Coombs S and Montgomery JC (1999). The enigmatic lateral line system. In: Fay RR and Popper AN (eds) *Comparative Hearing: Fish and Amphibians*, pp. 319–362. New York: Springer-Verlag.

Fay RR and Popper AN (eds) (1999) *Comparative Hearing: Fishes and Amphibians*. New York: Springer-Verlag.

Mann DA, Lu Z, Hastings MC and Popper AN (1998) Detection of ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the American shad (*Alosa sapidissima*). *Journal of the Acoustics Society of America* 104: 562–568.

Montgomery JC, Coombs S and Halstead M (1995) Biology of the mechanosensory lateral line. *Reviews in Fish Biology and Fisheries* 5: 399–416.

Myrberg AA Jr (1981) Sound communication and interception in fishes. In: Tavolga WN, Popper AN and Fay RR (eds) *Hearing and Sound Communication in Fishes*, pp. 395-426. New York: Springer-Verlag.

Popper AN and Carlson TJ (1998) Application of the use of sound to control fish behavior. *Transactions of the American Fisheries Society* 127: 673–707.

Popper AN and Fay RR (1999) The auditory periphery in fishes. In: Fay RR and Popper AN (eds) *Comparative Hearing: Fish and Amphibians*, pp. 43–100. New York: Springer-Verlag.

Popper AN and Lu Z (2000) Structure–function relationships in fish otolith organs. *Fisheries Research* 46: 15–25.

Zelick R, Mann D and Popper AN (1999) Acoustic communication in fishes and frogs. In: Fay RR and Popper AN (eds) *Comparative Hearing: Fish and Amphibians*, pp. 363–411. New York: Springer-Verlag.

FISH LARVAE

E. D. Houde, University of Maryland, Solomons, MD, USA

doi:10.1006/rwos.2001.0026

Introduction

Most marine teleost (bony) fishes produce thousands to millions of planktonic eggs and larvae. Newly hatched larvae, usually 1–5 mm in length, are delicate, poorly developed, and retain many embryonic characteristics. They usually hatch with undeveloped mouth parts, fins, and eyes. Larvae drift and disperse in the sea. Most die before transforming into the juvenile stage. The larval stage originates as a nonfeeding, yolk-sac larva that derives nutrition from stored yolk and develops into an actively feeding larva that eventually transforms to a juvenile morphologically resembling a small adult. Transformation, which occurs from a few days to more than a year after hatching, often involves major changes in morphology (e.g. eels, flounders, herring) or may be less dramatic (e.g. cods, basses, sea breams). Lengths at metamorphosis are usually < 25 mm, but can range from a few millimeters to many centimeters (some eels). The diverse, sometimes bizarre, suite of larval types that are collected represents a range of adaptations that promote survival and fitness in marine environments ranging from estuaries to the deep sea (**Figure 1**).

Fisheries scientists and managers are concerned about growth and survival during the earliest life stages of fishes because variability in those processes can lead to 10-fold or greater differences in numbers of recruits that survive to catchable size. Causes of mortality are seldom evaluated. Since early in the twentieth century, scientists have realized that ocean circulation, frontal systems, and turbulence might be key physical factors controlling larval survival. Biological factors, especially larval nutrition and predation also are major controllers of survival and growth. The physical and biological factors combine to determine success of the reproductive effort, termed ‘recruitment’ by fisheries scientists. Recruitment processes are not confined to the larval stage but act on earlier (eggs) and later (juveniles) stages. The larval stage is important but does not stand alone as a ‘critical stage’, and its relative importance in determining recruitment success can vary annually and seasonally.

Fish Larvae and the Plankton

Larvae of marine fishes, termed ichthyoplankton, usually are pelagic, drifting in the sea and interacting with pelagic predators and planktonic prey. Most fish larvae, even of species that ultimately are herbivores as juveniles or adults, are primarily carnivorous during the larval stage, feeding upon smaller planktonic organisms. In turn, larval fishes are the prey of larger nektonic and planktonic organisms. Escape from the precarious larval stage is accomplished via growth and ontogeny. Only a few individuals from thousands of newly hatched larvae survive the ever-present threats of starvation and predation during planktonic life.

Eggs and larvae of marine fishes are collected in fine-meshed plankton nets or specially designed traps. Surveys at sea estimate distributions, abundance, diversity, and structure of 'ichthyoplankton' communities, including associations of larvae with their predators and prey. Such surveys sometimes are a component of stock assessments used in fisheries management.

Larval distributions within nursery areas, including vertical distributions, differ among species. Most larvae are in the upper 200 m of the water column, although buoyant eggs, which gradually rise towards surface after spawning, may be deeper if adults spawned at depth. Accurate estimates of abundances and production of eggs and small larvae are possible because these stages usually cannot avoid samplers. Declines in abundances of older (and larger) larvae in plankton collections provide the means to estimate mortality rates if dispersal losses by water currents can be determined, and if the probability of sampler avoidance is known.

Larval Survival

The larval stage may be most important in controlling levels of subsequent recruitment. Early in the twentieth century, Johann Hjort (1914) offered the 'critical period' hypothesis, proposing that incidence of starvation at the time of yolk-sac exhaustion, when larvae first required plankton as food, was the primary factor determining variability in year-class recruitment success. In combination, probabilities of starvation and transport to unsuitable nursery habitats constitute the two elements of Hjort's hypothesis. Although the hypothesis cannot be rejected after 85 years, it is now apparent that recruitment variability is generated by a multitude of processes acting throughout the early-life stages in fishes.

Hjort's hypothesis provided a foundation for subsequent attempts to explain recruitment variability. The potential for high and variable larval stage mortality led many scientists to hypothesize that coarse controls on the magnitude of recruitment are set during the larval stage rather than later in life. The 'match-mismatch' hypothesis proposed by Cushing builds upon Hjort's ideas, emphasizing the importance of temporal coincidence in spawning and bloom dynamics of plankton, the primary food of larval fish. There is support for this hypothesis, especially for species with short spawning seasons in high-latitude seas. A 'match' between spawning and spring plankton blooms ensures larval growth and survival, while a 'mismatch' results in high mortality. The 'stable ocean' hypothesis, proposed by Lasker in the 1970s, is another nutrition-related explanation for variability in larval survival. Lasker hypothesized that relaxation of storm winds and intense upwelling resulted in a stable, vertically stratified ocean in which strata of fish larvae and their prey coincide, promoting larval nutrition and survival. The hypothesis is strongly supported for species inhabiting coastal upwelling regimes.

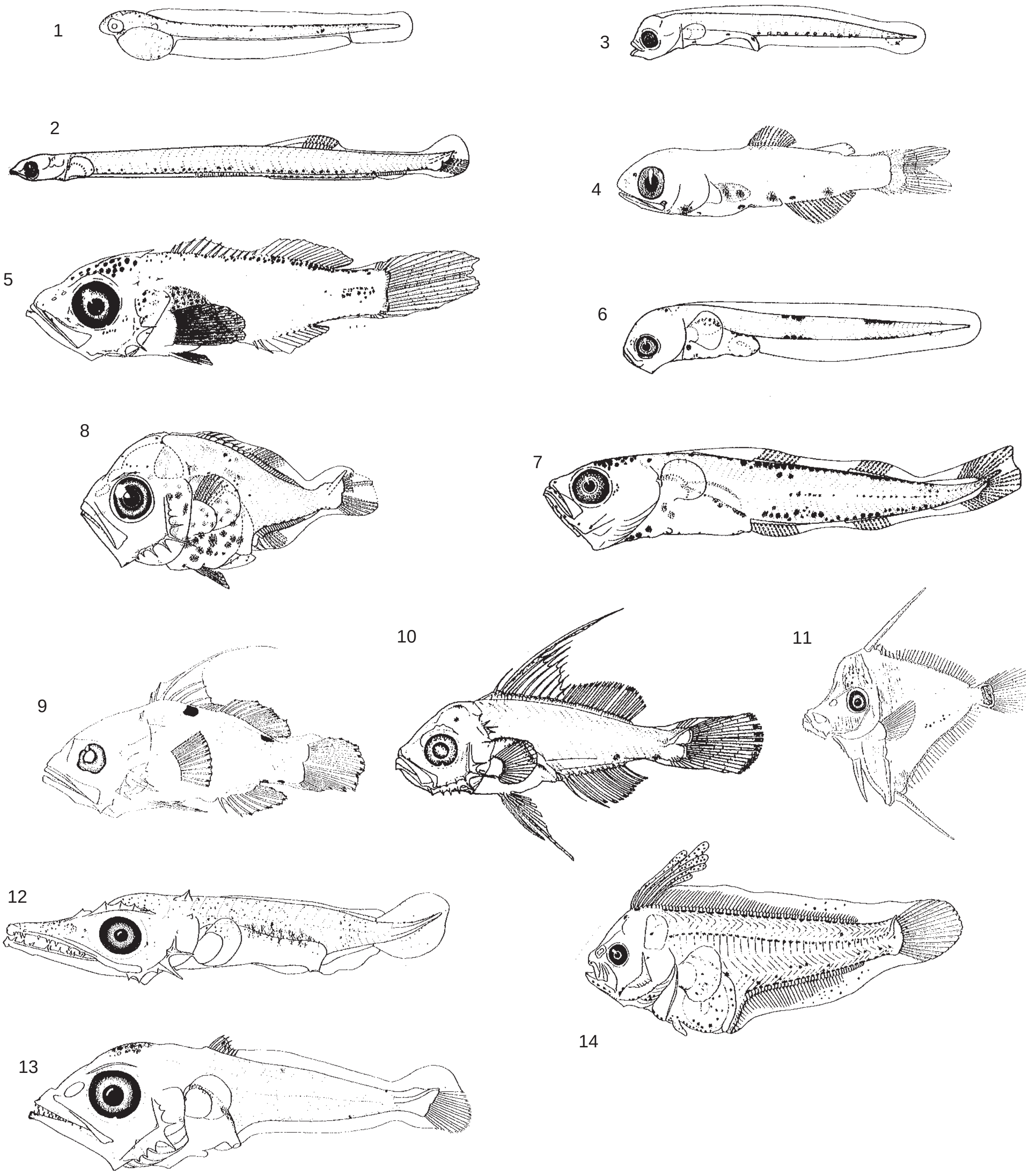
Contrasting with the match-mismatch hypothesis is the proposal by Sinclair and Iles that gyre-like circulation features in well-mixed coastal waters define spawning areas while retaining eggs and larvae. This hypothesis emphasizes physics and circulation features, rather than nutritional factors, as the controller of recruitment variability. The hypothesis gains support from evidence on recruitment of numerous herring (*Clupea harengus*) and some cod (*Gadus morhua*) stocks in the North Atlantic. Sinclair and Iles argued that high larval retention promotes strong recruitment while failed retention diminishes success. Retention not only reduces larval losses to dispersal, but ensures genetic integrity of a stock by confining reproduction within the retention area. Although this hypothesis differs from the 'match-mismatch' hypothesis, there is evidence from some cod stocks that 'match-mismatch' and retention mechanisms operate together to promote larval survival.

In the tropics and especially on coral reefs, scientists have debated whether supply of larvae or post-settlement mortality of juveniles is the primary factor generating variability in recruitment levels. The 'lottery' hypothesis, of Sale, proposes that fish larvae are delivered by ocean currents to reefs where they settle onto structure that, if by chance is free of predators or competing fish, will lead to successful recruitment. Recent evidence supports both larval supply and post-settlement controls as important for recruitment success. Also, there is accumulating evidence that long-range dispersal, once assumed to dominate early-life processes in tropical seas, may in fact be limited and that retention near islands and reefs is common as larvae develop from hatching to settlement stages.

Foods and Feeding

Fish larvae must feed frequently to ensure fast growth, a prerequisite for high survival. Successful initiation of feeding depends upon availability of suitable kinds and sizes of prey, which usually is zooplankton 50–100 µm in width. Sizes of prey that are consumed are strongly related to larval size (specifically mouth size). Nauplii of copepods are perhaps the most common prey of small fish larvae. Concentrations of nauplii and other zooplankton have often been analyzed to evaluate feeding conditions for larvae in the sea. Recent research has demonstrated that many species of fish larvae initiate feeding on a diverse spectrum of small planktonic organisms, including some phytoplankton and protozoa that are often more abundant than copepod nauplii. Laboratory experiments indicate that concentrations of copepod nauplii exceeding 100 per liter may be required to support feeding and growth of larval fish, leading to hypotheses and simulation models that implicate patchiness of prey and small-scale turbulence as mechanisms promoting prey encounter, successful feeding, and growth. Such enhancing mechanisms clearly are important, but if diverse diets are the norm, as recent evidence suggests, then availability of suitable larval prey in the sea may be higher than once believed.

As development and growth proceed, feeding success increases. Maximum prey sizes in larval diets increase substantially, but the mean size increases only slowly because larvae continue to consume



small prey while adding larger prey to the diet. This ontogenetic shift occurs gradually in most fishes, but in some mackerels, tunas, and other species the shift is dramatic, and piscivory on larval fish becomes their primary source of nutrition during the earliest larval stage. Large amounts of prey must be consumed. Marine fish larvae typically consume $>50\%$ of their body weight daily to achieve average growth. Some larvae from warm seas, e.g. tunas and anchovies, consume $>100\%$ of their body weight each day to grow at average rates. Such high food requirements have reinforced the belief that poor feeding conditions, slow growth, and starvation are major causes of larval mortality in the sea.

Starving fish larvae are seldom observed in the sea because such larvae are believed to be selectively preyed upon, then disintegrating rapidly in stomachs of predators. Thus, dead or starving larvae are infrequent in ichthyoplankton collections. Nutritional condition of fish larvae can be evaluated by morphological, histological, and biochemical approaches. Nucleic acid analysis, when properly conducted, shows that poorly fed larvae in environments with low prey have low RNA/DNA ratios, indicating poor potential for growth. Fish larvae that fail to initiate feeding soon after yolk depletion will become nutritionally compromised and poorly conditioned, reaching a 'point-of-no-return' within 2–10 days, from which they cannot recover even if adequate food is provided.

Little is known about specific feeding behaviors of fish larvae. Larvae mostly feed visually and must be in close proximity (e.g. less than one body length) to successfully encounter and capture prey. Most feeding occurs during daylight, although threshold light levels are low, in the range 0.01–0.10 lux, levels equivalent to dawn and dusk periods. In elongate, herring-like larvae, a typical 'S-flex' behavior has been described in which a larva, upon encountering a prey, flexes its body into an S-shape before striking at the prey (**Figure 2**). Other kinds of larvae use a modified 'S-flex' behavior or a 'cruise and strike' searching behavior. As in other life stages, successful feeding by larvae depends on the relationship: $P = E \cdot A \cdot C$, where E, A, and C are probabilities of encountering, attacking, and capturing a prey. Modeling and understanding this relationship, and changes in it during larval development, are important to evaluate larval survival potential.

Predation

Much evidence indicates that predation is the major direct cause of mortality to early-life stages of fish. This conclusion does not exclude starvation and nutritional deficiencies as causes of, or contributors to, larval mortality. Because predation in the sea is strongly size-dependent and predators are size-selective, fish larvae that are slow-growing or starving will remain in small, highly vulnerable size classes

Figure 1 (Left) Larval fishes. (1) *Sardinella zunasi* (Clupeidae), 4.8 mm. (Reproduced with permission from Takita T (1966).) Egg development and larval stages of the small clupeoid fish *Harengula zunasi* Bleeker and some information about the spawning and nursery in Ariake Sound. *Bulletin of the Faculty of Fisheries, Nagasaki University* 21: 171–179. (2) *Clupea pallasi* (Clupeidae), 10.4 mm. (Reproduced with permission from Matarese AC, Kendall AW Jr, Blood DM and Vinter BM (1989).) *Laboratory Guide to Early Life History Stages of Northeast Pacific Fishes. NOAA Technical Report, NMFS 80* Seattle, WA: National Marine Fisheries Service.) (3) *Diaphus theta* (Myctophidae), 4.6 mm. (Reproduced with permission from Matarese *et al.*, 1989.) (4) *Benthosema fibulatum* (Myctophidae), 8.7 mm. (Reproduced with permission from Moser HG and Ahlstrom EH (1974).) Role of larval stages in systematic investigations of marine teleosts: the Myctophidae, a case study. *Fishery Bulletin, US* 72: 391–413. (5) *Sebastes melanops* (Scorpaenidae), 10.6 mm. (Reproduced with permission from Matarese *et al.*, 1989.) (6, 7) *Theragra chalcogramma* (Gadidae), 6.2 and 13.7 mm. (Reproduced with permission from Matarese *et al.*, 1989.) (8) *Carangoides* sp. (Carangidae), 4.4 mm. (Reproduced with permission from Leis JM and Trnski T (1989).) *The Larvae of Indo-Pacific Shorefishes.* Sydney: University of New South Wales Press.) (9) *Plectranthrias garupellus* (Serranidae), 5.5 mm. (Reproduced with permission from Kendall AW Jr (1979).) *Morphological Comparisons of North American Sea Bass Larvae (Pisces: Serranidae). NOAA Technical Report NMFS Circular 428.* Rockville, MD: National Marine Fisheries Service. (10) *Lutjanus campechanus* (Lutjanidae), 7.3 mm. (Reproduced with permission from Collins LA, Finucane JH and Barger LE (1980).) Description of larval and juvenile red snapper, *Lutjanus campechanus. Fishery Bulletin, US* 77: 965–974. (11) *Naso unicornis* (Acanthuridae), 5.9 mm. (Reproduced with permission from Leis JM and Richards WJ (1984).) Acanthuroidei; development and relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW Jr, and Richardson SL (eds) *Ontogeny and Systematics of Fishes*, pp. 547–551. American Society for Ichthyologists and Herpetologists, Special Publication 1. (12) *Xiphias gladius* (Xiphiidae), 6.1 mm. (Reproduced with permission from Collette BBT, Potthoff T, Richards WJ, Ueyanagi S, Russo JL and Nishikawa Y (1984)) Scombroidei: development and relationships. In: Moser HG *et al.* (eds) *Ontogeny and Systematics of Fishes*, pp. 591–620. American Society of Ichthyologists and Herpetologists, Special Publication 1. (13) *Thunnus thynnus* (Scombridae), 6.0 mm. (Reproduced with permission from Collette BB *et al.*, 1984.) In: Moser HG *et al.* (eds) *Ontogeny and Systematics of Fishes*, 591–620. American Society of Ichthyologists and Herpetologists Special Publication 1.) (14) *Paralichthys californicus* (Paralichthyidae), 7.0 mm. (Reproduced with permission from Ahlstrom EH, Amaoka K, Hensley DA, Moser HG and Sumida BY (1984).) In: Moser HG *et al.* (eds) *Ontogeny and Systematics of Fishes*, pp. 640–670. American Society of Ichthyologists and Herpetologists, Special Publication 1.)

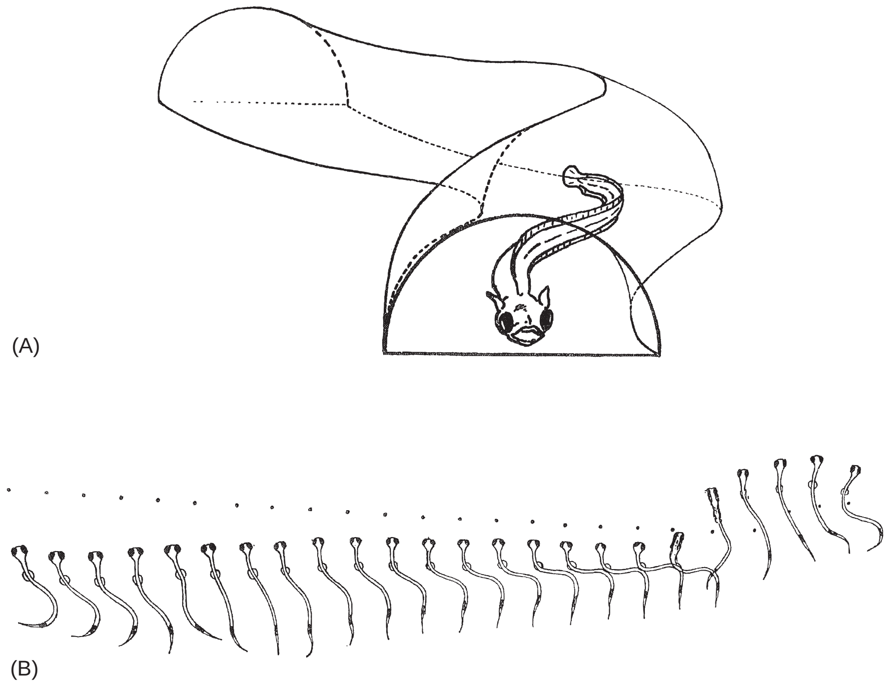


Figure 2 Typical feeding behavior of an Atlantic herring larva. (A) 'Tube' search. Only those food items in the tube are available to the larva. (B) S-flex feeding. Sequence of stages during an unsuccessful feeding attempt by a larva. (Reproduced with permission from Rosenthal H and Hempel G (1970).) Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.) In: Steele JH (ed.) *Marine food chains*, pp. 344–364. Berkeley: University of California Press.)

longer and may have higher predation risk. Thus, larval growth rate and its dependence on nutrition links the predation and starvation processes. Larval growth rate under many circumstances is an important measure of susceptibility to predation.

There are many kinds of predators on fish eggs and larvae. Predators include jellyfishes (ctenophores and medusae), fish, and crustacea (e.g. euphausiids, large copepods). Cannibalism on eggs and larvae occurs and can be an important population regulatory mechanism. The relative importance of the various predators is poorly known. Although a suite of predators of different taxa and sizes eat larvae of preferred sizes, the integrated effects of complex, multispecific predation on recruitment outcomes have hardly been evaluated in the sea or in laboratory experiments. Models of predation also generally have focused on single predators of near-uniform size preying on fish larvae of a single species. In natural ecosystems a community of predators of varying kinds and sizes, which are distributed patchily in time and space, interacts with an assemblage of fish early-life stages. Outcomes are difficult to predict and will be modified by availability of alternative prey resources.

Vulnerability of larval fish to a predator of defined size can often be represented by dome-shaped responses in which vulnerability peaks at an intermediate larval size or by a consistent decline in vulnerability as larval size increases (**Figure 3**). Predation rate on larvae is frequently a dome-shaped function of the ratio of prey size : predator size, where larval fish (the prey), are consumed most efficiently when they are 5–15% of a predator's length, a ratio that is consistent for predators as diverse as jellyfish or fish. Vulnerability of larval fish to predation is the product of encounter rate (dependent upon abundances, sizes, and swimming speeds of both predators and prey) and susceptibility (attack probability × capture probability) of larvae. Thus, sizes and swimming speeds of predators and larvae determine vulnerability of an individual larva. At the population level, size-specific abundances of the predator clearly will be important in determining whether a particular predator can control or inflict significant mortality on a population of larval fish. Many common predators, e.g. some medusae and fish, span a broad range of sizes and may be predators on populations of fish larvae over a wide size range.

Although size is the dominant factor determining vulnerability of fish larvae to predation, ontogeny plays an important role. Fish larvae can react to predators by sensing vibrations via free neuromasts that are present at hatching. As growth occurs, neuromasts proliferate, the lateral line develops, and vision may become increasingly important to detect

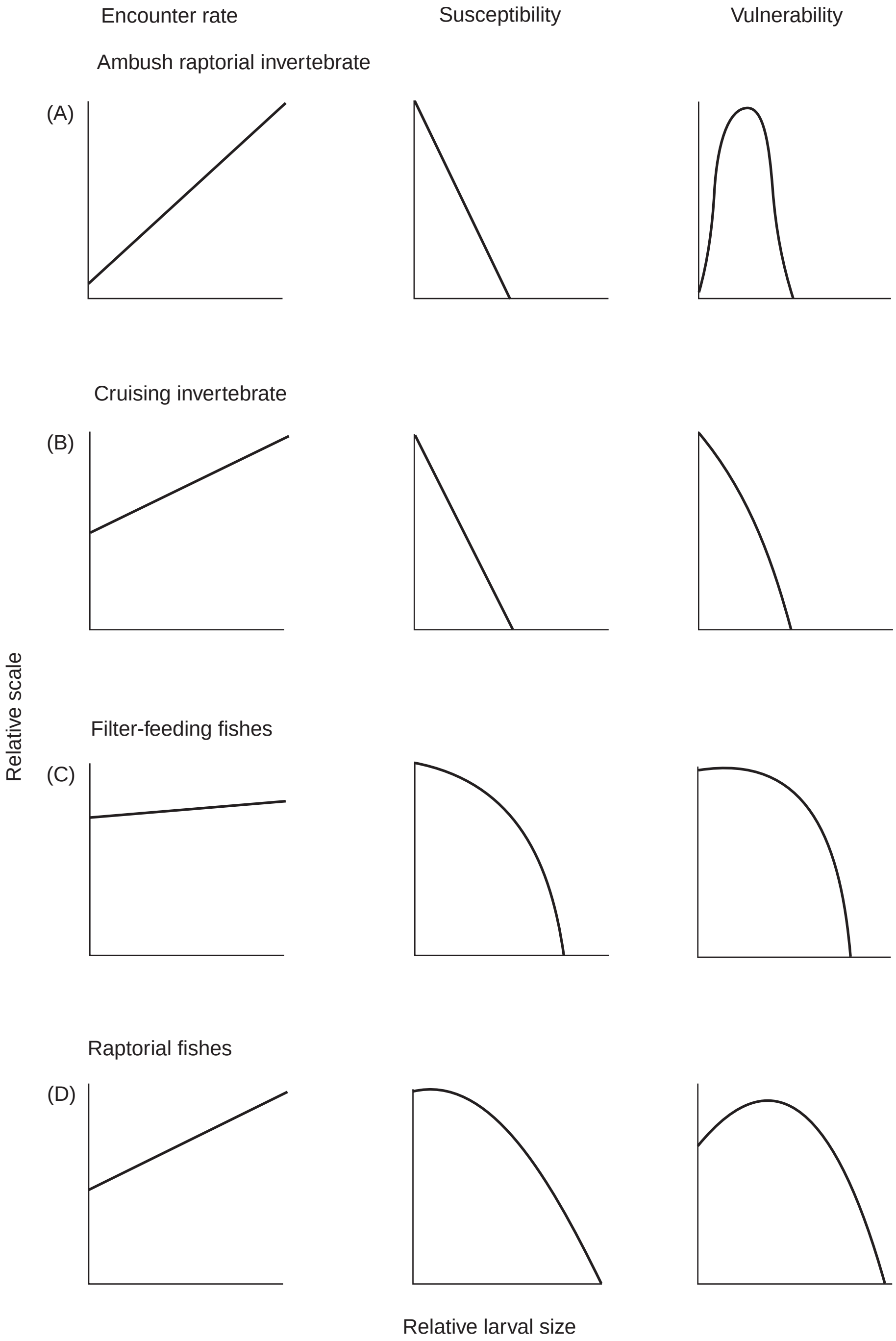


Figure 3 Conceptual models showing relative encounter rates, susceptibility, and vulnerability of fish larvae to different predator types. (Reproduced with permission from Bailey KM and Houde ED, 1989.)

and escape predators. Development of musculature and fins, especially the caudal fin complex, increases the swimming power and escape ability of larval fishes. Ontogenetic improvements in larval ability to avoid predators are counteracted to an extent by the increased sizes of predators targeting larger larvae and juvenile fish. Mortality rates of large larvae and juveniles generally decline, indicating that survival advantages attained through ontogeny and growth outweigh increased suitability of these fish to a suite of larger predators.

Temperature and Salinity

Temperature exerts strong control over rate processes associated with metabolism and growth in larval fishes. Temperature and body size may be the two most important controlling variables in the early lives of fishes. Temperature also controls rate processes in predators and thus indirectly controls rates at which larvae die from predation. Furthermore, seasonal development of planktonic prey of fish larvae depends in part upon temperature, and is especially important in seasonally variable mid and high latitudes where combined effects of temperature and prey levels control larval growth potential. Salinity generally is of secondary importance, but it too can be critical for some anadromous fishes whose larvae inhabit estuarine zones along the salinity gradient or at the interface between fresh water and salt waters.

Growth rates of marine fish larvae are surprisingly plastic. Weight-specific growth rates may vary by more than fourfold in response to temperature differences within tolerable ranges, which imparts high variability to larval stage durations. Although temperature can exercise physiological control over growth, prevailing temperatures in many continental shelf and oceanic nursery areas differ only slightly during a spawning season or between years, and larval growth may in fact be controlled more by prey availability in those ecosystems. However, in shallow estuaries and neritic habitats, fluctuations in temperature induced by weather fronts or shifts in circulation patterns may be sufficiently strong to influence larval growth rates or to directly cause mortality. Ranges of temperature tolerated by larvae are generally lower than for juveniles and adults.

Temperature and body size control bioenergetics relationships in marine poikilotherms, including larval fish. Growth rates, metabolic rates, and possibly growth efficiencies and assimilation rates of fish larvae, are sensitive to changes in temperature. Each fish species has a temperature at which it performs optimally. In meta-analyses across species and ecosystems, larval growth rates were demonstrated to increase as temperature increased. Species from high latitudes grow slowly (often $<10\%$ body weight per day) while tropical species grow fast ($>30\%$ per day). In the meta-analysis, mortality rates are positively correlated with growth rates, and thus also are temperature-dependent.

Salinity controls water balance in osmotic regulation. Marine fish larvae often have surprisingly broad tolerances of salinity. Even anadromous fishes, whose larvae normally live in salinities <1 psu, may perform well in laboratory experiments at salinities of 5–10 psu. At high salinities marine fish larvae drink sea water to regulate water balance. Drinking rates increase as either salinity or temperature increases. Salinity and temperature often act together to affect the physiological performance of larvae. In particular, optimum salinity–temperature combinations determine hatching success and larval performance. Moreover, temperature and salinity combinations in the sea determine the density field (σ_t) in which larvae are located. The density field controls pycnocline and thermocline depths, which define strata, discontinuities, shear zones, and transition depths that may aggregate prey and predators of fish larvae as well as the larvae themselves.

Behavior

Except for larval feeding behavior (see above), relatively little is known about the behavior by individuals with respect to environmental cues or other stimuli. Swimming behaviors are documented for some species. Larvae with elongate bodies (e.g. sardines) swim with an anguilliform motion, while larvae with more compact bodies (e.g. cod-like or bass-like larvae) adopt a modified carangiform, 'cruise-pause' swimming behavior. When searching for food, swimming typically is slow, one or two body lengths per second, and is the predominant behavior of feeding-stage larvae during daylight hours. Feeding-stage larvae generally can cruise at sustained swimming speeds of 3–10 body lengths per second, but newly-hatched, yolk-sac larvae are incapable of strong, directed swimming in a horizontal plane. Burst swimming to escape predators, at >10 body lengths per second is observed. Predator detection and avoidance behaviors become increasingly effective during ontogeny as sensory systems develop.

Fish larvae may migrate vertically over tens of meters on a diel basis. This ability allows larvae to track food by adjusting depth distributions to coincide with depths where prey is abundant. In addition, larvae can potentially avoid parts of the water column where predators prevail or where environmental conditions and water quality (e.g. low dissolved oxygen) are unfavorable. Dispersal of larvae or, alternatively, retention on nursery grounds can depend on depth selection that promotes 'selective tidal stream transport.' This behavioral mechanism requires that larvae coordinate vertical migrations with tides and currents to ensure transport to, or retention within, favorable nursery areas. This mechanism is particularly important in estuaries, but may also regulate larval drift or retention on continental shelf nursery areas.

Integration

Larval populations of many marine fishes are distributed over tens to thousands of kilometers and have early-life durations that range from days to months. However, the fates of individual larvae depend upon interactions with their environment, prey, and predators measured on spatial scales of micrometers to meters and on timescales of fractions of seconds to hours. Events at all spatial and temporal scales are potentially important and can generate significant variability in larval survival.

The potential for recruitment success is indicated by both survival and proliferation of cohort biomass during early life. While numbers decline steadily, biomass of successful cohorts increases. Stage-specific survival during early life depends upon relative rates of mortality (M) that reduce a cohort's numbers and growth (G) that controls accumulation of individual mass. Biomasses of most marine fish cohorts decline during the larval stage to levels $<1\%$ of their biomasses at hatching because $M/G>1.0$. In many marine and estuarine fish larvae (e.g. walleye pollock *Theragra chalcogramma*, American shad *Alosa sapidissima,* bay anchovy *Anchoa mitchilli*), the body size at which the transition from $M/G>1.0$ to <1.0 occurs, after which cohort biomass increases, varies annually. Cohorts that are strong contributors to recruitment make the transition at smaller size than unsuccessful cohorts (**Figure 4**).

Important processes may act sequentially during development (**Figure 5**). Initially, density-independent processes are believed to dominate as controllers of growth and mortality. As growth proceeds and the young fish are less dominated by physical conditions of their immediate environment, density-dependent processes related to competition for prey or predation pressure will become increasingly important in regulating recruitment.

The ability to assign ages to sampled fish larvae from daily increment counts in otolith microstructure and thus to estimate sizes-at-age, growth rates, and mortality rates provides a powerful tool to retrospectively analyze cohort dynamics and relate variability in larval-stage survival to environmental factors. Observed mortality rates of larval populations usually decline as size increases from hatching to metamorphosis, but patterns in growth rates are less predictable, differing among species and among cohorts within species. While the potential advantages of fast larval growth were cited by Cushing many years ago, convincing evidence supporting this hypothesis has been provided only recently in studies on larval cod, plaice *Pleuronectes platessa*, and other species. In these species, cohorts that grow fast often contribute disproportionately to recruitment. Although growth rate differences alone can generate strong variability in early-life survivorship, variability in larval mortality rates probably contributes most to fluctuations in recruitment.

Models to explore and simulate larval stage dynamics have proliferated in recent years.

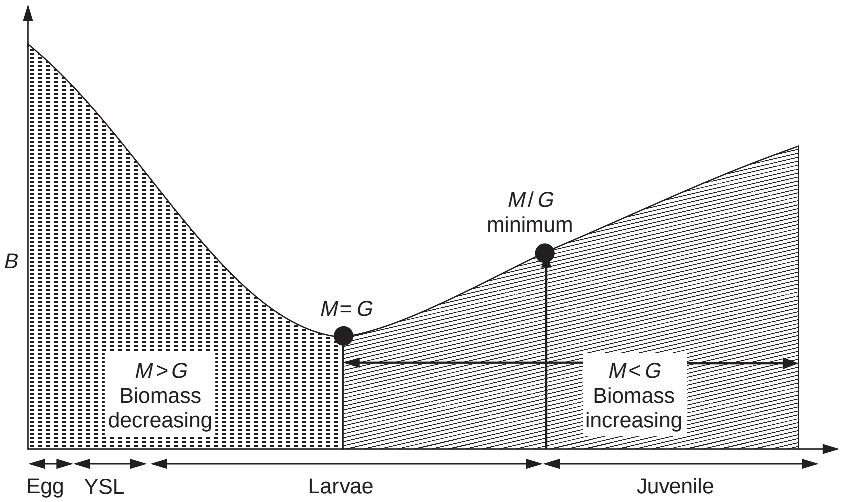


Figure 4 Conceptual diagram of trend in cohort biomass (B) during early-life stages. Cohort biomasses decrease during egg and yolk-sac larva (YSL) stages but may increase during the larval and juvenile stages. M is the instantaneous mortality rate and G is the weight-specific growth rate. A 'transition size' at which $M=G$ is the size of an individual at which cohort biomass begins to increase. (Reproduced with permission from Houde ED (1997) Patterns and consequences of selective processes in teleost early life histories. In: Chambers RC and Trippel EA (eds) *Early life history and recruitment in fish populations*, pp. 173–196. Dordrecht: Kluwer Academic Publishers.)

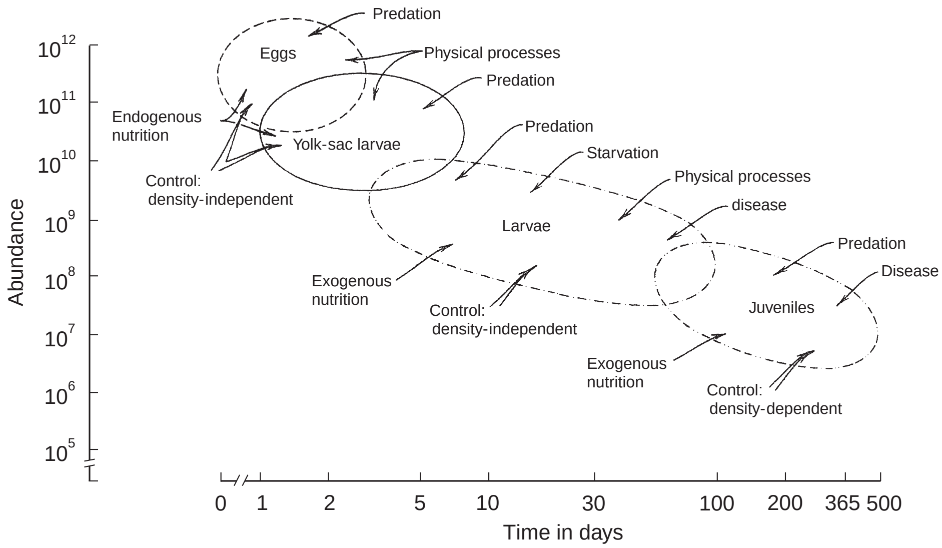


Figure 5 Conceptualization of the recruitment process including sources of nutrition, probable sources of mortality, and hypothesized mechanisms of control for four early-life stages. (Reproduced with permission from Houde ED, 1987.)

Individual-based models have proven to be useful in simulations of survival and growth responses of individual larvae, and to track the status and trajectory of cohorts over time with respect to variability in physical and biological factors. Coupled physical–biological models are making major contributions to understanding how circulation features transport or retain larvae and support larval production.

Research Needs

It remains difficult to accurately estimate abundances of fish early-life stages. As larvae grow their abundances decline, while they become increasingly more mobile and difficult to sample with conventional nets. This problem continues to plague attempts to estimate larval mortality rates and production, which require accurate abundance-at-age estimates. Improved samplers that allow depth-specific collections have been available since the 1970s and a new generation of collecting and sensing instruments (e.g. optics and acoustics) may partly resolve the problem. Distribution patterns and patchiness of early-life stages must be appreciated to design surveys that can adequately account for the temporal and spatial variability in distributions of early-life stages. The issues here are complex because critical spatial scales are poorly known and may change as larvae grow. Obtaining better abundance estimates ultimately depends upon an integrated knowledge of biotic and abiotic factors, especially larval behavior and ocean physics, and the interactions of the two at many scales.

There are few extensive time series of abundances of early-life stages of fish. Such series, while costly to obtain, provide information on annual variability in abundances with respect to long-term changes in climate and ocean environment. Fundamental advances in understanding causes of variability in larval production would emerge from surveys repeated over many years. It is quite probable that, in addition to annual variability, decadal and other low-frequency patterns of variability in ocean productivity also exercise controls over survival of fish early-life stages and levels of recruitment. Long time series of larval abundances and dynamics may not be essential to manage fisheries in a tactical sense, but they would be important strategically to document long-term trends and causes of variability in recruitment success.

It is essential to develop better knowledge of trophic relationships in the plankton because they largely determine the fate of larval fish cohorts. Better conceived, interdisciplinary, and integrated research programs that emphasize how physics at appropriate scales (e.g. microturbulence) accounts for interactions between larvae and prey and between larvae and predators are needed. Modeling research must play a major role to help explain and predict variability in larval survival. Existing models range from simple statistical models that describe allometric relationships of physiological responses during larval development to models of ecosystem-level complexity that include many environmental factors. Forecasting larval stage survival and recruitment are worthy, but elusive, goals of such modeling . It is important to build upon progress in development of coupled biological–physical models, including individual-based, spatially explicit models that predict larval survival (e.g. walleye pollock, Atlantic cod, Atlantic herring, Atlantic menhaden *Brevoortia tyrannus)*. Modeling physics at appropriate scales has progressed more rapidly than biological modeling. Improved models to elucidate biological variability in the larval stage are needed before forecasts of recruitment can be achieved.

Development of new technologies and adoption of technologies from other disciplines have advanced knowledge of larval stage ecology. Since the 1970s, analysis of microstructure in larval otoliths has provided the breakthrough that allows more or less routine aging of fish larvae from daily increments in otoliths. Biochemical methods, such as analysis of RNA/DNA and lipids, have proved useful to evaluate growth potential and nutritional condition of larvae. New biochemical indicators to assess larval condition or to categorize habitats (water quality) in which larvae were collected are being developed. Recent research combining analyses of otolith chemistry and microstructure holds great promise for hindcasting environmental conditions (temperature, salinity) that larvae experienced earlier in life. New genetic tools have potential to identify stocks, track larval dispersal, and differentiate survival potentials among closely related, but genetically distinct, stock units. The problem of obtaining adequate and representative samples of fish larvae is being addressed by applying new sensing technologies, e.g. *in situ* optical and acoustical samplers aboard ship or moored on buoy systems and designed to sense larval fish as well as their zooplankton prey and predators. Advances in remote sensing capability will allow better assessments of environmental conditions, hydrographic variability, and sea state, which will permit more critical evaluations of larval habitats and water quality.

Conclusions

Coarse controls on reproductive success and establishment of year-class abundances are exercised primarily during the embryonic and larval stages of marine fish during their drift in the plankton. The larval stage of marine fish is on average > 35 days long, during which time much of the variability in survival to recruitment may be generated. Control may be mostly density-independent during these stages, although theoretical and modeling research demonstrates that density-dependence, even at modest levels, could be a powerful regulator of early-life dynamics. Finer controls operate during the juvenile stage when a shift towards density-dependence may occur. Year-class size and recruitment level can be set in either the larval or juvenile stage. Importantly, effects of poor larval survival seldom can be compensated by high juvenile survival. The converse is not true, i.e. high larval stage survival does not guarantee recruitment success; year classes may fail during the juvenile stage.

Cushing (1975) referred to ‘the single process’ during early lives of marine fishes. Growth and mortality, nutrition and predation, and physical conditions in nursery areas all act together to control recruitment and mold a year class. It is not ‘starvation, predation or advective losses,’ but the net result of those combined processes that controls recruitment. The subtle, difficult-to-measure small differences in mortality or growth rates over weeks or months, rather than episodic events generating massive mortalities, usually dominate in determining recruitment success. Initially, eggs and larvae are very abundant, and their growth and mortality rates are high and variable. Even small differences in those rates, if not compensated in the juvenile stage, assure large fluctuations in cohort survival.

Survival of marine fish larvae appears to be strongly size-dependent. Compared with freshwater fish larvae, marine larvae tend to be small. Their hatch weights average nearly 10 times less than weights of freshwater larvae (**Table 1**). The difference in size is believed to be the primary factor determining the higher average mortality rates, longer stage duration, higher weight-specific respiration rates, and higher weight-specific food consumption by marine larvae. As a consequence and generalization, control over recruitment probably is exercised primarily in the relatively long larval stage of marine fish but in the juvenile stage of freshwater fish.

Table 1 Dynamic properties of marine and freshwater fish larvae

	Marine		*Freshwater*	
Variable	*Mean*	*Standard error*	*Mean*	*Standard error*
W_o	37.6	6.4	359.7	72.8
W_{met}	10 846	953	9277	1604
G	0.200	0.011	0.177	0.019
M	0.239	0.021	0.160	0.040
D	36.1	1.1	20.7	1.1

Temperature-adjusted mean values are presented. W_o = dry weight at hatch (μg); W_{met} = dry weight at metamorphosis (μg); G = weight-specific growth rate (d^{-1}); M = mortality rate (d^{-1}); D = larval stage duration (d). (Modified from Table 1 in Houde ED (1994). Differences between marine and freshwater fish larvae; implications for recruitment. *ICES Journal of Marine Science* 51: 91–97.)

An 'average' fish larva has little chance for survival. Typically, numbers are reduced by three orders of magnitude during the larval stage. Thus, larval survivors may have special qualities, in addition to extraordinary luck. Individuals that behave appropriately or grow faster will survive because they are proficient at feeding and avoiding predators, and perhaps better at selecting favorable habitat (e.g. by vertically migrating). Favored or selected characteristics may be phenotypic or inherited. As an example of the former, there is evidence that in many species bigger larvae hatch from eggs spawned by larger and older females. Such larvae have higher survival potential. Thus, the fates of fish larvae may be partly programmed by genes from their parents, but also will depend on selective fishing practices that target the largest adults, in addition to the myriad environmental factors that normally act on larval populations.

See also

Conservative Elements. Fish Ecophysiology. Fish Feeding and Foraging. Fish Locomotion. Fish Migration, Horizontal. Fish Migration, Vertical. Fish Predation and Mortality. Fish Reproduction. Pelagic Fishes. Plankton. Population Dynamics Models. Small-scale Physical Processes and Plankton Biology. Zooplankton Sampling with Nets and Trawls.

Further Reading

Bailey KM and Houde ED (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* 25: 1–83.

Beyer JE (1989) Recruitment stability and survival – simple size-specific theory with examples from the early life dynamics of marine fish. *Dana* 7: 45–147.

Blaxter JHS (1986) Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society* 115: 98–114.

Cushing DH (1975) *Marine Ecology and Fisheries*. Cambridge: Cambridge University Press.

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* 26: 250–293.

Hjort J (1914) Fluctuations in the great fisheries of northern Europe. *Rapport et Procés-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer* 20: 1–228.

Houde ED (1987) Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium* 2: 17–29.

Houde ED (1997) Patterns and consequences of selective processes in teleost early life histories. In: Chambers RC and Trippel EA (eds) *Early Life History and Recruitment in Fish Populations*. Dordrecht: Kluwer Academic Publishers.

Lasker R (ed.) (1981) *Marine Fish Larvae. Morphology, Ecology, and Relation to Fisheries*. Seattle: University of Washington Press.

Sale PF (ed.) (1991) *The Ecology of Fishes on Coral Reefs*. San Diego: Academic Press.

Sinclair M (1988) *Marine Populations. An Essay on Population Regulation and Speciation*. Seattle: University of Washington Press.

FISH LOCOMOTION

J. J. Videler, Rijksuniversiteit Groningen, Haren, The Netherlands

doi:10.1006/rwos.2001.0027

Introduction

After one thousand million years of evolution fish are extremely well adapted to various constraints set by the aquatic environment in which they live. In the dense fluid medium they are usually neutrally buoyant and use movements of the body to provoke reactive forces from the water to propel themselves. Propulsive forces overcome drag, are required for acceleration, and disturb the water. Animal movements are powered by contracting muscles and these consume energy. These basic principles of fish locomotion are used by more than 22 000 extant species. The variation in swimming styles, within the limits of these principles, is extremely large.

The Swimming Aparatus of Fish

Fish are aquatic vertebrates with a skull, a vertebral column supporting a medial septum dividing the fish into two lateral halves, and lateral longitudinal muscles segmentally arranged in blocks, or myotomes. The vertebral column is laterally highly flexible and virtually incompressible longitudinally. Consequently, contraction of the muscles on one side of the body bends the fish, and waves of curvature along the body can be generated by series of alternating contractions on the left and right side.