Ammodytoidei: Development and Relationships

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THE suborder Ammodytoidei consists of one family, Ammodytidae, with 5 genera and about 18 species. These are small (less than 100–350 mm SL), elongate fish occurring in the littoral and neritic waters of the Atlantic, Indian, Pacific, and Arctic Oceans. Adults form schools but also bury themselves in the sand. They are commercially valuable in the North Sea and off Japan.

The systematic position of Ammodytoidei, reviewed by Duncker and Mohr (1939), is unresolved, although the suborder is considered a perciform derivative by Berg (1940), Greenwood et al. (1966), and Gosline (1971). A second family, Hypoptychidae, has been included in this suborder by these authors and by Robins and Böhlke (1970), but was removed to the suborder Gasterosteoidei by Ida (1976), who considered it a prepercomorph family on the basis of jaw and caudal osteology, egg size, and reproductive behavior (see Fritzsche, this volume).

Development

The ammodytid genera, *Gymnammodytes, Hyperoplus*, and *Ammodytes* (11 species) are temperate and boreal; *Bleekeria* and *Embolichthys* (7 species) are more tropical in distribution. The confused nomenclature of the North Atlantic species was clarified by the synonomies in Reay (1970) and Russell (1976), where summaries of early life history data were also given. Other larval descriptions were given by Fage (1918) for *Gymnammodytes*; by Altukhov (1978), Kobayashi (1961c), Norcross et al. (1961), Richards (1965), Scott (1972), and Senta (1965) for *Ammodytes*; and by Macer (1967) for North Atlantic species. To date, eggs of 6 species and larvae of 9 species of these genera have been described. No early life history data are available for the tropical genera.

Eggs

Eggs of the six species that have been described are demersal and adhesive, forming clumps on sandy substrates in shallow water. Eggs, probably loosened by tidal currents, have been collected in plankton nets (Williams et al. 1964; Senta, 1965). Russell (1976) summarized studies made on eggs resulting from artificial fertilization. Incubation time ranges from 2.0 to 12.5 weeks. Eggs are irregularly shaped, but generally spherical, from 0.67 to 1.23 mm in diameter, with a single yellow oil globule, 0.17 to 0.42 mm. Embryos develop specific dorsal and ventral pigment, pigmented eyes, a moderate finfold, and pectoral buds prior to hatching at about 3.6 mm.

Larvae

Morphology.—Larvae of Ammodytidae typically are elongate, with rounded snouts which become pointed with age, and preanal length slightly more than 50% body length (Fig. 304). Newly hatched larvae range from 3.0 to 4.6 mm body length. In newly hatched and preflexion larvae the anus does not extend to the edge of the moderately wide finfold but opens to the side. Notochord flexion occurs at 10 to 12 mm body length in most

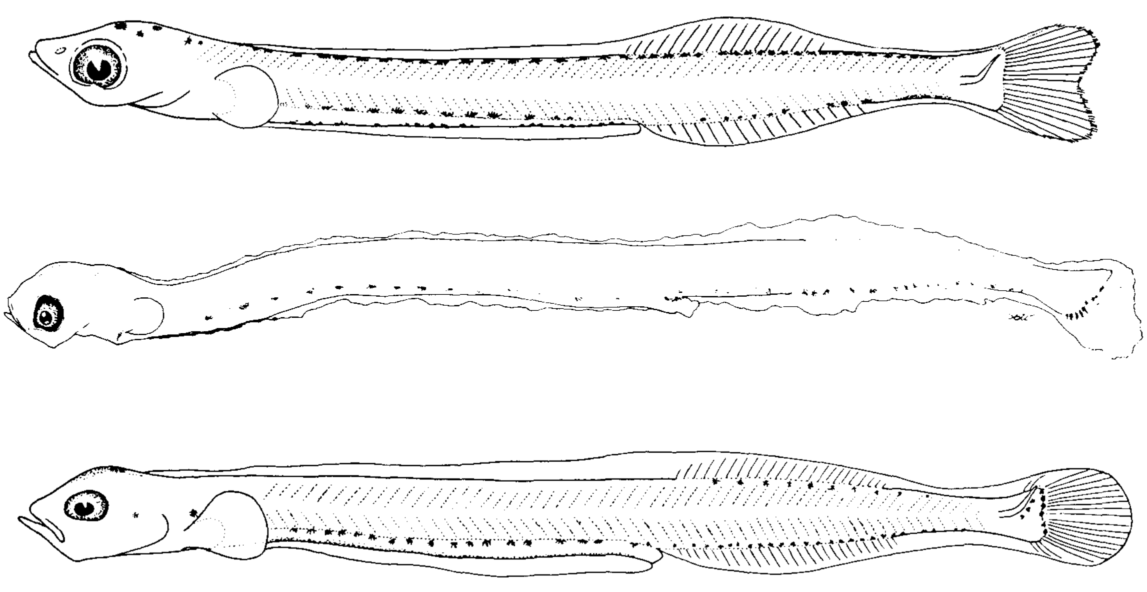

Fig. 304. Larvae of: (upper) *Hyperoplus lanceolatus*, 16 mm, redrawn by H. Orr from Einarsson (1951); (middle) *Ammodytes hexapterus*, 16 mm; and (lower) *Ammodytes marinus*, 16 mm, redrawn by H. Orr from Einarsson (1951).

TABLE 148. SELECTED PIGMENT CHARACTERS OF AMMODYTIDAE LARVAE. 0 = absent, + = present, ↑ = increasing with development, ↓ = decreasing with development, po = posterior, an = anterior.

Species	Stage	Body length (mm)	Head: Jaws	Head: Snout	Head: Brain	Head: Nape	Ventral gut	Dorsal midline	Caudal	Finfold	Sources
Gymnammodytes semisquamatus	preflexion	4.8	0	0	0	0	+	0	0	+	Cameron, 1959
	flexion	7.0	0	0	0	+	+	near tail	+	+	Macer, 1967
	postflexion	11.8–38.0	0	+	+, 0	+	+↓	↑+	+	+	
G. cicerellus	preflexion	7.0	0	0	0	+	0	+	+	0	Fage, 1918
	postflexion	11.0–25.0	0	0	+	+	0	↓	+		
Hyperoplus lanceolatus	flexion	6.0	0	0	+	+	+	po 1/3	0	0	Einarsson, 1951
	postflexion	11.0–25.0	0, +	0, +	+	+	+↓	+	↑		Macer, 1967
H. immaculatus	preflexion	5.5–9.0	0	0	0↑	0	an	po 1/4	0	0	Macer, 1967
	flexion	13.0	0	0	+	0	an	↑	+	0	
	postflexion	26.0	+	+	+	0	an	+	+		
Ammodytes tobianus	preflexion	4.0–5.0	0	0	0	+	an	0	0	0	Einarsson, 1955
	flexion	7.5–12.0	0	0	+	+, 0	an	near tail	0	0	Macer, 1967
	postflexion	16.0–27.0	0	0	+, 0	+, 0	0	↑	0↑		
A. marinus	preflexion	4.5–6.0	0	0	0	0	an	0	+	0	Einarsson, 1951
dubius	flexion	7.5–11.0	0	0	+	0	an	po 1/4	+	0	Macer, 1967
americanus	postflexion	19.0–33.0	0	0↑	+	0	+	↑	+		
A. hexapterus	preflexion	7.0–8.0	0	0	0	0	an	0	0	0	Kobayashi, 1961c
	flexion	11.0–13.0	0	+, 0	0	0	an	0	+	0	NWAFC, unpubl.
	postflexion	16.0–31.0	0↑	+	0↑	0	an	0↑	+		

species, and transformation to juveniles occurs at about 40 mm. The caudal fin is the first to ossify, followed by the pectorals, then the dorsal and anal. The median fin rays form in the posterior part of the body, and ossification proceeds forward. During larval development the body thickens somewhat, but maintains its elongate shape. All adult Ammodytidae have protrusible upper jaws, but *Gymnammodytes semisquamatus* is the only species in which this character is reported in larvae as small as 9 mm (Cameron, 1959). Postflexion larvae of *Hyperoplus* develop vomerine teeth which persist in the adult, while *Gymnammodytes* postflexion larvae develop both vomerine and premaxillary teeth which disappear at about transformation. During the larval period *Gymnammodytes, Hyperoplus,* and *Ammodytes* are pelagic. Juveniles and adults are both pelagic and benthic.

Pigment.—Pigment can be a useful diagnostic feature among the larvae of Ammodytidae, especially the location and development of melanophores on the ventral gut margin, the dorsal body margin, and the caudal area, i.e., the tip of the notochord and the edge of hypural elements. These pigment characters are summarized in Table 148. All species have a row of melanophores dorsally on the gut, beginning at or just posterior to the cleithrum, and a postanal row on the ventral body margin from the anus to the tail. The dorsal gut pigment becomes obscured with growth. Specific variations in pigment patterns can be seen in the 16 mm specimens illustrated in Fig. 304. At this length, dorsal midline pigment forms a complete row in *H. lanceolatus,* but occurs only on the posterior quarter in *A. hexapterus* and *A. marinus*; and ventral gut pigment extends the length of the gut in *H. lanceolatus* and *A. marinus* but is found only on the anterior ventral gut of *A. hexapterus.* Pigment patterns of *A. marinus, A. dubius* and *A. americanus* are nearly identical (Macer, 1976) although Richards (1982) has noted differences in the ranges of melanophore numbers, especially on the anterior ventral gut (stomach) and dorsal midline (supradorsal). Pigment appears variously on the head, increasing with age in all species reported. The only reported decrease in pigmentation is on the dorsal and ventral margins of *G. cicerellus* (Fage, 1918). *G. semisquamatus* has pigment on the ventral finfold margin, the only ammodytid species for which finfold pigment has been noted (Cameron, 1959).

Meristics.—Fin ray and vertebral counts for the family Ammodytidae are: Vert 54–78; D 40–69; A 14–36; Pec. 10–16; Pel. 0–I,5; and C 15–17 prin., 13 branched. In all genera the number of precaudal vertebrae exceeds the number of caudal. Robins and Böhlke (1970) report 9+8 principal caudal rays for *Embolichthys sarissa,* but all other ammodytid species, including *E. mitsukurii,* have 8 + 7. *Embolichthys* is the only genus with pelvic fins, which are thoracic. The caudal fin is the first to form, followed by the pectorals, dorsal, and anal. Posterior rays of the median fins form first and development proceeds forward. Fin formation is completed by 30 to 40 mm body length.

RELATIONSHIPS

Although early life history data of the suborder Ammodytoidei do little to clarify its phylogenetic position, larval pigment patterns and myomere-vertebrae counts are useful in separating sympatric species (Macer, 1967). General characters, such as the well developed state of newly hatched larvae and the sequences of fin development, are shared with other perciform derivatives and relatives, but essentially the problem of the systematic position of ammodytids is not yet resolved.

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