

Morphological and Functional Aspects of Marine Fish Larvae

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The notion that mortality during the larval stage is a major determinant of year class strength has been a part of fisheries theory since before the turn of the century (see Marr, 1956; May, 1974; Hunter, 1976, Lasker, this volume). I have been asked to talk about the systematic aspects of the larval stage, a subject as vast and diverse as systematic ichthyology itself. The importance of diversity to fisheries science is coming into prominence as we move beyond single species concepts. Since demersal and pelagic species from all depths supply larvae to the surface waters, nowhere else in the life histories of these species is there so great a potential for interaction. One might even characterize the larval stage as that period in ontogeny when major portions of a fish fauna come together and share prey, predators, and abiotic variables. Knowledge of direct and indirect species interactions during the larval stage will play an important role in the evolution of multispecies fisheries models.

The previous lecturers have discussed larval fishes from the points of view of behavior, physiology, and ecology. I would like to focus on the morphological aspects of larval adaptation. Marine teleost larvae have evolved an enormous array of morphological specializations, such that it seems we are looking at a distinct evolutionary domain quite separate from that of the adults. It is reasonable to assume that these remarkable structural specializations are adaptive and reflect each species' solution to the challenge of survival in a complex and demanding environment. In the course of an hour I could only hope to discuss a few of the adaptations found within selected teleost groups.

A good place to start is with a problem which puzzled Aristotle and remains somewhat of a puzzle today—the life history of the European eel, *Anguilla anguilla*. Since mature gonads were never found in the freshwater adults, their reproduction remained a mystery for millenia (Schmidt, 1932). Then just before the turn of this century, two Italian scientists, Grassi and Calandruccio (1897), captured some of the leaf-like marine larvae, known as leptocephali, and kept them in an aquarium, where they turned into the transparent glass eel stage of *Anguilla* (Fig. 1). Thus, it was shown that the species was catadromous. Seven years later Johannes Schmidt captured one of these leptocephali off the Faroe Islands north of Denmark. This initiated a wide-ranging plankton sampling program that employed four Danish research vessels and numerous merchant ships in the search for the newly



Figure 1. Transformation of the European eel, *Anguilla anguilla*, from the leptocephalus (at top, ca. 75 mm) to the juvenile (at bottom, ca. 64 mm). From Schmidt (1909).

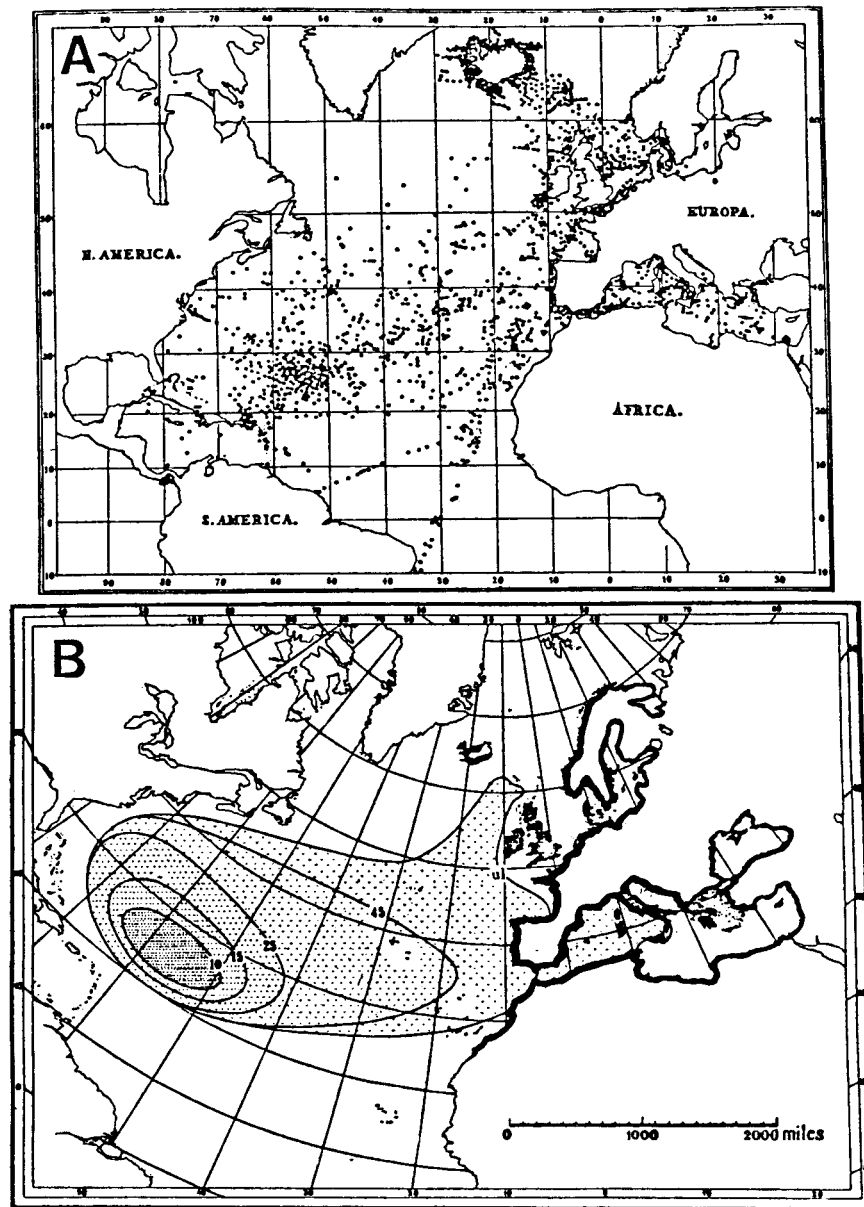


Figure 2. (A) Stations at which plankton collections were made during the Danish eel investigations, 1903-1922. (B) Areal distribution of *Anguilla anguilla* larvae based on plankton surveys. Contours indicate outer limits of occurrence of various sizes (mm) of larvae. Outermost contour refers to unmetamorphosed larvae. Black coastal strip shows distribution of juveniles and adults. From Schmidt (1925).

hatched larvae (Fig. 2). In 1922, with the discovery of newly hatched larvae in the Sargasso Sea, Schmidt concluded that “. . . the eels from Europe travel over the Atlantic to the Sargasso Sea where they spawn in the spring, and furthermore that the larvae, assisted by the North Atlantic current, make a journey in the opposite direction to Europe; a journey that lasts between two and three years” (Schmidt, 1932). Schmidt’s research program was the progenitor of the type of wide-ranging ichthyoplankton survey that continues to be a valuable tool in answering fundamental questions about the life histories of marine teleosts.

Since anguillid eels are a tropical group, the migration of *A. anguilla* adults from the fresh waters of Europe to the Sargasso Sea and the slow return journey of their larvae (via the clockwise North Atlantic gyre) may have been the mechanism by which this species penetrated northward to the fresh waters of Europe. The possibility that the intercontinental journeys of this species have evolved gradually in relation to continental drift and the widening of the Atlantic during the Cretaceous, as suggested by Hulet (1978), in no way diminishes the immensity of the adaptations involved.

The nutrition of the eel larva during its journey is enigmatic since no food has ever been found in the gut of any eel leptocephalus. Furthermore, the gut is poorly differentiated and the lumen of the midgut is often occluded. The suggestion that dissolved organic compounds are absorbed directly through the epidermis is plausible since the epidermis is only from one to several cells thick and the surface cells are covered with microvilli (Hulet, 1978). Such a mode of nutrition would be remarkable since the leptocephali of some eels are the largest of all fish larvae. The leptocephalus of *Thalasseenchelys coheni* attains a length of 30 cm (Smith, 1979) and a 25-cm specimen of this species in our care has a wet weight of 21 gm. The highly attenuate leptocephalus of a notacanthiform eel known as *Leptocephalus giganteus* attains a length of 184 cm (Nielsen and Larsen, 1970).

Hulet (1978) has suggested that an alternative nutritional source might be afforded by the extraordinarily large fang-like teeth typical of eel leptocephali. They could be used to puncture organisms and the protoplasmic juices could be swallowed and absorbed by the epithelium of the esophagus and stomach. Such predaceous strategy might account for the emphasis on eye development and for the many eye specializations found among the eel leptocephali (Smith, 1979). If dissolved organic compounds are the source of leptocephalus nutrition, then the function of the huge teeth becomes problematical. Often it has been suggested that they could function in calcium metabolism. Considering the duration of the larval stage for many eels, another possibility is that they could serve as a defense against predators.

In addition to the 22 families of anguilliform eels and the three families of notacanthiform eels, leptocephali are found in the Order Elopiformes, a group which includes the tarpons, bonefishes, and ladyfishes. This was a major character used by Greenwood et al. (1966) to group the three orders into the Supraorder Elopomorpha.

Elopiform leptocephali share many morphological features with eel larvae, including the leaf-like body form, fang-like teeth, well-developed eyes, and distinct renal blood vessels, but differ markedly in having a well-developed caudal fin that is separate from the dorsal and anal fins. The caudal fin ray formula of elopiforms (10 + 9 principal rays, 4 + 3 hypurals, multiple ural centra) is also typically found in the next orders we will consider—the Clupeiformes, Salmoniformes and Myctophiformes (Ahlstrom and Moser, 1976).

Clupeiform larvae have elongate bodies with long straight intestines and are characterized by their relative uniformity and subtlety of morphological specialization (Fig. 3). Likewise, their conservative pigment patterns are dominated by serially arranged melanophores along the gut and on the ventral midline between the anus and caudal fin. It seems probable that, when expanded, the gut melanophores help conceal the larvae by masking light refracted from gut contents. Similarly, the melanistic shield which forms over the gas bladder reduces light refraction as a visual cue to potential predators. The melanistic pigment found on the oil globules of so many teleost eggs and yolk sac larvae may function in a similar way. Linear gut pigmentation and dorsal gas bladder pigment are recurrent larval characters represented in almost every teleost group in a myriad of arrangements, their universality attesting to their adaptive contribution.

Suggesting a function for the linear series of post-anal melanophores poses more of a problem. Since larvae are transparent and have a body outline that is imperceptible, or nearly so, it is unlikely that the post-anal linear series functions in concealment in the sense that Cott (1940) has shown for organisms with distinct body outlines. Moreover, if post-anal series were to function in this manner one would expect the pigment to be in the form of bars or saddles running at right angles to the body edge. Indeed, in a host of teleost species, melanistic bars and saddles are found in late larvae and pelagic juveniles, ontogenetic states where body outline is more likely to be an important cue to predators. Rather, it would seem that the distinctive post-anal melanophore series, present in so many species throughout almost every teleost group, would call the attention of potential predators. This does not negate the possibility of a protective role for post-anal pigment, since the zoological realm provides numerous examples where visual prominence of a prey species affords protection from predators.

One such example, the phenomenon of "flicker fusion," might be responsible for the widespread occurrence of post-anal melanophore series in teleost larvae as suggested by Joseph Copp (pers. comm.) of Scripps Institution of Oceanography. Describing the phenomenon in banded snakes, Shaw and Campbell (1974) state the following:

As the snake moves forward, seeking a hiding place, the bands on its back follow one another like the spokes on a wheel. Depending on the nearness of the predator, the width of the bands and the intensity of the light on the snake . . . the results may be startling. At the very least an astigmatic

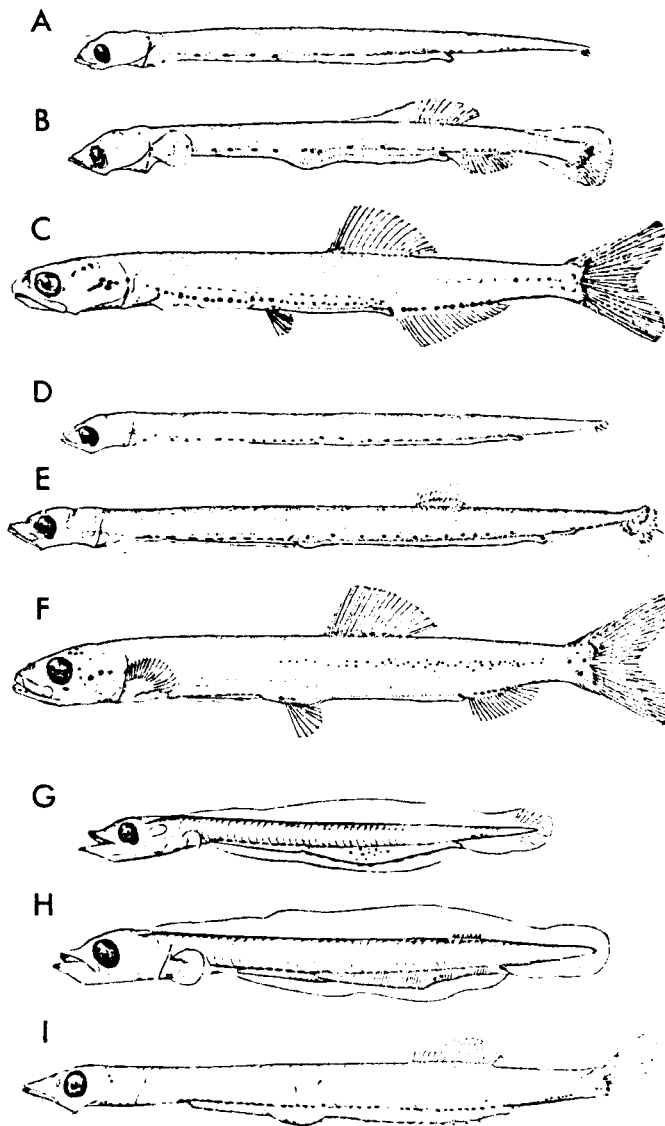


Figure 3. Larvae of clupeiforms. (A-C) northern anchovy, *Engraulis mordax*, 7.5, 11.5, 31.0 mm, from Kramer and Ahlstrom (1968); (D-F) Pacific sardine, *Sardinops sagax*, 9.1, 14.0, 31.3 mm, from Kramer (1970); (G-I) round herring, *Etrumeus teres*, 5.6, 8.2, 16.7 mm.

condition may be produced in the onlooker. Most often, however, the flicker fusion phenomenon brings a fusing in the beholder's perception of the snake's bands, a greying of them, to the point where bands and the snake no longer exist. The beholder stares fixedly at the spot where he first saw the snake and misses the fact that the snake is passing from his view.

The serially arranged post-anal melanophores of teleost larvae may function in just this manner, and indeed the obfuscation may even be more effective owing to the rapid lateral beats of the larval tail. Flicker fusion may be another reason for the widespread occurrence of serially arranged lateral gut melanophores, and the effect may be even further heightened in species where the lateral gut series and the post-anal series form a continuum. Another possible adaptive advantage of melanophores is related to the specificity of their pattern. Melanophore pattern is one of the most useful characters for distinguishing among species of teleost larvae. It is possible that unique melanophore patterns could serve an infraspecific recognition function and aid in the location and exploitation of food patches. That is, the feeding movements of one or more larvae of a species, made visible and instinctively recognizable by their unique melanistic pattern, could serve to attract other members of the species to the patch and thus provide a selective advantage. This hypothesis is consistent with the survival premium placed on patch feeding as a compensation for overall low prey densities (outlined in Dr. Hunter's lectures), and one could see how such a mechanism could lead to the proliferation of the intricate melanophore patterns, so characteristic of teleost larvae. Additionally, in many schooling fishes (e.g., clupeiforms) the onset of schooling is within the larval phase, and here again melanophore pattern may be an important factor in intraspecific recognition. One could even speculate that the behavioral mechanisms of early larval patch feeding could have been intimately involved in the evolutionary origin of schooling and other aggregation phenomena.

A remarkable feature of clupeiform larvae, which they share with elopiforms, is the phenomenon of fin migration. Fage (1920) and Lebour (1921) described how, in the late larvae of many clupeiforms, the dorsal and anal fins migrate anteriorly with respect to the myomeres. Anterior migration of the dorsal fin is greatest in the European pilchard, where the fin moves forward 11 myomeres during transformation. In the herring and sprat the fin migrates 7 and 5 myomeres respectively. Anterior migration of the anal fin is less pronounced in the above species (1, 6, and 4 respectively). In the Pacific sardine the dorsal fin migrates 10 myomeres and the anal fin 6, whereas in the northern anchovy the migration is barely perceptible (dorsal, 3; anal, 1). The functional significance of fin migration is unknown; perhaps the more posterior placement of the dorsal and anal fins during the larval stage could involve them in tail beat thrust.

In salmoniform fishes the larvae have undergone an extraordinary radiation, particularly among two deep-sea groups—the argentinoid smelts and the stomiatooids. These fishes have invaded deep oceanic waters, and the morphological specializations of the larvae must have played an important role

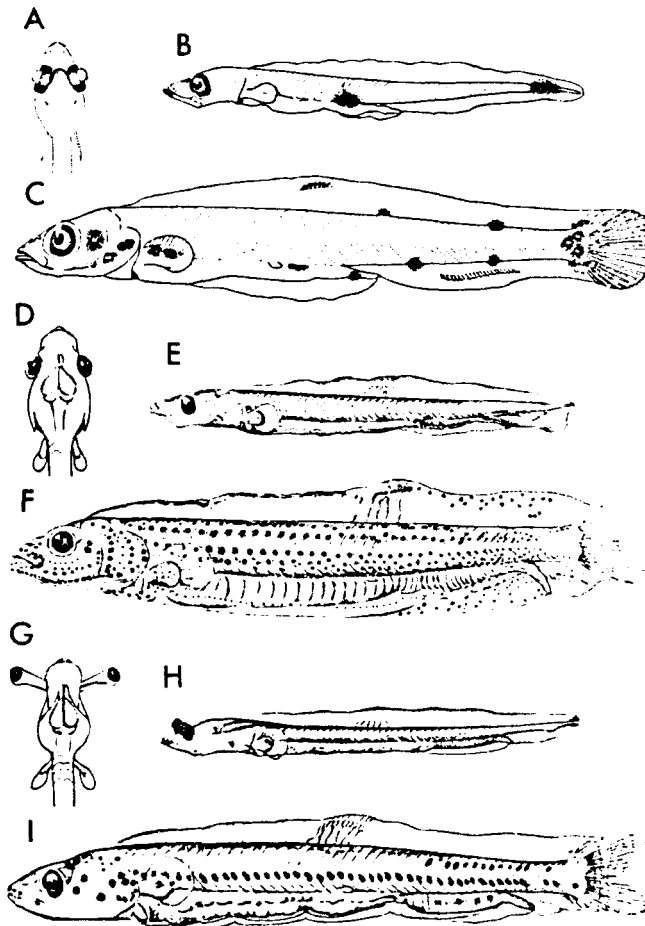


Figure 4. Larvae of argentinoid smelts showing various eye types. A-C, *Bathylagus milleri* with round eyes: (A) dorsal view of head of 10.6-mm larva, (B) 10.6-mm larva, (C) 27.5-mm larva; (D-F), *Bathylagus wesethi* with elliptical eyes, (D) dorsal view of head of 8.5-mm larva, (E) 8.8-mm larva, (F) 24.5-mm larva, from Ahlstrom (1965); G-I, *Bathylagus ochotensis* with stalked elliptical eyes, (G) dorsal view of head of 8.5-mm larva, (H) 10.2-mm larva, (I) 21.5-mm larva.

in the penetration and exploitation of this demanding environment. The fin fold has become a prominent feature and, in many salmoniforms, the dorsal and anal fins develop within the fin fold tissue at some distance from the body. The extreme is found in some argentinoids where the dorsal and anal fins form at the fin fold margin and are connected to the body by a series of hyaline strands (Fig. 4). At metamorphosis the fins become connected with the body in the normal position. The voluminous fin folds may enhance buoyancy and are probably involved in locomotion by high frequency/low amplitude vibration as Hunter (1972) has described for anchovy larvae in the S-strike position. The peripheral location of the developing dorsal and anal fins in argentinoids may serve to support the fin fold while allowing maximum freedom for vibratory locomotion.

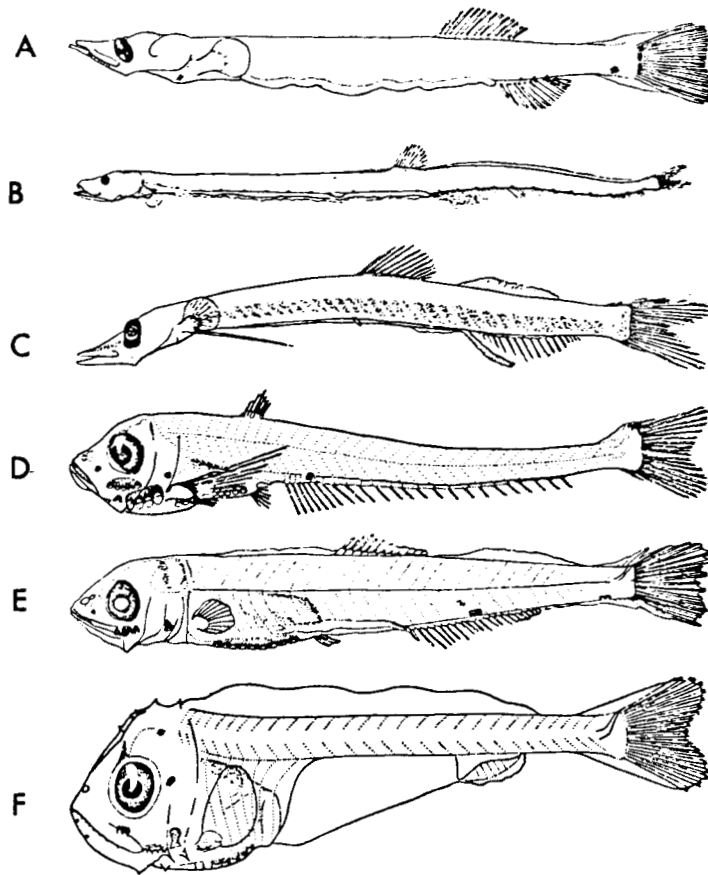


Figure 5. Larvae of stomiatoidei. (A) *Vinciguerria lucetia*, 9.0 mm, from Ahlstrom and Counts (1958); (B) *Diplophos taenia*, 44 mm, from Jespersen and Taning (1919); (C) *Ichthyococcus ovatus*, 15 mm, from Jespersen and Taning (1926); (D) *Danaphos oculatus*, 22.4 mm, from Ahlstrom (1974); (E) *Maurolicus muelleri*, 10.3 mm, from Okuyama (1971); (F) *Sternoptyx* sp., 8.8 mm.

A characteristic of argentinoid larvae is the specialization of the eye. In many species the eyes have become narrowed and elliptical and in some species they are borne on stalks (Fig. 4), the possible function of which we can consider when we take up the stomiatoidei.

The Stomiatoidei is dominated by two major groups, the gonostomatids and relatives and the melanostomatids and their relatives. Gonostomatid larvae have achieved a diversity of form (Fig. 5). Some, such as the clupeoid-like *Vinciguerria*, are slender with a long intestine. *Diplophos* and *Ichthyococcus* are even more attenuate, and in the latter the posterior section of the elongate intestine trails free from the body (a feature that is widespread throughout the melanostomatids) and the lower pectoral fin rays are extraordinarily elongate (a condition encountered in the larvae of some myctophid

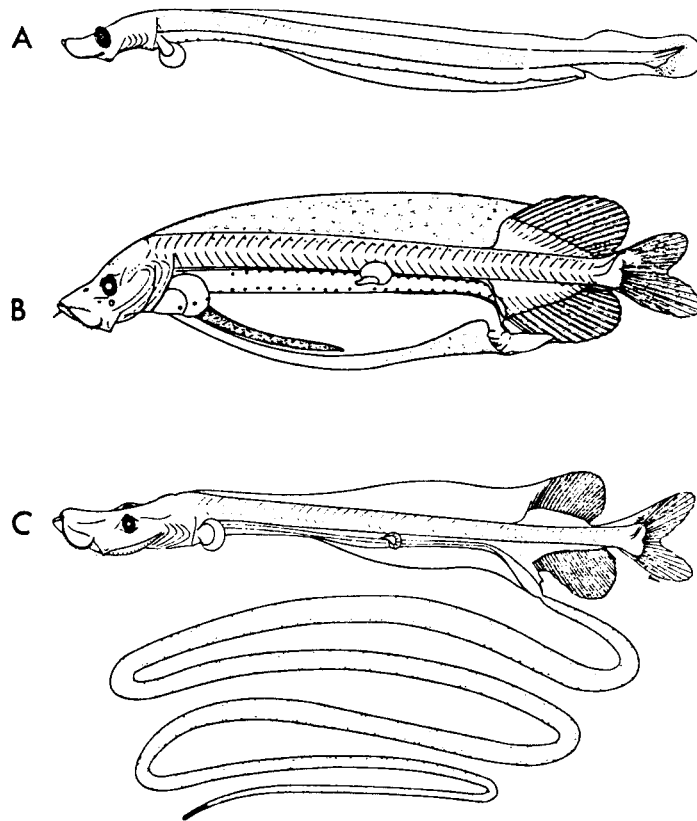


Figure 6. Larvae of stomiatoids. (A) *Stomias atriventer*, 10.0 mm; (B) *Bathophilus nigerrimus*, 21.7 mm, from Sanzo (1931); (C) Melanostomiid, 34.5 mm.

species). In another direction, genera such as *Maurolicus* and *Danaphos* are less attenuate, have shorter intestines, and begin to develop their clumps of photophores well before transformation. The foreshortening of the gut, deepening of the body, and development of larval photophore clumps is most pronounced in the larvae of hatchet fishes, a group closely allied with the gonostomatids.

Morphological specialization reaches a zenith in larvae of the Melanostomiidae and relatives (Fig. 6). They range from highly attenuate forms with long intestines such as *Stomias* to rather deep-bodied forms such as *Bathophilus* with its voluminous sac-like intestine. The large jaws and expansive gut of the latter would appear to allow it to utilize large prey. Elongation of the gut beyond the confines of the body is a common feature of many melanostomiid genera, and nowhere is this more apparent than in a larva tentatively identified to the genus *Leptostomias* (Fig. 6), where the gut is five times the length of the body and exceeds it in mass. One may speculate that, in this remarkable expression of alimentary dominance, digestion and absorption efficiency is improved while permitting a greater variety of prey types.

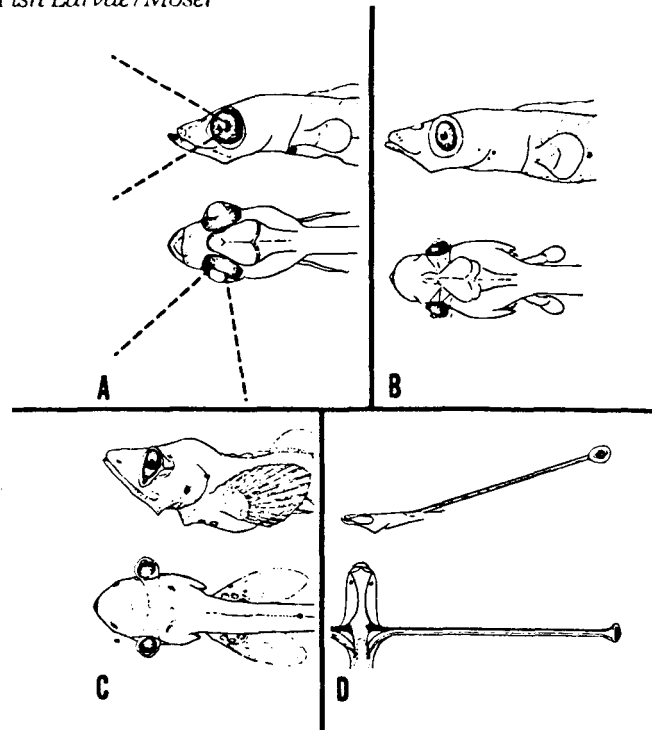


Figure 7. Various eye shapes of marine teleost larvae. (A) Round eye of *Bathylagus milleri*, lateral view (above) of 10.6-mm larva and dorsal view (below) of 9.5-mm larva; (B) Narrow sessile eye of *Bathylagus wesethi*, lateral view of 8.8-mm larva and dorsal view of 8.5-mm larva; (C) Narrow slightly stalked eye of 7.0-mm *Myctophum nitidulum* larva; (D) Markedly stalked eyes of 16-mm *Idiacanthus fasciola* larva. Figure from Weihs and Moser (1981).

Among the most specialized of all fish larvae are those of the stomiatoid family Idiacanthidae (Figs. 7 and 8). The eyes are borne on stalks that grow to one-fourth the length of the body and are then resorbed at transformation. Weihs and Moser (1981) have proposed a theory that might explain the adaptive advantage of this extraordinary specialization. If one assumes that the major causes of larval fish mortality are starvation, predation, and the interactions between them (Hunter, 1976), and that feeding and predator avoidance are largely dependent on vision, then eye specializations that improve feeding efficiency and predator avoidance are to be expected. Hunter (1972) showed that anchovy larvae notice and strike at food particles located within a 60° cone with a maximum height of about one body length and demonstrated that sighting distance and visual field are major limitations for feeding larvae.

Weihs and Moser (1981) suggest that enlargement of the visual field has evolved progressively through several stages, the first being a narrowing of a sessile round eye (Fig. 7B). In contrast to the round cup-shaped eye which lies flat in the developing orbit, the elliptical eye would have an increased rotational ability around the long axis, thus enlarging the volume observable from a given point. The next stage would be the extension of the eyes on short

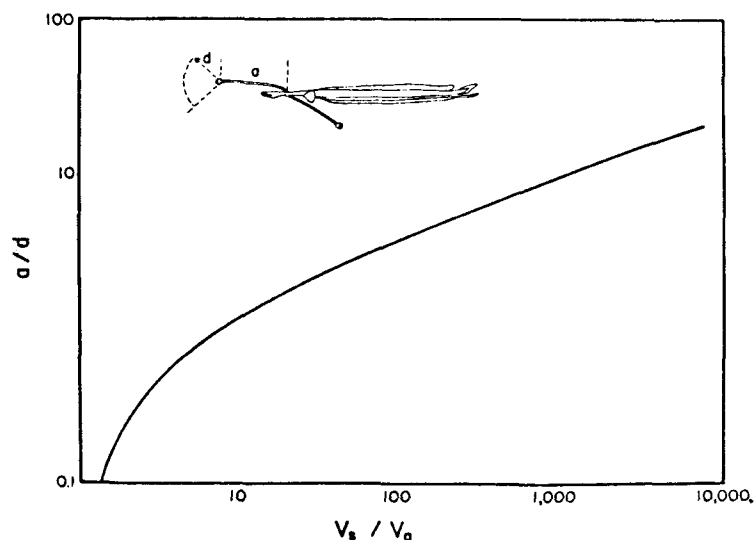


Figure 8. Theoretical relation of eye stalk length to perception distance in fish larvae. Ratio of the volume sighted by stalked eyes V_s to that covered by fully rotatable eyes attached to the head V_a , versus the ratio of stalk length "a" to perception distance "d." *Idiacanthus* larva is shown to illustrate the geometrical parameters. From Weihs and Moser (1981).

stalks so that they lie just outside the margin of the eye (Fig. 7C). Such eyes could be even more freely rotated so that the observable volume would approach that of a sphere. Extension of the eyes on pedunculate stalks would further increase this volume (Fig. 7D).

These specializations raise the possibility of detecting prey from greater distances with a minimum of body motion, thus both conserving energy and reducing predator cues. Weihs and Moser (1981) calculate a tenfold increase in visual volume for elliptical eyes compared with round eyes and as much as an additional tenfold advantage for eyes borne on stalks (Fig. 8). The fact that protruding eyes have evolved independently in larvae of three families of anguilliform eels, in argentinoid and stomioid salmoniforms, and in the myctophiform lanternfishes points to the evolutionary value and persistence of the adaptation.

The order Myctophiformes is in some ways the most varied and interesting teleost order from the standpoint of larval development. Shallow-water benthic forms such as the synodontid lizardfishes have elongate larvae with long strait intestines, reminiscent of clupioid larvae (Fig. 9A). The large conspicuous melanistic blotches spaced evenly along the sides of the gut are characteristic of lizardfish larvae. Other benthic forms such as *Aulopus* and *Chloropthalmus* have shorter intestines with a single dorsally located melanistic blotch (Figs. 9B,C). Some deep-living benthic and benthopelagic forms have larvae with magnificent enlarged diaphanous fins (Fig. 9D). Larvae of the pelagic myctophiforms display great diversity of form. Notosudids have

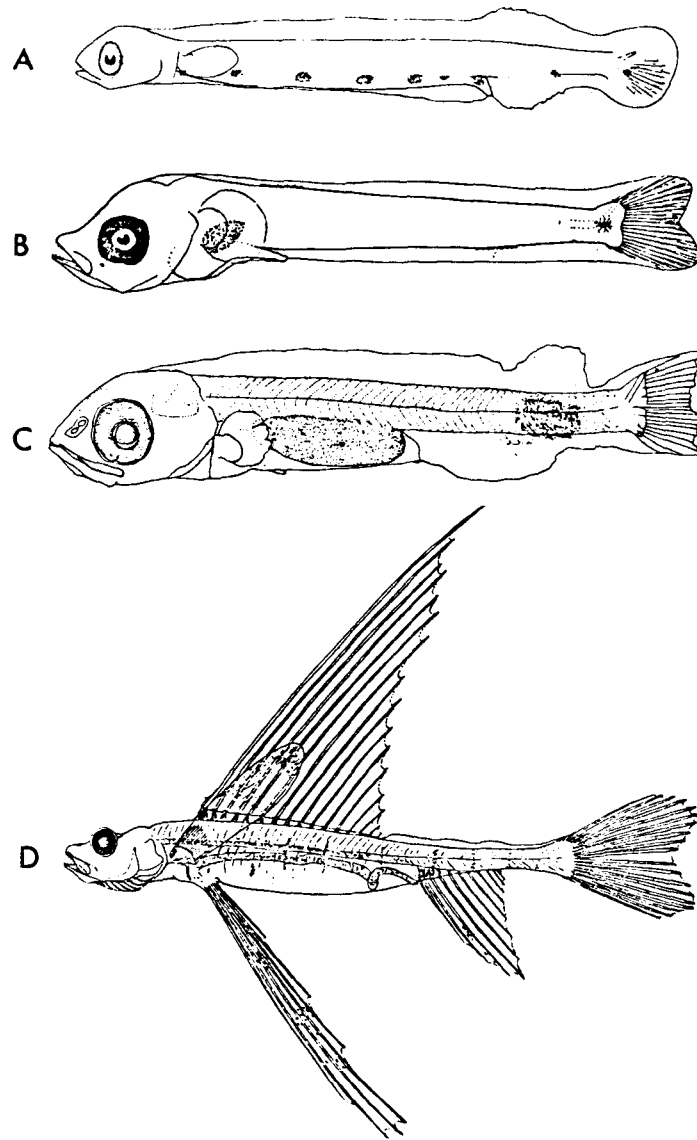


Figure 9. Larvae of demersal myctophiforms. (A) *Synodus lucioceps*, 10.5 mm; (B) *Chlorophthalmus agassizi*, 9.5 mm, from Taning (1918); (C) Aulopid, 12.3 mm, from Okiyama (1974, courtesy of Springer-Verlag New York, Inc.); (D) Bathysaurid, 33 mm, from Marshall (1961).

elongate larvae with narrow elliptical eyes and curiously complex melanophore patterns in the caudal region (Fig. 10A). Larvae of the paralepidids, midwater predators, are elongate and have extremely short intestines that lengthen markedly during the larval stage. Their characteristic pigmentation consists of large melanistic blotches that are added serially along the dorsal aspect of the gut as it elongates and may function in maintaining a masking capability commensurate with gut length (Fig. 10C-E). Larvae of another

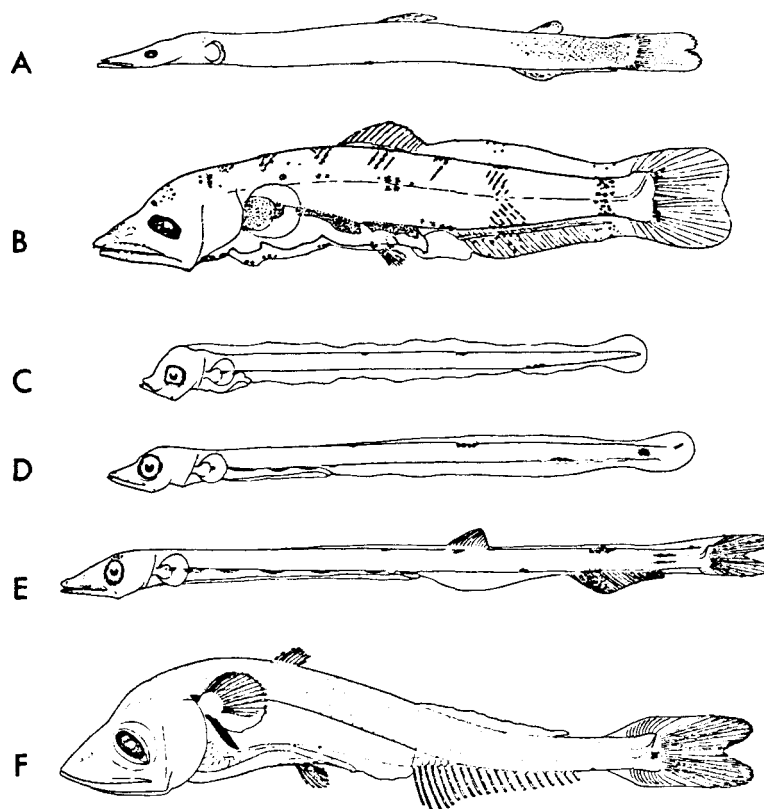


Figure 10. Larvae of midwater myctophiforms. (A) *Ahliesaurus berryi*, 30.5 mm, from Bertelsen et al. (1976); (B) *Evermannella balbo*, 11.5 mm, from Schmidt (1918); (C-E) *Lestidiops ringens*, 9.4, 16.5, 28.5 mm; (F) *Scopelarchoides nicholsi*, 23.0 mm.

midwater predatory group, the Scopelarchidae, have large jaws and a short bulbous gut that is covered by one or two very large melanistic blotches positioned directly over the saccular portion of the gut (Fig. 10F). Larvae of this group have also developed remarkably narrow eyes with pendant chorioid tissue.

In no other teleost group have the larvae explored so many pathways of evolutionary diversity as in the myctophid lanternfishes. As the largest family in the order (more than 30 genera and about 200 species), myctophids are ubiquitous in the world ocean. In a typical oceanic plankton tow about half the total fish larvae are those of lanternfishes, and Barham (1970) may be justified in suggesting that lanternfish have the largest biomass of any vertebrate group. Dr. E.H. Ahlstrom and I have been studying lanternfish larvae from a taxonomic viewpoint for over fifteen years, and our findings are detailed in four papers (Moser and Ahlstrom, 1970, 1972, 1974; Ahlstrom et al., 1976). Today I will only have time to describe some of the most prominent morphological specializations and discuss possible adaptive significance.

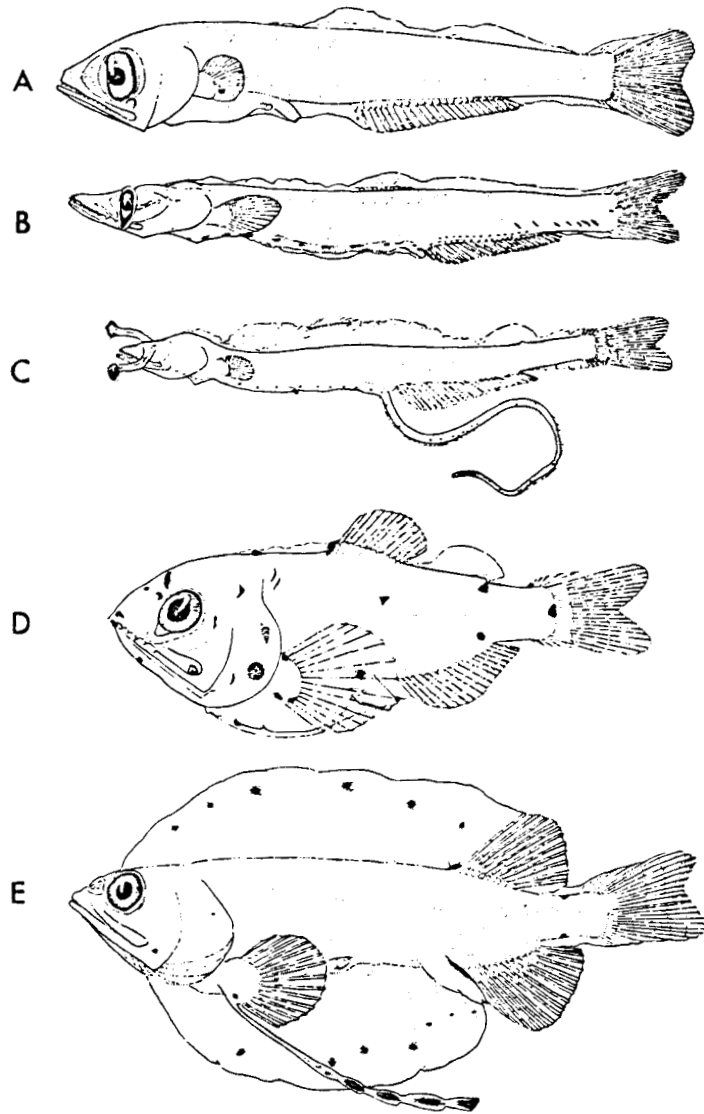


Figure 11. Larvae of myctophine lanternfishes. (A) *Protomyctophum crockeri*, 14.2 mm, from Moser and Ahlstrom (1970); (B) *Hygophum reinhardti*, 12.8 mm, *ibid*; (C) *Myctophum aurolaternatum*, 26.0 mm, from Moser and Ahlstrom (1974); (D) *Myctophum asperum*, 6.8 mm, *ibid*; (E) *Loweina rara*, 17.6 mm, from Moser and Ahlstrom (1970).

Paxton (1972) divided the family into two subfamilies, Myctophinae and Lampanyctinae, on the basis of adult osteology and photophore characters. Moser and Ahlstrom (1970) showed that characters of the larvae also divide the family, with a distribution of genera that mirrors that of Paxton. Myctophine larvae have narrow elliptical eyes and most lampanyctine larvae have round eyes, although some genera (*Triphoturus*, *Notolychnus*, *Lobianchia*) of

the latter have experimented with narrowing of the eye (Figs. 11–14). Stalked eyes are found in three of the narrow-eyed myctophid genera. Practically every larval teleost body form is represented among myctophid genera, and we have been able to delineate a unique larval morph for each genus. Body form ranges from slender to stubby to leaf-like. The uncoiled intestine has distinctive transverse rugae and ranges from short, to elongate, to trailing free from the body (Fig. 11). The intestinal rugae, which are pronounced enough in myctophids and relatives to serve as an identifying character of the group, provide a mechanism for increasing the digestive and absorptive surface of an uncoiled gut.

Myctophid larvae exhibit a diversity and specificity of melanophore pattern that is unmatched among teleosts, and indeed each genus has a pigment morph that is as taxonomically useful as the structural morph. I believe that the specificity and often limited variation of pigment patterns in this group, perhaps in concert with the unique structural morphs, relate to the species recognition/patchfeeding idea presented earlier in the lecture.

A remarkable feature of lanternfish larvae is the development of one or more pairs of photophores, a character we saw in gonostomatids and sternoptychids. Larvae of almost every lanternfish species develop a photophore (later to become the middle branchiostegal photophore of juveniles and adults) below each eye. Considering the position and universality of occurrence of these photophores it is reasonable to suggest that they are functional and may lure and/or illuminate potential prey.

Additional pairs of photophores develop during the larval stage in three myctophine genera (*Benthoema*, *Diogenichthys*, and *Myctophum*) and in numerous lampnactine genera. These additional photophore pairs appear consistently in several areas— anterior to the eye, on the outer surface of the pectoral fin penduncle, and along the ventrum. The preorbital photophores, like the branchiostegal photophores, may be utilized in feeding. The light organs on the highly motile pectoral fin base may also be involved in feeding, possibly as lures. Typical locations for the ventral organs among the various genera are below the pectoral fin base, just anterior to the developing pelvic fin, and posterior to the anus; however, the sequence of appearance of the photophores is often highly specific (Figs. 12–14). In genera such as *Diogenichthys* (Fig. 12), where the sequence of appearance of multiple photophores is highly specific, the photophore patterns may function as infraspecific recognition signals in feeding as suggested for the melanophore patterns. Since each photophore has a heavily melanistic cup, they could enhance the specificity of the melanophore patterns during the day and provide a specific luminous pattern during dim light conditions.

In larvae of two genera (*Loweina* and *Tarletonbeania*) the lowermost pectoral finrays become elongate and bear serially arranged pigmented fleshy spatulations (Fig. 11E). These elongate ornamented rays, along with some neighboring rays, are resorbed at transformation. Larvae of these same genera have voluminous fin folds which are accommodated by the posteriad

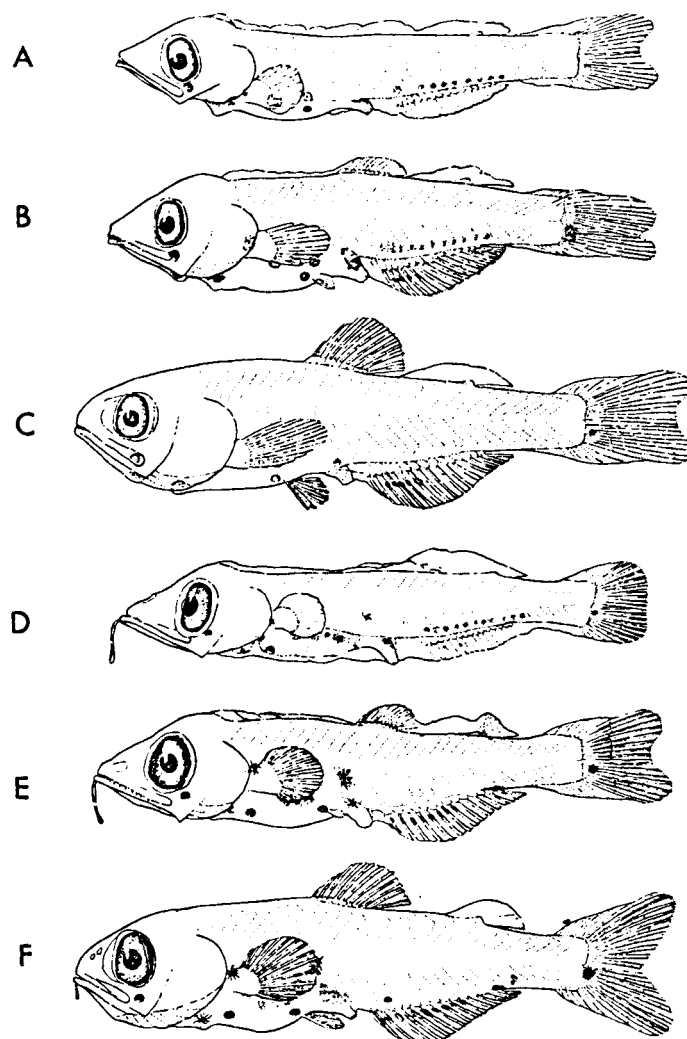


Figure 12. Larvae of myctophine lanternfishes. (A-C) *Diogenichthys lanternatus*, 6.6, 7.7, 12.3 mm; (D-F) *Diogenichthys atlanticus*, 7.2, 8.8, 12.8 mm. From Moser and Ahlstrom (1970).

displacement of dorsal and anal fins. One could postulate hydrostatic (energy saving) or nutritional (energy storage) functions for these remarkable structures. These functions could be related to orienting/stabilizing and sensory functions for the elongate rays. Another possibility is that both the voluminous fin folds and the elongate trailing pectoral fin rays enhance the apparent size of the larvae and thus function as a deterrent to potential predators. The facts that the fin folds are emphasized by an even distribution of large melanophores and that the elongate pectoral rays are provided with large melanistic spatulations support this idea.

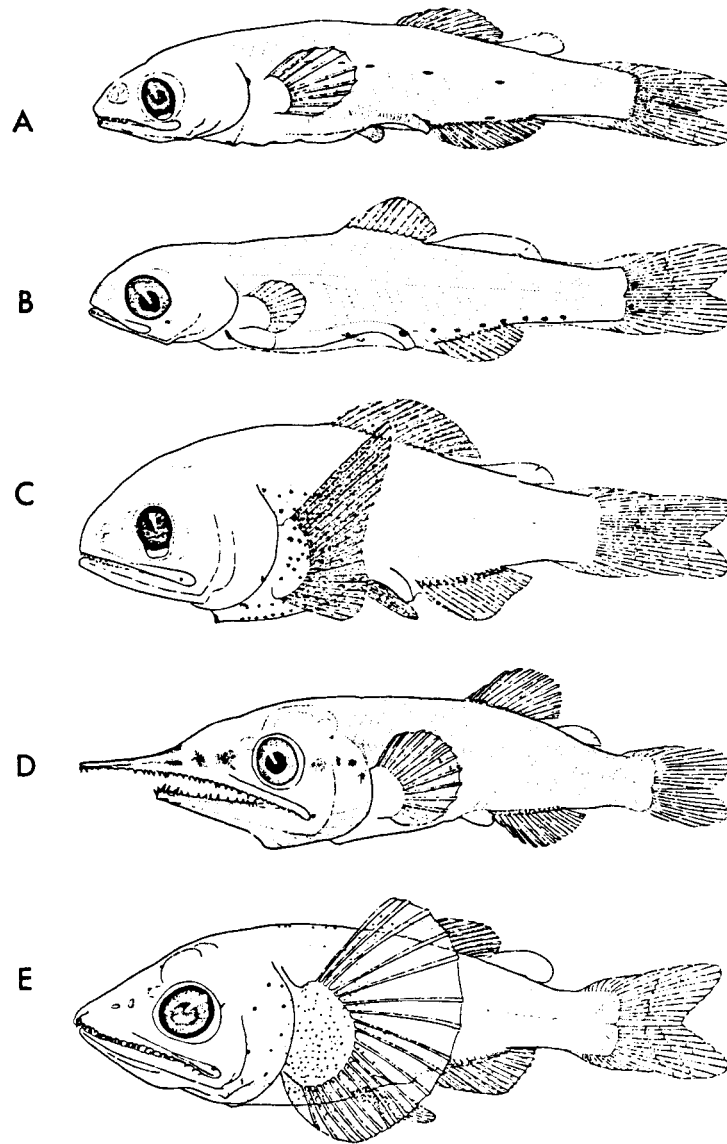


Figure 13. Larvae of lampanyctine lanternfishes. (A) *Triphoturus nigrescens*, 8.5 mm; (B) *Diaphus theta*, 6.9 mm, from Moser and Ahlstrom (1974); (C) *Lobianchia do-fleini*, 8.2 mm, *ibid*; (D) *Lampanyctus achirus*, 13.4 mm, *ibid*; (E) *Lampanyctus sp.*, 9.4 mm.

Enlarged pectoral fins with supernumerary rays also occur in *Myctophum* and *Symbolophorus* and, in the other subfamily, have reached a peak of specialization in one group of *Lampanyctus* (Moser and Ahlstrom, 1974). In these species, fin enlargement is accompanied by increasing robustness of the body and prolongation of the extraordinarily toothy jaws, giving them a distinct predatory appearance (Fig: 13D, E). The body form of these larvae is

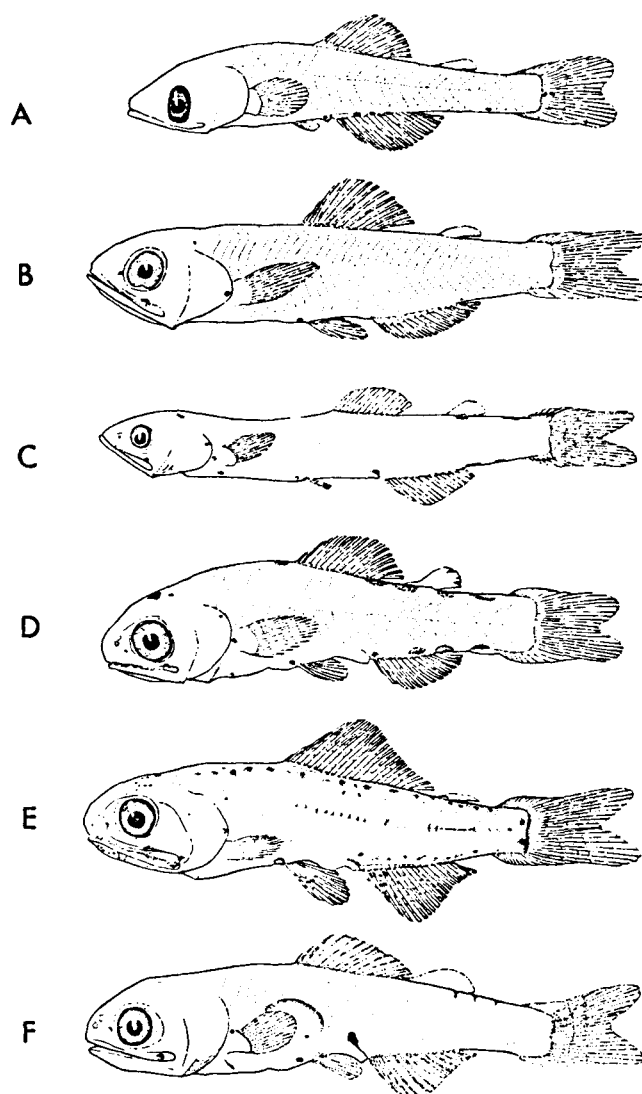


Figure 14. Larvae of notolychnine and gymnoscopeline lanternfishes. (A) *Notolychnus valdiviae*, 9.2 mm, from Moser and Ahlstrom, 1974; (B) *Ceratoscopelus townsendi*, 16.6 mm, *ibid*; (C) *Lepidophanes gaussi*, 13.5 mm, *ibid*; (D) *Lampadena urophaos*, 13.4 mm; (E) *Notoscopelus resplendens*, 16.2 mm; (F) *Lampanyctodes hectoris*, 11.7 mm, from Ahlstrom et al. (1976).

not commensurate with an S-shaped feeding strike, and one could speculate that pectoral fin thrust could play a part in the feeding strike. The “independence” of larval evolution is exemplified by these species when their robust, presumably motile and predatory larvae transform into soft-bodied, sluggish juveniles and adults. This is highlighted by the species with the largest larval pectoral fins, having the highest ray count of any myctophid, where the fin is lost completely in adults (Fig. 13E).

A major characteristic of gadiform larvae is a coiled gut, a feature found in larvae throughout the higher teleost groups. A coiled gut in the larval stage would appear to have certain advantages over the straight condition. By compressing the intestine in a mass behind the head, the digestive and propulsive systems become spatially separated and can specialize independently. Coiling would seem a natural prerequisite for the development of specialized digestive regions, separated by sphincters, that allow a more controlled rate of passage and digestion. A coiled gut with specialized functional regions is found in adults of most teleosts, whether or not their larvae have straight or coiled intestines. The development of the coiled specialized condition early in the ontogeny of most "advanced" teleosts appears to be a major evolutionary shift, permitting more efficient digestion and absorption and a greater variety of prey types.

In the gadoids, the cods and relatives, the larvae have large heads and jaws and an intestinal mass of large capacity (Fig. 15A–C). The ability of early larval stages to capture and retain prey items of a wide size range would seem advantageous to a group whose larvae are found typically in relatively deeper colder water (Sumida and Moser, 1980). In many species of morids, the pelvic fins appear early in the larval stage and develop elongate rays, sometimes ornamented with pigmented spatulations (Fig. 15E). Similarly, the macrurids develop large specialized pelvics, but also develop elongated dorsal rays and have curious paddle-shaped, highly peduncular pectoral fins (Fig. 16A).

Remarkable appendages are found in the larval stages of ophidioid fishes. Pearlfish larvae develop a highly modified dorsal appendage that bears leaf-like pigmented spatulations and in many species is directed anteriorly, possibly functioning as a lure (Fig. 16B).

What may be an example of mimicry is found in certain highly specialized ophidioid larvae that possess an ornate free trailing intestinal loop (Fig. 16C). Two such "exterilium" larvae have been reported, one taken in a trawl off Brazil (Nielsen, 1963) and the other captured alive after washing up on a beach near East London, South Africa (Fraser and Smith, 1974). A third specimen shown in Figure 16C was captured alive by a diver off New Guinea and deposited in the Scripps Institution of Oceanography Fish Collection (Cat. No. SIO 76–68). Although this larva is specifically distinct from the South African specimen (based on contrasting melanophore pattern, relative gut length, and other characters) both larvae have a fringe of fleshy cirri along the ventral edge of the intestinal loop and an arborescent appendage attached to the distal end of the loop. The cirri are marked with conspicuous large melanophores, and the resemblance of the entire structure to a siphonophore or other poisonous coelenterate prompted Fraser and Smith (1974) to suggest that the larvae may be discouraging potential predators through mimicry. One would associate such a large, highly specialized structure with prolonged pelagic life, and the authors may be correct in speculating that these are the larvae of some yet unknown group of slope or deep-sea ophidioids.

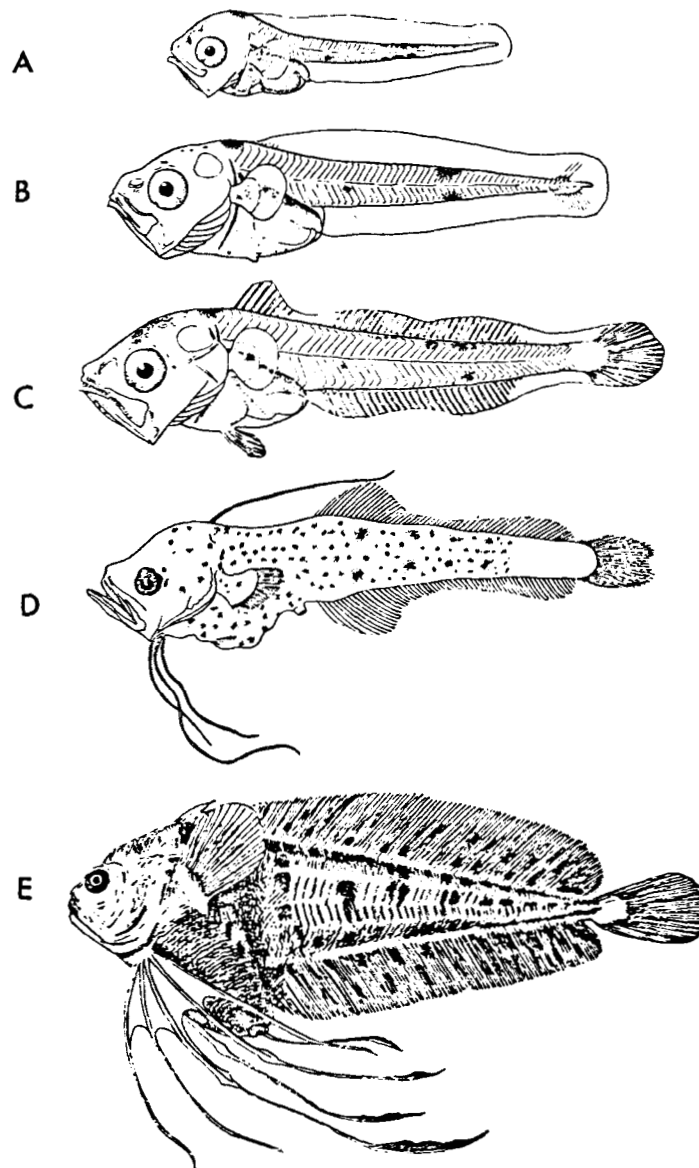


Figure 15. Young of gadiforms. (A-C) *Merluccius productus* larvae, 4.3, 7.7, 11.0 mm, from Ahlstrom and Counts (1955); (D) *Bregmaceros maclellandii* larvae, 10 mm, from D'Ancona and Cavinato (1965); (E) *Eretmophorus kleinbergi* pelagic juvenile, 105 mm, from D'Ancona (1933).

This remarkable adaptation probably arose secondarily from an adaptation associated with nourishment. Elongation of a straight intestine is common among salmoniforms and myctophiforms (Figs. 6, 11), presumably as an adaptation for improved digestion and absorption. Larvae of some higher teleosts have increased the gut mass by projecting an intestinal loop beyond the ventral body contour. This is particularly evident in bothid flatfishes such

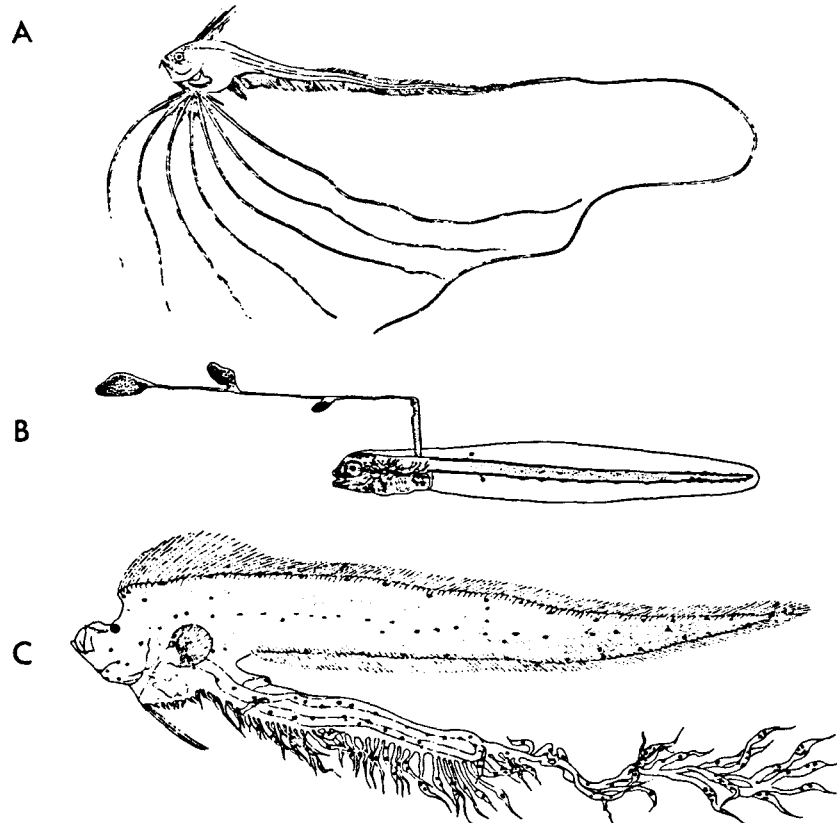


Figure 16. Young of gadiforms. (A) *Krohnius filamentosus* pelagic juvenile, 120 mm, from Sanzo (1933); (B) *Carapus acus* larva, 3.8 mm, from Padoa (1956); (C) *Exterilium* larva, 64 mm, from Scripps Institution of Oceanography Fish Collection, Cat. No. SIO 76-68.

as *Laeops* (Amaoka, 1972) and in cynoglossid flatfishes. Presumably the trailing gut loop began as a nutritional adaptation in exterilium larvae and evolved through increasing levels of ornamentation to culminate in a structure of dual function.

Specialized elongate and often ornamented pelvic and dorsal fin rays are found widely among higher teleosts, particularly among the perciforms, pleuronectiforms, and lampridiforms. In the latter the character achieves its earliest ontogenetic expression (Figs. 17, 18). Lampridiforms produce large eggs, up to several millimeters in diameter, in which the larvae develop to an advanced state and form their elongate ornamented pelvic and anterior dorsal rays before hatching. The fact that enlarged specialized pelvic and anterior dorsal rays appear in larvae of many phylogenetically diverse higher teleosts speaks for the importance of these adaptations, whose possible functional significance was discussed earlier.

Another group with large eggs and advanced development before hatching are the atheriniform fishes—the flying fishes, sauries, and silversides. The eggs often have attachment filaments or spike-like processes, and the larvae



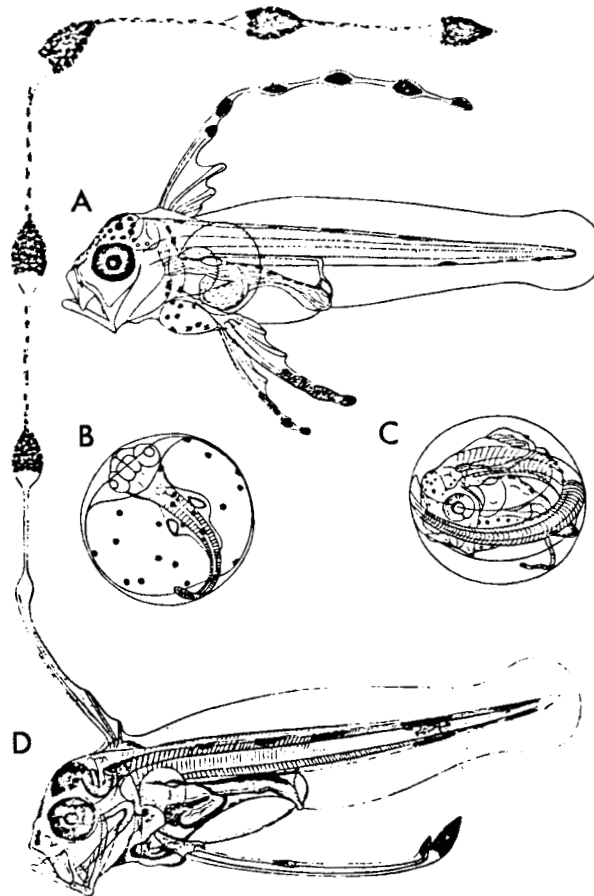


Figure 17. Larvae of lampridiforms. (A) *Trachipterus* sp., 7.6 mm, from Mito (1961); (B-C) *Trachipterus* sp., eggs, 1.8 mm, ibid; (D) *Lophotus* sp., 12.1 mm, from Sanzo (1940).

hatch with well-developed, highly functional pectoral fins and ontogenetically advanced and functional caudal fins (Fig. 19). The large egg, early fin development, and early-forming heavy melanistic pigmentation are adaptations to their stressful neustonic habitat that is characterized by high solar radiation, wind stress, and predation (by birds, invertebrates, and other fish).

The suggestion that ultraviolet radiation is the primary factor selecting for the heavy melanistic pigmentation found universally among neustonic fish larvae is supported indirectly by the experiments of John Hunter and his collaborators. Newly hatched anchovy larvae surviving four days of UV-B radiation equivalent to summertime levels off Southern California developed necrotic lesions of the eye and brain and had retarded growth and development (Hunter et al., 1979). Further experiments by Hunter et al. (in press)



What then is the major attraction of the neustonic zone? Zaitsev (1970) found relatively high concentrations of invertebrate plankters, of appropriate size for feeding larval fish, at the surface of the Black Sea. Similar studies yet to be carried out in oceanic waters may show that the neustonic zone is a kind of permanent food patch available to larval fish. Evolutionary requirements for successful exploitation of this "patch" appear to be a large, often attached, egg that permits advanced development before hatching, and a new-hatched larva that is relatively large, heavily pigmented, tough bodied, and capable of feeding and avoiding predators. That this neustonic morph has been achieved by species from so many phylogenetically divergent groups suggests a habitat of richness and complexity worthy of detailed study.

A major evolutionary theme in higher teleosts is spination. Within the dominant group of spiny-rayed teleosts, the Acanthopterygii, calcium metabolism and mobilization has reached a degree of perfection, and the array of fin spine, head spine, and dentitional arrangements is unmatched in complexity within the animal kingdom. The propensity to evolve specialized bony structures extends back into the larval period, where the diversity of fin and head spine specializations exceeds that of adult acanthopterygians (Figs. 20–26).

Primary sites for the accentuation and ornamentation of spines are at the anterior end of the dorsal and pelvic fins and on the head, usually posteriorly, where the head is widest and deepest, on bones such as the frontals, parietals, pterotics, posttemporals, preoperculars, and the opercular series (Figs. 20, 21). By having elongate fin and head spines at the widest region of the body the larva increases its size, from the standpoint of a potential predator, to a degree that is a function of spine length. Spines on the opercle can be extended laterally by flaring the gill covers to produce the same effect. The result is a prey item that is effectively larger, painful to ingest, thus more resistant to predation. Such a protective effect may be enormous at the size range of fish larvae, where small increments in actual or apparent prey size may have a disproportionately large effect in reducing predation by the smaller classes of organisms that prey on fish larvae.

Another effect of the elaboration of bony material into spines is to increase the specific gravity of the larva, thus posing a flotation problem. This is partially ameliorated in many larvae where structurally elegant spines are formed by supporting rods and thin serrated veins. Moreover, the center of gravity is shifted well forward in larvae with spiny heads. This appears to be compensated for in these larvae by a corresponding, more anterior location of the gas bladder. Many acanthopterygian reef fishes (beryciform and perciform) produce larvae which inhabit open ocean waters and must have extended larval periods for their survival. They are among the spiniest of all fish larvae, leading to the often stated notion that spines enhance flotation. It is likely that increased spination in acanthopterygian fishes has the opposite effect and that flotation is the province of the gas bladder, even in fishes

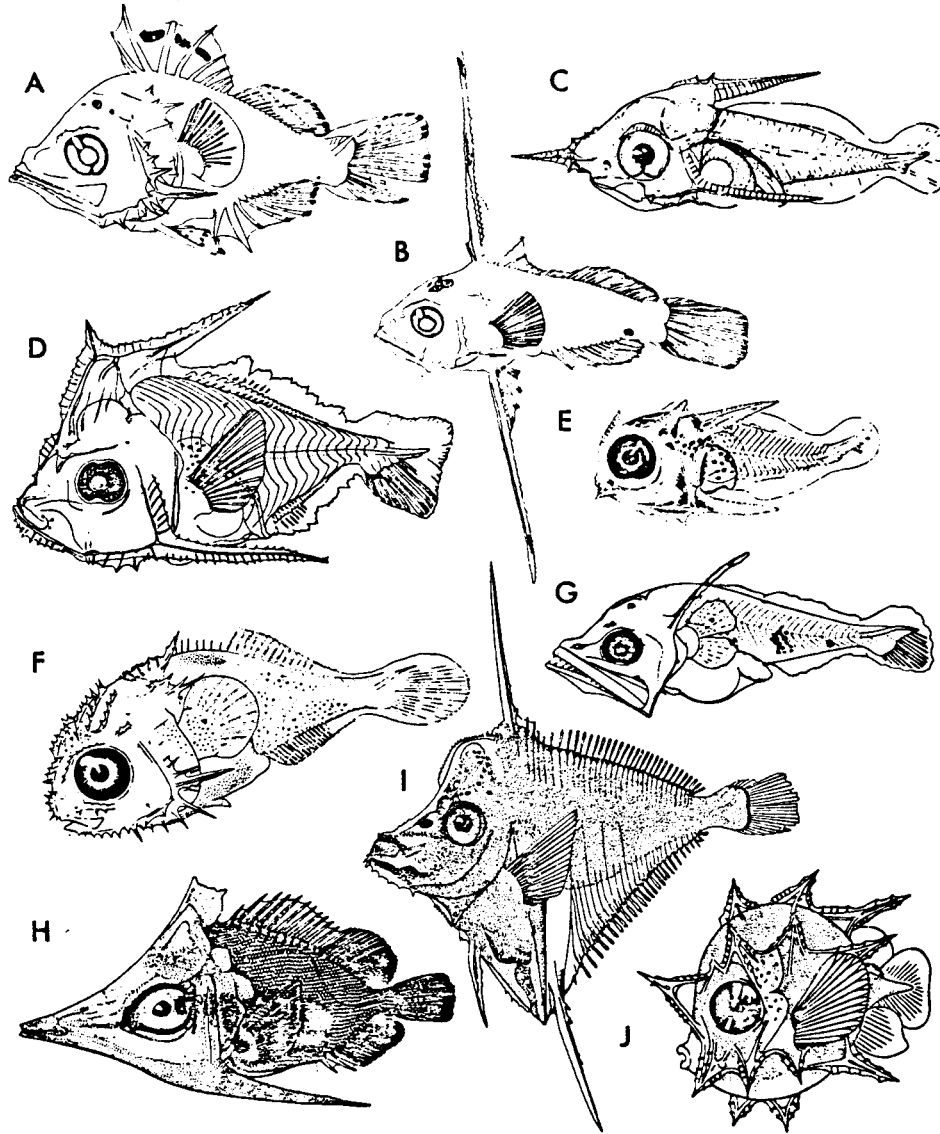


Figure 20. Larvae of acanthopterygii showing well-developed spination. (A) *Anthids gordensis*, 6.0 mm, from Kendall (1979); (B) *Epinephelus* sp., 8.4 mm, *ibid*; (C) *Holocentrus vexillarius*, 5.0 mm, from McKenney (1959); (D) *Antigonia rubescens*, 4.5 mm, from Uchida (1936); (E) *Dactylopterus volitans*, 3.5 mm, from Sanzo (1934); (F) *Caulolatilus princeps*, 6.0 mm; (G) *Champsodon snyderi* 4.6 mm, from Mito (1962); (H) *Forcipiger longirostris* (tholichthys stage), 17 mm, from Kendall and Goldsborough (1911); (I) acanthurid, 7 mm, from Weber (1913); (J) *Ranzania laevis*, 2.8 mm, from Tortonese (1956).

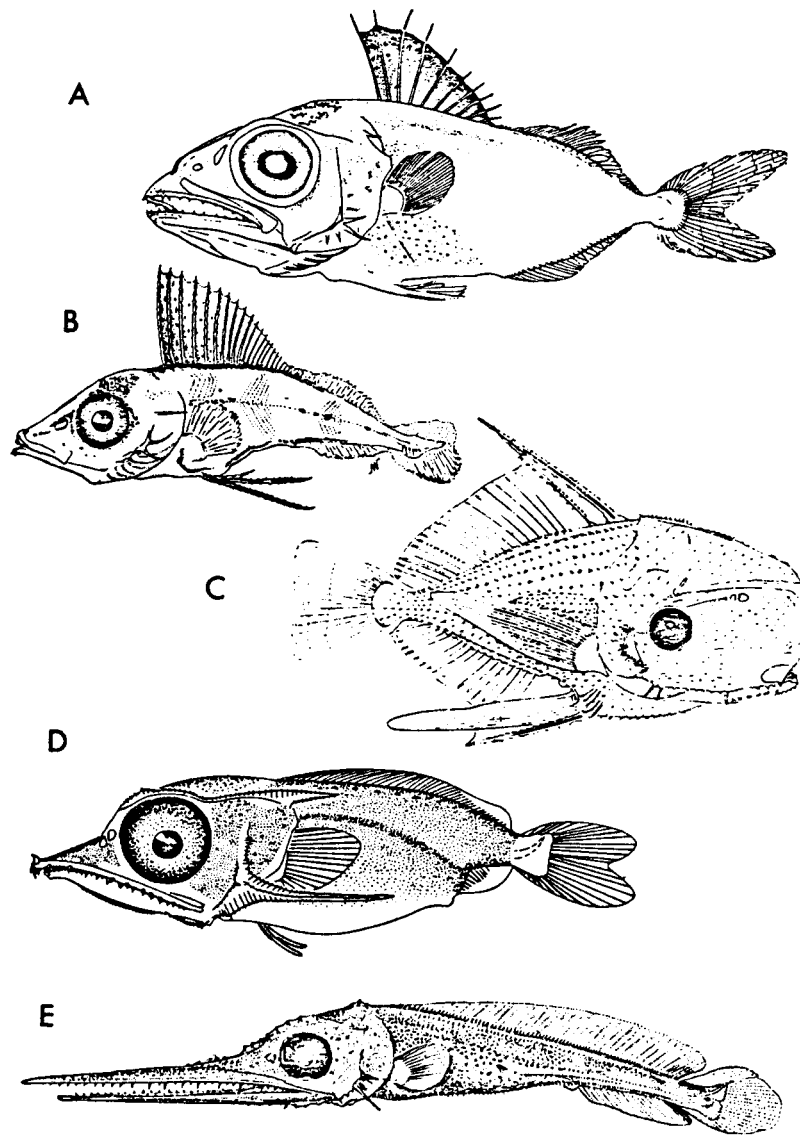


Figure 21. Larvae of scombroids. (A) *Thunnus albacares*, 14.2 mm, from Matsumoto (1958); (B) *Gempylus serpens*, 6.9 mm, from Voss (1954); (C) *Luvarus imperialis*, 11.9 mm, from De Gaetani (1930); (D) *Istiophorus americanus*, 8.1 mm, from Gehringer (1956); (E) *Xiphias gladius*, 15.6 mm, from Taning (1955).

where the bladder is lost during ontogeny. Voluminous finfolds (as in *Loweina*), distended gelatinous body envelopes (e.g., in lophiiforms and tetraodontiforms) and enlarged diaphanous fins may also serve to maintain buoyancy. It seems probable that the highly developed spination of many marine teleost larvae reflects the importance of predation as a major mortality factor during an extended larval period. In some reef and shore species a specialized pelagic juvenile stage is interposed between the larval and benthic juvenile stages. They have a unique morphology, with spines often accentuated beyond that of the larval period (Fig. 20H) and are capable of rapid transformation upon sensing bottom.

Although the adults of most spiny-rayed fishes are smooth-headed, the adults of some families within the acanthopterygian order Scorpaeniformes have complex and highly specific arrangements of head spines. Certain of these spines are well developed during the larval period and aid in identification, at least to the generic level (Moser et al., 1977; Richardson and Laroche, 1979). One group of scorpaenids, the rockfishes (*Sebastes* and relatives), have undergone extensive speciation in temperate and boreal waters. A major evolutionary trend in rockfishes is towards a more pelagic mode of life, with associated flexibility and streamlining of the body form, lightening of the skeleton, and reduction and loss of head spines. However, even the smooth-headed species have larvae with prominent head spines, many of which are lost gradually after the larval period (Moser, 1972; Moser and Ahlstrom, 1978; Richardson and Laroche, 1979; Laroche and Richardson, 1980). Retention of the ancestral pattern in their larvae suggests that the rockfishes are derived from warm-water benthic forms resembling the contemporary tropical genera, and also points out the ontogenetic and evolutionary plasticity of spine formation in this group (Moser and Ahlstrom, 1978).

Pigmentation has evolved to a high degree in larvae of acanthopterygians. In addition to the recurring types of melanistic pigment (e.g., gas bladder, oil globule, gut, post-anal series), whose possible functions were discussed earlier, unique melanopore patterns are found among the species of many groups. The possible role of pattern specificity in patch feeding was presented earlier. In addition to melanistic pigment, well-developed xanthic (yellow) pigment is encountered among the larvae of acanthopterygian fishes. The xanthophores may be in the same locations as the melanophores in a species, or they may be arranged in a distinctly different pattern, thus affording the larva two separate and unique patterns of pigmentation (see Mito, 1960, 1963, for examples). Where the xanthophores co-occur with the melanophores they may enhance the melanophore pattern signal, and where they are complementary they could serve to increase the specificity of the overall pattern. Xanthophore patterns seem to be best developed in coastal fishes, where reduced water clarity may obscure the melanistic pattern. An interesting feature of xanthophores is that they appear brown or black when viewed in transmitted light and have the appearance of melanophores when illuminated from the back. Much is to be learned about this dual capacity

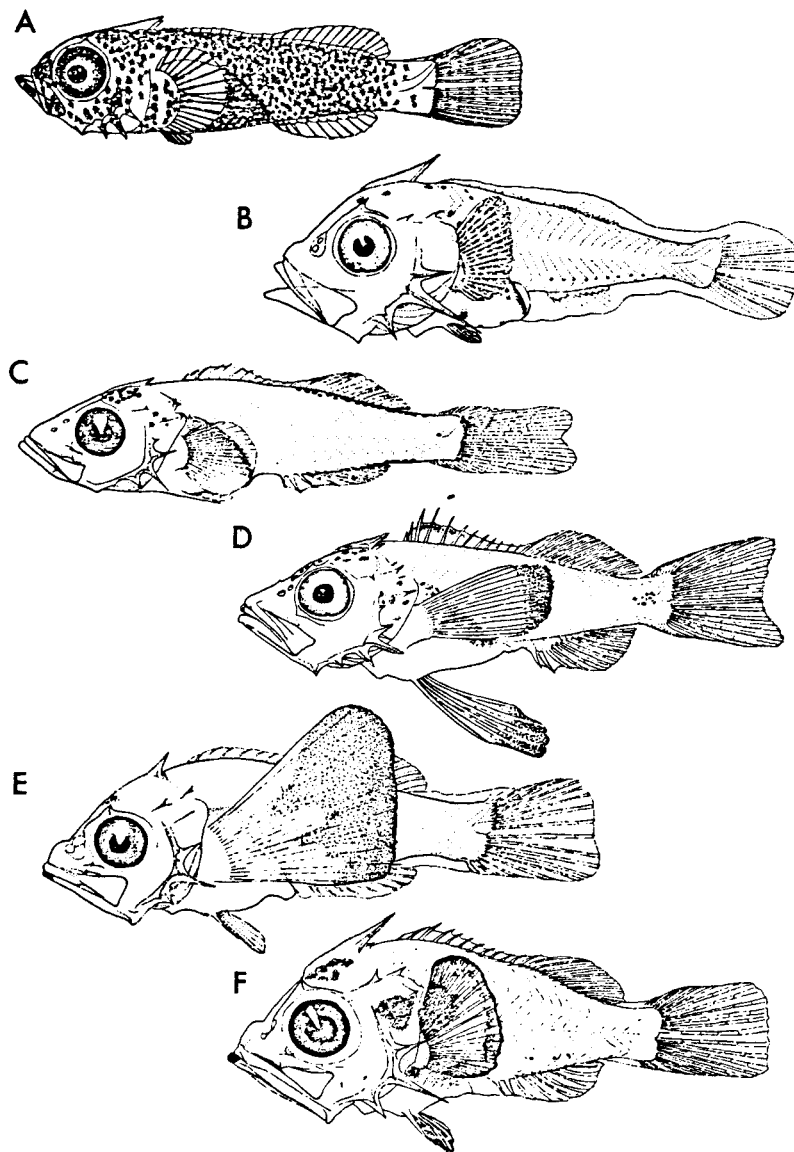


Figure 22. Larvae of *Sebastes*. (A) *S. oblongus*, 14 mm, from Fujita (1958); (B) *S. macdonaldi*, 9.0 mm, from Moser et al. (1977); (C) *S. jordani*, 15.5 mm, *ibid*; (D) *S. paucispinis*, 14.0 mm, *ibid*; (E) *S. levis*, 10.4 mm, *ibid*; (F) *S. melanostomus*, 8.2 mm, from Moser and Ahlstrom (1978).

and about the synthesis, arrangement, and role of xanthic pigment in fish larvae.

The flatfishes (Pleuronectiformes) are a large group of fishes which have become highly specialized for life on the seafloor and have both eyes on the side away from the substrate. In all flatfishes the eyes are symmetrical during

the larval stage and migrate to their asymmetrical position during metamorphosis. In the pleuronectids (the highly successful group of northern seas) and the soleids (the true soles of temperate and tropical waters), the left eye migrates over to the right side of the head and the left side faces the substrate. The opposite is true for the diverse bothid and cynoglossid flatfishes of tropical and subtropical waters. Early in the larval stage, flatfish are not unlike larvae of typical acanthopterygians; however, they soon develop a deep, laterally compressed body form and a markedly coiled gut that is positioned well forward in the body.

Pleuronectiform larvae have a large array of morphological specializations (Figs. 24–26). The most prominent specialization is size. Size has played an important evolutionary role in larval flatfishes, perhaps more than in any other group of teleosts. To begin with, pleuronectiform eggs span the entire range of teleost egg size. Species with small eggs (ca. 0.6 mm in diameter), approaching the lower limit of teleost egg size, are found throughout the flatfish groups, and several species in the pleuronectid genera *Hippoglossus*, *Hippoglossoides*, and *Reinhardtius* approach the upper size limit for pelagic teleost eggs. Most notably, the eggs of the Greenland halibut, *Reinhardtius hippoglossoides*, are 4.0–4.5 mm in diameter and the larvae are 10–16 mm at hatching (Jensen, 1935).

The range of sizes encountered among flatfish larvae is greater than in any teleost group. Larvae of the achirine soles are among the smallest of all teleost larvae. For example, larvae of the lined sole, *Achirus lineatus* (Fig. 26), are 1.6 mm long at hatching and complete metamorphosis before they are 5.0 mm (Houde et al., 1970). In contrast, the larvae of some pleuronectids and bothids attain very large sizes (Figs. 24–25). Dover sole (*Microstomus pacificus*) larvae exceed 60 mm in length, and those of the rex sole (*Glyptocephalus zachirus*) reach a maximum of about 90 mm (Pearcy et al., 1977). Larvae of bothid genera such as *Kamoharaia*, *Laeops*, and *Taeniopsetta* reach sizes in the 70–90 mm size range, and those of *Chascanopsetta* exceed 100 mm (Nielsen, 1963; Amaoka, 1970, 1971, 1972). Barham (1966) observed from a submarine a remarkable bothid larva that he estimated to be more than 220 mm in length. The point is that, in flatfish, egg and larval size (and accordingly age) has been explored as a major adaptation.

Shallow or estuarine forms, such as the achirine soles, have solved the problem of recruitment of planktonic larvae to an areally limited bottom habitat by reducing the length and therefore the dispersal of the larval state. In contrast, the deepest living species have protracted the larval state through sustained growth, thus increasing the probability of settling success following shoreward and bottomward drift or migration. Not only is the time interval available for settling extended, but the length and time range over which metamorphosis can occur is increased in the species with larger larvae. This phenomenon is clearly demonstrated among the species of *Pleuronichthys* where there is a gradation in size at metamorphosis (Fig. 24). The bay and nearshore species transform and settle at small sizes, and the deeper water

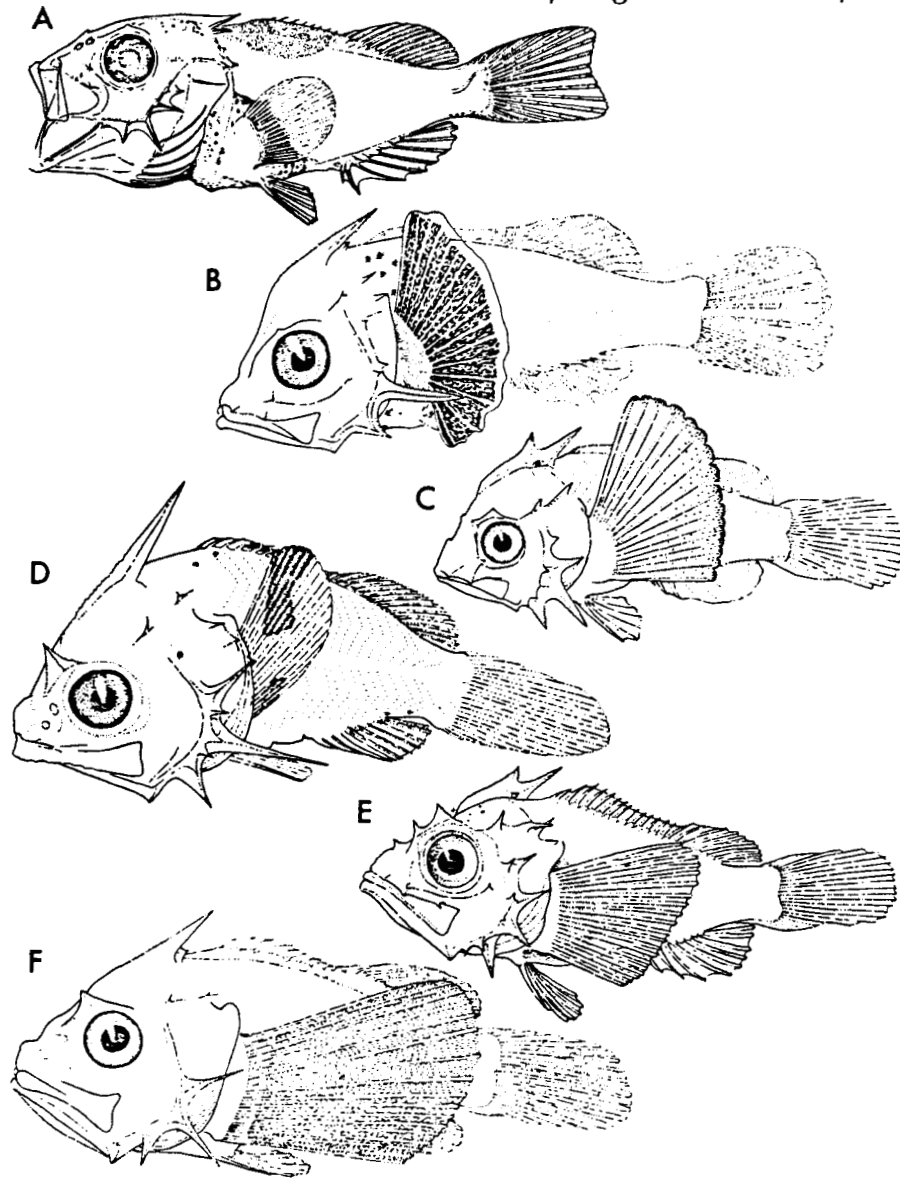


Figure 23. Larvae of scorpaenids. (A) *Helicolenus dactylopterus*, 19.0 mm, from Tanning (1961); (B) *Scorpaena guttata*, 6.2 mm, from Moser et al. (1977); (C) *Scorpae-nodes xpris*, 6.2 mm, *ibid*; (D) *Pontinus* sp., 5.0 mm, *ibid*; (E) *Sebastolobus altivelis*, 11.2 mm, *ibid*; (F) *Ectreposebastes imus*, 6.7 mm, *ibid*.

species attain larger sizes before metamorphosis (Sumida et al., 1979).

The heavily pigmented larvae of *Pleuronichthys* are taken frequently in our neuston collections. Particularly prominent in these collections are fully transformed juveniles of the deeper water species, *P. coenosus* and *P. decurrens*. Since transformed flatfish have a blind side, they would be at a disadvantage in finding food and avoiding predators prior to settling. These disadvantages might be reduced in the neustonic zone, where juvenile

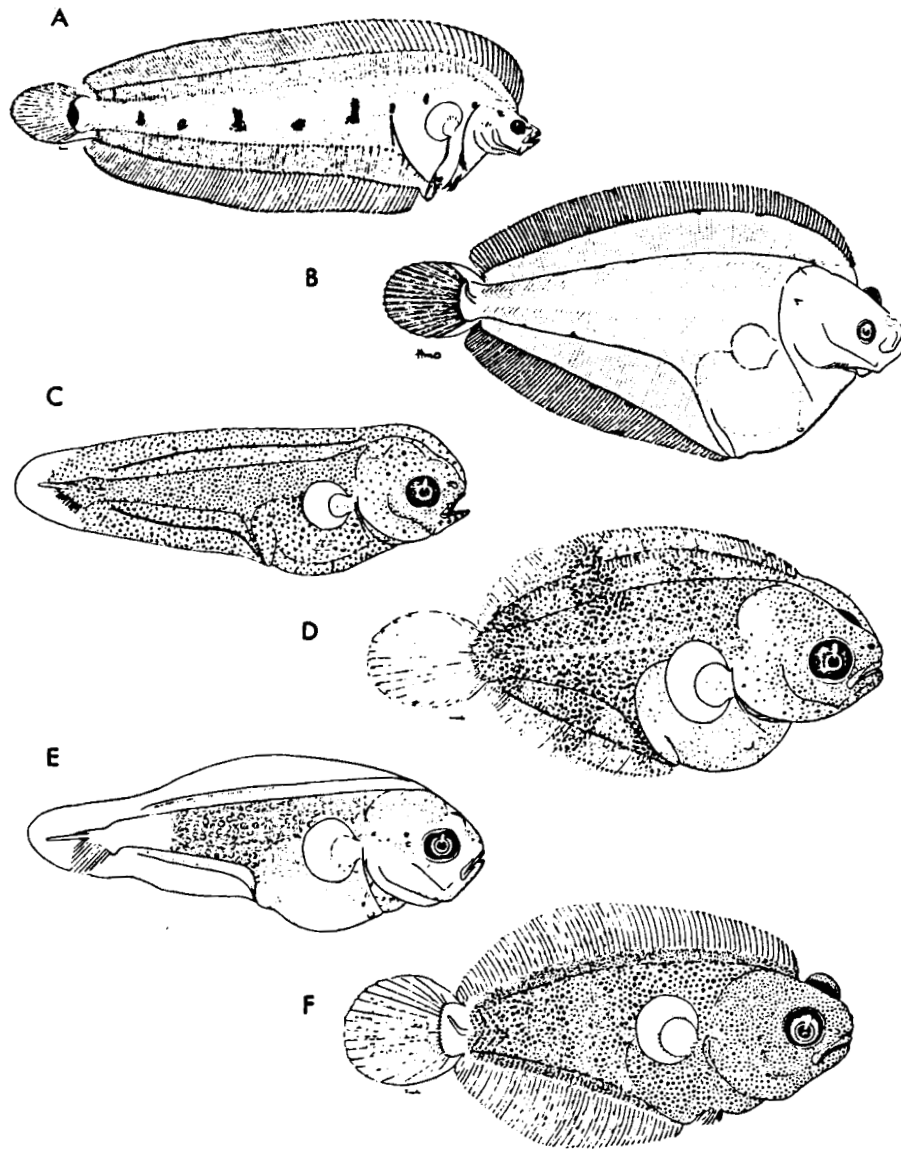


Figure 24. Larvae of pleuronectid flatfishes. (A) *Glyptocephalus zachirus*, 47.0 mm; after Ahlstrom and Moser (1975); (B) *Mierostomus pacificus*, 14.6 mm; (C) *Pleuronichthys decurrens*, 9.7 mm, from Sumida et al. (1979); (D) *P. decurrens*, 10.0 mm, showing initial eye migration, *ibid*; (E) *Pleuronichthys ritteri*, 5.6 mm, *ibid*; (F) *P. ritteri*, 6.4 mm, showing initial eye migration, *ibid*.

Pleuronichthys could feed efficiently on surface organisms while gaining some measure of disguise from their orientation just below the sea boundary. In effect, they may have "settled" temporarily at one surface before they arrive at water of appropriate depth for benthic settling.

The fact that flatfish species and genera with large larvae typically have broader zoogeographic distributions has led to the suggestion that increased

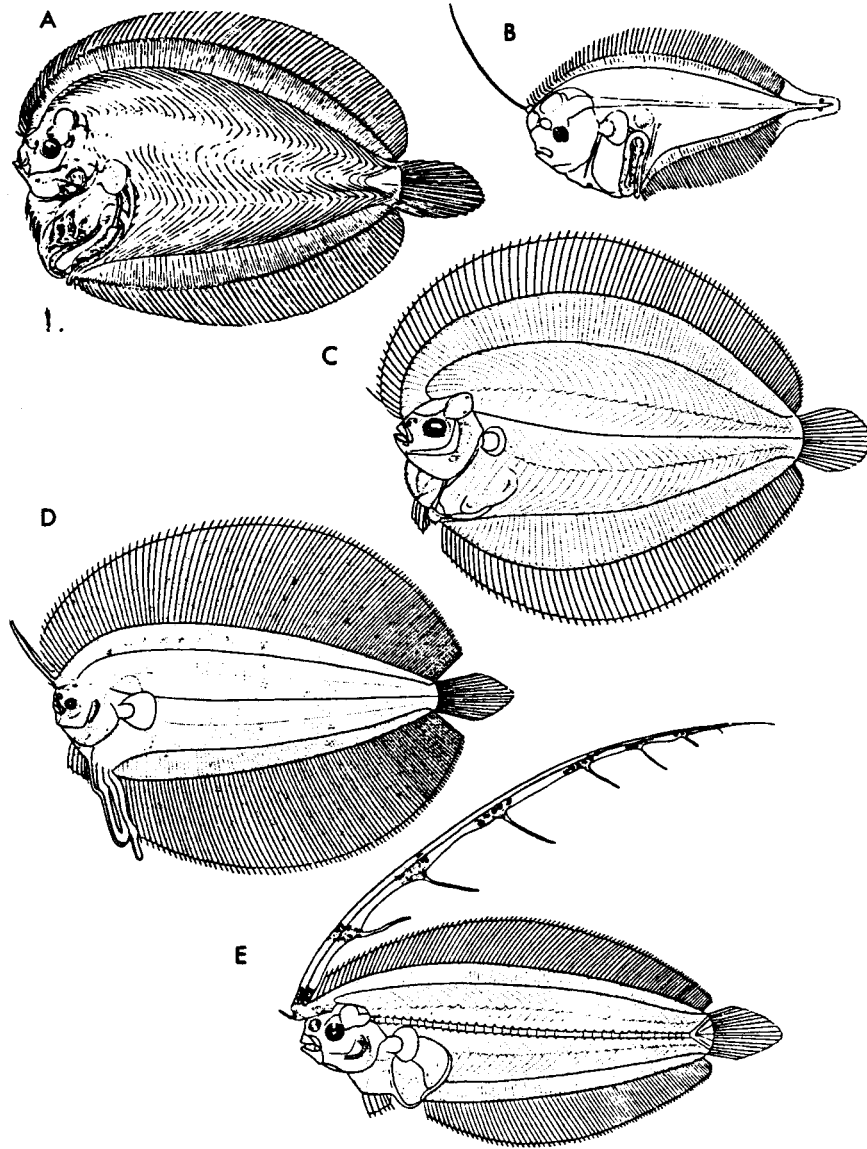


Figure 25. Larvae of bothid flatfishes. (A) *Bothus constellatus*, 27.1 mm; (B) *B. constellatus*, 6.2 mm; (C) *Taeniopsetta ocellata*, 59 mm, from Amaoka (1970); (D) *Laeops kitaharae*, 79 mm, from Amaoka (1972); (E) *Arnoglossus japonicus*, 30.5 mm, from Amaoka (1973).

size is a dispersal mechanism that increases species fitness (Brunn, 1937). An alternative hypothesis is that wide dispersal is a secondary consequence of increased larval size (and time) as a solution for the problem of larval settling in deep-living species.

The deep, sometimes leafshaped, body form of many larger flatfish larvae is related to a major locomotive adaptation. The deep body form results

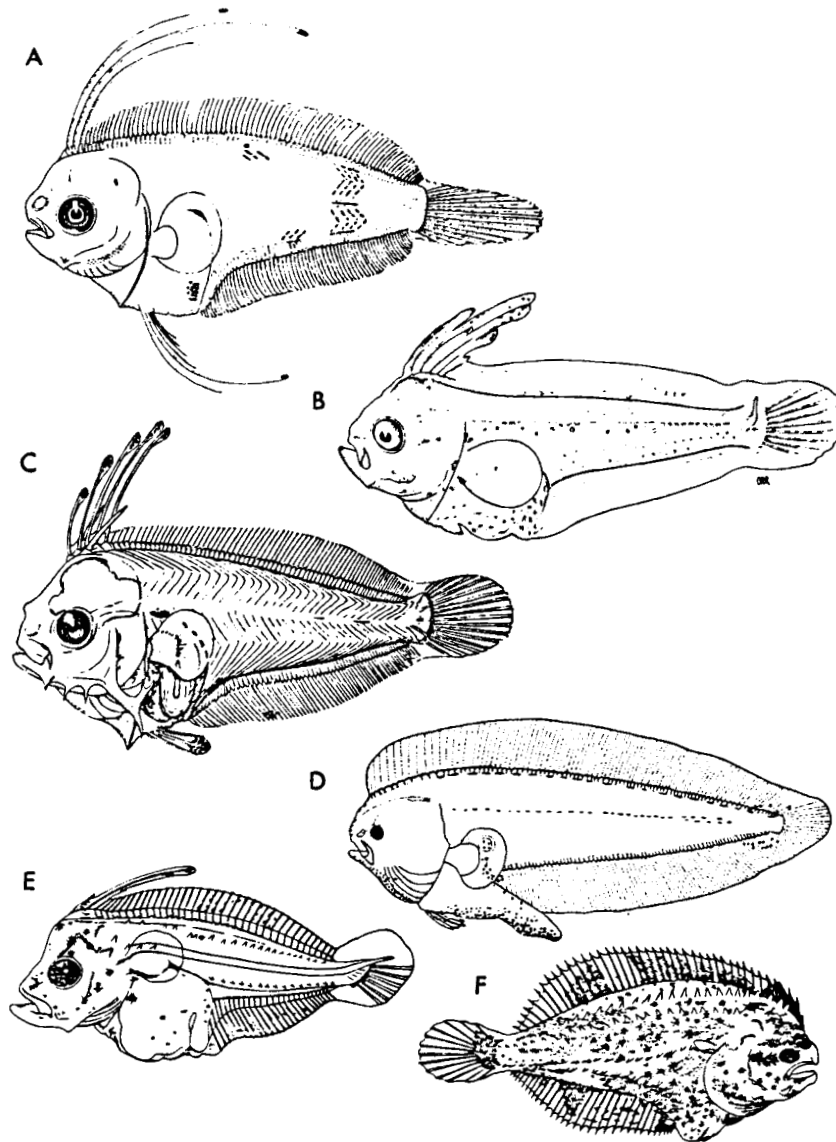


Figure 26. Larvae of paralichthyid, cymoglossid and soleid flatfishes. (A) *Citharichthys platophrys*, 8.6 mm; (B) *Paralichthys californicus*, 5.9 mm; (C) *Syacium ovale*, 6.5 mm; (D) *Symphurus atricauda*, 12.8 mm; (E) *Achirus lineatus*, 3.1 mm, from Houde et al. (1970); (F) *A. lineatus*, newly transformed specimen, 5.4 mm, *ibid.*

from the laterally compressed nature of the epaxial and hypaxial muscle masses, a widening of the dorsal and anal fin pterygiophore zones, and a lengthening of the dorsal and anal fin rays. The relative contribution of the pterygiophore zone to total body depth varies among species of flatfish. In some large deep-bodied larvae it contributes more to the total body depth than does the body musculature zone. Since flatfish larvae are extremely thin-bodied and flexible, the pterygiophore zone essentially enlarges the dorsal

and anal fins, thus enhancing the power and precision of fin undulation. Barham's (1966) account of undulatory propulsion in the large unidentified flatfish larva and his estimate of 0.5 m/sec swimming speed highlight the importance of dorsal and anal fin undulation, with its associated enhanced directionality, in larval flatfish locomotion.

Further specialization of the dorsal fin is seen in bothid larvae (Fig. 25), which develop an elongate, sometimes ornamented, second dorsal ray and in many paralichthyid larvae (Fig. 26) which have a group of elongate anterior dorsal rays forming a comb-like structure. The elongate ray in bothids might have a sensory function. Barham (1966) observed that the dorsal fin "comb" was held erect during undulatory locomotion of his giant larva, and John Butler and I have observed that the smaller dorsal fin comb of reared California halibut (*Paralichthys californicus*) larvae is also held erect during locomotion, suggesting that the comb may function as a rudder during undulatory locomotion and possibly as a stabilizing vane during caudal-fin-generated feeding strikes. In some paralichthyid larvae, the pelvic fins are also enlarged by ray elongation and may function during undulatory locomotion.

Another possible function for the elongate dorsal ray in bothids and the elongate dorsal and pelvic rays in paralichthyids is to increase the apparent size of the larva as a means of reducing predation. In some species of the bothid genus *Arnoglossus* (Fig. 25E), the produced dorsal ray bears fleshy streamers and heavy pigmentation, and in paralichthyids such as *Citharichthys* and *Syacium* (Fig. 26A,C), the tips of the elongate dorsal and pelvic rays have pigmented spatulations. These highly emphasized rays produce the effect of a second body contour and thus may increase the apparent size of the larva, as suggested earlier in the lecture for groups with similar larval appendages.

Other specializations of flatfish larvae include a vast array of head spine patterns, the secondary elongation of the gut coil to a trailing condition in bothids and cynoglossids, and the development of highly complex and specific melanistic pigment patterns, particularly in the pleuronectids (Figs. 24-26).

One could not leave a survey of teleost larval specialization without mentioning the remarkable larvae of lophiiform angler fishes (Fig. 27). Goosefish (*Lophius*) larvae, with their elongate dorsal and pelvic fin rays, huge pectoral fins, balloon-like outer skin, and large size are among the most beautiful of all fish larvae (Fig. 27A). The adaptations are associated with prolonged pelagic life and presumably are related to the evolution of deeper-living benthic species, as suggested above for deep-water flatfish. Ontogeny in the deep-water pelagic angler fishes (Ceratioidei) is fully described in Bertelsen's (1951) definitive monograph. Dr. Richard Rosenblatt's suggestion (pers. comm.) that the deep water pelagic angler fishes are neotenic derivatives of benthic coastal forms via extended pelagic larval or juvenile stages is fascinating to consider; the gelatinous balloon-like skin of adult ceratioids

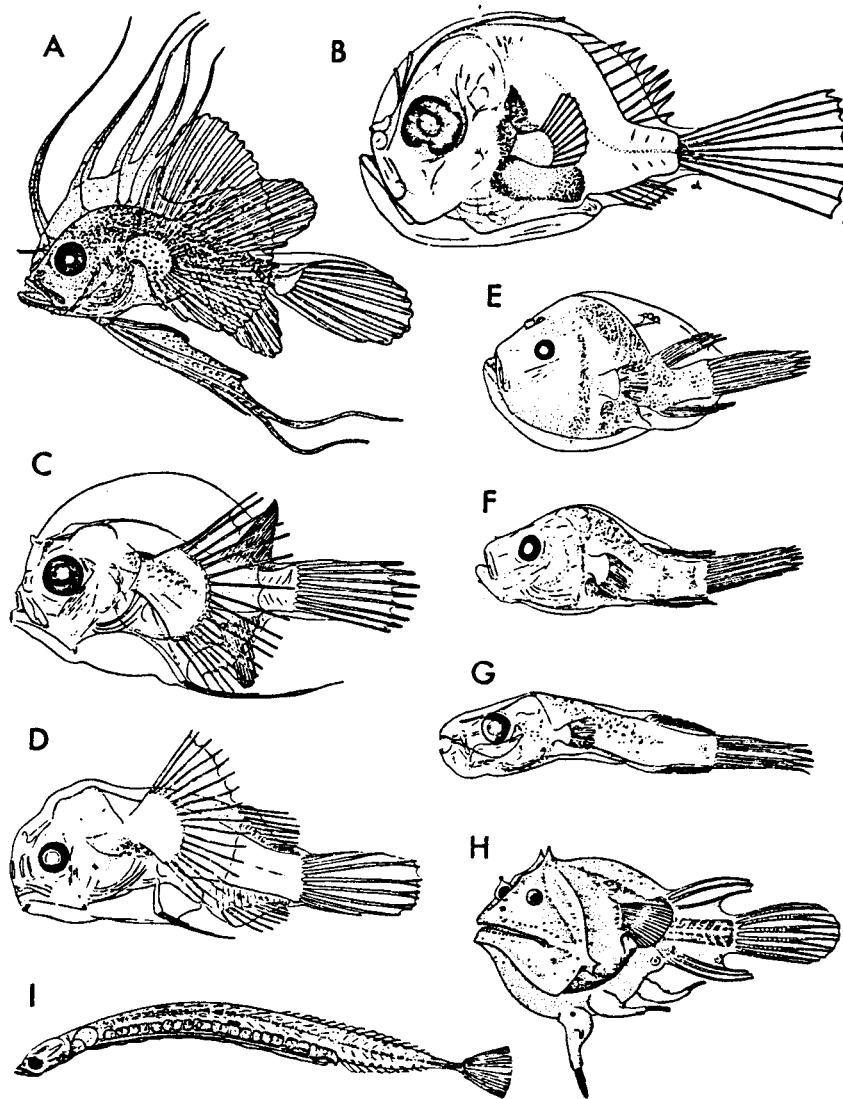


Figure 27. Larvae of lophiiforms and *Schindleria*. (A) *Lophius piscatorius*, 26 mm, from Taning (1923); (B) *Histrio histrio*, 2.0 mm, from Adams (1960); (C) *Caulophryne jordani*, 9.5 mm, from Bertelsen (1951); (D) *C. jordani*, 10.0-mm metamorphic male, *ibid.*; (E) *Cryptosaras couesi*, 11.8-mm female, *ibid.*; (F) *C. couesi*, 9.8-mm metamorphic male, *ibid.*; (G) *C. couesi*, 14.3 mm, oldest free-living stage of male, *ibid.*; (H) *Edriolychnus schmidti*, 70-mm adult female with 3 parasitic males, *ibid.*; (I) *Schindleria praematurus*, 15-mm ripe female, from Brunn (1940).

could be considered a retention of a pelagic larval character. The larvae of many ceratioids are sexually dimorphic and the mature males are distinctly larvoid in appearance. The reduction of ceratioid males to short-lived gamete carriers and the further reduction to attached "parasitic" sperm sacs in at least four families are well known. Larvoid males are also found in the stomioid, *Idiacanthus*, and the gobiid genus *Crystallogobius* appears neotenic. This tendency reaches the extreme in *Schindleria* (Fig. 271), where adults range from 10.5 to 20.5 mm SL, weigh 2.0–8.0 mg, and in all appearances are larvae (Brunn, 1940). Here neoteny has been explored to the lower limits of vertebrate size and marks a convenient point to end the lecture.

Acknowledgments

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