# Early Life History Stages of Fishes and Their Characters

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### PATTERNS OF TELEOST EARLY
### LIFE HISTORY

IN discovering that Atlantic cod lay free-floating planktonic eggs which develop into pelagic larvae, G. O. Sars, in 1865 (see Hempel, 1979; Ahlstrom and Moser, 1981) had also come upon an example of the widespread life history pattern of marine fishes. Most marine fishes, regardless of systematic affinities, demersal or pelagic habits, coastal or oceanic distribution, tropical or boreal ranges, spawn pelagic eggs that are fertilized externally and float individually near the surface of the sea (Fig. 5). These eggs range from about 0.6 to 4.0 mm in diameter (mode about 1 mm) and generally are spherical. Within a species there is little variation in egg characters such as size, number and size of oil globules, and pigmentation and morphology of the developing embryo. Development time is highly temperature dependent and also species-specific. The eggs hatch into relatively undeveloped yolk-sac larvae which swim feebly and rely on their yolk for nourishment while their sensory, circulatory, muscular, and digestive systems develop to the point that they can feed on plankton. Even these yolk-sac larvae have characters (pigment patterns, body size and shape, myomere number) that reflect their heritage. After the yolk is utilized, they develop transient "larval" characters such as pigment patterns and, in some, specialized head spines and fin structures that are apparently adaptive for this phase of their life history. During this period more characteristics of the adult (e.g., meristic characters) gradually develop. At the end of the larval stage, they may go through an abrupt transformation to the juvenile stage, particularly if they move from a pelagic to demersal habitat, or the transformation may be gradual. In some fishes, there is a prolonged and specialized stage between the larval and juvenile stages. These pelagic (often neustonic) forms eventually transform into demersal juveniles. The juvenile stage is characterized by specimens having the appearance of small adults—all fin rays and scales are formed, the skeleton is almost
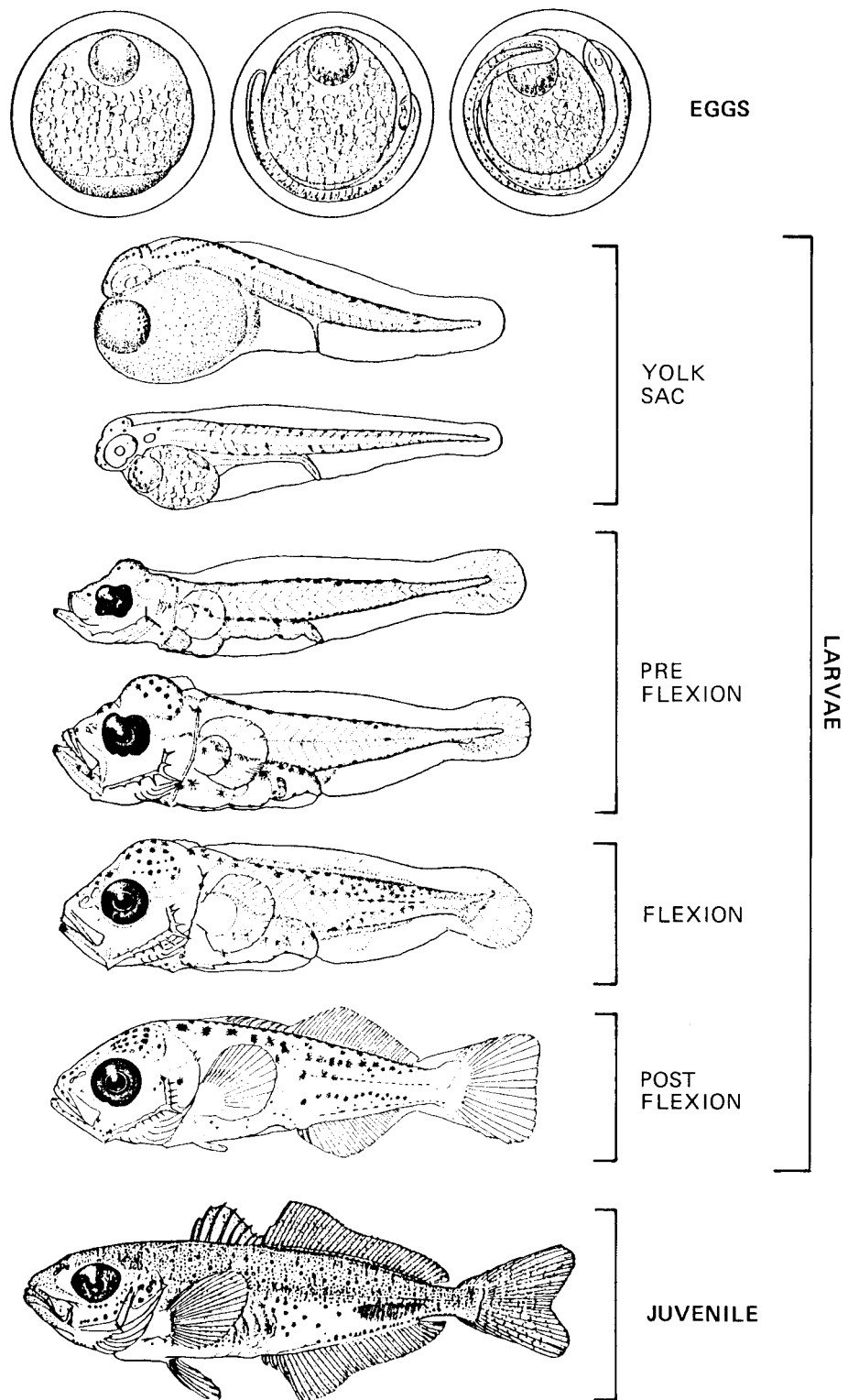
EGGS

YOLK SAC

PRE FLEXION

FLEXION

POST FLEXION

LARVAE

JUVENILE

Fig. 5. Early life history stages of *Trachurus symmetricus* from Ahlstrom and Ball (1954).

| END POINT EVENTS | Spawning | Blastopore closure | Tailbud free | Hatching | Yolk sac absorbed | Notochord starts to flex | Notochord flexion complete | Metamorphosis begun | Full finray complement present, squamation begun, loss of larval characters | Attain juvenile body proportions, pigment, habits | Attain adult body proportions, pigment, habits |

**TERMINOLOGY**

Primary developmental stages: Egg | Larva | Juvenile

Transitional stages: Yolk sac larva | Transformation larva

Subdivisions: Early | Middle | Late | Preflexion larva | Flexion larva | Postflexion larva | Pelagic or special juven.

**OTHER TERMINOLOGIES**

Hubbs, 1943, 1958: Embryo | Prolarva | Postlarva | Prejuvenile

Sette, 1943: Larva | Postlarva

Nikolsky, 1963: Embryo

Hattori, 1970: Prelarva

Balon, 1975 (phases): Cleavage egg | Embryo | Eleutheroembryo | Protopterygiolarva | Pterygiolarva

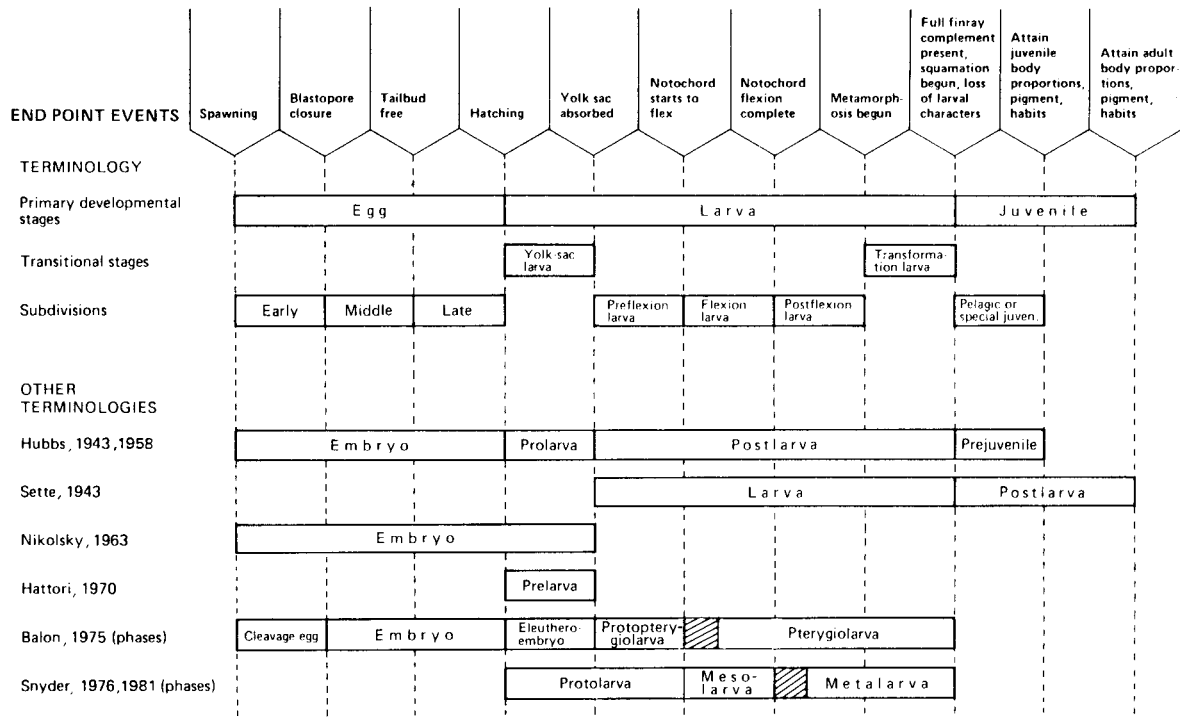Snyder, 1976, 1981 (phases): Protolarva | Mesolarva | Metalarva

Fig. 6. Terminology of early life history stages.

completely ossified, the larval pigment pattern is overgrown or lost and replaced by dermal pigment similar to that of the adults, and the body shape approximates that of the adults.

Although this is the most frequently observed life history pattern, there are many variations (see Breder and Rosen, 1966) often related to increased parental investment in individual progeny with a concomitant decrease in fecundity and larval specializations. There is scant information on the young of many deep-sea fishes, and this may be due in part to life history strategies that do not include eggs and larvae that occur in the epipelagic zone (where most of the collecting is done). Marshall (1953) discussed life history adaptations of these fish such as the production of few, large yolky eggs that hatch into relatively advanced larvae. These young may remain far below the more productive surface layers, and thus not be susceptible to most sampling procedures. Markle and Wenner (1979) cite evidence for demersal spawning of two species of groups (Alepocephalidae, Zoarcidae) that are seldom collected in the plankton as larvae.

Many coastal marine and nearly all freshwater fishes lay demersal eggs which are generally larger than the 1 mm mode of pelagic eggs. In such fish development from hatching through juvenile stage is direct and the larvae gradually attain adult characters of shape, pigmentation, and meristic features. The demersal eggs frequently are adhesive and laid in some sort of nest. Parental care of the nest is observed in many species, and this care may extend to the larvae after hatching (e.g., mouth brooding in cichlids, ariids). Parental care takes another form in *Sebastes*, where development through the yolk-sac stage takes

place in the ovary and first-feeding larvae are extruded. Viviparity, in which nourishment is supplied by maternal structures, has evolved many times (e.g., poeciliids, some zoarcids, embiotocids), whereby the larval stage is bypassed and the fish are extruded ("born") as juveniles (Wourms, 1981).

### EARLY LIFE HISTORY STAGES

Between spawning and recruitment into the adult population, most fishes undergo dramatic changes in morphology and hab-

TABLE 2. EXAMPLES OF CHARACTERS OF PELAGIC EGGS THAT MAY BE USEFUL FOR SYSTEMATIC STUDIES OF CERTAIN FISHES.

| Character | Character states | Systematic groups |
|---|---|---|
| Egg size | <1 mm–>5 mm | Pleuronectidae |
| | >3 mm–>5 mm | Anguilliformes |
| Egg shape | Round—oblong | Engraulidae |
| | | Ostraciontidae |
| Envelope sculpturing | Varying distances between pores | Gadidae |
| | Varying length/density of filaments | Atheriniformes (Exocoetidae) |
| Oil globule position | Anterior to posterior in yolk sac | Perciformes |
| Embryonic characters | State of development of various organs/organ systems at various developmental mileposts | Gadidae |
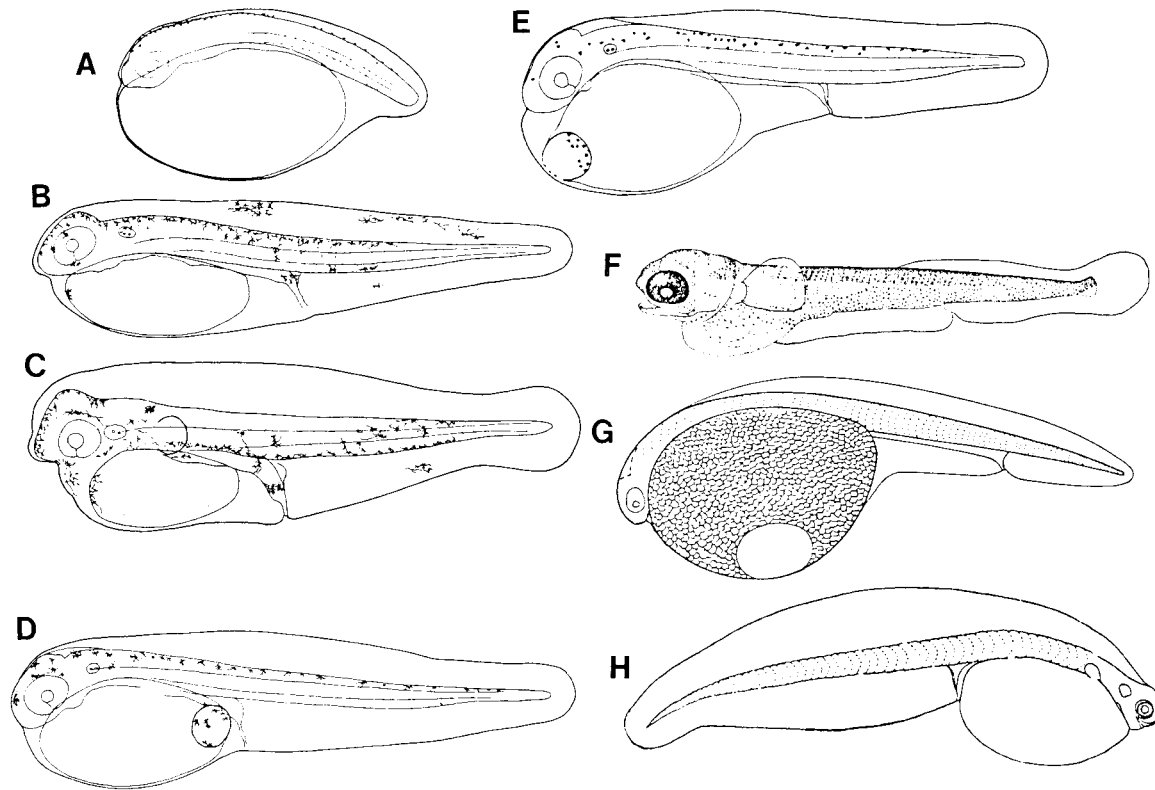
Fig. 7. Examples of features of yolk-sac larvae of teleosts. (A–C). *Paracallionymus costatus*. A. soon after hatching 0.98 mm NL; B. 1.8 mm NL; C. 1.9 mm NL. From Brownell (1979). Features demonstrated in: (A) include the small size of the larva, the lack of an oil globule, the segmented yolk, and the dorsally arranged melanophores; (B) demonstrates the migration of melanophores ventrally and the formation of the anus producing a preanal finfold; (C) demonstrates further ventral migration of melanophores, beginning of larval pectoral fin formation, the decrease in yolk-sac size, and beginning of pigment in the eye; (D) *Diplodus sargus*. 2.4 mm NL. From Brownell (1979). Single pigmented oil globule posterior in the unsegmented yolk and a short preanal finfold are demonstrated; (E) *Trachurus t. capensis*. 2.2 mm NL. From Brownell (1979). Single pigmented oil globule anterior in segmented yolk with moderately long preanal finfold demonstrated; (F) *Cololabis saira*. 5.1 mm SL. (original). Well-developed, heavily pigmented yolk-sac larva at hatching with notochord flexion beginning and some caudal rays formed; (G) *Argentina silus*. 7.7 mm. Redrawn from Schmidt (1906c). A large but poorly developed yolk-sac larva at hatching with a large oil globule; and (H) *Hippoglossus stenolepis*. 9.5 mm. From Pertseva-Ostroumova (1961). A large but poorly developed yolk-sac larva at hatching with no oil globule.

its. As mentioned earlier, at hatching, particularly in marine fishes with pelagic eggs, the fish is in an extremely undeveloped state and then, as a free-living individual, it gradually develops the adult characters. This process is continuous, but there are morphological and ecological mileposts that are significant in the life of the fish and which allow us to subdivide this process so that we can communicate results of our studies and compare different fishes at the same moment in development.

Fish early life history has been and continues to be studied from a number of different perspectives (Ahlstrom and Moser, 1976). Some studies deal directly with embryology and later ontogeny, others emphasize functional morphology of larval structures, apply larval features to taxonomic and systematic studies, investigate the ecology of eggs and larvae, or use these stages to address fishery-related problems such as assessment of spawning stock size and recruitment success. All of these

studies have in common the need to subdivide early life history and communicate information based on processes and events occurring during these subdivisions. As with any communication, it is vitally important to use terms that are clearly defined and this is particularly true with the diverse disciplines that are involved in larval fish studies. Historically, several disciplines have used different names for the same stage, or subdivided development differently [see Okiyama (1979a) and Fig. 6 in this paper]. This has led to confusion rather than communication.

Several criteria seem appropriate for defining stages of development to be used by students of any discipline. The variety of developmental patterns should be recognized and the definitions should apply to as many patterns as possible. Thus, stages should be based on very widespread, fundamental features of development. The stages should have some significance in the life history of the fish, both morphologically and func-
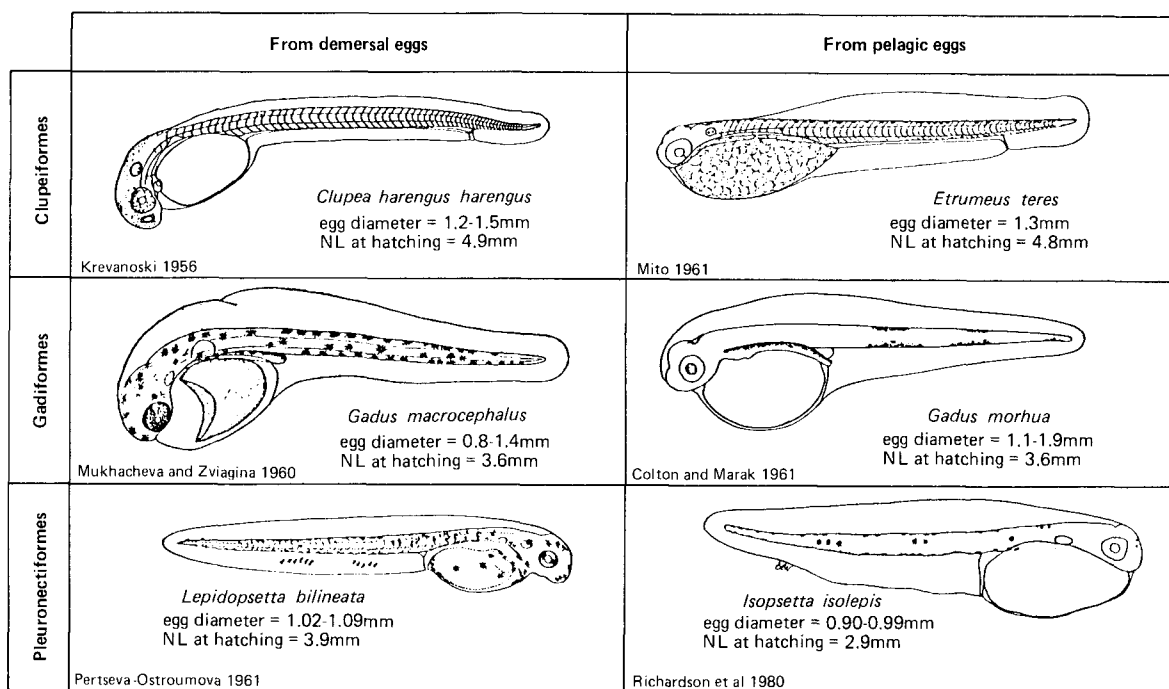
| From demersal eggs | From pelagic eggs |
|---|---|
| **Clupeiformes** Clupea harengus harengus egg diameter = 1.2-1.5mm NL at hatching = 4.9mm Krevanoski 1956 | Etrumeus teres egg diameter = 1.3mm NL at hatching = 4.8mm Mito 1961 |
| **Gadiformes** Gadus macrocephalus egg diameter = 0.8-1.4mm NL at hatching = 3.6mm Mukhacheva and Zviagina 1960 | Gadus morhua egg diameter = 1.1-1.9mm NL at hatching = 3.6mm Colton and Marak 1961 |
| **Pleuronectiformes** Lepidopsetta bilineata egg diameter = 1.02-1.09mm NL at hatching = 3.9mm Pertseva-Ostroumova 1961 | Isopsetta isolepis egg diameter = 0.90-0.99mm NL at hatching = 2.9mm Richardson et al 1980 |

Fig. 8. Newly hatched yolk-sac larvae of related fishes with pelagic and demersal eggs of comparable sizes.

tionally, such as a particular type of nourishment or locomotion. Also the endpoints for the stages should be easily observed and sharply defined.

The most general scheme of terminology of early development of fishes includes (Fig. 5):

The "egg stage" (spawning to hatching). The egg stage is used in preference to the embryonic stage because there are characters present during this stage other than just embryonic characters (e.g., those associated with the egg envelope).

The "larval stage" (hatching to attainment of complete fin ray counts and beginning of squamation). One of the fundamental events in development of most fishes is the flexion of the notochord that accompanies the hypochordal development of the homocercal caudal fin. It is convenient to divide the larval stage on the basis of this feature into "preflexion," "flexion," and "postflexion" stages. The flexion stage in many fishes is accompanied by rapid development of fin rays, change in body shape, change in locomotive ability, and feeding techniques.

The "juvenile stage" (completion of fin ray counts and beginning of squamation until fish enters adult population or attains sexual maturity).

Transitional stages can also be recognized: the "yolk-sac larval stage" (between hatching and yolk-sac absorption); and the "transformation stage" (between larva and juvenile). Metamorphosis occurs during this stage and is considered complete when the fish assumes the general features of the juvenile.

The life histories of some fishes include other specialized ontogenetic stages that have received various names. In some cases, these are the generic names under which these stages were described before they were recognized as larvae of other species (e.g., the leptocephalus stage of Anguilliformes, the scutatus stage of Antennarius, the vexillifer stage of Carapidae, and the kasidoron stage of Gibberichthys). In other cases, consistent features of development of a group permit useful subdivisions of stages (e.g., in leptocephali the engyodontic and euryodontic stages).

## THE EGG STAGE

Hempel (1979) reviewed the egg stage relative to fisheries investigations. Ahlstrom and Moser (1980) presented a concise review of the range of characters observed in pelagic fish eggs, particularly those useful in identifying eggs in plankton samples. Sandknop and Matarese in this volume also discuss this subject in detail. The characters that have proven useful for egg identification include egg size and shape, size of perivitelline space, yolk diameter and character (homogeneous or segmented), number and size of oil globules, texture of the egg envelope (smooth or with protrusions), pigment on the yolk and embryo, and characters of the developing embryo (relative rate of development of various parts, body shape, number of somites) (Table 2).

The egg stage has been subdivided by a number of workers (e.g., Apstein, 1909). Fishery biologists need to determine the age of eggs at the time of collection for production, drift, and mortality estimates. Embryologists have designated stages to coincide with significant developmental features. While the stages of fishery biologists are designed to divide the embryonic stage into several easily recognized portions, embryologists are more

TABLE 3. EXAMPLES OF USE OF CHARACTERS OF EARLY LIFE HISTORY STAGES IN TAXONOMIC AND SYSTEMATIC STUDIES. X indicates range of stages and taxonomic levels at which characters vary. (X) indicates infrequent state.

| Character | Egg | Yolk-sac | Pre-flexion | Flexion | Post-flexion | Trans-formation | Species | Genus | Family | Order | References Keyed to Table 4 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Meristic characters** | | | | | | | | | | | |
| Fin spines/soft rays | | | (X) | X | X | | | | (X) | X | 20 |
| Principal caudal rays | | X | X | X | (X) | | | | (X) | X | 20, 29 |
| Pelvic fin | | | (X) | X | X | | | | (X) | X | 2, 38 |
| Dorsal/anal fin | | | | X | X | | X | X | | | 1, 2, 11, 19, 24, 27, 39 |
| Pectoral fin | | | (X) | X | X | | X | | | | 11, 19, 24, 27, 39 |
| Vertebrae | | | | X | X | | X | X | X | | 1, 2, 3, 5, 11, 15, 17, 19, 20, 25, 27, 28, 33, 34 |
| Branchiostegals | | X | X | X | (X) | | | | (X) | X | 27, 38 |
| Gill rakers | | | | | X | X | X | | | | 19 |
| **Larval characters** | | | | | | | | | | | |
| Body shape | | X | X | X | X | X | X | X | | | 2, 3, 4, 5, 10, 11, 13, 14, 19, 20, 23, 24, 25, 26, 27, 28, 29, 31*, 33, 37, 40 |
| Snout shape | | | X | X | X | | X | X | | | 28, 33, 35, 36, 38 |
| Pigment patterns | X | X | X | X | X | X | X | X | X | X | 1, 2, 3, 4, 8, 9, 11, 13, 14, 15, 17, 19, 20, 21, 22, 25, 27, 28, 29, 33, 36, 38, 39, 40 |
| Head spines | | | X | X | X | | X | X | X | X | 9, 11, 23, 24, 25, 27, 36, 38, 40 |
| Fin ray elongation | | | X | X | X | | X | X | | | 1, 9, 14, 23, 27, 29, 33 |
| Fin ray ornamentation | | | X | X | X | | | X | | | 14, 27, 29 |
| Fin ray serration | | | | X | X | | | X | | | 27 |
| Finfold size/shape | | X | X | | | | | X | | | 8, 10, 14 |
| Preanal finfold | | X | X | | | | | X | | | 36 |
| Pectoral size shape | | | X | X | X | | | X | | | 8, 14, 15, 33 |
| **Larval gut** | | | | | | | | | | | |
| Shape | | X | X | X | X | | | X | | | 20, 33, 38, 39 |
| Length | | (X) | X | X | X | | | X | | | 14, 20, 29, 33, 38 |
| **Larval eye** | | | | | | | | | | | |
| Shape | | | X | X | X | | | X | | | 8, 10, 14, 20, 33 |
| Stalked | | | X | X | X | | | X | | | 14, 20, 33 |
| Choroid tissue | | | X | X | X | | X | | | | 10, 14, 20 |
| Migration | | | | | | X | | | | X | 29 |
| **Other characters** | | | | | | | | | | | |
| Egg characters | X | | | | | | X | X | | | 6, 19, 20, 30, 32 |
| Osteological development | | | (X) | X | X | X | | X | X | X | 7, 16, 19, 23, 29, 33, 40 |
| Scale formation | | | | X | (X) | X | X | | | | 11, 27 |
| Photophore formation | | | | X | X | X | X | X | | | 12, 14, 21 |
| Size at developmental stage | X | X | X | X | X | X | X | X | | | 10, 11, 22, 23, 29, 30, 39 |
| Fin development sequence | | | (X) | X | X | | X | X | | | 13, 14, 20, 26, 27, 34 |

* Emphasis on oil globule placement in yolk-sac larvae.

interested in tracing the sequence of development. The embryologist's approach will probably provide more useful information for systematic investigations.

Although excellent, early descriptive work was done on teleost embryology (e.g. Wilson, 1891), comparative research on development needs to be done to allow an evaluation of its value to systematics, a subject that has proven so fruitful among invertebrates. It appears, from the characters that have been studied in greatest detail, that convergence may overshadow phyletically significant information. For instance, the egg envelope sculpturing on *Pleuronichthys*, a pleuronectiform, was found even on scanning electron microscope examination to be quite similar to that on *Synodus*, a myctophiform (Sumida et al., 1979). Phylogenetically diverse fishes often have round pelagic eggs, about 1 mm in diameter, with a single oil globule. Demersal eggs from equally diverse fishes are generally larger than 1 mm and develop a vitelline circulatory system. Yolk segmentation seems to be a character of more primitive fishes, but some carangids and other perciforms have yolks that are secondarily segmented in an evolutionary sense. Detailed studies are needed to sort out these and other features of the teleost egg and its embryonic development in a systematic context.

TABLE 4. SOME CONTRIBUTIONS IN WHICH ONTOGENETIC CHARACTERS HAVE BEEN USED TO EXAMINE SYSTEMATIC RELATIONSHIPS (UPDATED FROM AHLSTROM AND MOSER, 1981).

| No. | References | Date | Group dealt with | Egg | Lar-vae | Juv. ad. | Among spe-cies | Among genera | Among subfam. or families | Among orders |
|---|---|---|---|---|---|---|---|---|---|---|
| 1, 3, 5 | Ege, V. | 1930, 53, 57 | Paralepididae | — | + | ± | X | X | | |
| 2 | Bertelsen, E. | 1951 | Ceratioidei | — | + | + | X | X | X | |
| 4 | Bertelsen, E., and N. B. Marshall | 1956 | Miripinnati | — | + | ± | X | X | X | |
| 6 | Pertseva-Ostroumova, T. A. | 1961 | Pleuronectidae | + | + | ± | X | X | | |
| 7 | Berry, F. H. | 1964a | Mar. teleosts | — | + | — | | | | X |
| 8 | Pertseva-Ostroumova, T. A. | 1964 | Myctophidae | — | + | — | | X | | |
| 9 | Gutherz, E. J. | 1970 | Bothidae | — | + | — | | X | | |
| 10, 14 | Moser, H. G., and E. H. Ahlstrom | 1970, 74 | Myctophidae | — | + | ± | X | X | X | |
| 11 | Mead, G. W. | 1972 | Bramidae | — | + | + | X | X | | |
| 12 | Ahlstrom, E. H. | 1974 | Sternoptychidae | — | + | ± | | X | | |
| 13 | Johnson, R. K. | 1974b | Scopelarchidae | — | + | + | X | X | | |
| 15 | Okiyama, M. | 1974a | Myctophiformes | — | + | — | | X | X | |
| 16 | Potthoff, T. | 1974 | Scombridae | — | + | + | X | | | |
| 17 | Richards, W. J., and T. Potthoff | 1974 | Scombridae | — | + | ± | X | | | |
| 18 | Aboussouan, A. | 1975 | Carangidae | — | + | — | | X | | |
| 19 | Ahlstrom, E. H., J. L. Butler, and B. Y. Sumida | 1976 | Stromateoidei | ± | + | ± | X | X | X | |
| 20 | Ahlstrom, E. H., and H. G. Moser | 1976 | Mar. teleosts | + | + | + | | | | X |
| 21 | Ahlstrom, E. H., H. G. Moser, and M. J. O'Toole | 1976 | Myctophidae | — | + | + | | X | | |
| 22 | Bertelsen, E., G. Krefft, and N. B. Marshall | 1976 | Notosudidae | — | + | ± | X | X | | |
| 23 | Futch, C. R. | 1977 | Bothidae | — | + | — | | X | X | |
| 24 | Moser, H. G., E. H. Ahlstrom, and E. Sandknop | 1977 | Scorpaenidae | — | + | ± | X | X | X | |
| 25 | Okiyama, M., and S. Ueyanagi | 1978 | Scombridae | — | + | — | | X | X | |
| 26 | Powles, H., and B. W. Stender | 1978 | Sciaenidae | — | + | ± | | X | | |
| 27 | Kendall, A. W., Jr. | 1979 | Serranidae | — | + | + | | X | X | |
| 28 | Ueyanagi, S., and M. Okiyama | 1979 | Scombridae, Istiophoridae | — | + | + | | X | | |
| 29 | Amaoka, K. | 1979 | Pleuronectiformes (in part) | — | + | — | | X | X | |
| 30 | Dotsu, Y. | 1979 | Gobiidae | + | + | — | | X | | |
| 31 | Suzuki, K., and S. Hioki | 1979a | Percoidei | ± | + | — | | X | X | |
| 32 | Mito, S. | 1979a, b | Mar. teleosts | + | — | — | | X | X | |
| 33 | Okiyama, M. | 1979b | Myctophoidei | — | + | — | | | X | |
| 34 | Potthoff, T., W. J. Richards, and S. Ueyanagi | 1980 | Scombrolabracidae | — | + | + | | X | X | |
| 35 | Zahuranec, B. J. | 1980 | Myctophidae (Nannobrachium) | — | + | + | X | X | | |
| 36, 37 | Richardson, S. L. | 1981a,c | Cottidae | — | + | + | | X | | |
| 38 | Washington, B. B. | 1981 | Cottidae | — | + | | X | X | | |
| 39 | Johnson, R. K. | 1982 | Scopelarchidae Evermannellidae | — | + | + | X | X | X | |
| 40 | Kendall, A. W., Jr., and B. Vinter | 1984 | Hexagrammidae | — | + | + | X | X | | |

## THE YOLK-SAC LARVAL STAGE

At hatching, larvae can be at various states of development, dependent to a large degree on the size of the yolk (Fig. 7). Larvae from eggs with small yolks are less developed at hatching than those that hatch from eggs with larger yolks. Since the bulk of marine fish spawn eggs that are about 1 mm in diameter and have a narrow perivitelline space, the yolk is only slightly less than 1 mm. Larvae from such eggs generally lack a functional mouth, eye pigment, and differentiated fins. They possess a large yolk sac relative to the size of the larva which supplies nourishment while the larvae develop to become self-feeding. Newly hatched larvae from demersal eggs are generally further advanced in development than larvae from pelagic eggs of comparable size (Fig. 8). In these and other fish with large eggs, hatching may be delayed until the yolk sac is absorbed and the larvae are ready to feed at hatching, having bypassed the yolk-sac larval stage. The delayed absorption of yolk reaches an extreme in fishes such as salmonines in which the yolk-sac larva transforms directly into a juvenile; Hubbs (1943) proposed the term "alevin" be applied to this yolk-sac larval stage.

At hatching, locomotion and orientation of most yolk-sac larvae are aided by a continuous median finfold (dorsal, caudal, anal) and larval pectoral fins. During egg development, many fish embryos develop melanophores that originate in the neural
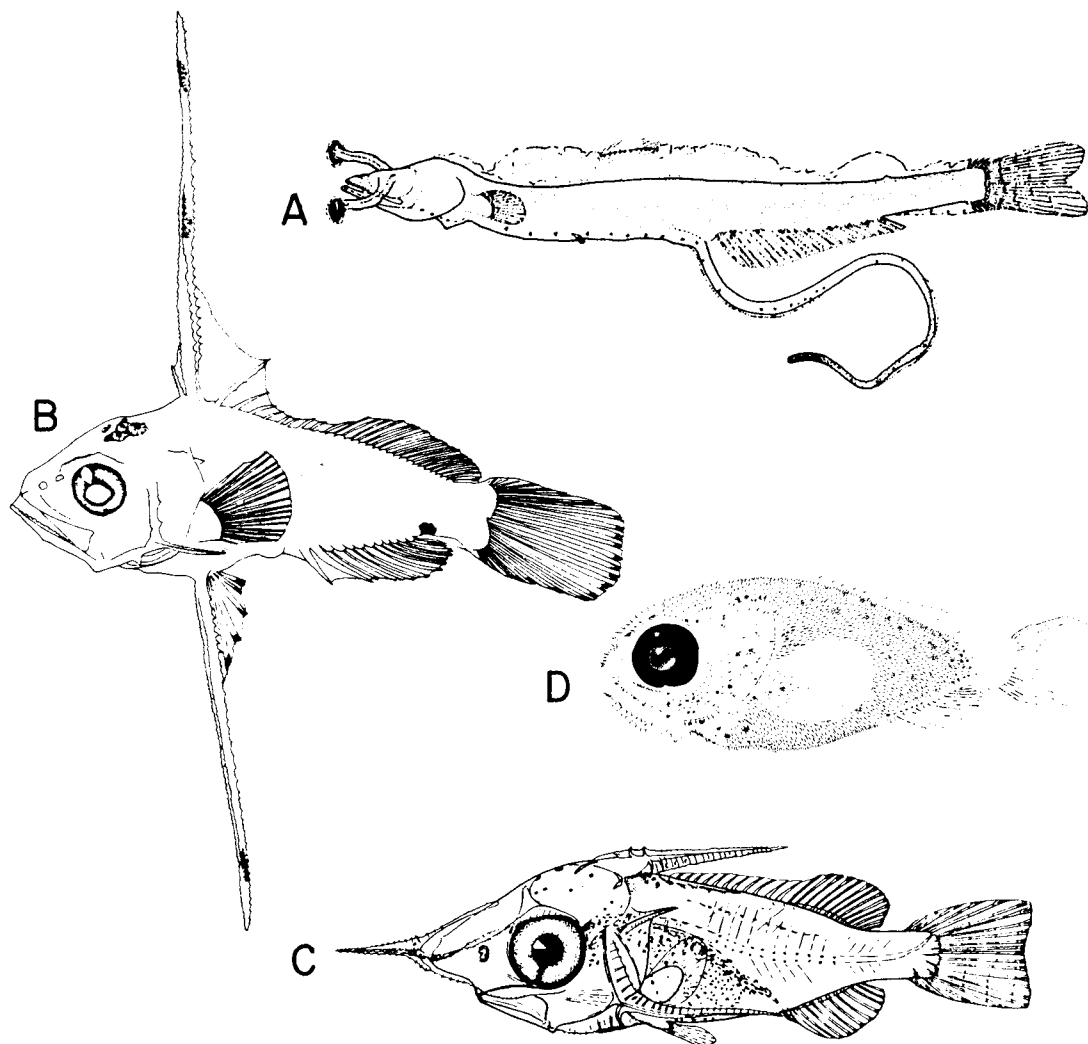
Fig. 9.   Examples of teleost larvae illustrating extremes of some systematically useful larval characters. (A) *Myctophum aurolaternatum*, 26.0 mm (Moser and Ahlstrom, 1974). Note stalked oval eye with choroid tissue, trailing gut, and dorsal fin developing in finfold; (B) *Epinephelus* sp., 8.4 mm (Kendall, 1979). Note elongate, serrate dorsal and pelvic spines; (C) *Adioryx* (*Holocentrus*) *vexillarius*, 8.5 mm (McKenney, 1959). Note head spines; and (D) *Lopholatilus chamaeleonticeps*, 6.0 mm (Fahay and Berrien, 1981). Note spines on head and body.

crest and are generally aligned along the dorsal surface of the embryo. During the yolk-sac stage, these melanophores move laterally and ventrally to establish the beginning of the larval pigment pattern. Orton (1953a) describes these events in detail in *Sardinops sagax*. This realignment may begin during the late embryonic stages, before hatching. Some species hatch with few if any melanophores, and when they first appear, they are in ventral positions. Apparently, the pigment cells migrate before pigment formation occurs.

The presence and position of oil globules in yolk-sac larvae vary and can be of diagnostic value. In fishes with single oil globules, it can be far forward (e.g., labrids, most carangids, mullids, and lethrinids), in the middle of the yolk sac (e.g., some clupeids, serranids, and argentinids), or more usually near the rear of the yolk sac. The shape and relative size of the yolk sac itself are variable and provide additional taxonomic characters.

In summary, although the yolk-sac stage starts at hatching and ends when the yolk is absorbed, fish are at different stages of development with regard to such features as pigmentation, eye development, and fin formation during this stage. The striking pigment rearrangements that occur during this stage provide further emphasis that the yolk-sac stage is a transitional stage between the egg and larval stages.

### THE LARVAL STAGE

During the larval stage many ontogenetic changes occur (Moser, 1981). Some of these relate directly to the development of the adult form while other changes and structures are specialized
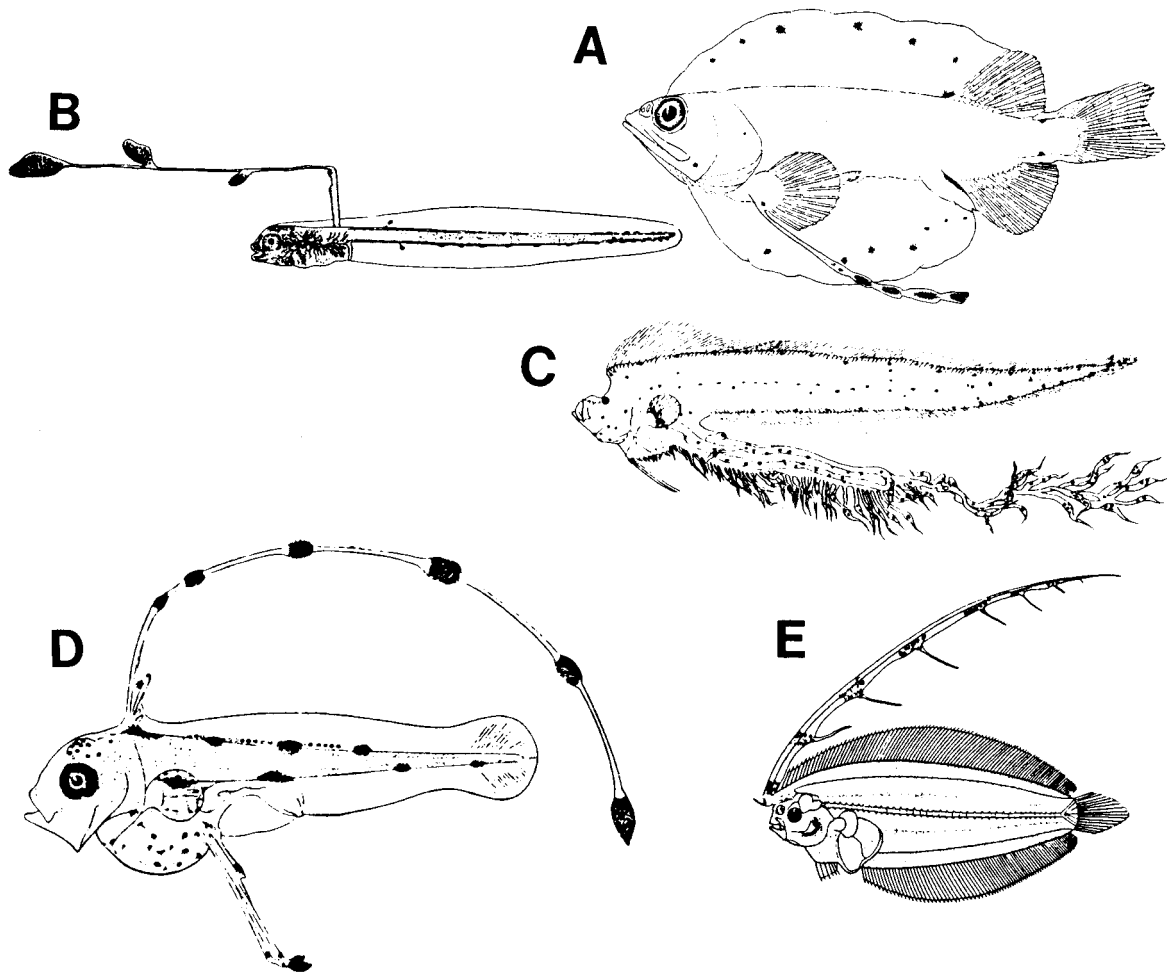
Fig. 10. Apparent convergence in siphonophore-mimicking appendages on larval fish. (A) *Loweina rara,* 17.6 mm. Note lower pectoral fin ray (Moser and Ahlstrom, 1970); (B) *Carapus* sp., 3.8 mm (Padoa, 1956j). Note elongate dorsal fin ray; (C) Exterilium larva, 64 mm. Note trailing gut (Moser, 1981); (D) *Lophotus* sp., 12.1 mm. Note elongate dorsal and pelvic ray (Sanzo, 1940); and (E) *Arnoglossus japonicus,* 30.5 mm. Note elongate dorsal ray (Amaoka, 1973).

and of presumed functional significance primarily for planktonic existence (Fig. 9). These latter features are of particular interest in systematic studies of larval fish ontogeny. They include pigment pattern, larval body shape, armature on head bones, and precocious (early forming), elongate, or serrate fin spines. The sequence and way of developing adult structures, such as the skeleton and fin rays, are also useful larval characters. All of the characters of the larvae—whether they are specialized larval characters or merely characters observable in the larvae—may have potential systematic value at some taxonomic level; however, the usefulness of most of the characters has not been evaluated (Tables 3 and 4).

Among the most taxonomically useful larval characters, generally at the specific or generic level, is the pigment pattern. Usually, each species has a distinct larval pigment pattern. In some the number and placement of individual melanophores

are diagnostic, while in others the location, shape, and size of groups of melanophores are key characters. At a higher taxonomic level, in the myctophiforms for example, the peritoneal pigment blotches seem to indicate relationships on a suborder-family level. Problems associated with the usefulness of pigment patterns include 1) the widespread distribution of some patterns, and 2) the variable state of melanophore contraction on larvae of the same species. An example of the first problem is the frequent occurrence of a row of small melanophores along the ventral midline from just behind the anus to the tip of the tail. Another example is a pigmented area midlaterally on the caudal peduncle which occurs in numerous groups. A ventral spot at the junction of the cleithra is also quite common. These are just a few examples of widespread, presumably convergent pigment patterns that limit the usefulness of pigment in systematic studies of larvae. The causes for the observed differences in degree

velopment are characteristic of larvae at the generic or familial level, although subtle differences in body shape may be characteristic of species. Size at stage of development can be environmentally modified (e.g., by temperature or food) to some extent, but is primarily genetically determined. There appears to be some convergence in larval body shape, such as on a long tubular body in several divergent groups (e.g., Clupeiformes, Argentinidae, Blennioidea), just as there is on the "herring" morph of adults.

A valuable and fairly widespread set of larval characters concerns the development of spines and armature on bones of the head and cleithral region. Such armature has provided diagnostic larval characters as well as material for systematic inference at levels from species to order. Larval head armature appears to be a mark of the Acanthopterygii. Only a few scattered examples of such armature appear in fishes which have only soft rays as adults (e.g., *Sudis*). Within the spiny-rayed fishes, beryciforms are quite heavily armed with spines on many head bones. Perciforms usually do not have spines on the parietals but the supraoccipital is armed in some. The Scorpaeniformes are just the opposite: they tend to have head armature that includes spines on the parietals but do not have spines on the supraoccipital.

Nowhere are larval specializations more evident or varied than in the fins. Elongation of particular spines or soft rays or enlargement of whole fins are frequently seen. Such elongations have been described for rays of the dorsal, pelvic, pectoral, and caudal fins; thus they occur with both spines and soft rays. In some, these long rays may bear pigmented "bulbs" or appear like flagellae. Such specialized rays are produced in the dorsal, pectoral, or pelvic fins of taxonomically diverse fishes. The extended gut of "exterilium" ophidioid larvae (Fraser and Smith, 1974) and the serial pigment pattern of some leptocephali (Smith, 1979) may give the same appearance to potential predators as these elongate rays. All of these structures may be mimicking siphonophores: a remarkable example of convergence (Fig. 10 and 11). Elongate fin spines are heavy and armed with serrations in some. Elongated rays are often precocious in development, with some even forming in the egg. These fin characters seem to vary at the family-species levels. Other characters associated with fin development include the sequence of formation and movement and loss of whole fins or some of the rays. Dorsal and anal fins move forward along the body during larval development in elopiform and clupeiform fishes. They develop in "streamers" in the finfold of argentinoids and attach to the body proper just before or during transformation. The shape of the finfold, presence or absence of a preanal finfold, and shape of the pectoral fin base provide additional characters at the family-genus level.

Gut characters of fish larvae include length and shape as well as the development of a protruding, trailing hindgut in some. In fishes with photophores, their placement and sequence of development are excellent characters at the subfamily-species levels. The eye of a larva is specialized in a number of ways.



Fig. 11.   *Liopropoma* sp., 11.0 mm. Collected by G. R. Harbison, 16 May 1981, 6°31.8′S, 150°21.8′E. Note elongate dorsal spines.

of contraction of melanophores are not well understood although they may be partially related to ambient light intensity. The relative size and placement of melanophores are genetically determined and therefore useful in a systematic context, while the degree of contraction seems to be physiologically determined.

In general, the body shape and size at various stages of de-

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Fig. 12.   Examples of special juvenile stages. (A) *Hexagrammos lagocephalus*, 28.0 mm. A neustonic or epipelagic form of a species that is demersal as an adult (from Kendall and Vinter, 1984); (B) *Forcipiger longirostris*, 17 mm. A spiny form that lives on tropical reefs as an adult (from Kendall and Goldsborough, 1911); (C) *Sebastolobus altivelis*, 26.8 mm. A barred pelagic form of a species that is demersal on the continental slope as an adult (from Moser et al., 1977); (D) *Oncorhynchus kisutch*, 37 mm. The freshwater alevin or parr stage of an andromous salmonid (from Auer, 1982); and (E) *Kali macrodon*, 45 mm. The juvenile of a bathypelagic species. Originally described as *Gargaropteron pterodactylops* (see Johnson and Cohen, 1974).

A

B

C

D

E
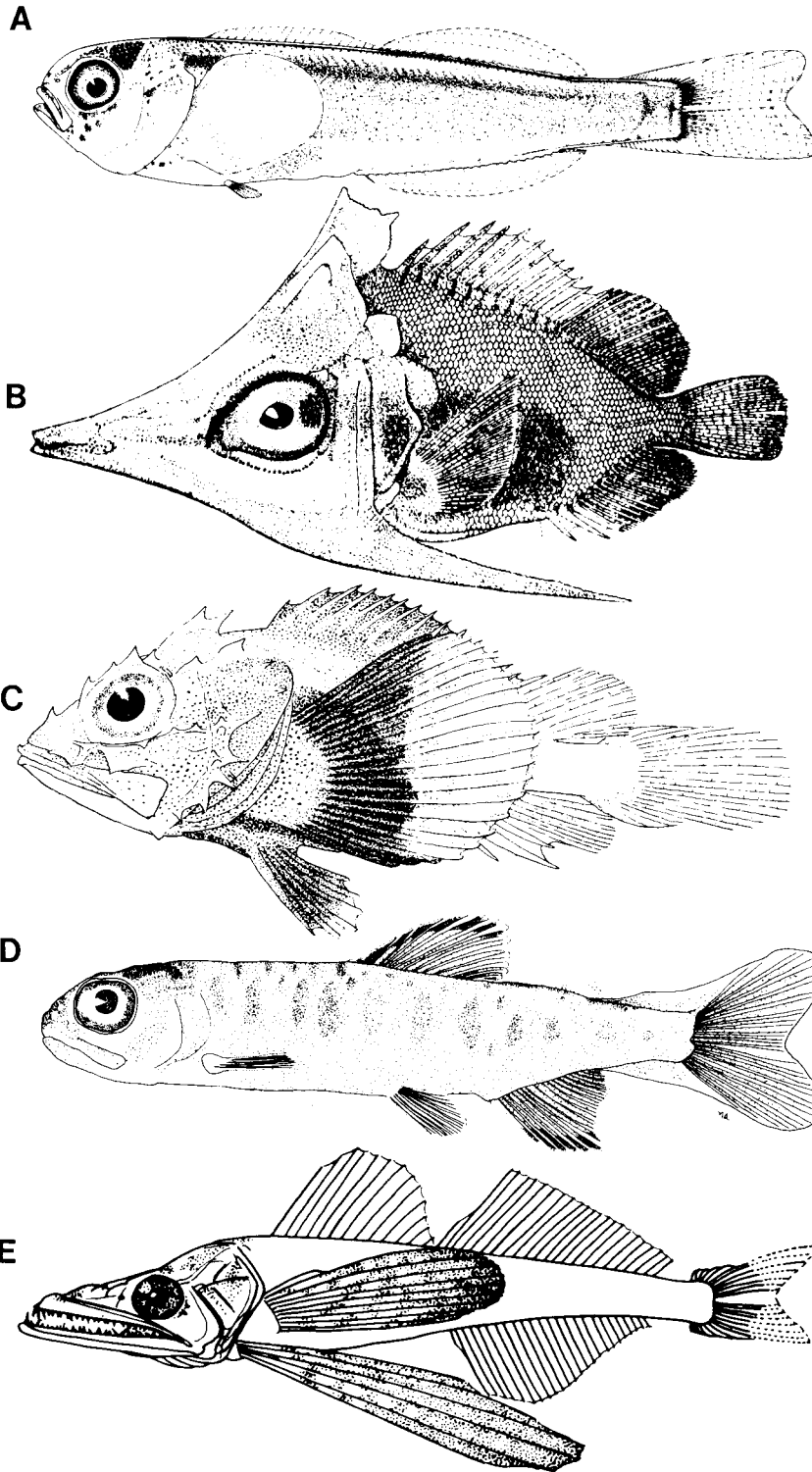
Its size and rate of development are useful, as well as whether it is round or oval. Some fish larvae have eyes borne on stalks that reach an extreme in *Idiacanthus*, while others develop an area of choroid tissue. Migration of the eye in flatfish larvae from a symmetrical position to one side of the head is well known. The sequence of development of ossified structures is proving to be a powerful tool in systematic studies of fish larvae. The losses and fusions of bones, which are generally assumed based only on adult material, can and should be tested using developmental studies. The caudal fin skeleton has provided excellent developmental characters to be used for systematic inferences, mainly at the order-generic levels. The development of scales has been little studied but may prove valuable, especially in fishes with precocious scales (e.g., some anthiins, holocentrids).

### THE TRANSFORMATION STAGE

Between the larval and juvenile stages, there is a transitional stage which may be abrupt or prolonged and which, in many fish, is accompanied by a change from planktonic habits to demersal or schooling pelagic habits (Fig. 12). In some fishes migration to a "nursery" ground occurs during or just before this stage. Morphologically the transformation stage is characterized by a change from larval body form and characters to juvenile-adult body form and characters. At the end of this stage the fish generally looks similar to the adult, with major differences only in pigmentation patterns. Two ontogenetic processes occur during this stage of transition between the larva and juvenile: 1) loss of specialized larval characters, and 2) attainment of juvenile-adult characters. Changes that occur during this stage include pigment pattern, body shape, fin migration (e.g., in clupeids and engraulids), photophore formation, loss of elongate fin rays and head spines (e.g., in epinepheline serranids and holocentrids), eye migration (pleuronectiforms), and scale formation.

In several groups, where the transformation stage is prolonged, the fish have developed specializations that are distinct from both the larvae and juveniles. This stage has been designated the prejuvenile stage (Hubbs, 1943). The specializations generally involve body shape and pigmentation. In many, the morph resembles a herring-like fish and is apparently adapted for neustonic life. The dorsal aspect of the fish is dark green or blue and the lateral and ventral is silvery or white. The body tends to be herring shaped and the mouth terminal. Fins are generally unpigmented. Such a stage is present in Gadiformes (*Urophycis*), Beryciformes (*Holocentrus*), Perciformes (e.g., *Pomatomus*, Mullidae, Mugilidae) and Scorpaeniformes (e.g., *Scorpaenichthys*, *Hexagrammos*). In other fishes, such as some myctophiforms and carapids, the prolonged transformation stage may have distinctive body and fin shapes.

### IMPLICATIONS OF LARVAL FISH MORPHOLOGY

When studying the appearance of larval fishes, one is immediately struck with their diversity and morphological dissimilarity to adults. This dissimilarity led early workers to establish names for several of these forms, not realizing that they were the young stages of known adults. After establishing the identity of many fish larvae in a variety of groups, we hypothesize that the larvae of all species are recognizably distinct. The use of diversity of larval form in vertebrate systematics was discussed some time ago by Orton (1953b, 1955c, 1957) and in this volume we examine this use in detail in numerous groups of fishes.

*Why are the larvae so diverse?*—Despite the tremendous mortality associated with living in the planktonic realm during the larval period, survival must be sufficient to maintain the species and provide a dispersal mechanism for it. To different degrees, various taxa apparently rely on survival and longevity of individual larvae. The amount of reliance is presumably related to fecundity and importance of dispersal and colonization to the taxon. A number of structures have evolved that would be expected to enhance larval survival in the plankton. Practically no experimental work has been done to investigate the function of larval structures, but some structures probably assist flotation and feeding while others decrease predator mortality. Convergence on characters that are apparently functionally important to larval survival in the plankton is seen. These specializations develop in conjunction with the basic ontogeny of the taxon. In studying systematics using larval fishes, both the basic pattern of development and the specialized structures must be analyzed.

*Why are these larvae so morphologically unlike the adults?*— Most larvae are adapted to survive in an ecological realm (generally the plankton) that is far different from that of the adult. These are small organisms, compared to adults, and they live in the plankton, having to find and capture food there and avoid becoming food. They float and migrate vertically in a milieu that may be moving much faster than they are. During this larval period, these fish undergo extreme changes in morphology yet remain a functioning (eating, avoiding predators) organism and eventually end up in a suitable nursery area for the juvenile stage.

*How then can larval morphology help us understand the evolution of these fishes?*—After recognizing that each species has a morphologically distinctive larva, generally we see that species of the same genus are phenetically similar, and larvae of members of a family also share common features. Even larvae of suborders and orders share some larval characters. This would be expected since evolution operates on all stages in the life cycle, not just the adult. Evolutionary pressures on the larval stage seem to be particularly intense in those groups that rely on the larvae for widespread dispersal in the ocean. Here the larvae appear well adapted for life in the planktonic realm, and it can truly be said that the larva and the adult perform in "two quite separate evolutionary theaters" (Moser and Ahlstrom, 1974). In this volume we are focusing on what we know to date about larval evolution within various groups of fishes (Table 4).

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