54.0)	22.0 ± 0.05 (14.0–33.0)	28.0 ± 0.05 (18.0–38.0)
Predorsal fin length/SL	17, 92, 30	24.0 ± 0.03 (21.0–31.0)	23.0 ± 0.02 (17.0–32.0)	24.0 ± 0.02 (19.0–28.0)
Snout-to-anus length/SL	19, 97, 31	32.0 ± 0.03 (29.0–39.0)	29.0 ± 0.03 (24.0–39.0)	27.0 ± 0.03 (22.0–32.0)
Mandible-to-anus length/SL	19, 94, 32	27.0 ± 0.03 (20.0–33.0)	25.0 ± 0.04 (9.0–38.0)	22.0 ± 0.03 (12.0–28.0)
Preanal fin length/SL	19, 94, 31	33.0 ± 0.05 (14.0–39.0)	32.0 ± 0.02 (27.0–42.0)	32.0 ± 0.01 (30.0–34.0)
Body depth at pectoral fin base/SL	19, 97, 32	17.0 ± 0.02 (12.0–22.0)	15.0 ± 0.02 (9.0–21.0)	18.0 ± 0.02 (14.0–24.0)
Body depth at anal fin origin/SL	19, 97, 32	10.0 ± 0.02 (6.0–13.0)	9.0 ± 0.01 (6.0–13.0)	11.0 ± 0.02 (9.0–15.0)
Upper pectoral fin length/SL	17, 79, 27	10.0 ± 0.04 (5.0–18.0)	11.0 ± 0.02 (5.0–15.0)	14.0 ± 0.03 (9.0–19.0)
Notch length/SL	15, 63, 27	2.0 ± 0.01 (1.0–4.0)	2.0 ± 0.01 (1.0–5.0)	5.0 ± 0.02 (2.0–11.0)
Lower pectoral fin length/SL	15, 61, 26	3.0 ± 0.02 (1.0–8.0)	7.0 ± 0.02 (3.0–12.0)	14.0 ± 0.04 (8.0–22.0)
Caudal fin length/SL	19, 92, 31	8.0 ± 0.02 (5.0–13.0)	7.0 ± 0.02 (3.0–13.0)	8.0 ± 0.02 (4.0–14.0)

Measurements given as mean percent ± standard deviation; range in parentheses
F, flexion; PF, postflexion; J, juvenile

increasing after flexion. Eye diameter and interorbital width decreasing after flexion. Postorbital and suborbital head length constant throughout development. Gill opening large, increasing after flexion. Predorsal-fin length constant throughout development. Snout to anus and mandible to anus length decreasing after flexion. Preanal fin length constant throughout development. Upper, lower, and pectoral fin length, and pectoral fin notch length, increasing after postflexion. Caudal fin length constant throughout development.

Cephalic pores.—At approximately 14.9 mm SL, first to third infraorbital pores and first nasal pore present; first to third preoperculomandibular pores weakly formed but present. By 20.5 mm SL, all cephalic pores are developed.

Pigmentation.—Yolk-sac larvae completely unpigmented except eyes (Fig. 5A). By 10 mm SL, punctate melanophores present dorsally over hindbrain and nape, laterally on posttemporal region (Fig. 5C). Peritoneum densely pigmented, increasing in darkness and intensity throughout development. Small melanophores scattered on head and upper jaw by 15.0 mm SL (Fig. 5D). Pigmentation gradually increases on head and nape; melanophores present on operculum and lateral body by 18.0 mm SL (Fig. 5E). Light-colored orobranchial cavity covered with small- to medium-sized melanophores. Two irregularly shaped pigmented areas on lateral body present around fifth and ninth caudal myomeres. Skin covering dorsal pterygiophores pigmented to about dorsal fin ray 22 (approximately 40% body length). By 40.0 mm SL, posttemporal pigmentation no longer visible, but opercular melanophores present, smaller and more numerous than in smaller larvae (Fig. 5F). Entire body covered with melanophores, and irregularly shaped pigmented areas on lateral body no longer apparent. Peritoneum completely dark and opaque. Skin covering dorsal and anal pterygiophores pigmented, additional melanophores present on dorsal fin.

Developmental osteology. *Head region.*—Branchiostegal rays ossify at approximately 13.2 mm SL. Upper (maxilla, maxillary teeth, premaxilla) and lower (mandible, angulars) jaws, suspensorium, opercular, and parasphenoid in the neurocranium ossify at approximately 14.8 mm SL. Remaining bones in head region completely formed and ossified by 17.2 mm SL.

Vertebral column.—Vertebrae differentiated with neural and hemal spines present in yolk-sac larvae by 7.7 mm SL. Vertebrae, neural spines, and hemal spines completely ossified in postflexion larvae at 14.8 mm SL (Table 3). Pleural ribs developed and ossified in juveniles.

Fins.—At 7.7 mm SL, yolk-sac larvae with completely formed but unossified dorsal, anal, pectoral, and caudal fins (see Fig. 5A,B). By 13.2 mm SL, caudal fin rays ossified and dorsal- and anal-fin rays begin to ossify from posterior to anterior (Table 3). Pectoral fin rays ossified around 14.8 mm SL. By 15.6 mm SL, dorsal and anal fins completely ossified;

Table 3. Meristics of cleared and stained *Paraliparis homelas* larvae and juveniles

Standard length (mm)	Rays			Branchiostegal rays	Neural spines			Hemal spine	Centra			Caudal fin rays
	Dorsal fin	Anal fin	Pectoral fin		Abdominal	Caudal	Total		Abdominal	Caudal	Total	
7.7												
9.5												
11.5												
13.2	22	20		6								6
15.6	59	52	20	6	10	52	62	52	10	53	63	6
17.2	59	52	20	6	9	54	63	53	9	53	64	6
19.1	59	54	19	6	10	53	63	52	10	54	64	6
22.8	59	53	20	6	9	53	62	53	9	54	63	6
36.8	58	52	20	6	9	53	62	53	9	54	63	6
40.9	58	52	19	6	9	52	63	52	9	53	64	7
46.5	59	52	20	6	9	52	61	52	9	53	62	—

Specimens above dashed line were undergoing notochord flexion
Counts are of ossified elements only
—, Caudal fin rays missing

dorsal and anal fin pterygiophores ossified by 17.2 mm SL.

Caudal skeleton.—The urostyle, superior hypural plate, inferior hypural plate, and 6 or 7 caudal-fin rays comprise the caudal skeleton. Superior and inferior hypural plates fuse at their posterior ends, leaving a small gap between them, and the caudal skeleton is ossified by 19.1 mm SL. The gap between the hypural plates continues to decrease in size with development but the plates never completely fuse.

Distribution. Adult *P. holomelas* range from the Sea of Okhotsk to the northern Gulf of Alaska (see Fig. 2A). Other reports of this species from the Sea of Okhotsk, Kuril Islands, and off southeastern Kamchatka are not shown on this map (see remarks). The specimen first reported by Mecklenburg et al. (2002) (SIO 63-536-56A) represented a northeasterly range extension of approximately 720 km. Nearly all collections have occurred close to shore, with the greatest depth of capture being the paralectotype from the southeastern Bering Sea at 2972 m. The least depth of capture was 55 m for the specimens collected off Cape Alitak near the southwest end of Kodiak Island, Alaska (UBC 62-526). Larvae and juveniles were all collected in or around Shelikof Strait and the Shelikof Sea Valley, Alaska, at depths of 176–346 m (see Fig. 2B).

Comparisons. *Paraliparis holomelas* is most similar to *Paraliparis dactylosus* Gilbert, 1896 but differs primarily by having fewer pectoral-fin rays (19–23 vs. 28–30), fewer caudal fin rays (6–7 vs. 8), fewer pyloric caeca (7–10 vs. 17–23), a larger gill opening (extending down in front of 8–15 pectoral fin rays vs. 2–4 pectoral-fin rays), and simple rather than trilobed teeth. In addition, the uppermost pectoral fin ray in *P. dactylosus* is positioned well below level with the ventral margin of the eye whereas in *P. holomelas* it is inserted on vertical nearly level with the center of eye, and the pectoral-fin notch in *P. dactylosus* is shallow rather than deep. The chin pores in *P. dactylosus* have a narrow interspace, less than half that of *P. holomelas*, and they are imbedded in folds of loose tissue. *Paraliparis holomelas* is also similar to *Paraliparis latifrons* (see Stein, 1978), but differs in having a dark (vs. pale) stomach and usually having more dorsal-fin rays (57–61 vs. 54–57) and more anal fin rays (52–55 vs. 48–50). *Paraliparis latifrons* has not been reported from Alaska. *Paraliparis deani* differs from *P. holomelas* in having fewer anal fin rays (44–48 vs. 52–55) and usually fewer dorsal fin rays (56–57 vs. 57–61). In addition, the uppermost pectoral fin ray in *P. deani* is positioned on a vertical level with the ventral margin of the eye whereas in *P. holomelas* it is inserted on a vertical nearly level with the center of the eye. Rays in the lower pectoral fin lobe in *P. deani* are greatly exerted from the fin membrane, unlike *P. holomelas*.

Remarks. The distribution of *P. holomelas* in the Sea of Okhotsk is now less clear with our determination that the larger of the two specimens reported by Schmidt (1950; ZIN 26318, 95 mm TL) has 69 vertebrae (vs. 60–65 in *P. holomelas*) and 65 dorsal-fin rays (vs. 57–61) and is most likely *Paraliparis rosaceus* Gilbert, 1890. Although in very poor condition, it is complete enough to determine that it is not *P. holomelas*. Dudnik and Dolganov (1992) reported *P. holomelas* from the Sea of Okhotsk at depths of 617–1988 m, and Sheiko and Fedorov (2000) reported it from the northern Kuril Islands and off southeastern Kamchatka. However, none of those specimens was preserved after collection, and the identifications cannot be verified (B.A. Sheiko, personal communication, June 2002). Although Mecklenburg et al. (2002) described the habitat of *P. holomelas* as benthic, our data suggest they are epi- and mesopelagic, and are likely only epibenthic during spawning and perhaps when nest-guarding [if male *Paraliparis* exhibit this behavior, as suggested by Stein (1980)]. Their pelagic distribution is supported by our collection of at least two adults in midwater trawls (UW 044363 and UW 046118). Unfortunately, it is unclear from the collection data what type of gear was used to collect several of the other adult specimens. If a bottom trawl was used, these individuals

could have been caught in midwater during deployment or retrieval of the net. Early larvae are epibenthic, as evidenced by our collections of numerous individuals with an epibenthic sled, whereas later-stage larvae evidently are planktonic because many were collected with bongo nets.

Most collections of *P. holomelas* larvae were made using an epibenthic sled in the Shelikof Sea Valley, March through April (see Fig. 2B). These tows resulted in collections of *P. holomelas* in all stages of development, yolk-sac through juvenile stages, in relatively large numbers (≤38) at some stations. The presence of larvae in various degrees of development and juveniles at these stations and throughout the Shelikof Sea Valley indicates a protracted spawning season for *P. holomelas*, perhaps in late winter, January through March.

Snailfishes of the genus *Paraliparis* remain poorly known and inadequately documented in the Gulf of Alaska and Bering Sea. Although this study clarifies the identity, development, and distribution of *P. holomelas*, several new and unusual species of *Paraliparis* remain to be described from this region (Busby and Cartwright, unpublished data).

Comparative materials. Adults: *Paraliparis rosaceus*?, ZIN 26318, sex unknown, 95 mm TL (identified as *P. holomelas* in Schmidt 1950), southern Sea of Okhotsk, 46°41′30″ N, 147°28′00″ E, R/V *Gagara*, 2 Aug. 1932, depth 3350 m. *Paraliparis latifrons*, USNM 214613, sex unknown, 87 mm SL, northeastern Pacific Ocean off Oregon, 46°03′12″ N, 125°35′12″ W, R/V *Yaquina*, 3 Oct. 1969, depth 2156 m. *Paraliparis dactylosus*, UBC 65-0097, 2 specimens, sex unknown, 79–80 mm SL, southeast of Tigalda I., Alaska, 53°38′01″ N, 164°39′00″ W, 13 Aug. 1964, depth unknown. UW 045268, 14 specimens, sex unknown, 130–155 mm SL, eastern North Pacific Ocean, 37°08′48″ N, 122°09′41″ W, R/V *Miller Freeman*, 30 Oct. 1997, depth 925 m. UW 113895, 2 specimens, sex unknown, 118–125 mm SL, Bering Sea, 55°09′58″ N, 168°01′38″ W, F/V *Northwest Explorer*, 27 July 2004, depth 1010 m. UW 048667, sex unknown, 118 mm SL, eastern North Pacific Ocean, 42°03′49″ N, 124°14′50″ W, R/V *Miller Freeman*, 11 Nov. 1997, depth 861 m. *Paraliparis deani*, UW 014761, sex unknown, length undetermined, Alexander Archipelago, Stevens Passage, Alaska, R/V *John N. Cobb*, 26 Mar. 1951, depth unknown. BCPM65-4, 6 specimens, 5 females, 1 sex unknown, 48–75 mm SL, British Columbia, Canada, off Sherringham Light, 48°23′00″ N, 123°55′00″ W, 2 Feb. 1965, depth 115 m, coll. W.E. Barraclough.

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