Size. A comparatively small species reaching a maximum known size of 260 mm SL (Gibbs and Stauger 1970).

Biology. Western Atlantic females caught in June and August contain ovarian eggs 1.8–1.9 mm in diameter, the same size as living, just-fertilized eggs (Gibbs and Stauger 1970). The eggs are covered with filaments. Juveniles have a pair of slender barbels that persist until about 160 mm SL.

General Range. Found on both sides of the Atlantic (Gibbs and Stauger 1970: Fig. 8). The western Atlantic population occurs close inshore throughout the Antilles, inshore and offshore in the Caribbean Sea and Gulf of Mexico, and in the Gulf Stream and adjacent waters to about 40° N, 66° W.

Acknowledgments. Drafts of the beloniform section were reviewed by Thomas A. Munroe and Rodney A. Rountree.

Killifishes. Order Cyprinodontiformes

Monophyly of this order is based on several derived characters such as symmetrical dorsal fin supported internally by one epural bone and first pleural rib on the third or fourth vertebra as occurs in other atherinomorphs (Parenti 1981; Nelson 1994). The lateral line is present on the body as pitted scales; nasal openings paired; and protrusible upper jaw bordered only by premaxilla. A number of species of this order are popular aquarium and experimental fishes. Eight families with 88 genera and about 807 species (Nelson 1994).

Killifishes. Family Fundulidae

Kenneth W. Able

Killifishes are small, stout fishes of shallow water habitats. They are recognizable by a small mouth, single dorsal fin that originates about halfway along the body, a relatively deep caudal peduncle, and abnormally large pelvis fins. The family Fundulidae (following Parenti 1981) contains five genera and about 48 species occurring in fresh, brackish, and coastal marine areas from southern Canada to Yucatán, Bermuda, and Cuba (Nelson 1994). Of the approximately 32 species of Fundulus, two occur in the Gulf of Maine. A related species, Cyprinodon variegatus, was included in Bigelow and Schroeder based on an account by Storer. To the best of our knowledge it has not been collected in the area subsequently, but it is common on the southern shores of Massachusetts.

KEY TO KILLIFISHES OF THE GULF OF MAINE

1a. Preorbital scales present; short, narrow, irregular bars on sides of body .............................................. Mummichog

1b. Preorbital scales absent; 12–20 long and dark vertical bars on sides of males; adult females with horizontal stripes .............................................. Striped killifish

Mummichog / Fundulus heteroclitus macrolepidotus (Walbaum 1792) / Bigelow and Schroeder 1953:162–164

Description. Stout-bodied, with a flattened head, deep caudal peduncle and rounded caudal fin (Fig. 128). Mouth small, oriented somewhat dorsally. Dorsal and anal fins originate just behind midpoint of body. Head and body covered with large, round scales except for preorbital region, which is naked. Sexual dimorphism pronounced (Newman 1907, 1909a; Relyea 1983). Females have a sheath or ovipositor on the anterior edge of the anal fin, which is especially prominent during the spawning season. Males have numerous dermal contact organs on the posterior rim of selected scales and on the rays of the dorsal, anal, and pelvic fins during the breeding season.

Meristics. Dorsal fin rays 10–15; anal fin rays 9–12; pectoral fin rays 16–21; caudal fin rays 14–21; branchedepgital rays 5. Details of meristic and morphometric variation can be found in Relyea (1983).
Color: Color is especially variable and can differ between the sexes, in and out of the reproductive season, and dependent upon the substrate over which they are found (Parker 1925). Females are olive green, darker on the dorsal surface. They sometimes show subtle vertical bars on the posterior half of the body. Males become much brighter and more colorful during the spawning season. Prior to the spawning season they are dark green with whitish or silvery spots and dark irregular vertical bars on the lateral surfaces and dark motting on the dorsal surface. The fins are dark and the dorsal fin may have an ocellus on the posterior portion. The belly is much lighter.

Size. Maximum size attained in Canadian waters is 10–13 cm (Needler 1940; Fritz and Garside 1975) but they are seldom more than 10 cm in the Gulf of Maine or in the New Jersey and North Carolina marshes (Kneib and Sliven 1978; Able 1990b).

Distinctions. Fundulus heteroclitus can be distinguished from F. majalis, the only other Fundulus in the Gulf of Maine, because F. heteroclitus lack preorbital scales while F. majalis have them (Relvy 1983). Typically, the vertical bars on the body of F. majalis are longer and darker than those of F. heteroclitus and only adult female F. majalis have horizontal stripes. In addition, the anal sheath of female F. heteroclitus is much longer than in F. majalis, reaching to almost half the length of the anal fin ray.

Taxonomic Remarks. Variation in adult and egg morphology, reproductive behavior, and genetic variation (Able and Felley 1986; Marteinsdottir and Able 1988; Gonzalez-Villasenor and Powers 1989; Powers et al. 1993) has resulted in resurrection of two subspecies as recognized by Jordan and Evermann (1896). The northern subspecies, F. h. macrolepidotus, is present in the Gulf of Maine. Characteristics of the more frequently studied southern subspecies should not be assumed for the northern subspecies.

Habits. This shallow water species is euryhaline, with some freshwater populations reported (Klaue 1957; Hastings and Good 1977; Denoncourt et al. 1978; Sartarian and Schmidt 1982). Under laboratory conditions, adults and larvae can survive salinities higher than 110 ppt (Griffith 1974; Joseph and Scalesena 1966). They occupy an array of marsh habitats from salt marshes, where they are especially abundant, to eelgrass beds, open shores, and many altered and impacted habitats where few other fish can survive (Bigelow and Schroeder; Nixon and Oviatt 1973; Able and Fahay 1998). They are especially tolerant of low dissolved oxygen (Packard 1905; Smith 1993; Layman et al. 2000).

Food. Larval, juvenile, and adult F. heteroclitus feed, apparently opportunistically, on small crustaceans, annelids, and gastropods, and although detritus is ingested it does not appear to have any nutritional value (Clymer 1978; White et al. 1986; Kneib 1987; Petrillo 1987). Food habits change during early life history with diets of the smallest individuals (<20 mm SL) composed of harpacticoid copepods and annelid worms whereas the diets of larger individuals (up to 30 mm SL) comprised primarily Spartina detritus and aggregates of other food particles (Smith et al. 2000). All life-history stages depend to a large degree on marsh surface food sources (Weisberg and Lotrich 1982, 1986). The high annual production and mortality of F. heteroclitus (Valiela et al. 1977; Meredith and Lotrich 1979) implies that they are important in trophic dynamics of salt marshes, yet their roles in salt marsh ecosystems are hard to quantify (Clymer 1978; Kneib 1987, 1997).

Parasites. Mummichog is parasitized by every major parasite group including dinoflagellates, sporozoans, monogenetic trematodes, digenetic trematodes, cestodes, nematodes, and copepods (Dillon 1966; Marigoñese 1995).

Predators. They are probably preyed upon by a variety of birds and fishes but data are often lacking (Daiber 1982; Kneib 1982; Tupper and Able 2000), particularly for the Gulf of Maine. There are reports of predation by herons, terns, kingfishers, mergansers, and a variety of other birds (White 1953,
Reproduction. Reproductive characteristics vary between the two subspecies (Marteinsdottir and Able 1988, 1992; Able and Felby 1998). The following account is based on Gulf of Maine populations of the northern subspecies whenever possible. Maturation, at least for some populations, occurs as individuals enter their second year at sizes as small as 40–50 mm TL (Able 1990b). Maturation appears to occur under conditions of increasing photoperiod and temperature (Taylor 1986). Fertilization appears to be affected by salinity (Able and Palmer 1988) but can be altered by acclimation (Palmer and Able 1987). Spawning occurs in early spring through summer, but timing and duration of spawning may vary between subspecies (Marteinsdottir and Able 1992). Reproduction occurs in Massachusetts from May to July (Wallace and Selman 1981). All populations appear to spawn intermittently (Taylor 1986). Populations of *F. h. macrolepidotus* may spawn daily during the reproductive season in Massachusetts (Wallace and Selman 1981; Taylor 1986) and on Long Island (Conover and Kynard 1984). They do have semilunar peaks in reproduction (Taylor 1986) although perhaps not as pronounced as in more southern populations.

Field observations of spawning of a *F. h. macrolepidotus* population from Massachusetts (Able and Hata 1984) differ in several respects from earlier accounts (Newman 1907; Foster 1967). In a salt marsh creek at low tide, males and females concentrated in isolated pools (Able and Hata 1984). As the tide began to flood a small tributary of the creek, adults moved into the area for spawning. By this time males assumed typical spawning coloration with the eyes becoming very dark and the posterior portions of the dorsal, anal and caudal fins becoming yellowish green. The dominant male in a given area was always the brightest and usually defended a territory around a mat of dead eelgrass (*Zostera marina*) and decaying algae. Courtship consisted of a male following a female and contacting her lightly on the top of her head with his lower jaw. At this time the female often jumped the spawning site and then the male attempted to wrap his dorsal and anal fins around the female while she inserted her anal fin ovipositor into the substrate. While clasping, the male and female vibrated for 1 or 2 s as eggs and sperm were released. Females, regardless of subspecies, deposited eggs in small interstices, a behavior that is facilitated by the female's anal sheath or ovipositor (Able 1984b). Populations of *F. h. macrolepidotus* deposit their eggs in the substrate or in mats of vegetation in intertidal or shallow subtidal areas (see Able 1984b for summary).

Early Life History. The demersal eggs are smaller (*F. h. macrolepidotus* [1.6–1.9 mm diameter] than those of *F. majalis* [2.0–3.0 mm]). In addition, the eggs have longer chorionic filaments than those of *F. majalis*, which are very short and difficult to observe except with scanning electron microscopy (Able 1984a). Embryonic development of *F. heteroclitus* from Woods Hole has been described in detail (Armstrong and Child 1965). Daily increment formation in otoliths of embryos, larvae and juveniles has been validated (Radke and Dean 1982). Hatching normally occurs in 9–18 days but may be a function of temperature and elevation at the intertidal spawning site, as part, because hatching is cued to immersion on high tides (Di Michele and Taylor 1980; Di Michele and Westerman 1997, Williamson and Di Michele 1997). If hatching is delayed (Taylor et al. 1977; Di Michele and Powers 1982), the larvae are more advanced developmentally (fin ray formation, pigmentation [K. W. Able, pers. obs.]). After hatching, larvae resemble those illustrated by Armstrong and Child (1965). They differ from recently hatched *F. majalis* in the smaller size (*F. h. macrolepidotus* [4.8–5.1 SL] [Marteinsdottir and Able 1992] vs. *F. majalis* [7.0 mm]) (Hjard 1978a), as well as the number of branchiostegals, with *F. heteroclitus* typically having five and *F. majalis* possessing six (Richards and McBean 1966). At larger sizes (>10 mm) they differ in pigment patterns, head scale pattern, and a number of body proportions (Richards and McBean 1966). Recently hatched individuals are distributed on the marsh surface in shallow pools, ponds, ditches, and depressions (Kneib and Stiven 1978; Wang and Kneib 1979; Taylor et al. 1979; Talbot and Able 1984; Smith 1995; Able et al. 1996; Able and Hagen 2000). On several occasions in Nauset Marsh on Cape Cod, schools of small individuals were observed at the edge of larger marsh creeks in eddies behind peat reefs (K. W. Able, pers. obs.). Many of the young-of-the-year remain in marsh pools during the first summer (Talbot and Able 1984; Able and Hagen 2000). Recently hatched individuals have a wide salinity tolerance (<1 to >10 ppt) but growth is retarded at the extremes (Jose and Salesa 1966).

Age and Growth. Age of larvae and adults has been determined from otoliths (days) and scales (years), respectively, as well as modal increases in length (Valiela et al. 1977; Kneib and Stiven 1978; Radke and Dean 1982). In New Jersey salt marshes, young-of-the-year grew approximately 1.8-3 mm-week<sup>−1</sup> (Clymer 1978; Rountree 1992) and attained 23–58 mm TL by the fall and 35–63 mm TL by the end of the first year (Able 1990b). Most studies commonly report 2- to 3-year classes and occasionally age 4 (Fritz and Garside 1975; Valiela et al. 1977; Kneib and Stiven 1978; Able 1990b). This species probably spawns for the first time at about 12 months (Kneib and Stiven 1978; Able 1990b). Young-of-the-year are estimated to suffer an annual mortality rate of 99.3% (Kneib and Lottich 1979), whereas mortality estimates for older year-classes are considerably lower (Kneib and Stiven 1978; Valiela et al. 1977). Abundance of this species makes it a dominant component of many shallow water estuarine systems especially salt marshes (Nixon and Oviatt 1973). Annual production from Delaware marsh creeks was estimated as 8.14 gdw (grams dry weight) m<sup>−2</sup> year<sup>−1</sup> (Meredith and Lottich 1979) to 7.37 gdw·m<sup>−2</sup>·year<sup>−1</sup> (Tao and
able, unpublished data). Estimates from a Massachusetts marsh, after recalculation, were 1.6 gdw-m⁻² year⁻¹ (Valiela et al. 1977; Teo and Able, unpublished data).

**General Range.** Mummichog occur from southwestern Newfoundland and Prince Edward Island in the Gulf of St. Lawrence (Scott and Scott 1988) to northern Florida (Relyea 1983). The northern subspecies occurs throughout the Gulf of Maine as far south as Long Island and northern New Jersey, where it intergrades with the southern form, *F. h. heteroclitus* (Able and Selley 1986; Marteinsdottir and Able 1988, 1992).

**Occurrence in the Gulf of Maine.** Found in shallow waters throughout the Gulf. See Collette and Hartel (1988) for details of distribution in Massachusetts Bay.

**Movements.** Although mummichog are among the most sedentary of fishes, especially during the summer (Horton 1963; Lotrich 1975; Clymer 1978; Murphy 1991; Halpin 1997), they appear to move greater distances during the winter (Fritz et al. 1975). More recent observations indicate that the summer home range can be as much as 15 hectares (Teo and Able, unpublished data). A spring migration from high-salinity waters into brackish and freshwaters has also been reported (Chidester 1920). More recent observations in southern New Jersey indicate that they leave marsh creeks to overwinter in pools on the marsh surface (Smith and Able 1994), where they are reported to bury 15–20 cm in the mud (Chidester 1916).

During the summer, homing is evident in marsh pools and creeks (Horton 1965; Lotrich 1975; Murphy 1991). Movements within marshes have a strong tidal component, with juveniles and adults moving up creeks and onto the marsh surface on high tides (Clymer 1978; Werne 1981) and retreating on low tides usually to the same channel or creek (Butner and Brattstrom 1960; Kneib 1987). Access to the marsh surface is usually by intertidal creeks (Murphy 1991).

**Importance.** Mummichog are of some economic importance as baitfish (Hildebrand and Schroeder 1928; Livingstone 1933), but also have great value as an experimental laboratory animal in a variety of disciplines (Di Michele et al. 1986; Arr 1986) and for pollution studies (Bisler 1986).

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**Figure 159.** Striped killfish *Fundulus majalis*. Woods Hole, Mass. Male, 130 mm (above); female, 143 mm (below). Drawn by H. L. Todd.
Description. This fish resembles *F. heteroclitus* in relatively small body size, flattened head, small mouth, and deep caudal peduncle (Fig. 159). Dorsal and anal fins originate at same distance from snout, just behind midpoint of body. Both head and body covered with large, round scales. Adult males differ markedly from females (Newman 1907, 1909a; Relyea 1983) in color pattern and in absence of a short ovipositor on anterior edge of anal fin.

Meristics. Dorsal fin rays 11–16; anal fin rays 9–13; pectoral fin rays 16–21; caudal fin rays 14–20; branchiostegal rays 6. Details of meristic and morphometric variation can be found in Relyea (1983).

Color. Juveniles have vertical bars on the lateral surfaces. Males have 7–12 bars when young and 14–20 as adults. Transition from juvenile to adult pattern occurs with growth (Newman 1907). The adult color pattern is sexually dimorphic (Newman 1907). The vertical bars typical of juveniles are retained by the male, but at approximately 50 mm an ocellus appears on the posterior portion of the dorsal fin (Smith 1907). In females, the black vertical bars transform into horizontal stripes that first appear at approximately 32 mm. The belly is lighter than the dorsal surface.

Size. Adults reach 152–178 mm in the Gulf of Maine and a similar size in Chesapeake Bay (Hildebrand and Schroeder 1928; Young 1950; Clemmer and Schwartz 1964) and Long Island (Briggs and O'Connor 1971).

Distinctions. *Fundulus majalis* differs from the only other killifish in the Gulf of Maine (*F. heteroclitus*) in having precocial scales (Relyea 1983). The vertical bars on the body are large and darker than in *F. heteroclitus*, and only females have the horizontal stripes. The ovipositor on the anal fin is much shorter in this species.

Habits. Found in a variety of shallow habitats from open beaches to coves and bays. Seldom collected on the marsh surface (Weisberg 1986) but can be abundant in marsh creeks and along subtidal shorelines especially at higher salinities (Rountree and Able 1992; Able et al. 1995). They may prefer sandy sediments (Briggs and O'Connor 1971). They can bury completely in sandy substrate and frequently do so when surrounded by a seine. They can be abundant in small protected bodies of water, where they travel in schools of a few individuals to several hundred or more. On an ebbing tide they may be found on shallow flats in a few centimeters of water, but on a flood tide they are often abundant at the water's edge (Foster 1967; Weinstein 1975; Weisberg 1986). Lethal temperature–salinity experiments on juveniles and nonripe and ripe adults indicated that survival time and salinity tolerance varied with temperature, with the greatest survival at 20°C (Schmelz 1970). Ripe adults and larvae were least resistant to temperature and salinity extremes. Adults have survived salinities up to 106 ppt (Griffith 1974). Earlier experiments suggested an internal tidal rhythm and some ability to home (Mast 1915). A seasonal change in distribution from shallow habitats in the summer to deeper ones (1–3 m) in the winter has been reported (Able and Fahay 1998). Juveniles (as small as 24 mm TL) and adults have been observed to be cleaned by *Cymodocon arenariatus* while posing in an exaggerated head-down position (Able 1976).


Parasites. A broad spectrum has been reported including dinoflagellates, sporozoans, monogenean and digenetic trematodes, cestodes, nematodes, and copepods (Dillon 1966). Individuals parasitized with monogenean trematodes (*Swinglewiopsis*) and unidentified leeches posed for cleaning by other fish (Able 1976).


Reproduction. Adults probably mature in the second year (Tracy 1910); at 76 and 63 mm for females and males, respectively (Hildebrand and Schroeder 1928) or as small as 55 mm (Able and Fahay 1998). During spawning, the lateral surface of the head of a male is black and the ventral surface of an anal fin is yellow (Newman 1907; K. W. Able pers. obs.). Contact organs on the posterior rim of the scales are especially prominent at this time (Newman 1909a). Spawning occurs from April to September in Chesapeake Bay (Hildebrand and Schroeder 1928) and from May through July in New Jersey (Able and Fahay 1998), and has been reported from nearshore shallow water (Nichols and Breder 1927) and in intertidal pools (Able and Fahay 1998). Eggs are buried in the substrate during spawning (Newman 1909b) sometimes as much a 7–10 cm deep (Summer et al. 1913).

Early Life History. The eggs are 2.0–3.0 mm in diameter much larger than those of *F. heteroclitus*, with approximately 50 oil droplets, and are often amber in color (Hardy 1978a). Chloronellin filaments have been variously reported as absent or present, but many of the former accounts are incorrect (Able 1984A). The filaments are notable in that they possess microfilaments that give individual filaments a bottlebrush appearance (Able 1984a). Embryos tolerate a wide range of tempera
ature, salinity, and dissolved oxygen (Schmelz 1970). Hatching takes 22 or 23 days (Newman 1908, 1914). Descriptions of larval development are summarized by Hardy (1978a). The larvae differ from recently hatched F. heteroclitus in the larger size (7.0 mm, see Hardy 1978a), as well as in the number of branchiostegals with F. huebneri typically having six and F. heteroclitus having five (Richards and McBean 1966). Larger individuals of these two species differ in pigment pattern and a number of body proportions (Richards and McBean 1966). A series of experiments has examined the influences of temperature and crowding on meristic characters of embryos and larvae (Fahay 1978, 1979, 1980, 1982). Presence of multiple-size cohorts among recently hatched individuals in a New Jersey population suggests two or three spawning peaks that may be associated with spring tides (Able and Fahay 1998).

**Age and Growth.** Scales have been used for a Chesapeake Bay population (Clemmer and Schwartz 1964) to determine that males reached approximately 65 mm the first year and subsequently grew 4.4-21.0 mm/year\(^{-1}\). Females reached approximately 61 mm the first year and then grew at a rate of 8-28 mm/year\(^{-1}\). Another estimate indicated similar sizes (Able and Fahay 1998). Males older than age 1 were consistently smaller than females. Males and females lived 6 and 7 years, respectively. These estimates have been questioned (Foster 1967) based on comparisons with the lengths of presumed young-of-the-year collected by Warfel and Merriman (1944a).

**General Range.** Striped killifish (including the nominal F. similis) occur from New Hampshire to the Gulf of Mexico (Relyea 1983).

**Occurrence in the Gulf of Maine.** Striped killifish may have extended their range into the Gulf of Maine. Little evidence of their presence was found in the Gulf of Maine prior to 1937. Subsequently, they have become more abundant in Cape Cod Bay, perhaps as a result of completion of the Cape Cod Canal (Schroeder 1937). Their later occurrence as far north as New Hampshire has been verified (Jackson 1953). Recent collections have indicated that they are abundant in Waquoit Bay on the south shore of Massachusetts (Ayvazian et al. 1992) and in Nauset Marsh on the outer Cape Cod as well (K. W. Able, unpubl. data). See Collette and Kantel (1988) for details of their distribution in Massachusetts Bay.

**ACKNOWLEDGMENT.** A draft of the cyprinodontiform section was reviewed by Lynne Parenti.

### BERYC OID FISHES. ORDER B ERYCIFORMES

Beryciforms have traditionally been viewed as a morphologically diverse, but primitive, lineage of acanthomorph or spiny-finned fishes. Most beryciforms are deepwater species, as is the case for all taxa found in the vicinity of the Gulf of Maine. Large lateral line canals extend across the head, usually divided by narrow bony septae that often feature serrations or spines. Seven species from four beryciform families have been recorded from the Gulf of Maine. It would not be surprising if more beryciforms, such as other species of Dipturusidae, Trachichthyidae, Anoplogastridae, or Melampaeidae, are found someday in deeper portions of the Northeast Channel within the Gulf of Maine.

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<tr>
<th>KEY TO BERYCIFORM FAMILIES FROM THE GULF OF MAINE</th>
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<tbody>
<tr>
<td>1a. Two supracoaxials; pelvic fin 1, 7-13. ........</td>
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<tr>
<td>1b. One supracoaxial; pelvic fin 1, 6 .............</td>
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<tr>
<td>2a. Pelvic fins 1, 7; dorsal spines Xi or XII ..</td>
</tr>
<tr>
<td>2b. Pelvic fins 1, 7-13; dorsal spines IV ..</td>
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<tr>
<td>3a. No spines in dorsal or anal fins; no lateral line</td>
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<tr>
<td>3b. Dorsal fin with 3-8 spines; anal fin with 2 or 3 spines; lateral line present</td>
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### SQUIRRELFISHES AND SOLDIERFISHES. FAMILY HOLOCENTRIDA E

**Jon A. Moore, Paul Geoghegan, and Joseph N. Strube**

Squirrelselves and soldierfishes are small to medium-sized (10-30 cm SL) benthopelagic fishes associated with rocks and coral reefs (0-300 m depth). They are recognizable by their large eyes; hard scales with spiny posterior edges; a single vertical row of scales along anterior edge of the operculum; radiating bony edges on the skull above the eyes; and laterally compressed bodies, which are red to silvery pinkish in most species. They are active nocturnal predators on benthic invertebrates or zooplankton. They typically hide in crevices, caves, or under ledges during the day. Larvae to young juveniles (<30 mm SL) have prominent spines on the head projecting forward from the snout (nasal bone), backward from the crown (supraocipital bone), and backward from the lower corner of each gill cover (preopercle). Larvae and postlarvae