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Chapter 9

Collection, Preservation, and Identification of Fish Eggs and Larvae

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9.1 INTRODUCTION

This chapter is an introduction to methods for collecting, processing, and identifying early life stages of fishes and summarizes the diversity of both marine and freshwater studies on fish eggs and larvae. We review various gears used to collect eggs and larvae, their relative effectiveness in different sampling situations, and the effects of physicochemical characteristics and larval behavior (e.g., vertical migration and phototaxis) on sampling design. We also include a discussion of sample preservation and processing, as well as discussions of early life stage terminology and techniques and taxonomic guides used for egg and larval identification.

Early investigators studying the growth, reproduction, and mortality of fish populations documented the critical importance of early life stages (eggs and larvae; see section 9.6.3) to overall abundance (Hjort 1914; May 1974; Hempel 1979). Fishes typically have high fecundity, and fish populations generally have high egg and larval mortality (>90%) and substantial year-to-year variation in survival of early life stages. Ichthyoplankton mortality is usually attributed to inherited defects, egg quality, starvation, disease, and predation. In addition, periods of high mortality may be associated with critical events in early ontogeny (e.g., hatching, first feeding, and initiation of swimbladder function; Blaxter 1988). Because the timing and duration of these critical periods are closely tied to physicochemical conditions, environmental variability can have substantial effects on egg and larval growth and mortality and ultimately on recruitment to adult stocks (Thorisson 1994).

The importance of early life stage survival to population abundance and fisheries harvests (Smith and Morse 1993) has led to numerous studies on distributions of fish eggs and distributions and behavior of larvae. Egg and larval collections have been used to identify spawning and nursery areas (Heath and Walker 1987) as well as temporal and spatial differences in spawning characteristics of exploited populations (Graham et al. 1984). Larval fish studies have also yielded information on ontogenetic changes in movement patterns (Lough and Potter 1993) and foraging behavior (Brown and Colgan 1985). Because larval survival may be closely linked to rapid growth, several recent investigations have focused on the use of RNA:DNA ratios (Bulow 1987) and larval otoliths to assess growth rates (e.g., Karakiri and von Westernhagen 1988; Zhang et al. 1991; see Chapter 16). Improvements in egg and

larval rearing techniques (Hunter 1984) have increased the number of fish species that can be cultured and have provided material for a diversity of physiological experiments (see Hoar and Randall 1988) as well as taxonomic and systematic studies (Moser et al. 1984). In addition, because abundance and survival of fish eggs and larvae may be closely tied to environmental changes, studies of fish early life stages have been important in the assessment and reduction of anthropogenic effects (e.g., entrainment; Dempsey 1988) on aquatic systems.

Because eggs and larvae of marine and freshwater fishes differ in size, vertical and horizontal distribution, temporal availability, and susceptibility to various gears, effective collection techniques are critical to the design of a sampling program. In addition, a well-designed study requires proper handling, preservation, and identification of collected organisms (see Chapter 5). Because of characteristics unique to early life stages (e.g., small size and patchy distribution), techniques used for collection and identification of eggs and larvae are considerably different from those devised for adult fishes.

9.2 COLLECTION OF FISH EGGS AND LARVAE

The diversity of fish reproductive modes combined with species-specific differences in spawning habitats, larval growth, and behavior have resulted in the development of a diverse array of egg and larval collecting gears. Most gears designed for collecting pelagic eggs and larvae involve filtration of water through fine-mesh material, whereas harvest of demersal or attached eggs and larvae usually involves the use of artificial substrates and traps. Many modifications of traditional collecting gears can be found in the literature, and it is frequently necessary to alter the design of a particular gear to fit specific sampling conditions. Regardless of the sampling problem involved, choice of a particular gear must include consideration of the advantages and disadvantages of each gear type (Table 9.1). In addition to the sampling characteristics of each gear, characteristics of the organisms being sought and the habitat being sampled must also be considered. Marcy and Dahlberg (1980) and Bowles et al. (1978) summarized the major mechanical problems associated with sampling fish eggs and larvae, some of which can be minimized by choice of sampling gear.

9.2.1 Active Collecting—Low-Speed Gears

Use of plankton nets (Figure 9.1A) to collect ichthyoplankton can be traced to 1828 (Fraser 1968). Since that time, many modifications of gear design and sampling methodology have been developed to increase accuracy and precision of ichthyoplankton abundance estimates. Choice of sampling gear should be based on consideration of expense, ease of use, relative effectiveness, and sampling bias.

9.2.1.1 Plankton Nets

Conical plankton nets (Figure 9.1) with mouth diameters ranging from about 0.1 m to over 1 m in diameter have been used extensively to sample fish eggs and larvae. Larger nets (>0.5 m in diameter) are usually towed at speeds under 2 m/s for periods ranging from 30 s to an hour, depending primarily on ichthyoplankton density and the abundance of debris (clogging). Nets typically consist of a nylon mesh cone or a cylinder-cone combination attached at the proximal end to a steel or brass ring, which is in turn connected to the towing cable with a three-stranded bridle (Figure 9.1A). The distal end of the net usually ends in a collection bucket (Duncan 1978;

Table 9.1 Advantages and disadvantages of various types of collecting gears for fish eggs and larvae.

Gear type	Examples	Advantages	Disadvantages	
Low-speed nets	Vertical tows	Buoyant net	Reduced net avoidance Useful in shallow, vegetated habitats	Small volume filtered
	Horizontal tows	Meter nets	Large water volume in short time period	Clogging of mesh reduces efficiency
		Bongo nets	Inexpensive	Efficiency variable in turbulence
		Benthic sleds	Can be towed or anchored	Net avoidance increases with size of larvae
		Tucker trawl	Only small vessels required	Without modifications, limited use in littoral areas
Neuston nets	Small conical nets can be towed by hand			
Henson nets				
High-speed nets	Miller high-speed sampler	Reduced net avoidance	Extrusion, damage to collected organisms	
	Jet net	Large water volume can be sampled over extensive areas	Larger vessels required	
	Gulf III LOCHNESS		Winches required for deployment and retrieval	
Plankton recorders	Hardy plankton recorder	High-speed sampling possible	Damage to sampled organisms	
	Longhurst-Hardy plankton recorder	Discrete samples at depth possible	Extrusion of organisms through mesh Sampling bias due to variations in passage through net	
Midwater nets	Isaacs-Kidd midwater trawl	Pelagic sampling	Large nets, increased personnel needs	
	Tucker trawl	Large volume of water	Constant boat speed important	
	MOCHNESS RMT 1-8	Multiple samples	Increased net handling times	
Pumps	Centrifugal pumps	High-volume samples from turbulent areas	Damage to organisms	
	Trash pumps	Low personnel needs Easy replication	Handling problems with large pumps Reduced efficiency for some species Avoidance by larger larvae	

Graser 1978; Figure 9.1A) into which organisms are washed after net retrieval (although Miller 1973 reported that the use of a 333- μ m-mesh cod end bag reduced damage to collected larvae). Paired nets mounted on a rigid frame attached to the towing cable are called bongo nets (Figure 9.1B). These nets have the advantage of not obstructing water flow with the towing bridle and also provide replicate samples to determine sample variability (Smith and Richardson 1977; Colton et al. 1980; Choat et al. 1993).

Flow meters should be mounted in the net mouth (Figure 9.2A) to determine sample volumes (Gehring and Aron 1968) and should be positioned to measure

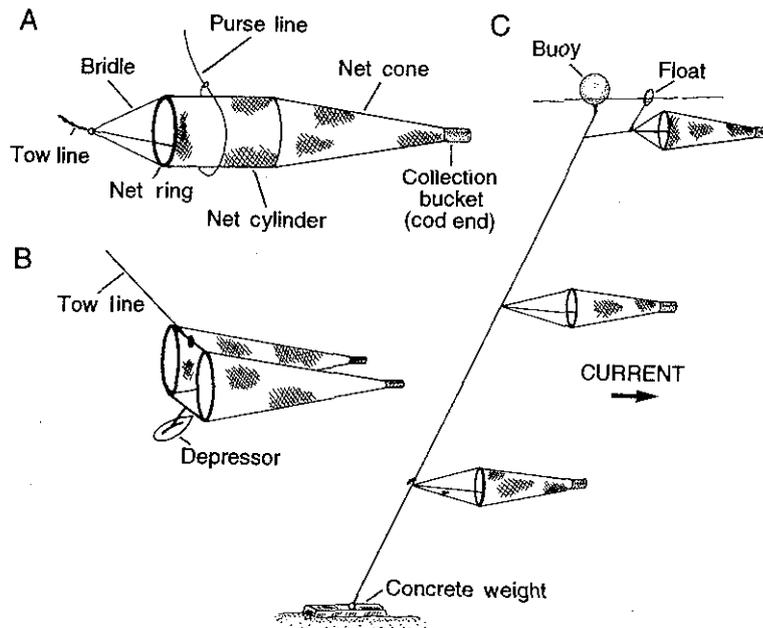


Figure 9.1 Several methods of plankton net sampling: (A) simple cylinder-cone plankton net with a purse line for sampling at discrete depths; (B) paired bongo nets fitted with a depressor to maintain the nets at a prescribed depth; (C) three plankton nets rigged vertically to sample drifting eggs and larvae in lotic habitats.

average velocity through the net. For unbridled nets, the center of the mouth provides a reasonable estimate of average velocity (Mahnken and Jossi 1967); for bridled nets, the flow meter should be located in the net mouth about 20% of the net diameter from the net edge (Figure 9.2A; Trantor and Smith 1968).

The ratio of the open area of a net (exclusive of net material) to its mouth area has been termed the open-area ratio. Studies indicate that filtering efficiency of a net with an open-area ratio exceeding 3 would approach 85%, whereas a ratio of 5 or more would result in up to 95% efficiency (Trantor and Smith 1968). Net efficiency can be increased with a mesh cylinder (40% of the total gauze area) ahead of the conical net (60% of the gauze area); the cylinder acts as additional filtering surface and is much less susceptible to clogging (Figure 9.1A; Smith et al. 1968; Schnack 1974). Additionally, use of a mouth-reducing cone (see Figure 9.4) increases filtering efficiency by creating a low-pressure area that draws a column of water larger than the mouth diameter into the net (Trantor and Smith 1968).

Numerous modifications of standard plankton nets have been reported for specific sampling conditions. Brown and Langford (1975) developed a frame-mounted plankton sled fitted with buoyant floats for sampling ichthyoplankton near the surface. Netsch et al. (1971) incorporated a depressor weight (Figure 9.1B) mounted just ahead of a meter net (a net with a 1-m-diameter mouth) for horizontal towing at depth, and Bath et al. (1979) used a similar design to collect simultaneous bottom, middepth, and surface samples with 0.5-m nets (dimension is mouth diameter). Faber (1968) eliminated the towing bridle and incorporated a purse line to close the net and allow sampling at discrete depths (Figure 9.1A). Nester (1987) developed a

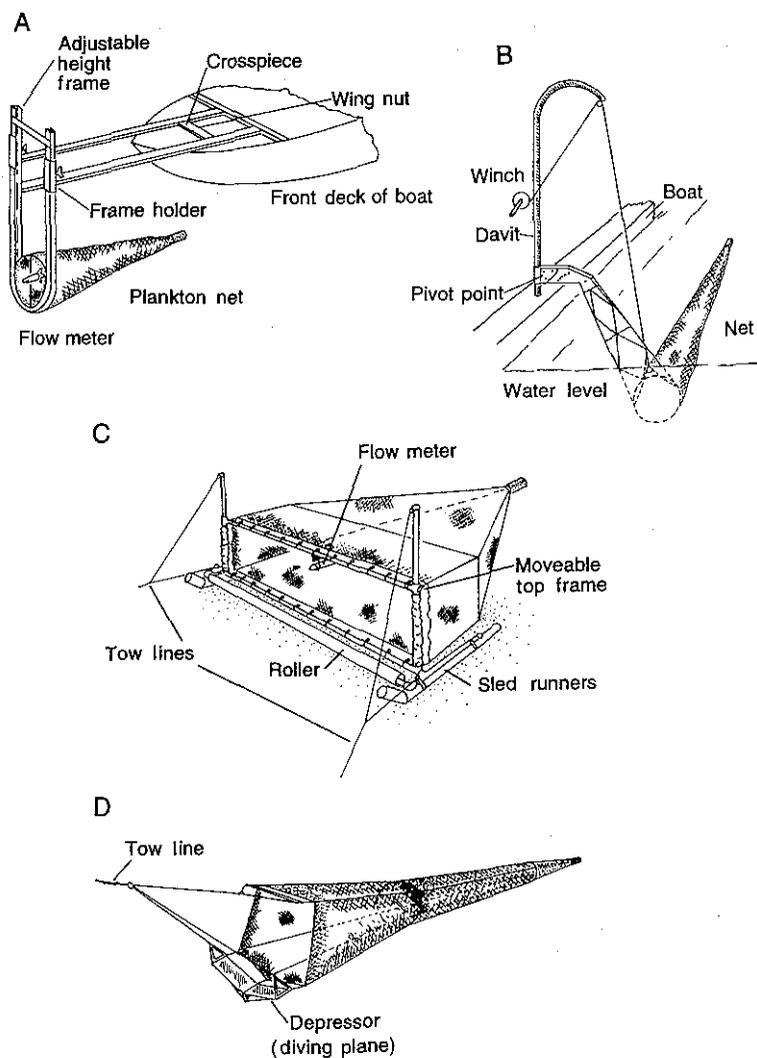


Figure 9.2 Designs for towed or pushed nets: (A) a vertically adjustable push net; (B) a side-mounted ichthyoplankton net; (C) a benthic sled for shallow-water sampling; and (D) an Isaacs-Kidd midwater trawl fitted with a depressor for improved performance at depth (adapted from Meador and Bulak 1987 and La Bolle et al. 1985, with permission).

0.5-m cylinder-cone net and depressor weight mounted on a fixed frame to study vertical distribution of Great Lakes ichthyoplankton. Contamination of samples during vertical retrieval was prevented by collapse of the net over the frame. Dovel (1964), Cooper (1977), Tarplee et al. (1979), and Hermes et al. (1984) described side-mounted frames for sampling surface ichthyoplankton with 1.0-m and 0.5-m nets (Figure 9.2B). Miller (1973) used paired nets suspended from the bow to sample ichthyoplankton in shallow bays in Hawaii.

9.2.1.2 Benthic Plankton Samplers

The need to sample eggs and larvae on or just above the bottom has led to the development of benthic plankton sleds (Figure 9.2C). Frolander and Pratt (1962)

mounted a cylindrical net (Clarke and Bumpus 1950) on a benthic skimmer for sampling demersal organisms in a lake. Dovel (1964) used a much larger net mounted on an aluminum benthic sled for sampling estuarine ichthyoplankton associated with bottom currents of more saline, higher-density water; however, the net was positioned 0.28 m from the bottom of the sled. Yocum and Tesar (1980) mounted a 0.5-m plankton net in a rectangular sled frame and sampled within 5 cm of the bottom in littoral areas of Lake Michigan. This study and that of Madenjian and Jude (1985) indicated that, relative to a standard plankton net, the plankton sled provided better abundance estimates for fish eggs and demersal fish larvae. The rectangular sled developed by La Bolle et al. (1985) included an adjustable net that could effectively fish the entire water column in depths ranging from 0.15 to 0.70 m. Phillips and Mason (1986) developed a sled fitted with a self-adjusting grate to sample demersal adhesive and nonadhesive fish eggs on irregular coastal substrates.

9.2.1.3 Pelagic Trawls

Several low- to moderate-speed (0.5–3 m/s) midwater trawls have been developed to sample zooplankton and early life stages of pelagic fishes. The Isaacs–Kidd midwater trawl (Isaacs and Kidd 1953; Figure 9.2D) is of simple design and has been used extensively to sample large larvae and small juveniles in pelagic areas (Pearcy 1980). A steel-framed trawl (1.8 m × 1.8 m) developed by Tucker (1951; Figure 9.3A) was used by Haldorson et al. (1993) to monitor ichthyoplankton abundance in an Alaskan bay and was modified by Houser (1983) to include a diving plane for maintenance of position in the water column without the use of ballast. Siler (1986) reported Tucker trawl estimates of juvenile and adult threadfin shad abundance in a North Carolina lake were superior to those obtained with rotenone samples. However, Choat et al. (1993) found the Tucker trawl was ineffective for estimating the density or size composition of pelagic reef fish larvae, particularly small individuals. Clarke (1969) described a rectangular (2.8 m × 4 m) trawl that could be opened and closed acoustically, and Baker et al. (1973) used a similar design for the RMT 1–8 (rectangular midwater trawl) which incorporated two opening–closing nets for sampling at depths up to 2,000 m. The MOCHNESS trawl (multiple opening–closing net and environmental sensing system; Wiebe et al. 1976) was similar to that reported by Frost and McCrone (1974) and incorporated nine sequentially opening and closing nets (1 m × 1.4 m × 6 m long, 333- μ m mesh) as well as sensors to monitor depth, temperature, specific conductance, flow, net angle, and net deployment. Sameoto et al. (1977) incorporated a depressor and rigid net frames in a similar 10-net (1-m² mouth area, 243- μ m mesh) sampler (BIONESS; “—NESS” denotes a net with environmental sensing systems) that could be towed at speeds up to 3 m/s. The BIONESS net proved to be superior to a Tucker trawl for sampling small (<10 mm) Atlantic cod larvae, although the trawl was most effective for larger larvae and juveniles (Suthers and Frank 1989). Because of the small mouth size of the BIONESS nets and the dependence of effective mouth areas on towing speed in the RMT 1–8 and MOCHNESS nets (higher speeds caused the bottom of the net mouth to move back and up, reducing the effective mouth area), Dunn et al. (1993) developed the LOCHNESS sampler. This sampler was designed for larger organisms (2-mm mesh) and incorporated five 2.3-m square nets and environmental sensors for simultaneous collection of organisms and environmental data.

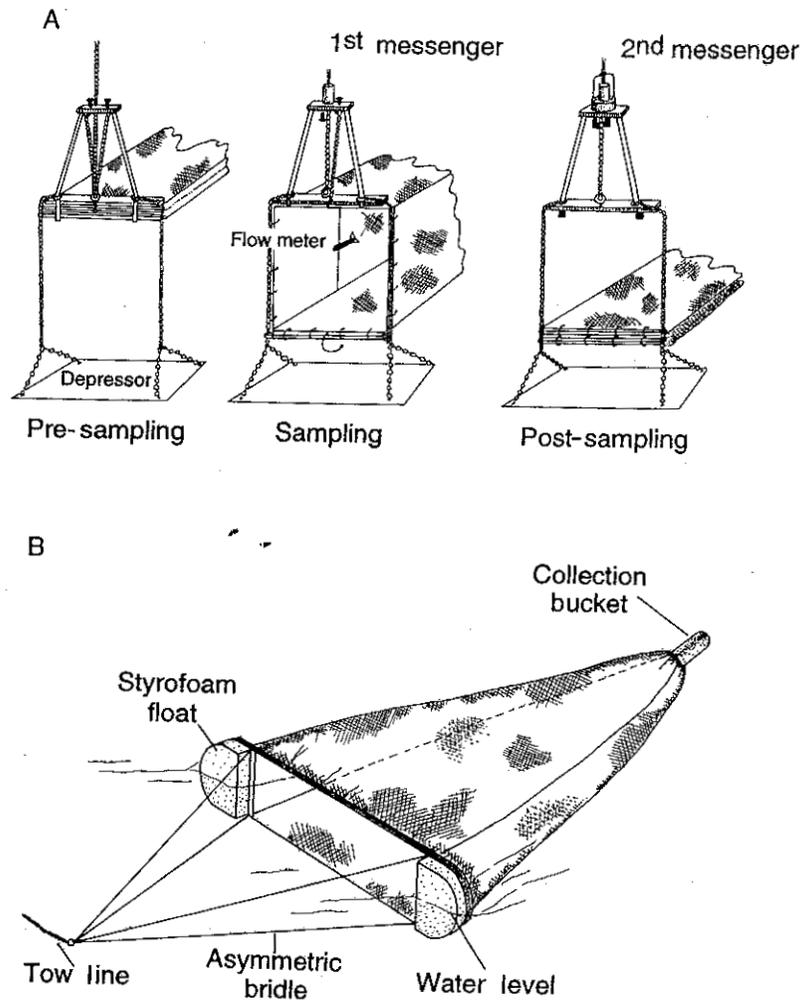


Figure 9.3 Two gears for sampling specific depth strata: (A) a modified Tucker trawl for sampling at depth, and (B) a neuston net for sampling surface eggs and larvae (adapted from Sameoto and Jaroszynski 1976 and Brown and Cheng 1981, with permission).

9.2.1.4 Neuston Nets

Several nets that are towed with the top edge of the net above the water surface have been developed to sample neustonic organisms (Figure 9.3B; Hempel and Weikert 1972; Lippincott and Thomas 1983). Eldridge et al. (1978) tested 4.9-m- and 8.5-m-long Boothbay neuston nets (pipe frame 2 m wide \times 1 m high, 947- μ m mesh) at speeds from 1 to 3 m/s and found that the 4.9-m net was easier to handle and caused less damage to collected specimens. Hettler (1979) modified the Boothbay net for stationary sampling in a tidal current and incorporated a wooden collection box for retrieval of live larvae. Brown and Cheng (1981) developed the Manta net, which was designed with fixed wings and asymmetrical towing cables to maintain the net at the surface and away from the boat. The authors reported that the net was superior to other neuston net designs for sampling in choppy waters (waves higher

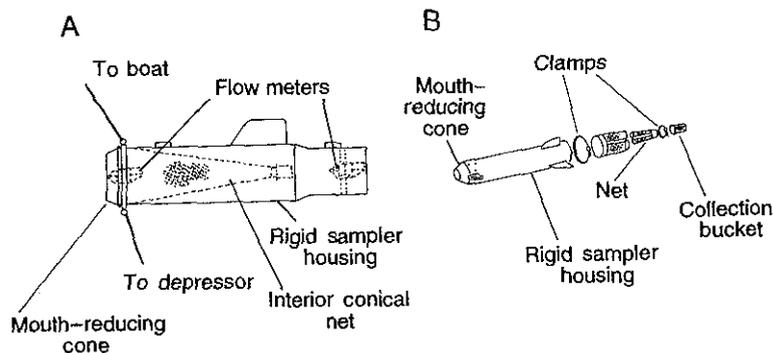


Figure 9.4 High-speed samplers: (A) a cutaway of the Gulf III sampler (note the fore and aft flow meters) and (B) exploded view of a Miller high-speed sampler (adapted from Gehringer 1952 and Miller 1961, with permission).

than 10 cm). Shenker (1988) also found the Manta net to be an effective sampler for larval fishes and crabs off the Oregon coast, although a larger neuston trawl (3.5 m wide \times 1 m deep) was more effective for larger juveniles.

9.2.2 Active Collecting—High-Speed Gears

Conical plankton nets mounted inside hollow cylinders fitted with mouth-reducing nose cones (Figure 9.4) have been used extensively as high-speed samplers in studies of both marine and freshwater ichthyoplankton (Gehringer and Aron 1968). These samplers are typically large (>50 kg; the Miller high-speed net is an exception) and require power winches for deployment and retrieval. Although high-speed samplers reduce net avoidance by mobile larvae (larval avoidance can still occur; Bjørke et al. 1974) and can sample large volumes of water over extended distances in short periods of time, the net-within-cylinder design appears to be more subject to clogging (but see the unencased "Nackthai" high-speed net in Schnack 1974). The Gulf 1-A high-speed sampler (12-cm-diameter tube, 4-cm opening) was described by Arnold (1952) and was modified by Smith et al. (1964) to sample at speeds up to 9 m/s. The Gulf III net (Gehringer 1952) incorporated a 0.5-m net in a rigid housing to sample a greater volume of water than the Gulf 1-A (Figure 9.4A). Bridger (1958) reported that a reduction in nose cone diameter from 40 cm to 20 cm substantially improved net efficiency and resulted in increased diurnal catches of larval Atlantic herring. Beverton and Tungate (1967) modified the Gulf III net to sample larval pleuronectids, phytoplankton, and zooplankton simultaneously.

In freshwater systems, Miller high-speed nets (Miller 1961) have been widely used to sample fish eggs and larvae (Figure 9.4B). These samplers are lightweight and can be operated by a single person from a small boat. Noble (1970) evaluated Miller high-speed samplers attached to side-mounted 3-m poles and found that sampling performance was improved by increasing speed, sampling nocturnally, incorporating an electroshocking grid in front of the samplers, and using clear rather than opaque materials to construct the sampler. Coles et al. (1977) incorporated a small pump to continuously empty the contents of a high-speed Miller-type net that was used to study spatial heterogeneity of Eurasian perch larvae. Such a design seems particularly well suited for studying vertical and horizontal patchiness in egg and larval

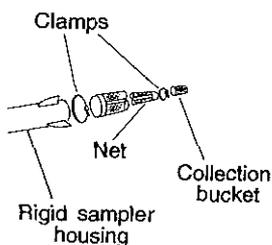


Figure 9.2.3. Gulf III sampler (note the fore and aft samplers) (adapted from Gehring)

to be an effective sampler for a larger neuston trawl (3.5 miles).

ers fitted with mouth-reducing high-speed samplers in studies (Gehring and Aron 1968). These high-speed net is an exception) and although high-speed samplers can still occur; Bjørke et al. (1970) extended distances in short to be more subject to clogging (Schneck 1974). The Gulf 1-A (Figure 9.2A) was described by Arnold (1958) at speeds up to 9 m/s. The net is in a rigid housing to sample (Figure 9.2A). Bridger (1958) reported that a 10 cm substantially improved efficiency of larval Atlantic herring. This design to sample larval pleuronec-

(1961) have been widely used. These samplers are lightweight and can be used (1970) evaluated Miller (1970) and found that sampling is more effective nocturnally, incorporating a clear rather than opaque net. Miller incorporated a small pump to operate the net that was used to collect a design seems particularly effective in egg and larval

distributions. An alternative design for a high-speed sampler was the jet net, which was developed to reduce damage to collected organisms by slowing the velocity of water as it moved through the sampler into the collecting net (Clarke 1964).

Opening-closing high-speed samplers have also been developed for sampling at discrete depths (Bé 1962). The Clarke-Bumpus sampler (Clarke and Bumpus 1950; Trantor and Heron 1965) has been used extensively in zooplankton studies. It uses a messenger-operated closing gate (Paquette and Frolander 1957) to eliminate sample contamination. Kinzer (1966) modified a Gulf III net with a messenger-activated, spring-loaded closing mechanism, and Bary and Frazer (1970) incorporated a similar electrically activated closing mechanism and an improved flow meter design on the Catcher II, a modification of the Catcher sampler developed by Bary et al. (1958).

An alternative method for obtaining discrete plankton samples was developed by Longhurst et al. (1966) from a Hardy plankton recorder (Hardy 1936). The Longhurst-Hardy plankton recorder incorporated, at the end of a plankton net, a unique collection box that continuously filtered collected organisms through a gauze strip, which was overlaid by a second strip, both of which were wound up in the box. The plankton recorder has been used extensively and has been reported to be more effective than meter nets (Colton et al. 1961), MOCHNESS, and pump samplers (Brander and Thompson 1989) for assessing the distribution of larval Atlantic herring. However, the recorder may not be effective at low concentrations of larvae (<0.1/m³; Colton et al. 1961), and there may be problems with extended residence of organisms in the netting before capture in the recorder (Haury et al. 1976).

9.2.3 Other Active Gears

9.2.3.1 Shallow-Water Nets

Gear modifications have also been developed for collecting larvae in shallow areas not easily sampled with towed nets. For qualitative surveys, fine-mesh (505 μ m or less) dip nets can be used to obtain presence-absence data and to collect eggs and larvae from structurally complex areas. Seines can also be used in areas with smooth bottoms but are of limited use in vegetated habitats (Dewey et al. 1989). Although these gears are easy to use, removal of larvae from seines and dip nets may be time consuming and may result in considerable damage to collected specimens. In addition, because of difficulties in quantifying seine haul and dip-net effort (depth, speed, habitat differences, or amount of water filtered), data obtained with these gears probably should not be analyzed quantitatively without careful assessment and standardization of techniques.

Other shallow-water gears have been designed that incorporate nets in fixed or adjustable boat-mounted frames. Hodson et al. (1981) used side-mounted meter nets to obtain replicate samples of ichthyoplankton from surface waters. Bryan et al. (1989) mounted paired 0.5-m nets on vertically adjustable side frames braced with support wires; the design permitted discrete sampling at two depths up to 4 m at speeds up to 1.3 m/s. Holland and Libey (1981) and Meador and Bulak (1987) used 0.5-m nets in adjustable bow-mounted frames to sample shallow littoral areas (Figure 9.2A). Burch (1983) mounted two 0.5-m nets on a bicycle-type push net to be manually operated in depths up to 1.5 m. Ennis (1972) used a diver-operated device consisting of a 0.5-m net attached to two underwater towing vehicles to sample larvae in shallow coastal areas.

An alternative design developed by Bagenal (1974) for sampling shallow-water

areas incorporated a buoyant net ring to allow vertical sampling of larvae in shallow, vegetated areas. These nets, sometimes called pop nets, are deployed with an anchor or weighted frame to take the net to the bottom. After a period of time (10–30 min), a release mechanism is triggered, and the cylindrical net rises to the surface. Although the volume of water sampled is small, Bagenal (1974) indicated no avoidance of the net by cyprinid larvae, and Dewey et al. (1989) and Dewey (1992) found that pop nets provided quantitative estimates of juvenile fish abundance in vegetated habitats of a Minnesota lake. Portable drop nets have also been used to collect larval and postlarval fishes (Kushlan 1981). One design incorporates a square or rectangular frame with a surrounding net suspended along the top. In contrast to the buoyant net, the frame is set in place for a period of time, and then the net is released to fall quickly to the bottom (Dewey 1992). Alternatively, lightweight frames with mesh on all four sides can be thrown to the sample location and collected fishes can be removed by dip nets (Kushlan 1981). La Bolle et al. (1985) used a rectangular drop sampler constructed of clear plexiglass (to reduce visual avoidance) to sample larval fishes in littoral areas of the Columbia River. Similarly, Baltz et al. (1993) used a circular (1.2-m diameter) plexiglass drop sampler deployed from a boat-mounted boom to study microhabitat use by marsh fishes. After deployment, organisms were retrieved from the sampler by means of rotenone and dip nets.

9.2.3.2 Pumps

Centrifugal pumps have been used since about 1887 to collect demersal eggs and larvae and also to study the spatial distribution of pelagic ichthyoplankton (Aron 1958). Most systems involve pumping a target volume of water from an intake hose into a net (Figure 9.5) or a filtering drum (to reduce damage to collected larvae). Such a system has several advantages: depth of sampling and volume of water through the system (duration of pumping) can be easily controlled, discrete quantitative samples can be obtained by intermittent collection of organisms from the filtering surface, and the system can be operated from a stationary or moving platform. Conversely, pumping volumes can be small, pump intakes and filtering screens can be subject to clogging, the effective pumping area of most systems is limited to several centimeters from the pump intake—avoidance by mobile larvae can be significant (e.g., threadfin and gizzard shad; Petering and Van Den Avyle 1988), and most larvae are killed or damaged during sampling (Gale and Mohr 1978).

Aron (1958) reported that pump collections of pelagic fish eggs in Puget Sound were quite similar to collections taken concurrently with a 0.5-m net, although abundance estimates for several copepod taxa differed between the two gears. Harris et al. (1986) found a high-volume pump was particularly useful for sampling larvae and associated food organisms from discrete depths. A pump system was used successfully by Manz (1964) to collect viable walleye eggs from Lake Erie, although pump performance was reduced over mud, silt, and sand substrates because of clogging. Leithiser et al. (1979) found the abundance of fish larvae (particularly those longer than 5 mm) taken from a coastal power plant intake was significantly higher in pump samples than in concurrent samples taken with 0.5-m and 1.0-m plankton nets. Stauffer (1981) tested three pump designs for collecting lake trout eggs and early life stages and reported adequate collections only with a system incorporating a diver-directed intake. Novak and Sheets (1969) also used scuba divers to direct the pump intake for collecting smallmouth bass larvae.

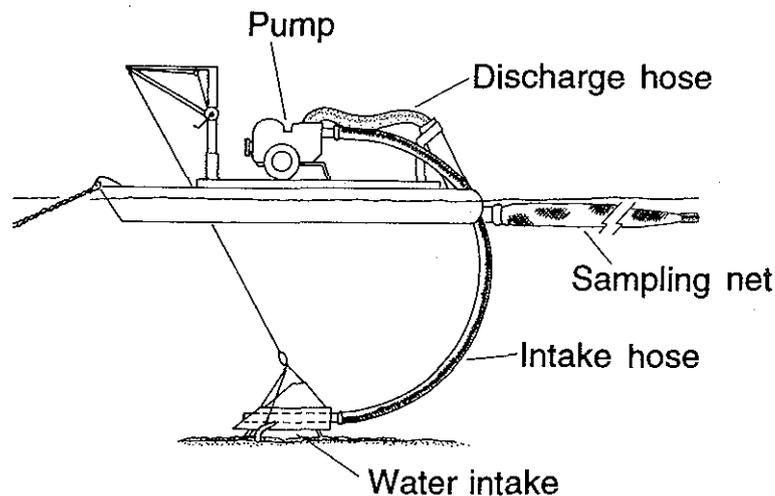


Figure 9.5 A towable pump sampler with adjustable intake for sampling at discrete depths (adapted from Gale and Mohr 1978, with permission).

Other types of pumping devices have also been used to collect eggs and larvae. Dorr et al. (1981) used diver-operated underwater diaphragm pumps (Flath and Dorr 1984) to sample alewife and lake trout eggs as well as age-0 sculpins. Vogele et al. (1971) used compressed air from a scuba cylinder in a portable, diver-operated suction device for collection of centrarchid (sunfish) eggs and larvae in Arkansas reservoirs.

9.2.3.3 Electrofishing Gear

Electrofishing equipment has not been widely employed to sample fish larvae. However, battery- or generator-powered electrofishing gear is particularly well suited for sampling fishes in shallow, structurally complex areas by wading or from small boats and may be much less species selective than are nets or pumps. Electrofishing was successfully used by Braem and Ebel (1961) to sample sea lamprey ammocoetes in Great Lakes tributaries. The electrofishing unit was battery powered and 20-cm-square, wire-mesh dip nets mounted on 1.2-m handles were used as electrodes; the authors reported that interruption of the current was most effective in attracting larvae from their burrows. For sampling lamprey larvae in deeper waters, McLain and Dahl (1968) developed an electrified plankton sled (pulsed DC) that successfully collected larval (>30 mm) sea, American brook, northern brook, and silver lampreys. Copp and Peñáz (1988) used electrofishing for sampling larval and juvenile fishes in floodplain habitats of the upper Rhône River. The electrofishing unit was modified to include a 10-cm diameter anode to create a steep voltage gradient; at 200 V and 400 Hz, the battery-charged unit created a voltage gradient ranging from 3.6 to 0.13 V/cm (minimum effective gradient for galvanotaxis of 20-cm trout; Cuiat 1967) at 10 and 30 cm from the anode, respectively. The unit collected 1,048 larvae representing 12 species, and larval lengths ranged from 5 to 22 mm. Modified electrofishing gear probably deserves increased use for collection of larval and juvenile fishes. However, further studies are needed on the effects of fish size, water chemistry, electrode design, voltage gradient, current level, and pulse width and shape on sampling effectiveness.

9.2.3.4 Other Active Sampling Methods

Many situations unique to various fish species require other methods to sample eggs and larvae. Many species spawn on vegetation (e.g., northern pike), and collection of epiphytic eggs or larvae may require clipping and examination of submerged macrophytes. Collection of rocks or debris from the bottom may be best for species that shed adhesive demersal eggs over such substrates (e.g., darters and sculpins). Demersal eggs and larvae in or on the substrate can be collected with dredges or corers (although damage to larvae from these gears can be substantial), and eggs and early larvae of benthic-nesting species can sometimes be retrieved with small suction devices such as pipettes or slurp guns. Snorkeling, scuba diving, and underwater video photography (Chapter 18) can be used to gather important data on spawning locations, egg deposition, and larval behavior (Aggus et al. 1980).

9.2.4 Passive Collecting Gears

9.2.4.1 Egg Traps

Although pumps (Nigro and Ney 1982), jet tows (Haug et al. 1984), drift nets (Johnston and Cheverie 1988; Pitlo 1989), and scuba surveys (Newsome and Aalto 1987) have been used in studies of fish egg distribution and abundance, egg traps have also been used extensively to capture and protect demersal eggs as they are spawned in the water column. Gammon (1965) used a simple wooden frame fitted with a fiberglass screen bottom and a 6.4-mm screen top (protecting eggs from minnow predation) to collect esocid eggs. Eggs of cavity spawners such as the channel catfish can be collected easily with spawning containers (Moy and Stickney 1987); other types of samplers have been designed for various other substrate-spawning fishes. Downhower and Brown (1977) used slate tiles to collect egg masses of the mottled sculpin in an Ohio creek, and Fridirici and Beck (1986) devised a series of stacked plastic plates for laboratory collections of eggs of crevice-spawning spotfin shiners. Stauffer (1981) used bucket samplers filled with substrate material to collect lake trout eggs in Lakes Michigan and Superior. Buckets were placed in holes in the substrate that had been excavated by scuba divers and were retrieved after lake trout had spawned. Additional gears used in studies of lake trout egg deposition have included nets (Horns et al. 1989) and egg traps (Marsden et al. 1991) strung together on collection lines. Egg traps proved to be a more effective gear than nets in terms of both the number of eggs retrieved and the percentage of undamaged eggs in the samplers (Marsden et al. 1991).

9.2.4.2 Drift Samplers

Drifting eggs and larvae are usually collected with stationary sets of standard plankton nets, although nets with mouth-reducing cones have also been used (Franzin and Harbicht 1992). Mesh size depends on the size of the target organisms and mesh clogging tendencies but typically ranges from 116 μm (Lindsay and Radle 1978) to over 1 mm (Graham and Venno 1968). Horizontal (Carter et al. 1986; Winnell and Jude 1991) and vertical location of drift nets in the water column depends on the drift characteristics of the species under study. Drift nets have been set to sample ichthyoplankton throughout the water column (Johnston and Cheverie 1988), as well as at the surface (Gale and Mohr 1978; Lindsay and Radle 1978; Carter et al. 1986), middepth (Franzin and Harbicht 1992), surface and bottom (Clifford 1972), and at several depths simultaneously (Dovel 1964). Graham and Venno (1968) attached drift nets to swivel-mounted vanes for sampling larval Atlantic

herring in tidal areas of the Gulf of Maine. The weight of the cod end of the net collapsed the net at slack tides to prevent escape of larvae, and the vane ensured that the net was aligned with the current when tides were flowing (Figure 9.6A). Winnell and Jude (1991) obtained replicate samples of drifting fishes and macroinvertebrates from paired nets attached at several depths to fixed poles. In addition to summer sampling, the authors were able to deploy the gear through the ice during winter. Lewis et al. (1970) developed a versatile net to capture Atlantic menhaden in estuarine channels. The net resembled a bag seine (3-mm mesh in the wings, 500- μ m mesh in the bag) and was held stationary by a 1-m \times 3-m frame that could be moved up and down in the water column on fixed poles (Figure 9.6B). Pitlo (1989) used rigid drift nets (15-cm \times 46-cm frame; 61-cm bag) constructed of window screening (6.1 meshes/cm) to collect walleye and sauger eggs and define habitat boundaries in the Mississippi River.

9.2.4.3 Emergence Traps

Fishes such as salmonids (trouts) that deposit their eggs in gravel nests below the surface of the substrate provide the opportunity to capture offspring from individual spawnings as larvae emerge. Several investigators have developed traps to sample larvae as they leave the nest. Phillips and Koski (1969) used a covering net with an attached collecting bag to sample emerging larvae from individual coho salmon redds and reported near 100% trap efficiency. Porter (1973) designed an oval-shaped mesh and canvas trap with a downstream collecting box; the box was designed to reduce water velocity and resulted in 100% survival of rainbow trout larvae (Figure 9.6C). Gustafson-Marjanen and Dowse (1983) used the Porter trap to study emergence of Atlantic salmon, and Field-Dodgson (1983) developed a larger Porter trap and successfully captured emerging chinook salmon larvae. A slightly different trap was used by Bardonnet and Gaudin (1990) to study emergence of grayling larvae from artificially spawned eggs placed in the trap. The trap incorporated a downstream compartment that was filled with gravel and connected by pipe to an upstream above-gravel compartment; the trap was oriented at 45° into the current. Collins (1975) and Stauffer (1981) used pyramidal emergence traps (Figure 9.6D) that relied on vertical migration by larvae into the trap to study emergence of lacustrine salmonids. Although the trap was designed to sample redds, it also collected larvae of broadcast-spawning lake whitefish after emergence from demersal eggs.

Trap design (e.g., trap size) for emergence studies depends on the species being studied, as well as on the characteristics of the water body (e.g., water velocity and substrate composition). Temporal emergence patterns of the target fishes may also be important in the design of trapping studies. Most salmonid larvae emerge at night (but see Bardonnet and Gaudin 1990 for grayling), and the bulk of emergence occurs over restricted (approximately 10-d) periods (Gustafson-Marjanen and Dowse 1983; Brännäs 1987). More importantly, de Leaniz et al. (1993) and others have reported within-gravel movements of salmonid larvae, which could substantially bias results of trapping studies unless traps are large relative to the magnitude of lateral movements of larvae from the nest or trap aprons are buried deep enough in the substrate to minimize within-gravel dispersal.

9.2.4.4 Activity Traps

Several investigators have developed traps for free-swimming larvae and juveniles in littoral habitats. A simple trap consisting of two mesh cones mounted inside a

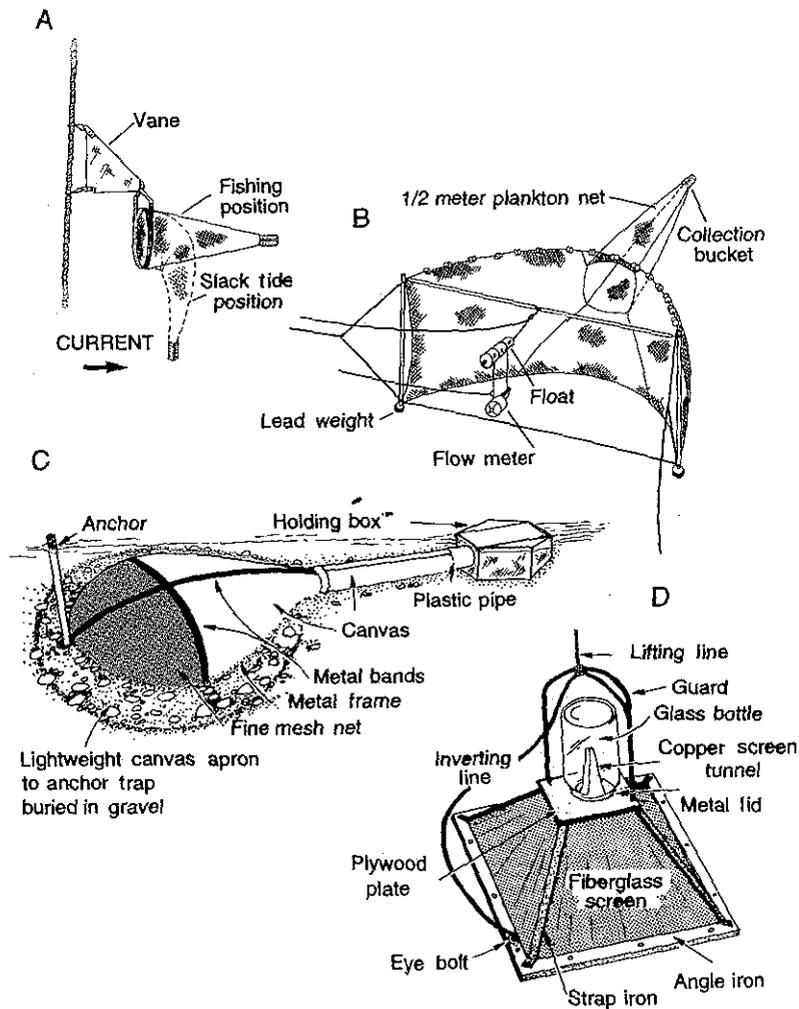


Figure 9.6 Various types of passive collecting gears: (A) a plankton net attached to a vane for sampling in tidal currents; (B) a channel net developed to collect larvae in flowing currents; and (C) and (D) emergence traps for demersal larvae (adapted from Graham and Venno 1968; Lewis et al. 1970; Porter 1973; and Collins 1975, with permission).

mesh cylinder was used by Baugh and Pedretti (1986) to catch 8- to 60-mm fishes in a shallow desert spring. Breder (1960) constructed a box trap of clear plexiglass that had removable wings which directed fish to a slot in the interior of the trap (Figure 9.7A). This design served as the basis for traps developed by Casselman and Harvey (1973) and a collapsible plexiglass and net trap designed by Trippel and Crossman (1984). These traps are low cost, easy to build, and highly adaptable to various sampling conditions. In particular, the size of the entrance slots into the trap can be adjusted to capture small larvae or larger juveniles, and the traps can be fished at various depths and positions in the water column, depending on the behavior of the target fishes. Small versions of fyke nets (Beard and Priegel 1975) and trap nets (Beamish 1973) have also been used to sample larval and juvenile fishes in lentic

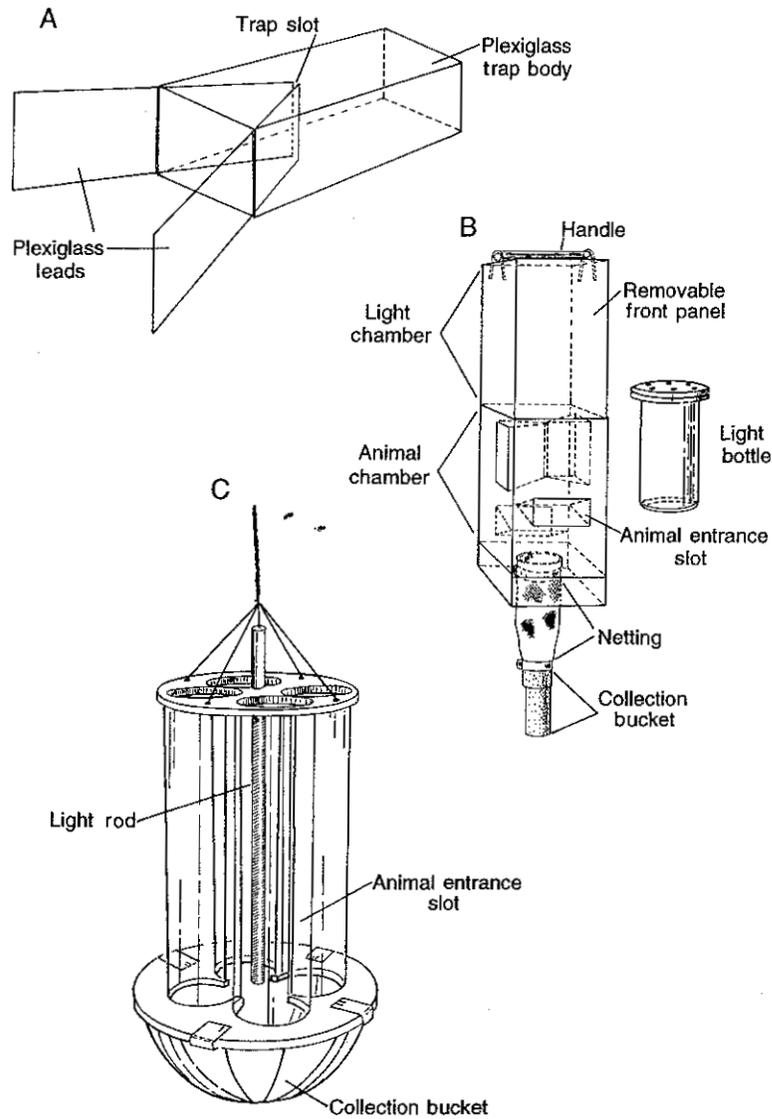


Figure 9.7 Larval and juvenile fish traps: (A) plexiglass activity trap; (B) rectangular light trap with horizontal and vertical entrance slots; and (C) the Quatrefoil trap (adapted from Breder 1960; Faber 1982; and Floyd et al. 1984a, with permission).

systems. Plexiglass or net traps are easy to set and are particularly appropriate for vegetated habitats, as long as the taxa and life stages under study are mobile and tend to move laterally along a visible or invisible barrier. However, because of interspecific differences in larval susceptibility to traps (due to differences in mobility, behavior, and microhabitat preferences), comparison of catch-per-unit-effort data among species may not accurately reflect relative species composition.

9.2.4.5 Light Traps

Larvae and juveniles of many fishes are positively phototactic, and the use of artificial light sources in nocturnally fished traps has been an effective method for

collecting larvae of some species. Dennis et al. (1991) used a light mounted above a lift net to assess abundance of 12 ichthyoplankton taxa in reef, seagrass, and mangrove habitats in Puerto Rico. Paulson and Espinosa (1975) used cylindrical, wire mesh (6.4-mm mesh) light traps to collect juvenile (approximately 40-mm) threadfin shad from midwater depths in Lake Mead, Nevada; Kindschi et al. (1979) used a similar design to assess spatial and temporal trends in ichthyoplankton abundance in Rough River Lake, Kentucky. Faber (1981) designed a box-shaped plexiglass light trap (Figure 9.7B) that was used by Faber (1982) and Gregory and Powles (1988) to determine seasonal abundance patterns of larval fishes in vegetated habitats of Lac Heney, Québec, and Chemung Lake, Ontario, respectively. In both studies, collected taxa represented about 50% of the species in the lakes; collections indicated differences in trap susceptibility among species and larval developmental stages. Muth and Haynes (1984) developed a smaller, floating plexiglass trap that incorporated plexiglass leads to guide larvae to the trap entrance slots. Field trials indicated the trap effectively sampled larvae and juveniles from 11 to 60 mm and captured three taxa not found in concurrent seine samples.

Floyd et al. (1984a) developed a trap with a central light-distributing rod surrounded by four plexiglass cylinders milled to three-fourths of a full circle (the Quatrefoil trap, Figure 9.7C). Advantages of this trap design include large trapping slots relative to the size of the trap as well as easy adjustment of trap size (length of the plexiglass cylinders) and sampling depth. Floyd et al. (1984b) used Quatrefoil traps, seines, and drift nets to collect larvae and juveniles in a small Kentucky stream. Of the 28 taxa collected during the study, the Quatrefoil trap collected 25, compared with 21 in seine hauls and 11 in drift nets; the light trap was particularly effective for cyprinid larvae. The Quatrefoil trap was modified by Secor et al. (1992) to include a chemical light source, a flotation device, and a collection bucket and proved to be an effective trap for pond-reared larval and juvenile striped bass (7–35 mm).

Because of differences in movement patterns, microhabitat preferences, and phototactic behavior among species, light traps are probably best suited for determining species presence or absence, as opposed to providing estimates of species relative species composition. Light traps are also useful for investigating intraspecific patterns of temporal or spatial abundance through time (Doherty 1987); however, changes in phototactic behavior with increasing larval size (e.g., Bulkowski and Meade 1983) must be considered in interpretation of temporal data. Light traps may be particularly effective for early larval stages (but see Doherty 1987 and Choat et al. 1993) and typically provide larvae in excellent condition if traps are checked at frequent (e.g., 1-h) intervals (Faber 1981). Gregory and Powles (1988) found light traps to be much more effective than Miller high-speed nets for 2.5–7.5-mm Iowa darter larvae, whereas length distributions of yellow perch and pumpkinseed larvae captured by the two gears were similar.

9.3 SAMPLING CONSIDERATIONS

Formulation of specific research objectives is the first step in selection of egg and larval sampling methods. Budget, personnel, equipment, and time limitations will affect the study design (see Chapter 1), as will numerous physicochemical, ecological, biological, and statistical factors. Larval fish are morphologically and behaviorally distinct from juveniles and adults (Snyder 1990), and knowledge of fish reproductive life history and larval behavior and ecology are important factors in the choice of

collecting methods, gear types, sampling periodicity, and sampling habitat. There is a large volume of information on fish reproduction (Balon 1975). Data on sampling-related topics such as reproductive habitat preferences, seasonality, and diel periodicity can be found in Wootton (1990); temperature preferences and substrate and flow requirements are discussed in Breder and Rosen (1966), Carlander (1969, 1977), and Potts and Wootton (1984). Additional information is available in numerous regional summaries (Bigelow and Schroeder 1953; Scott and Crossman 1973; Lee et al. 1980; Becker 1983; Jenkins and Burkhead 1993), and larval fish bibliographies (Smith and Richardson 1979; Lathrop and Snyder 1986; Simon 1986; Hoyt 1988 [available as an ASCII file from American Fisheries Society Computer User Section]; Richards 1990).

9.3.1 Spatial and Temporal Effects on Sampling Design

Distributions of fish eggs and larvae vary both temporally and spatially, and this variability must be accounted for in the study design. Duration of the spawning season for various fishes ranges from a few days to several months (Potts and Wootton 1984), and although spawning times of some species are remarkably constant (Cushing 1970), spawning activity may vary temporally both within and between years based on seasonal and annual variability in rainfall, temperature, or other physicochemical variables (Bye 1984). Several studies have focused on temporal succession of larval fishes over various time periods (Amundrud et al. 1974; Gallagher and Conner 1980; Floyd et al. 1984b), and although initiation, cessation, and frequency of egg and larval sampling depend on study objectives, sampling typically commences just prior to spawning of the target species and continues at hourly to biweekly intervals until catches cease or decline to low levels.

9.3.1.1 Marine Systems

Numerous reports attest to the horizontal and vertical patchiness of egg and larval distributions due to passive and active aggregations in marine systems (Haug et al. 1984), which can have substantial effects on abundance estimates (Wiebe and Holland 1968). Vertical patterns of distribution depend on egg and larval buoyancy and larval behavior and can be affected by factors such as temperature and current patterns (Bailey 1980), salinity, light (Cada et al. 1980), and the distribution and movement of predators and prey. Eggs of Atlantic halibut are most abundant at intermediate depths, where temperature and salinity render the eggs neutrally buoyant (Haug et al. 1984). In contrast, in Mobile Bay, Alabama, fish eggs were most abundant in bottom strata during periods of high river discharge and were uniformly distributed in the water column during periods of low river discharge (Marley 1983). Demersal eggs typically show disjunct distributions related to depth and substrate (Newsome and Aalto 1987; Marsden et al. 1991), and spawning habitat specificity may play a large role in determining effective egg sampling methods.

The importance of tidal transport of marine fish eggs and larvae to estuarine nursery grounds has led to several studies on spatial and temporal variability in the distribution of estuarine ichthyoplankton (Miller et al. 1984; Pietrafesa and Janowicz 1988). In Gulf of Maine estuaries, Graham and Venno (1968) found differences in the vertical distribution of Atlantic herring larvae between flood (greatest numbers at 10–15 m) and ebb (greatest numbers at the surface) tides. Similarly, Atlantic croaker larvae were found to occupy lower, inward-flowing stratified waters of the Chesapeake Bay (Norcross 1991). Rijnsdorp et al. (1985) found demersal plaice larvae moved into the water column during nocturnal flood tides. Diel variability in

catch was evident for 41 of 47 taxa of marine ichthyoneuston (0–50 cm in depth) studied by Eldridge et al. (1978); 29 were more abundant nocturnally, whereas 12 were more abundant diurnally. Larval clupeids (herrings; Harris et al. 1986), gadids (cods; Lough and Potter 1993), and cupelin (Fortier and Leggett 1983) were patchily distributed vertically, and abundance patterns were related to diel period, thermocline position, and larval length. Larval fishes collected in Narragansett Bay were found to exhibit an overall downward migration at night from surface waters, whereas eggs were found predominantly (72%) at 0–3-m depths (Bourne and Govoni 1988). The importance of identifying larval microhabitat preferences was demonstrated by Lindsay and Radle (1978) in their study of inland, Atlantic, and rough silverside larvae. Silversides were abundant in only the 0–5-cm surface layer in mesohaline areas of the Delaware River and were virtually absent from deeper strata.

9.3.1.2 Freshwater Rivers and Streams

In freshwater lotic systems, spatial and temporal variability in ichthyoplankton distributions have been reported for many taxa. Sager (1987) reported increased density of gizzard shad larvae in backwater areas relative to main-stem habitats of the Cape Fear River, North Carolina. In the Susquehanna River, Gale and Mohr (1978) found limited numbers of larval fishes near the bottom during the day, peak drift of cyprinid and catostomid larvae between 2400 and 0300 h, and a night:day drift abundance ratio of 3.8:1. Carter et al. (1986) found similar increases in nocturnal abundance of drifting larval fishes in the upper Colorado River but reported significantly higher abundance of larvae along the shoreline compared with the midchannel surface zone. Gallagher and Conner (1980) also found the highest larval densities at turbulent, nearshore stations in the lower Mississippi River, whereas larval fishes in the St. Mary's River, Michigan–Ontario, were more abundant in the upper half of the water column in midchannel (Winnell and Jude 1991). Larval distribution may also be related to temporal changes in stream physicochemistry. The diel pattern of larval drift of anadromous blueback herring in an Atlantic coastal stream was temperature dependent; higher abundances of larvae occurred nocturnally at temperatures less than 13°C, and abundance of larvae increased diurnally at temperatures over 15°C (Johnston and Cheverie 1988).

9.3.1.3 Freshwater Lakes

Similar spatial and temporal heterogeneity in larval fish distributions has been reported in freshwater lentic systems. Conrow et al. (1990) found substantial differences in distributions of larval fishes in areas of open water, panic grass *Panicum* spp., *Hydrilla* spp., and floating and emergent vegetation in Orange Lake, Florida. Larval clupeids typically exhibit diel vertical movements, with highest densities at dusk in open water near the surface, whereas freshwater drum larvae have been reported to be most abundant at depths of 3–6 m during the day and to move to deeper waters at night (Tuberville 1979). Ontogenetic changes in larval distribution (e.g., from limnetic to littoral habitats [Werner 1969] or from high-density to low-density macrophyte beds [Gregory and Powles 1985]) must also be considered in the sampling design. Golden shiner larvae (5–10 mm) were reported by Faber (1980) to be scattered in shallow (10 cm) shoreline areas, whereas larger individuals (10–30 mm) schooled among floating and emergent macrophytes at depths of 0.25–1 m. These ontogenetic changes in habitat preferences, combined

with increasing size and decreasing susceptibility to ichthyoplankton samplers, often result in biased abundance estimates for late larvae and early juveniles.

9.3.2 Fish Density and Sample Volume Effects on Sampling Design

Studies cited above attest to the importance of considering vertical, horizontal, and temporal discontinuities in ichthyoplankton distributions when a sampling program is designed. Sampling a large volume of water increases the chances of encountering patches of eggs and larvae; 100 m³ is generally accepted as a target volume in fresh water, whereas sample volumes of 250 to 1,500 m³ have been filtered in studies of marine eggs and larvae (Marcy and Dahlberg 1980). If objectives include a description of ichthyoplankton vertical and horizontal patchiness (Leslie 1986), the study design should include filtration of target volumes at discrete depths with opening-closing gears or pumps (Harris et al. 1986). In contrast, vertical tows (e.g., Smith et al. 1989) or oblique tows (deployment to specified depth and continuous sampling as the gear is towed to the surface at a constant tow angle; Smith and Richardson 1977) are commonly used if the study is designed primarily for collection of presence-absence data or assessment of temporal trends in egg and larval abundance (Rijnsdorp and Jaworski 1990). In addition to the towing path, towing speed can have a direct effect on the species and size composition of the catch, although the effects may vary among species (Aron and Collard 1969).

9.3.3 Statistical Considerations

Because most studies of ichthyoplankton involve estimates of egg and larval abundance and analyses of larval length distributions, care should be taken to ensure that data are both accurate and precise (see Chapter 2). Succeeding sections on sampling eggs and larvae discuss potential sources of bias associated with various collection methods. In particular, length distributions of sampled taxa may be biased due to extrusion of small larvae through net meshes and net avoidance by larger larvae; several formulas have been proposed to correct egg abundance estimates (D'Amours and Grégoire 1992) and larval length-frequency distributions due to avoidance (Barkley 1972; Murphy and Clutter 1972), extrusion (Lenarz 1972), or both (Somerton and Kobayashi 1989).

Because eggs and larvae of many fishes typically exhibit patchy distributions, data obtained from replicate samples may be subject to high variability and low precision. A set of observations (e.g., counts) at a single time and place (site) constitutes a sample; true replicates are similar independent and randomly collected samples (see Chapter 2). Replication allows for estimation of between-sample variance at a particular site, which is the basis for parametric tests of significant differences (e.g., mean length or abundance) between sites (see Waters and Erman 1990 for a discussion of statistical design). Accuracy of ichthyoplankton data depends on the ability of the sampling design to describe egg and larval characteristics effectively (e.g., abundance, distribution, or size composition). Precision is strongly affected by ichthyoplankton patchiness, and a given level of precision is dependent on the number of replicates taken. Cyr et al. (1992) reported that most larval fish surveys were based on low numbers (approximately four) of high-volume (approximately 300-m³) replicates. The authors found that half of the published studies on larval fish abundance could detect only order-of-magnitude differences among sites or time periods; 33 replicates were needed to detect a 50% change in population density ($\alpha = 0.05$) at larval abundances of 10 per replicate. Many ichthyoplankton studies have been based on two or three replicates at each site (e.g., paired net tows). Although

increasing the number of replicates may be problematic, larger numbers of lower-volume samples may be needed to increase the probability of detecting significant differences in egg and larval abundances between sites.

9.3.4 Effects of Gear Characteristics on Sampling Design

Passive avoidance of gears by eggs and larvae can be due to clogging of nets (Smith et al. 1968; Williams and Deubler 1968) or pump intakes. For towed nets (Aron et al. 1965) and filter nets used with pumps, clogging is primarily a function of gauze material, mesh size, density of organisms and debris in the water column, and duration of the sampling. Clogging can be a particular problem during oblique or vertical tows. Progressive clogging as the net is hauled up through the water column can lead to unequal sampling at different depths and inaccurate abundance estimates if eggs or larvae are not uniformly distributed (Schnack 1974). The magnitude of clogging can be assessed with flow meters mounted inside and outside the net, and clogging can be reduced by increasing the net area:mouth area ratio to at least 3:1 (preferably 5:1), incorporating mouth-reducing cones or prenet cylinders, and reducing the duration of sampling (Trantor and Smith 1968).

Extrusion of collected organisms through the mesh (Vannucci 1968) and damage to organisms in the net are primarily related to the size and shape of the collected taxa, mesh size (Lenarz 1972; Houde and Lovdal 1984), towing speed (Colton et al. 1980), tow duration, and water temperature. Thayer et al. (1983) reported catch of larvae in a modified Miller high-speed sampler (Figure 9.4B) increased with towing speed up to 7–8 m/s but declined at higher speeds due to either extrusion of larvae through the net or deflection of larvae by pressure waves ahead of the net mouth. Gregory and Powles (1988) also reported extrusion of small (<6.0 mm) Iowa darters through Miller high-speed nets. Extrusion of larvae and eggs can be reduced with smaller-mesh nets, but smaller mesh is more susceptible to clogging, reduced filtration, and increased net avoidance as larvae are deflected by pressure waves in front of the sampler.

Damage to collected organisms is more evident with high-speed samplers (towing speeds greater than 2 m/s) and is particularly important if it prevents identification. Several papers have documented changes in larval fish morphology due only to the effects of netting. Theilacker (1980) observed a decrease of up to 19% in the standard length of northern anchovy captured in plankton nets, and Hay (1981) and McGurk (1985) found up to 18% shrinkage in net-captured Pacific herring larvae. McGurk (1985) also found that netting effects on larval morphology were not consistent; that is, body depth and head width increased as standard length decreased, resulting in inaccurate assessment of larval condition.

Mesh sizes of nets used in ichthyoplankton studies typically range from 333 to 505 μm , and several studies have focused on gauze construction (Heron 1968) and selectivity of plankton net mesh (Saville 1958; Barkley 1972). Southward and Bary (1980) used high-speed samplers to study Atlantic mackerel egg abundance and concluded that previous studies employing larger-mesh nets had underestimated egg abundance due to egg loss through the net mesh. Loss of threadfin shad and gizzard shad larvae through 500- μm mesh during sampling and net washdown was documented by Tomljanovich and Heuer (1986), and studies by Leslie and Timmins (1989) in the Great Lakes indicated losses of 26 and 13% of larval fishes from nets with 1,000- and 480- μm mesh, respectively; all larvae were retained with a mesh size of 250 μm . O'Gorman (1984) compared catches of larval alewife and rainbow smelt

among 0.5-m nets with 355-, 450-, 560-, and 750- μm mesh and reported significantly fewer larvae with the latter three mesh sizes. A change in material and mesh size from 550- μm silk to 505- μm nylon was found to increase retention of larval northern anchovy in towed meter nets from 60% to near 100%, certainly an important factor affecting interpretation of data (Lenarz 1972).

Choice of mesh size in ichthyoplankton studies depends on a number of factors, including gear type, water velocity through the gear, and the size of the target organisms. Smith et al. (1968) concluded that capture of an organism depended on whether its width exceeded the mesh diagonal, and although this may be a conservative criterion (Lenarz 1972), it is likely a good guideline. Choosing the largest mesh that will collect the desired sizes of target organisms should maximize sampling effectiveness and minimize clogging problems and reductions in net performance. For small organisms in systems with large amounts of organic or inorganic debris, this may require several tows of short duration.

Gear failure can occur due to mechanical problems, operator inexperience, and collisions with debris or the substrate. Mechanical problems were particularly common with early opening-closing nets and have resulted in numerous gear modifications (Paquette and Frolander 1957; Bary and Frazer 1970). Several types of flow meters have been employed to measure sampled water volumes; meter accuracy may be dependent on towing speed and should be verified with frequent calibration. Contamination of samples can result from incomplete washing of nets and collection buckets (Figure 9.1A) between tows or sampling outside the target strata. Opening-closing nets can eliminate the latter problem and can be of a simple purse line design (Currie and Foxton 1956; Figure 9.1A).

9.3.5 Effects of Fish Behavior on Sampling Design

Fish behavior can have important effects on where, when, and how early life stages are collected (Bowles et al. 1978; Marcy and Dahlberg 1980). Active avoidance of towed nets and pumps is related to larval size (Lenarz 1973) and position relative to the net (Barkley 1964), light levels, physical characteristics of the sampling gear, and the velocity of the gear or water flow entering the gear. Visual signals (Clutter and Anraku 1968) and hydrostatic pressure waves may trigger avoidance responses in larval fishes, which can cause significant underestimates of the abundance of larger larvae. Conversely, slow growth of larval fishes may prolong their vulnerability to plankton nets, which can result in overestimates of larval fish abundance through time if the size distribution of the catch is not analyzed (Hamley et al. 1983). Noble (1971) used high-speed samplers to evaluate the effectiveness of a meter net for sampling yellow perch and walleye larvae, and reported avoidance of the meter net by larvae 10 mm and larger. Thayer et al. (1983) found the abundance of 10–16-mm spot and 19–26-mm Atlantic menhaden to be significantly underestimated by a 20-cm bongo net towed at 2 m/s.

Active avoidance of sampling gear by larvae has been examined with collection of diurnal and nocturnal samples, and many studies have documented increased catches of larvae at night (Bridger 1957). Cada and Loar (1982) found diurnal avoidance of a low-volume pump (compared with a 0.5-m Hensen net) by 5–10 mm clupeid larvae, and Graham and Venno (1968) reported that larval Atlantic herring were able to visually avoid diurnally fished stationary nets. Comparisons of pump and meter net samples by Leithiser et al. (1979) also indicated visual avoidance of a slowly towed (up to 0.4 m/s) meter net by larvae larger than 5 mm; however, higher towing speeds

may have made catches of the two gears more comparable. Murphy and Clutter (1972) compared efficiencies of a meter net and a miniature purse seine (Hunter et al. 1966; Kingsford and Choat 1985) for sampling larval engraulids. Meter net samples contained substantially fewer larvae greater than 5 mm, and improvements in nocturnal catch rates indicated that avoidance was primarily visual. In general, nocturnal sampling with low-velocity gears results in substantially higher catch rates compared with diurnal sampling (Cole and MacMillan 1984), although this phenomenon could be due to larval movements and temperature effects as well as reduced net avoidance (Marcy and Dahlberg 1980). Use of high-speed samplers can decrease active avoidance by larvae, although extrusion and damage of larvae may increase.

If study objectives include assessment of larval length-frequency distributions or growth, two or more types of gears can be used to improve accuracy and reduce mechanical or biotically related bias (Suthers and Frank 1989). Gallagher and Conner (1983) used a meter net and paired 0.5-m push nets to collect larvae in the Mississippi River and found that the relative effectiveness of the two gears varied by habitat (main stem versus slackwater) and time of day. If a study is designed to assess larval mortality (e.g., entrainment; Dempsey 1988) it is important that mortality due to sampling be quantified; larval mortality in nets has been found to be a direct function of water velocity (O'Conner and Schaffer 1977; Cada and Hergenrader 1978; see McGroddy and Wyman 1977 for a low-mortality collection device developed for entrainment sampling). Regardless of the type or number of gears used, sampling duration, gear characteristics (e.g., mesh size), sampling speed, and diel sampling periodicity should be quantified for each gear and be as consistent as possible among samples. In addition, interspecific variability in spatial distribution and susceptibility to various gear types must be considered when data are used to assess differences in relative species composition. Investigators must consider whether differences in the numbers of various taxa collected reflect true relative abundance or are a result of interspecific differences in swimming ability, behavior, and microhabitat preferences.

9.4 SAMPLE PRESERVATION

Maintenance of morphological integrity of eggs and larvae during initial fixation and long-term preservation is important for both taxonomic and ecological studies (e.g., length frequency and condition factors). Chemicals used for fixation and preservation should prevent microbial degradation and minimize autolysis and cellular damage due to osmotic changes (Jones 1976). The degree of specimen degradation (e.g., shrinkage or structural or pigmentation deterioration) from fixation and preservation depends primarily on developmental stage (Hay 1982), chemical concentration (Hay 1982), and osmotic strength (see studies in Tucker and Chester 1984). Fixation and preservation of eggs and larvae thus involve trade-offs between prevention of microbial-induced degradation and fixation-induced alterations.

9.4.1 Fixation and Preservation

Most methods for both fixation and preservation of ichthyoplankton (Lavenberg et al. 1984) involve the use of aldehyde-based solutions (e.g., formaldehyde and glutaraldehyde), which are excellent fixatives because they combine with tissue proteins and prevent proteins from reacting with other reagents (Pearse 1968). These

effects can be reversed by washing, and washing after fixation is not recommended (Taylor 1977). Although alcohol is used as a long-term preservative for some larval fish collections (DeLeon et al. 1991), it is not recommended because alcohol solutions cause significant specimen shrinkage and deformation due to dehydration. Formaldehyde is typically preferred to glutaraldehyde because it is less noxious and less expensive and is regarded to have superior long-term stability (Steedman 1976). In attempts to improve preservation qualities, formalin-based solutions have been mixed with buffers, acids and alcohols (e.g., Bouin's and Davidson's fluids; DeLeon et al. 1991).

Historically, fish eggs and larvae have been fixed in 5–10% formalin and preserved in 3–5% buffered formalin (Ahlstrom 1976; Smith and Richardson 1977). Formalin-based solutions are acidic (pH 2.5–5.0), and their acidity may increase over time through oxidation of formaldehyde to produce formic acid (Steedman 1976). Long-term storage of larval specimens in acidic formalin solutions can result in decalcification and demineralization of bone (Taylor 1977), including otoliths. (For age and growth studies, it is recommended that larvae be frozen after capture to eliminate preservative-related changes in otolith structure.) To prevent acid-induced degradation of specimens, a long-term preservative should have a neutral pH (7.0–7.5; Tucker and Chester 1984) and should be buffered with sodium borate (borax; Ahlstrom 1976), calcium carbonate (marble chips or limestone powder; Steedman 1976), sodium phosphate (Markle 1984), or sodium acetate (Tucker and Chester 1984). However, addition of buffers can raise the pH to levels (above ~8.0) that can increase larval transparency (clearing) and loss of pigmentation (sodium borate buffer; Taylor 1977), formation of calcium carbonate crystals on specimens (Tucker and Chester 1984), and precipitation of sodium phosphate on specimens (Markle 1984).

Larval fishes. Choice of a fixative and preservative may depend on the goals of the study. For long-term storage, Tucker and Chester (1984) found little shrinkage (97.4–100.7% of live standard length) and good pigment retention in larval southern flounder preserved in 4% unbuffered formalin in freshwater, although this preservative caused decalcification (pH < 6.0). They concluded that the best long-term preservative was 4% formalin in distilled water buffered with 1% sodium acetate. Alternatively, good preservation qualities have been reported for 5% formalin buffered with sodium phosphate (1.8 g sodium phosphate monobasic, 1.8 g anhydrous sodium phosphate dibasic [0.013 M, pH 6.8] in 1L of 5% formalin; Markle 1984).

Eggs. Oocytes have traditionally been fixed and preserved with formalin (4–10%) or modified Gilson's fluid (100 mL 60% methanol or ethanol, 880 mL of water, 15 mL of 80% nitric acid, 18 mL glacial acetic acid, and 20 g of mercuric chloride; Bagenal and Braum 1978). However, formalin fixation typically hardens ovarian tissue and makes oocyte separation difficult, and use of Gilson's fluid tends to result in degeneration of hydrated oocytes (Brown-Peterson et al. 1988) and oocyte shrinkage (15–24%; DeMartini and Fountain 1981). To avoid these problems and the toxicity of mercuric chloride (West 1990), Lowerre-Barbieri and Barbieri (1993) recommended physical separation of oocytes before fixation and preservation in 2% buffered formalin.

Fish eggs are not subject to the same preservation problems associated with larval fishes (i.e., decalcification and clearing), but eggs are often fixed and preserved

similarly (Ahlstrom 1976; Smith and Richardson 1977). Inadequate preservation of fish eggs has been reported for buffered (sodium phosphate and sodium borate) formalin solutions typically used in larval fish preservation (Ahlstrom 1976; Markle 1984; Gates et al. 1987). Markle (1984) recommended the use of 5% unbuffered formalin and Klinger and Van Den Avyle (1993) recommended the use of 4–7% unbuffered formalin for preservation of fish eggs.

Alternative preservation methods. Cooling or freezing of ichthyoplankton samples may be practical alternatives to formalin-based fixation if specimens are to be either processed quickly or used in biochemical studies. Genetic studies generally require that specimens be frozen rapidly in liquid nitrogen and stored at -76°C to ensure retention of the biochemical properties of proteins and DNA. If the effects of formalin-based fixation (i.e., shrinkage and clearing) are problematic for goals of a study, specimens should be placed on ice immediately after collection and processed quickly. Long-term freezing of specimens will result in some shrinkage (generally less than formalin-based solutions) and may cause cellular damage (Halliday and Roscoe 1969; Jones and Geen 1977).

Color preservation. Little research has been conducted on the addition of antioxidants to ichthyoplankton samples to maintain natural coloration. Brown and black melanins are generally well preserved in acidic to neutral formalin-based solutions without the use of antioxidants. Because color is not a commonly used character in identification of larval fishes, addition of antioxidants is not necessary. In collections in which natural color preservation is required (e.g., redds in larvae of tunas), addition of 0.2–0.4% solutions of IONOL CP-40 (40% butylated hydroxytoluene) in formalin-based preservatives has been recommended (Berry and Richards 1973; Scotton et al. 1973). Use of other antioxidants has been reported for adult (Gerrick 1968) and larval fishes (Ahlstrom 1976). If color attributes are important for larval fish identification, specimens should be examined immediately after collection, before fixation (Ahlstrom 1976).

9.5 SAMPLE PROCESSING

Processing egg and larval samples typically begins on site immediately upon collection. Depending on study objectives, fish eggs and larvae are either fixed in a formalin-based solution or frozen. To ensure specimen integrity, immediate processing is important (Ahlstrom 1976; Hay 1981). Samples are typically returned to the laboratory for sorting, enumeration, identification, measurement, and other study-specific analyses (e.g., age determination, gut analysis, or electrophoresis). Illustration of larval and egg characteristics (Faber and Gadd 1983; Lindsey 1984; Sumida et al. 1984) can be an important part of taxonomic studies, and use of photomicrography and photoimaging technology can greatly improve illustrative efforts. All data associated with egg and larval collections (e.g., date, location, collection personnel, and physicochemical data) should be stored with the specimens, which should be protected from excessive heat and sunlight and placed in either a teaching or museum collection for long-term curation (Lavenberg et al. 1984). These collections and related data provide important systematic references for future researchers.

9.5.1 Subsampling

Because fish eggs and larvae usually compose less than 1% of a plankton sample (Scotton et al. 1973), subsampling is typically not recommended. Time saved by

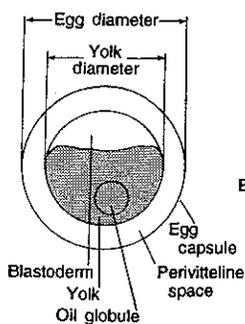
Table 9.2 Regional guides for the identification of fish eggs and larvae. Most manuals are illustrated and include regional notes on the distribution and ecology of fish eggs and larvae and on adult spawning.

Author(s) and publication date	Region	Comments
Fish 1932	Lake Erie	62 species accounts; several misidentified
Mansueti and Hardy 1967	Chesapeake Bay	45 species accounts; Acipenseridae through Ictaluridae
May and Gasaway 1967	Oklahoma	18 species accounts; photographs and key
Colton and Marak 1969	Northeast coast North America	27 species accounts
Scotton et al. 1973	Delaware Bay	56 species accounts
Lippson and Moran 1974	Potomac River	88 species accounts; keys
Hogue et al. 1976	Tennessee River	32 species descriptions; photographs and keys
Russell 1976	British Isles marine fishes	40 families; taxonomic characters and methods
Hardy et al. 1978	Mid-Atlantic Bight	278 species accounts; includes tidal freshwater zones
Drewry 1979	Great Lakes region	Key to yolk-sac larvae; illustrations
Wang and Kernehan 1979	Delaware estuaries	113 species accounts; keys
Miller et al. 1979	Hawaiian Islands	46 taxonomic accounts; illustrations
Elliott and Jimenez 1981	Beverly-Salem Harbor, Massachusetts	47 species accounts
Snyder 1981	Upper Colorado River, Colorado	19 species accounts; Cyprinidae and Catostomidae; keys
Wang 1981	Sacramento-San Joaquin estuary, California	74 species accounts; keys and comparison tables
Auer 1982	Great Lakes basin	148 species accounts; keys
Garrison and Miller 1982	Puget Sound, Washington	124 species accounts
Fahay 1983	Western North Atlantic	290 species accounts; comparison table
Leis and Rennis 1983	Indo-Pacific	49 family accounts
McGowan 1984	South Carolina	11 families, 18 species; illustrations
Conrow and Zale 1985	Florida	18 species accounts
Wang 1986	Sacramento-San Joaquin estuary, California	125 species accounts; keys and comparison tables
McGowan 1988	North Carolina reservoirs	10 families, 22 species
Leis and Trnski 1989	Indo-Pacific	54 family accounts
Matarese et al. 1989	Northeast Pacific	232 species accounts; keys and illustrations
Holland-Bartels et al. 1990	Upper Mississippi River	19 illustrated families, 63 unillustrated species
Wallus et al. 1990	Ohio River basin	24 species accounts; Acipenseridae through Esocidae
Olivar and Fortuno 1991	Southeast Atlantic	127 taxonomic accounts; illustrations
Kay et al. 1994	Ohio River basin	21 species accounts; Catostomidae
Ditty and Shaw 1994	Western central Atlantic	21 genera, 55 species; Sciaenidae
Farooqi et al. 1995	Western central Atlantic	7 genera, 28 species; Engraulidae

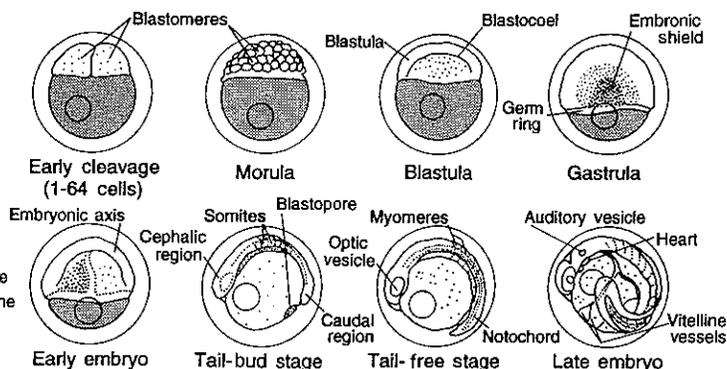
9.6.1 Egg Developmental Stages

Egg development is a dynamic process and is usually assumed to encompass the time period from ovulation until hatching. Egg structure consists of an outer membrane or chorion, perivitelline space, an inner egg membrane (present in some fishes), and yolk (Ahlstrom and Moser 1980; Kendall et al. 1984; Figure 9.8). Most fishes are oviparous: ovulation is followed by release of eggs to the external environment to be fertilized by sperm from associated males. Upon fertilization, eggs

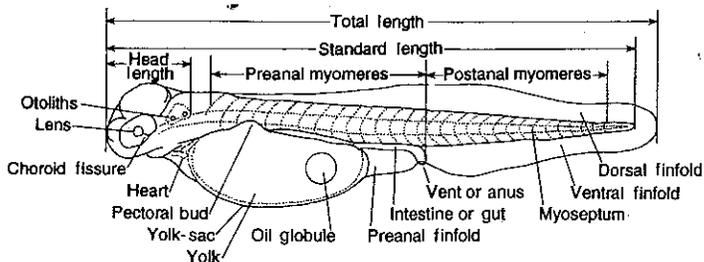
Egg structure



Egg development



Yolk-sac larva



Larva

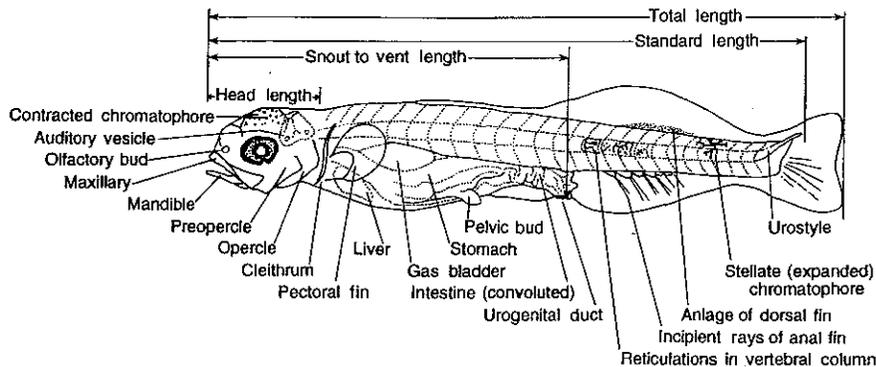


Figure 9.8 Developmental stages of a typical teleost egg and larva (adapted from Mansueti and Hardy 1967, with permission).

undergo changes in structure and function (egg activation) that prevent multiple fertilization (polyspermy), harden the chorion (water hardening; Redding and Patino 1993), and begin embryonic development. Cell division (cleavage) of the egg in fishes is most commonly meroblastic but is occasionally holoblastic (e.g., lampreys) or intermediate (e.g., South American lungfish, sturgeons, gars, and bowfin; Blaxter 1969; Lagler et al. 1977). For a general review of fish reproduction (e.g., gonad maturation, gonosomatic indices, and fecundity estimates) see Crim and Glebe (1990).

Several workers have described various stages of egg and embryo development useful in egg identification. Matarese and Sandknop (1984) adopted developmental stages proposed by Ahlstrom and Ball (1954), which included the following categories: early development, from fertilization to closure of the blastopore; middle development, from closure of the blastopore to tail bud lifting off the yolk; and late development, from tail bud lifting off the yolk to hatching. Mansueti and Hardy (1967) presented a more detailed description of egg development (see Figure 9.8): (1) early cleavage, 1-64 cells; (2) morula, blastomeres that form a cluster of cells; (3) blastula, formation of the blastocoel; (4) gastrula, differentiation of cells into ectoderm, mesoderm, and endoderm; (5) early embryo, formation of the embryonic axis; (6) tail-bud stage, prominent caudal bulge and cephalic development; (7) tail-free stage, separation of the tail from yolk; and (8) late embryo, embryo has developing characteristics of its hatching stage.

9.6.2 Egg Identification

Various egg types are found in both marine and freshwater fishes. Overall, fish eggs average 1 mm in diameter (although coelocanths have 90- μ m eggs; Potts and Wootton 1984). Eggs are typically translucent but may be dark (e.g., paddlefishes, sturgeons, and gars), they may be buoyant (pelagic) or nonbuoyant (demersal), adhesive or nonadhesive, and they may have modifications to aid in attachment or flotation. Eggs are typically spherical but may be ovoid or irregularly shaped. Oil globules may be present or absent, and may vary in number, size, color, position, and pigmentation. Yolk may have a characteristic segmentation, color, pigmentation, and circulation. The chorion may vary in surface topography, ornamentation, thickness, color, coatings, and micropyle size. The width of the perivitelline space and the location, presence, or absence of the inner egg membrane may also be variable among taxa. These characters, along with morphological information on the developing embryo, collection information (e.g., location, water temperature, season, and collection gear), and mode of reproduction are often used to aid in egg identification (Newell and Newell 1963; Hempel 1979; Ahlstrom and Moser 1980; Matarese and Sandknop 1984; Balon 1985; Blaxter 1988; Table 9.2). Difficulties in identifying fish eggs by means of morphological characters have led researchers to explore biochemical techniques to aid in identification, such as immunodiffusion and immunofluorescence (Johnson et al. 1975), molecular degradation (Valcarce et al. 1991), gas chromatography (Knutsen et al. 1985), isoelectric focusing (Mork et al. 1983), protein electrophoresis (Scobbie and Mackie 1990), and mitochondrial DNA analyses (Graves et al. 1989).

9.6.3 Larval Developmental Stages

Numerous terminologies have been proposed to describe early life history stages of developing larvae. None of the proposed terminologies is without problem because any attempt to categorize a dynamic and often species-specific process into a static framework is difficult (see Snyder 1976; Kendall et al. 1984; Snyder and Holt 1984; Balon 1985; and Blaxter 1988 for summaries of early terminologies). Most researchers agree that the term "embryo" encompasses development from fertilization to hatching (for exception, see Balon 1984), the "juvenile period" begins with acquisition of an adult body form and ends at sexual maturation, and the "larval period" is in between. Although the term "fry" has been used frequently in the larval fish literature for larvae from hatching to flexion of the notochord, there is little consensus on a precise definition for this term, and we have restricted our use of early

life stage terminology to larvae and juveniles. There are currently three commonly accepted terminologies used to categorize the phases of larval fish development.

1. Mansueti and Hardy (1967) and Hardy et al. (1978) described three phases of larval fish development based on the presence or absence of yolk material and fin ray development:
 - Yolk-sac larvae*: Phase between hatching and yolk absorption.
 - Larvae*: Phase between yolk absorption and the acquisition of adult fin ray complement.
 - Pre-juvenile or transitional*: Intermediate phase between larval and juvenile forms that begins with acquisition of the minimum adult fin ray complement and terminates in a more adultlike juvenile form.
2. Ahlstrom et al. (1976) described three phases of larval fish development based primarily on changes in the homocercal caudal fin:
 - Preflexion larvae*: Phase between hatching and upward flexing of the tip of the notochord or appearance of the first caudal rays.
 - Flexion larvae*: Phase characterized by upward flexion of the notochord (this phase terminates with formation of all principal caudal rays and the first appearance of secondary caudal rays).
 - Postflexion larvae*: Phase beginning after upward flexion of the tip of the notochord and terminating with a complete complement of fin rays. For some species prejuvenile or transitional phases are applied.
3. Snyder (1976, 1981) described three developmental phases based on morphogenesis of the median finfold and fins:
 - Protolarvae*: Phase between hatching and appearance of the first median fin ray or spine (dorsal, anal, or caudal fins).
 - Mesolarvae*: Phase beginning with the appearance of the first median fin ray or spine and terminating with acquisition of the pelvic fins or fin buds and a full complement of principal soft rays in the median fins.
 - Metalarvae*: Phase beginning with acquisition of pelvic fins or fin buds and a full complement of principal soft rays in the median fins and terminating with the loss of all finfolds and acquisition of the adult complement of spines and rays (including some ray segmentation) in all fins.

Each of these terminologies has been used successfully, and although there have been attempts to standardize larval fish terminology, no one method currently predominates in the early life history literature (Snyder 1976). Lack of standardization may be due to historical inertia as well as the broad array of topics (e.g., ontogeny, taxonomy, physiology, and ecology) addressed by early life history studies. Any terminology adopted to describe larval fish development should be inclusive of the diversity of forms, have some morphological and functional significance in the life history of the fish, and have observable and well-defined endpoints for each phase (Kendall et al. 1984). Although Snyder's (1976, 1981) terminology is typically used in studies of freshwater larval fishes in North America, several marine researchers recommend the terminology of Ahlstrom et al. (1976; see above) because of the functional importance of caudal fin development and associated changes in body shape and fin ray development and the terminology's simplicity and generality (Kendall et al. 1984; Blaxter 1988). Flexion of the notochord is a major developmental landmark that leads to increased larval mobility for pursuit of prey and

avoidance of predators. Ultimately, a combination of the terminologies (e.g., postflexion mesolarvae with yolk or yolk-sac mesolarvae; Snyder and Holt 1984) may prove most useful for standardization of terminology and definitions.

9.6.4 Larval Fish Identification

Many meristic, morphometric, and composite characters (e.g., pigmentation patterns, shape, size, and osteological development) have been used to aid in identification of larval fishes (Kendall et al. 1984; Figure 9.8). Morphological characters used for adult fish taxonomy are often not useful for larvae because of developmentally related structural differences. Some larvae possess specialized structures (e.g., eye stalks, elongated dorsal fins, sucker discs, unique spines, trailing gut, or photophores) that are unique to the larval stage and may be useful at some taxonomic level. More commonly used characters include myomere counts (total, preanal, and postanal) and the size, shape, and position of the gut, air bladder, yolk sac, oil globules, mouth, finfolds, and fins. Patterns of melanophore pigmentation have proven to be of particular value for species identification (Berry and Richards 1973; Snyder 1981; Kendall et al. 1984). In general, taxonomic characters tend to vary throughout the larval period; thus all meristic, morphometric, and composite characters must be related to size or developmental stage.

Myomere counts. Structurally, body muscles of postembryonic fishes are divided into myomeres, which are chevron-shaped serial segments separated by connective tissue (myosepta). Myomeres are conspicuous morphological features that approximate the number and position of vertebrae (typically number of myomeres minus one), although vertebral numbers are less variable (Snyder 1979; Fuiman 1982). Myomere counts (e.g., total, preanal, and postanal) are useful taxonomic characters because they are relatively consistent throughout the larval period. Total myomere counts include all myomeres from the first myomere, posterior to the occiput, to the urostylar myomere, posterior to the last myosepta (Fuiman 1982). Preanal myomere counts include all myomeres anterior to the posterior margin of the anus and include the myomere bisected by an imaginary vertical line drawn from the posterior margin of the anus; postanal myomeres are counted from this line posteriorly (Siefert 1969). Other partial myomere counts may be useful to reference the location of important structural features.

Morphometric analyses. Morphometric characters used for taxonomic purposes generally describe body form (e.g., body depth or eye width; Figure 9.8). Many morphometric characters are allometric (i.e., as larval fish grow there is a systematic change in shape). Differential growth rates are characteristic of the ontogeny of most organisms, but allometry is magnified during the larval period because of rapid growth. For comparative purposes, morphometric characters are often reported as ratios (proportions or percentage) in an attempt to remove the effect of body size (e.g., standard length, notochord length, or total length) from variation in body shape. Researchers have reported statistical problems with the use of ratios (e.g., inflated sampling errors, nonnormal frequency distributions, and erroneous character correlations; Atchley et al. 1976), and several regression methods have been applied to avoid statistical problems associated with ratios (see Strauss and Bond 1990).

Recent advances in morphological analyses may be particularly applicable to studies of larval fishes. Truss networks have been used to characterize differences in shape for adult fishes (Strauss and Bookstein 1982; Strauss and Bond 1990;

Bookstein 1991), but few studies have dealt with developmental changes in larval morphology (Strauss and Fuiman 1985). Truss analysis quantifies the shape (oblique, longitudinal, and vertical) of an organism with distance measurements among anatomical landmarks (see Douglas 1993 for application of videoimaging technology to truss analysis). Even though the number of landmarks in larval fishes is limited, several prominent morphological features (e.g., snout tip, bone articulations, tip of urostyle, and so on) can be identified to divide larvae into functional units. Landmarks are chosen to produce a series of contiguous quadrilaterals (anterior to posterior), with the landmarks forming the boundary of each quadrilateral (truss cell). Within a truss cell six pairwise measurements are made. The strength of truss analysis is based on the assumption that the anatomical landmarks are homologous among species. Multivariate methods (e.g., principal components analysis, sheared components principal analysis, and discriminant function analysis) are often used with morphometric character sets developed from the truss protocol to describe size and shape differences (Humphries et al. 1981; Bookstein et al. 1985; Strauss and Fuiman 1985; Strauss and Bond 1990).

Taxonomic guides. Because of the dynamic nature of anatomical characters during the larval period, comprehensive larval fish keys are difficult to prepare and thus are not common. Generally, keys or identification guides include only limited developmental ranges, distributional areas, and taxonomic groups (e.g., Fuiman 1979; Fuiman et al. 1983; Nishikawa and Rimmer 1987; Ditty 1989; Ditty et al. 1994; Richards et al. 1994). Because larval identification is typically based on a collection of anatomical (e.g., meristic and morphometric), ecological (e.g., adult spawning season), and zoogeographic (adult distribution patterns) characteristics that vary regionally, numerous regional identification guides have been developed (Table 9.2).

Supplemental identification techniques. Alternative techniques have been devised to aid in resolving larval fish taxonomic problems. Osteological features (Dunn 1984) often yield valuable taxonomic information, and methods for skeletal disarticulation (Mayden and Wiley 1984), whole organism clearing and staining (Taylor 1967; Galat 1972; Brubaker and Angus 1984; Potthoff 1984; Snyder and Muth 1990), X-ray radiography (Miller and Tucker 1979; Tucker and Laroche 1984), and histology (Govoni 1984) may enhance examination of internal structures (e.g., vertebrae). Scanning electron microscopy can be used to discern external characteristics (Boehlert 1984). As with fish eggs, biochemical techniques have been used to resolve taxonomic problems in some larval fishes (for a general review see Leary and Booke 1990; Beckenbach 1991; Park and Moran 1994). Most biochemical studies are designed to identify genetic differences between either closely related species (Morgan 1975; Sidell and Otto 1978; Comparini and Rodino 1980) or within stocks (Heath and Walker 1987; Graves et al. 1989; Grewe et al. 1994).

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