Larvae of *Liparis fucensis* and *Liparis callyodon*: Is the "Cottoid Bubblemorp" Phylogenetically Significant?

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ABSTRACT: Larvae of the slipskin snailfish, *Liparis fucensis*, and of the spotted snailfish, *Liparis callyodon*, are described; and fecundity/spawning information for these species is provided. Positive identification of larvae of both species required that they be laboratory reared up to identifiable juvenile stages. Too little taxonomic information exists on larvae of this genus to reveal diagnostic characters for northeast Pacific species. The early development patterns of these two species are contrasted; *L. fucensis* larvae grow from a very small to a very large size during the larval stage, and develop an enlarged subdermal space, the "cottoid bubblemorph", whereas *L. callyodon* larvae develop more typically. Evidence from the literature indicates that this bubble morphology is a convergent, derived character, and is unsuitable for use in determining phylogenetic relationships.

Larval descriptions do not exist for any of the 17 species of the genus *Liparis* that occur in the northeast Pacific Ocean (Matarese et al. in press), except for illustrations of newly hatched *Liparis fucensis* (Marliave 1975). Larvae of the subfamily Liparidinae were discussed generally by Able et al. (1984), with emphasis primarily on pigment and ontogenetic schedule of developmental landmarks. Able et al. (1984) included an illustration (their figure 236 bottom) of an unidentified cyclopterid from southern California with an enlarged cranial and thoracic subdermal space giving a bubble appearance, and suggested that such a feature might be of taxonomic value. Another cottoid larva sharing this bubble appearance is *Malacocottus zonurus* (Washington et al. 1984). This type of anomalous morphological feature of a larval fish must be considered as a possible character for elucidating phylogenetic relations (Kendall et al. 1984), and the extent to which such a feature is conservative, as opposed to immediately adaptive, is fundamental to assessing the utility of such a feature as a phylogenetic character (Cohen 1984). Thus, Haeckel's biogenetic law, that ontogeny recapitulates phylogeny, becomes a moot theory with developmental stages as intensely subjected to selective pressures as the planktonic larval stages of fish. This paper provides insight regarding the presence (*fucensis*) versus absence (*callyodon*) of the larval cottoid bubblemorph in two closely related, sympatric *Liparis* species.

Adults of slipskin snailfish, *L. fucensis*, and spotted snailfish, *L. callyodon*, look very similar and are close in morphometrics and meristics (Clemens and Wilby 1961; Hart 1973). *Liparis fucensis* is distributed over a greater depth range than the shallow-water *L. callyodon* (Clemens and Wilby 1961); but they do overlap in shallow water. Spawning in *L. fucensis* involves the male tending egg masses deposited among polychaete worm tubes (Marliave 1975) or inside empty mussel shells (DeMartini 1978) in shallow subtidal waters. No information has been published previously regarding reproduction of *L. callyodon*.

Two different approaches for obtaining larval specimens—captive rearing and plankton towing—provided developmental series for these two species. Both species were reared through transformation to the juvenile stage, permitting positive identification. This paper provides the first larval descriptions for northeast Pacific *Liparis* species. The bubble morphology of *L. fucensis* larvae is constrasted with the more typical larval morphology of *L. callyodon*.

METHODS

Eggs and a 67 mm ripe male of *L. fucensis* were collected at a depth of 10 m from among the tubes of *Eudistylia polymorpha* by divers in Barkley Sound, British Columbia (lat. 48°50'N, long. 125°08'30"W) on 26 May 1974. The embryos were not visibly developed and the yolks were

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light orange in color. The eggs were incubated at 11°C and hatched on 10 June 1974. Larvae were held in static seawater without food and preserved at 0, 3, and 7 d posthatch. From April to July 1988, older larval stages were taken in epibenthic plankton tows in southern British Columbia, using a sled trawl with a 1.5 m × 0.8 m mouth and 1 mm mesh. The larvae were killed in the cod end bucket with anaesthetic and fixed in 5% formosaline. Several of the largest larvae were removed live and transported to a 1,000 L laboratory tank with through-flowing seawater of 10°C, where they were fed *Artemia* nauplii. Two individuals survived past settlement and were preserved as juveniles.

Unidentified eggs, later found to be *L. callyodon*, were collected from among barnacles and rock crevices in the intertidal zone (0.6 m above low water, Canadian scale) outside Sooke Basin in the Strait of Juan de Fuca (48°20'N, 123°44'W) on 22 March 1987 and 13 March 1988. In 1987, egg masses and newly hatched larvae were directly preserved. A variety of egg masses taken in 1988, ranging in color from maroon to orange to green, were incubated in inflow water of a 1,000 L through-flowing seawater tank and hatches occurred from late March through mid-April from the different masses. Larvae were fed *Artemia* nauplii that had been fed supplemental omega-3 fatty acids (Cooper 1988). Larvae were preserved from the rearing tank at various intervals up to the benthic juvenile stage.

Positive identification of laboratory-reared juveniles was based on the full spectrum of external juvenile characters from the literature (e.g., Hart 1973); larval characters alone could not be used to positively identify to the species level. Median fin ray meristics of late larval stages for these two species overlapped too broadly to permit positive identification prior to the juvenile stage. Juveniles used for identification of both species were deposited in the British Columbia Provincial Museum (BCPM 988-945, BCPM 988-946, BCPM 988-947, BCPM 988-948, BCPM 988-949).

Eggs and larval morphometrics were taken with vernier dial calipers under a dissecting microscope. Upon sorting, measures of notochord length (NL) or standard length (SL) were taken from fixed specimens. Body depth was measured near the pectoral base, where the maximum body depth dimension occurred, including subdermal space (i.e., dorsal epidermis to ventral epidermis). Body length was measured from tip of snout to posterior margin of anus, not including any portion of the abdominal cavity posterior to the anus. Pelvic disk width, not length, was measured. Too few specimens were available to permit clearing and staining, although quick-staining with alizarin red permitted viewing of external features. Illustrations were drawn using a dissecting microscope and camera lucida. Specimens of newly hatched *L. fucensis* from 1974, together with the photographs, permitted redrawing of an illustration from Marliave (1975).

Larvae of *Liparis fucensis*

Pigment intensity varied between siblings hatched in 1974. Similarly, larvae of like sizes and stage, which were captured from the field in 1988, varied in pigment intensity. The overall pattern did not vary much, although a few of the more intensely pigmented individuals tended to prematurely develop sets of melanophores that average larvae develop later. Also, these few intensely pigmented individuals developed a broader extent of particular pigment patches and more numerous, regularly spaced melanophores in rows along the anal fin base and ventral fin fold. Postflexion stages, in particular, tended to show a variation in extent or absence of pigment. Loss of early melanophores and appearances of different sets of melanophores seemed to characterize the postflexion period of development. Overall, however, pigment corresponded clearly to the distribution patterns and intensities illustrated in Figures 1 and 2.

At all stages, the epidermis had a noticeably granular appearance (Fig. 1), except around the outer margins of the tail fin fold. The final development of the expanded subdermal space, or bubble, corresponded to the extent of this granular appearance. On the largest preflexion larva, this granular layer could be scraped away from a basement membrane, on which melanophores remained.

Hatching occurred at 2.9 mm NL; the larvae had a prominent yolk sac with a single anterior oil droplet (Fig. 2a). At hatching, dorsal gut melanophores, about 20 postanal ventral midline melanophores, and a hexagonal honeycomb pattern of melanin on the pectoral fin bases were evident. At 10°C, yolk resorption occurred over a period of seven days under starvation conditions. During that time, larvae grew to 3.3 mm NL; head length increased from 19 to 21.5%

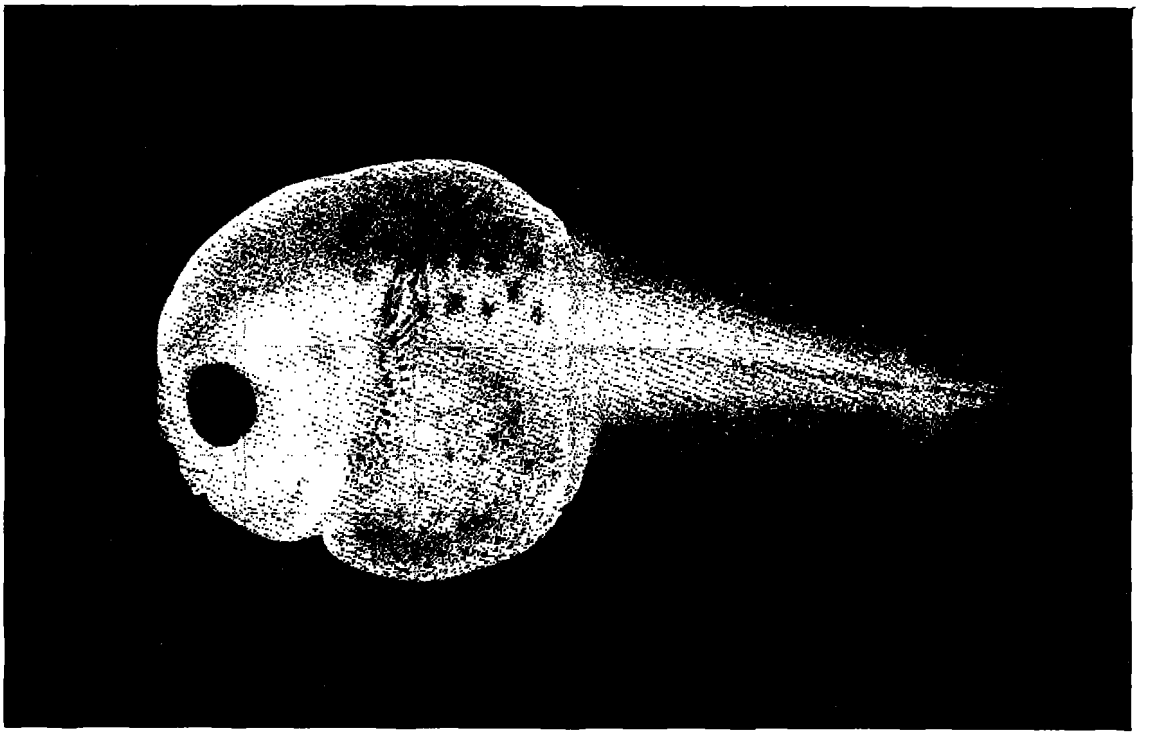

FIGURE 1.—Larva of *Liparis fucensis*, 6.9 mm NL preflexion. Note the granular appearance of the epidermis, visible especially in the cranial region, and the bubble shape of the expanded subdermal space.

NL, while snout-anus length remained at 38% NL. Body depth at yolk resorption was 27.6% NL, and the subdermal space had become prominent in the cranial area by this time. Pigment development during yolk resorption included the appearance of mandibular, ventral gut, and nape melanin, as well as a row of about 10 melanophores on the ventral margin of the fin fold. At hatching, the pectoral fin was only slightly larger than the eye; whereas, by yolk resorption it was 1.7 times as long and 2.3 times higher than the eye. It remained approximately this relative size through the remaining larval stages.

Through preflexion, relative head size increased largely through an increase in the bubble of the subdermal space. This bubble spread from the head region to include the nape and gut region. At 4.1 mm NL, snout-anus length had increased to 44% NL and body depth to 36% NL (Fig. 2b). The overall bubble appearance imparted by the subdermal space (see Figure 1) was evident by this stage, with the posterior margin of the bubble at the anus. Morphometric data on relative body depth and snout-anus length indicated that the development of the bubble is associated particularly with flexion (6–8 mm SL), the period of skeletal development. Just after flexion, a step-function increase in body depth and snout-anus length, relative to head length and standard length, marked the most rapid expansion of this bubble. Nostrils were prominently separated into dorsal and ventral nares by this stage. Through preflexion, pigment remained essentially the same as at the end of yolk resorption. Some preflexion larvae had up to 22 well-spaced, ventral, fin fold melanophores, and up to 24 postanal, ventral, midline melanophores. Such individuals also had denser mandibular melanophores, a few melanophores on the maxillary tip, and a few dorsal, midline melanophores posterior to the nape. Toward the end of preflexion, at 5.25 mm NL, the relative body depth had increased to 42%, and the snout-anus length, to 45%, giving the anterior body a nearly spherical bubble shape. At this size the position of the anus had become anterior to the posterior margin of the bubble portion of the subdermal space by two myomeres. The pelvic disk is not evident in preflexion larvae.

Late during the preflexion stage, larvae between 6 and 7 mm NL started forming dorsal and anal fin rays. These median rays started

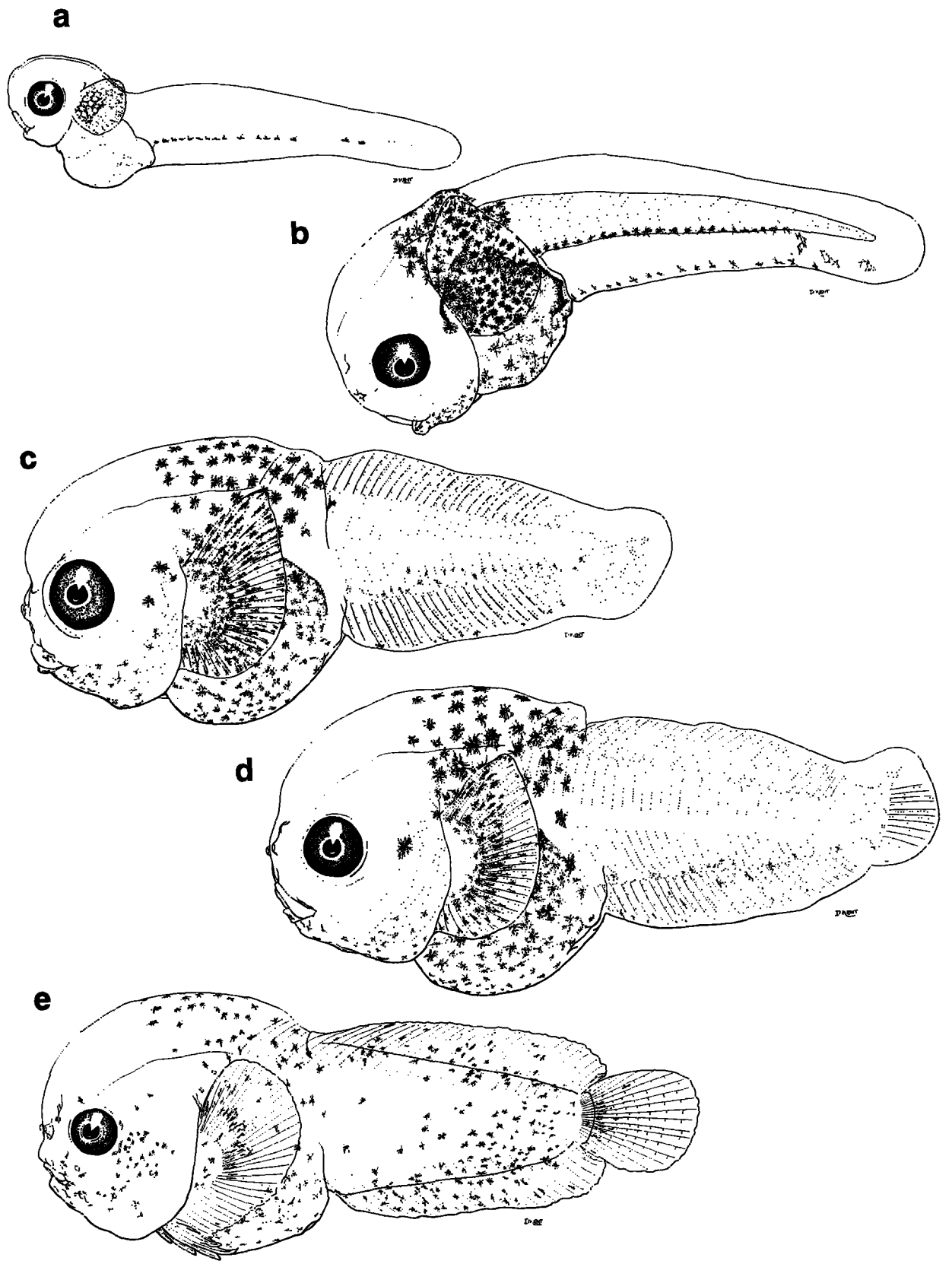

FIGURE 2.—Larvae of *Liparis fucensis*: a, 2.9 mm NL yolksac stage; b, 4.1 mm NL preflexion; c, 6.7 mm NL flexion; d, 8.7 mm SL postflexion; and e, 17.4 mm SL postflexion.

forming anteriorly, extending in decreasing length posteriorly. Pectoral rays were not evident in unstained material. Although the pectorals were very fully pigmented at this stage, the melanophores did not align with the underlying rays.

At the beginning of flexion, larvae between 6.7 and 7.3 mm NL developed dorsal, anal, and pectoral fin rays synchronously, prior to formation of caudal rays (Fig. 2c). Nape, gut, mandibular, and pectoral melanophores remained very prominent, with the addition of a few large melanophores in the opercular area. By this stage, the bubble was large and rather spherical, thus allowing epidermal melanophores to be distinguished readily from gut melanophores. The dorsal bubble melanophores around the nape were large and usually separated by a gap in epidermal pigment laterally, located in the plane of the large dorsal gut melanophores. The ventral bubble melanophores were markedly smaller by this stage, as were the mandibular melanophores. During flexion, postanal ventral, midline melanophores, particularly those in posterior positions, began migrating dorsally along the myosepta. Ventral fin fold melanophores eventually became aligned with the tips of anal fin rays.

During flexion, the final orientation of nares was attained, with the ventral naris on each side oriented anteriorly, and the dorsal naris, dorsally, and with the separation distance between the two nares of each pair similar to that of later stages, i.e., about 0.5 of eye diameter, slightly less than during preflexion. The pelvic disk was well developed and circular at this stage, slightly less than half of eye diameter in size. The pectoral fin did not extend ventrally to the pelvic disk, and no exserted lower rays were present.

During early postflexion, larvae up to 10 mm SL developed lower exserted pectoral rays but only in individuals in which caudal ray formation was completed (Fig. 2d). Early during postflexion, very small, mandibular, acousticolateralis pores became evident, three on each side. The pelvic disk was still small, embedded within an invagination of the bubble. The tail region formed a subdermal swelling, starting anteriorly, at sizes between 9 and 10 mm SL, extending out to under half the length of median fin rays.

Postflexion larvae tended to lose melanophores characteristic at earlier stages, while simultaneously developing new melanophores in other positions. Greater pigment variability between individuals was more evident at this stage than in earlier stages. All postflexion larvae lost the melanophores on the outer half of the pectoral fins, retaining rows of melanophores lining pectoral rays toward the fin base. A few individuals retained very small melanophores lining the fringe of the pectorals. These melanophores were frequently just on the dorsal tip of the pectoral fins, which tended to become less pointed via allometric reduction in ray length when the lower exserted rays formed. The exserted pectoral rays never developed pigmentation in larvae. Many individuals lost the small melanophores on the ventral bubble and mandibles, while the internal melanophores on the gut surface became obscured by the increasing thickness of the granular epidermis (cf. Fig. 1). Melanophores tended to develop along the margin of the tail swelling of the subdermal space, aligned with the midpoints of the dorsal and anal fin rays. At 16.8 mm SL (17.4 mm SL fresh, Fig. 2e), the outer skin was sparsely overlaid with melanophores everywhere except in the anterior cranial area. The melanin was most dense over the preopercular region and between the eye and the maxillary.

The largest postflexion larva, prior to the metamorphic allometry that yielded the juvenile morph, had tubular dorsal nares like the juveniles, but embedded in the bubble. The exserted, ventral, pectoral rays were the same length as the longest pectoral rays dorsally. The anterior portion of the dorsal fin was no longer visible within the bubble. Thus, only 25 posterior dorsal rays and 23 anal rays were evident. The mandibular, acoustico-lateralis pores were prominent and were aligned in a series of four on each side, extending toward the preoperculum. Two smaller pores were over the maxillary on each side. The pelvic disk had developed muscular papillae inside the margin; the shape was a flattened oval, with a width equal to the eye diameter.

The two larvae that survived to the juvenile stage in captivity underwent a metamorphic loss of the subdermal bubble. Over a period of nearly a month in the laboratory, the larvae were observed to show ambivalence between settlement and swimming in the water column. The pelvic disk was functional. Abruptly, the bubble appearance was lost on one juvenile that was observed at that stage; shrinkage occurred, giving the juvenile a slender, distinctively liparidine appearance. The other juvenile could not be

sighted until a later date when growth and deposition of intense dark pigment had occurred. Growth of the juveniles was very rapid compared with *L. callyodon*, as evident in Figure 2 versus Figure 3.

Larvae of *Liparis callyodon*

Preserved egg masses of *L. callyodon* numbered 409, 394, 203, 132, and 53 eggs (egg diameter 1.69 ± 0.02 mm, n = 10). Newly hatched *L. callyodon* averaged 5.21 ± 0.19 mm NL (n = 10). At hatching, snout-anus length averaged 39% NL (2.02 ± 0.16 mm); head length, 21% NL (1.08 ± 0.13 mm); body depth, 22.6% NL (1.18 ± 0.06 mm); and eye diameter, 9.5% NL (0.49 ± 0.02 mm). Pigment at hatching remained the same as in later preflexion stages (Fig. 3a) and consisted of large melanophores covering the entire body, except the posterior end of the notochord. There was also a row of elongated melanophores lining the ventral margin of the fin fold. At hatching, there was no pelvic disk, although the pectoral fin base extended ventrally toward the isthmus where the disk would form. The yolk included a single oil droplet, positioned anterodorsally within the yolk.

Considerable growth in size occurred during preflexion without any visible alteration in appearance (n = 17 specimens). Larvae less than 8 mm NL resembled the 5 mm yolk-sac larvae (Fig. 3). Pelvic disk width was about ⅓ eye diameter. At about 8 mm NL, growth in body depth occurred together with dorsal and anal fin ray formation; the rays formed synchronously along the entire fin lengths. In most specimens, dorsal and anal fin ray formation preceded both caudal and pectoral fin ray formation (Fig. 3b). Disk diameter was about ½ eye diameter at this stage. A few small melanophores had appeared in the dorsal fin area. The hypural primordia were present with no sign of notochord flexion. At lengths between 7 and 8 mm NL, morphometrics remained similar to those at hatching; the greatest changes were an insignificant increase in snout-anus length from 39 to 42% NL and a reduction in body depth from 22 to 19.5% NL.

Just beyond 8 mm NL, hypural plates formed at about the same time as pectoral fin ray bases. However, in a few specimens, these events just preceded anlagen of dorsal and anal fin rays, so the timing of these sets of events was very close and not entirely regular between individuals. At

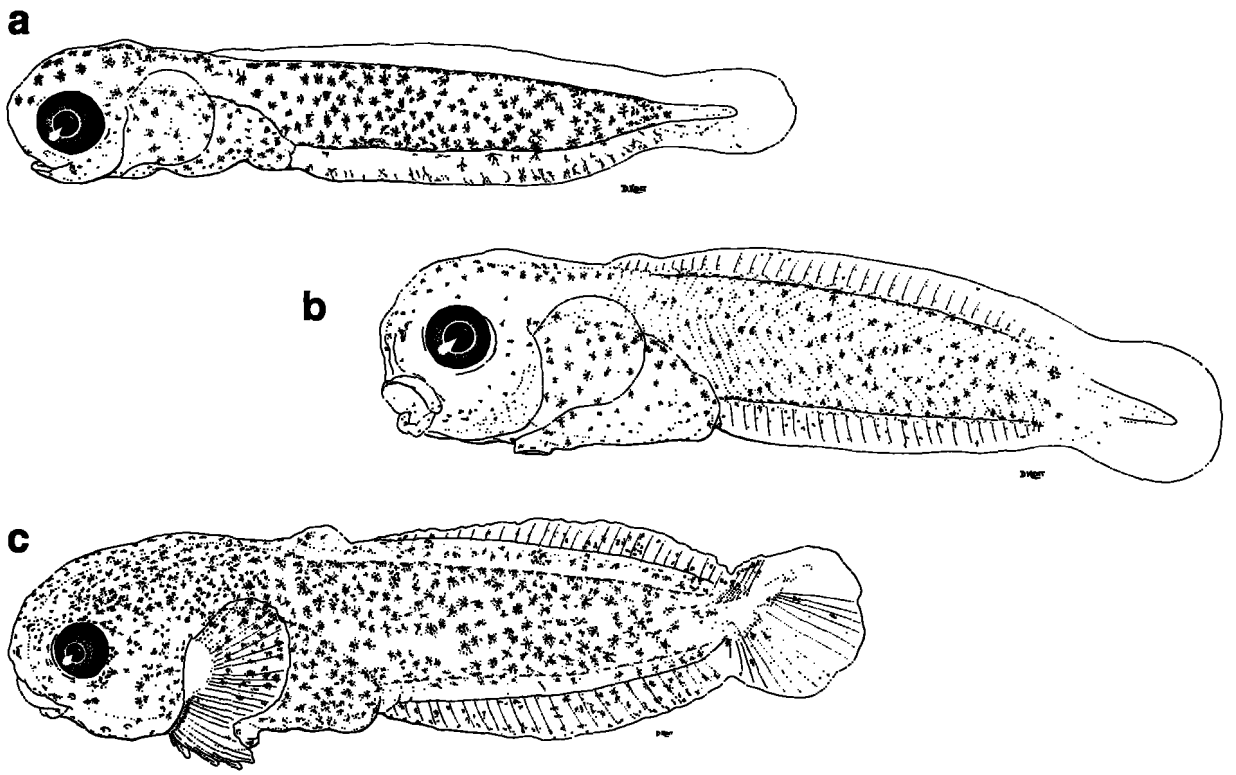

FIGURE 3.—Larvae of *Liparis callyodon*: a, 7.75 mm NL preflexion; b, 8.1 mm NL preflexion; and c, 10.45 mm SL postflexion.

a size of 8.8 mm NL, the hypurals were formed without caudal ray anlagen, and the pectoral fin ray bases were present. The anterior lobe of the dorsal fin (first dorsal) was becoming evident. The pelvic disk was only slightly smaller in diameter than the eye. At sizes between 9 and 9.9 mm NL, caudal rays formed, numbering 8 or 10 in different specimens, and pectoral rays developed from ½ to over ¾ of their length. All larvae under 10 mm NL were preflexion larvae. Larvae between 8.8 and 9.9 mm NL had the same morphometrics as smaller preflexion larvae, except a reduction from 9 to 7% NL in eye diameter.

Flexion occurred at sizes just beyond 10 mm NL, together with completion of caudal and pectoral fin ray formation. At 10.45 mm NL, the exserted lower pectoral rays were elongated, and the anterior lobe of the dorsal fin was becoming prominent. Disk width equalled eye width. Caudal pigment was forming, and the melanin on the rest of the body had become denser, although the pectoral fin remained unpigmented. The mandibular area was lined with 10 acousticolateralis pores (5 each side), and the maxillary region, with 8 pores. The nostrils were split into separate canals, with the ventral naris directed anteriorly in line with the eye pupil (about 66% pupil diameter) and with the dorsal naris directed up at a 45° angle to the level of the notochord (the opening half the diameter of the ventral naris). The cranial subdermal space was evident beneath the dense melanin. The operculum remained entirely open along the pectoral fin base and did not extend dorsally beyond the pectoral fin.

During postflexion (Fig. 3c), ambivalence between swimming and settlement became evident in the rearing tank (n = 3 individuals). Postflexion juveniles of about 12 mm NL had formed an acoustico-lateralis pore posterior to the eye, and two pores of the lateral line, immediately posterior to the dorsal end of the operculum. The operculum extended dorsally beyond the pectoral base, curving anteriorly as in adults. The opercular membranes with branchiostegals were fused with the isthmus up to about 7 rays from the top of the pectoral fin.

Juveniles of 20–22 mm SL showed different morphometrics from larvae: the snout-anus length was reduced from 42 to 36% SL; the eye diameter was further reduced to 5.7% SL; the head length increased from 21 to 24.4% SL; and the body depth slightly increased to 23.5% SL. In permanently settled juveniles at the largest sizes preserved, the opercular opening remained as low as the 4th or 5th pectoral ray; whereas, adult *L. callyodon* would not have this opening extending beyond the 1st ray (Hart 1973). The only other possible identifications from meristics were *L. cyclopus* and *L. florae*, but morphometrics, fin shape, and ecological information dictated against such determinations.

DISCUSSION

It must be reiterated that positive identification was, and now remains, possible only from juvenile material reared from known larvae. Future work may possibly permit identification from larval material for these Pacific *Liparis* species, but the present work serves only to focus such future efforts.

Taxonomic identification of *Liparis* species depends on numerous characters that are very difficult to determine in the smallest juvenile specimens. In addition, the opercular opening becomes smaller with development in *Liparis* species (Able et al. 1984). Therefore, rigid adherance to determining a restricted opercular opening size for identification of *L. callyodon* (cf. Hart 1973) should be expected to cause difficulty in identification of small juveniles. Further investigation of allometric reduction in opercular opening size in juveniles of the genus *Liparis* is required.

The fecundity (fewer than 400 eggs per mass) of *L. callyodon* was substantially less than the fecundity (about 1,500 to 5,000 eggs) determined for *L. fucensis* by DeMartini (1978). The average egg size, however, was larger at 1.7 mm for *L. callyodon* than for *L. fucensis* at 1 mm (Marliave 1975; DeMartini 1978). Adults of *L. fucensis* attain 30% greater maximum length than *L. callyodon* (Hart 1973). Furthermore, the *L. callyodon* egg masses collected, especially the counts of 132 and 53, may not have comprised the entire ovarian output of a female in every case because eggs were extruded into available interstitial spaces. This could sometimes restrict the number of eggs laid in one mass.

The larger eggs and apparent lower fecundity of *L. callyodon* resulted in considerably larger larvae at hatching than those for *L. fucensis*. Growth and development of *L. callyodon* occurred over a smaller range of lengths. Considering the cubic increase in volume with length for the bubblemorph of *L. fucensis* larvae, that unusual morph permitted enormous growth during the larval stage compared to the more typical *Liparis* larvalmorph of *L. callyodon*. Larvae of

L. callyodon resemble the few Atlantic species of *Liparis* that have been identified (Able et al. 1984), except for the unusually heavy melanization in larvae of this species. Intense melanization at hatching is more typical of cyclopterine than liparidine larvae (Able et al. 1984).

Although a relatively large subdermal space surrounding the entire body is typical of liparidine larvae, it is only as prominent as that illustrated in Figure 1 in *L. fucensis*, which may be the same species as that unidentified illustration previously referred to (by Able et al. 1984). That previously published illustration shows development of fin rays at a smaller size and with less melanin than in the present paper, but both of these features could result from the shrinkage and bleaching effects of long-term preservation. Another explanation for such differences is that regional differences might occur, as described for larvae of another cottoid species, *Oligocottus maculosus* (Marliave 1988). On the other hand, the unidentified illustration of a liparidine bubblemorph was drawn from a CalCOFI sample, which would be just south of the known range for *L. fucensis* (Hart 1973).

The larval bubblemorph of *L. fucensis* was collected in sled trawl tows taken within 1 m of the bottom at a wide variety of depths. In these same tows, larvae of Pacific whiting, *Merluccius productus*, were caught in the bottom tows at stages in which their swimbladder had developed, whereas earlier stages tended to be uniformly distributed through the water column (Marliave in press). Since cottoid fishes lack swimbladders at all stages, the evolution of a larval bubblemorph in the cyclopterid *L. fucensis*, in the cottid *Malacocottus zonurus* (Washington et al. 1984), and, to a less obvious extent, in the cottids *Gilbertidia sigalutes* and *Psychrolutes paradoxus* (Marliave 1975) may be an adaptation imparting neutral bouyancy, which would assist in maintaining a precise depth without costly swimming effort. The fluid of the subdermal space, if maintained at bodily osmolarity well below that of ambient seawater, would reduce overall density and lend to neutral bouyancy. Larvae possess swimbladders in certain other taxa that lack a swimbladder as benthic adults, as in the Gobiesociformes (Allen 1984); thus, the selective advantage of achieving neutral bouyancy appears to be relatively general among larval marine fishes.

Convergence toward the bubblemorph and midwater habitat is found in other genera. Most notably, Peden and Anderson (1978, 1979), Anderson (1977), and Peden (1979) discussed either the loose skin, which imparts a sort of bubble morphology, or the midwater habitat (i.e., neutral buoyancy) of the zoarcid genus *Lycodapus*. Anderson (1977, 1984) further noted that same habitat in *Melanostigma*, although this genus may possibly deposit demersal eggs in one species, *M. atlanticum*. Among liparidines, midwater habitat and bubble morphology are most specialized in *Nectoliparis* and *Liparisicus*; these genera retain this specialized larval character into adult life (see Peden 1981 regarding midwater habitat). In these four genera, representing two distinctly divergent families with demersal ancestors, eggs producing relatively large and well-developed young are apparently deposited and reared, for most species, in the same midwater habitat as adults. In the case of the better known *Lycodapus mandibularis* (Anderson 1977; Peden and Anderson 1978; Peden 1979), adults are not known to select bottom habitat except accidentally during diel migration (Peden observation from submersible). Young, as small as 19 mm, are found in the same midwater tows as adults (maturity is at 75–90 mm in northern samples); owing to the large size of the eggs (Anderson 1977), the young are assumed to have hatched at relatively large sizes. Given the development of loose skin, or bubble morphology, in the more specialized and diverse genera of liparidines *Careproctus* and *Paraliparis* (Burke 1930; Stein 1978), many of which are from midwater, the bubblemorph, which originally evolved in a *Liparis*-like ancestor, has apparently been exploited in adult life histories of a large number of species. In some of these liparidine and zoarcid genera, some species may be associated with near-bottom habitats, and the bubblemorph may allow adults to hover just off the bottom similar to fishes with swimbladders (observed in *Lycodapus parviceps* by Peden from submersible).

The relatively neutral bouyancy that seems probable for the cottoid bubblemorph might permit relatively greater overall growth during the planktonic stage than for larvae of related species that have more typical larval morphology; e.g., larval *Gilbertidia sigalutes* grow to about 75% of their average adult size during the planktonic stage (Marliave 1981). This difference in larval growth seems to be the case for the present two *Liparis* species; the normal-type *L. callyodon* settles from the plankton at a very small size compared with the bubblemorph of *L. fucensis*. Bouyancy and potential growth rate

are both features that should be under immediate selective pressure; thus the presence or absence of the bubble morphology would be a derived character not suitable for revealing phylogenetic relationships.

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