

Sustainable Swimming Speeds of Striped Bass Larvae

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Abstract.—Sustainable swimming speeds, defined as speeds maintained in 1-h tests, were measured for three size-classes (6–6.9 mm, 7–7.9 mm, and 8–8.9 mm) of larval striped bass *Morone saxatilis*. Probit analysis was used to find failure velocities (the water velocity at which 50% of the larvae fail to sustain swimming speed) and confidence intervals for each size-class. Failure velocities were 1.7, 2.1, and 3.0 cm/s for 6–6.9-mm, 7–7.9-mm, and 8–8.9-mm larvae, respectively. There was a general improvement in swimming performance with age. There was no difference in swimming ability due to the presence or absence of an inflated swim bladder. Striped bass larvae approached the upper range of swimming speeds recorded for other larval fishes and reached speeds of 3–4 body lengths/s, which are comparable to adult fish speeds. The relatively high speeds attained by striped bass larvae may improve feeding success rates by increasing the volume of water larvae are capable of searching for food.

Numbers of striped bass *Morone saxatilis* have declined dramatically in the Sacramento–San Joaquin estuary of California (Stevens 1977; Stevens et al. 1985) and Chesapeake Bay (Boreman and Austin 1985) since the early 1970s. In both cases a reduction in larval food supply is thought to be a contributing factor (Stevens et al. 1985; Tsai 1991). Previous laboratory studies have quantified prey densities required for larval striped bass growth and survival (Daniel 1976; Miller 1976; Eldridge et al. 1981, 1982; Houde and Lubbers 1986; Chesney 1989; Tsai 1991; Meng 1993), but these densities are often several times higher than prey densities found in the field in California (Stevens et al. 1985; Meng 1993). The discrepancy between laboratory and field results may be explained by the failure of laboratory studies to adequately evaluate the effect of swimming performance on larval searching ability and feeding success.

Swimming performance determines larval feeding rates and energy expenditures, as well as whether or not larvae remain in food-rich areas (Hunter 1981; Dabrowski et al. 1988; Miller et al. 1988). Larval swimming ability determines prey encounter rates because fish larvae alter their swimming speeds in response to changing prey densities (Rosenthal and Hempel 1970; Hunter and Thomas 1974; Theilacker and Dorsey 1980; Munk and Kiorboe 1985). Fish larvae may increase encounter rates by swimming faster at low prey densities (Theilacker and Dorsey 1980; Munk and Kiorboe 1985). Cruising or sustainable swimming speeds, defined here as speeds sustained for at least 1 h, are maintained by fish during routine activities such as feeding (Hunter 1981).

Cruising speeds of adult fish are well documented (Beamish 1978), but sustainable speeds of larvae have been more difficult to obtain. Fish larvae are delicate and easily damaged, and the low velocities attained by larvae are difficult to measure. Moreover, there is a large disparity in reported swimming speeds of fish larvae. Speeds of about 1 body length/s (BL/s) have been documented on film or videotape for free-swimming larvae (Rosenthal and Hempel 1970; Hunter 1972; Batty 1984). When larvae are subjected to currents in a flume, sustainable swimming speeds of some larvae increase to 3 BL/s or more (Houde 1969; Laurence 1972; Doyle et al. 1984). In flume studies, groups of striped bass larvae sustained speeds of 4 BL/s (Doyle et al. 1984) and larvae of largemouth bass *Micropterus salmoides* sustained 5 BL/s (Laurence 1972). Larvae of chub mackerel *Scomber japonicus* swam around the perimeter of a rearing tank for long periods at 3.8 BL/s (Hunter and Kimbrell 1980).

Because swimming speeds determine the amount of water a fish larva is able to search for food, swimming speed measurements are needed for inclusion in feeding models. Such models attempt to synthesize information on larval feeding, energy expenditure, and growth to quantify food levels necessary for larval survival (Blaxter 1986). The goals of my study were (1) to determine sustainable swimming speeds (maintained in 1-h tests) for three size-classes of first-feeding striped bass larvae (6–6.9 mm, 7–7.9 mm, and 8–8.9 mm, hereafter referred to as 6 mm, 7 mm, and 8 mm) in a current flume; (2) to evaluate the effect of swim bladder inflation on swimming performance; and (3) to relate swimming performance

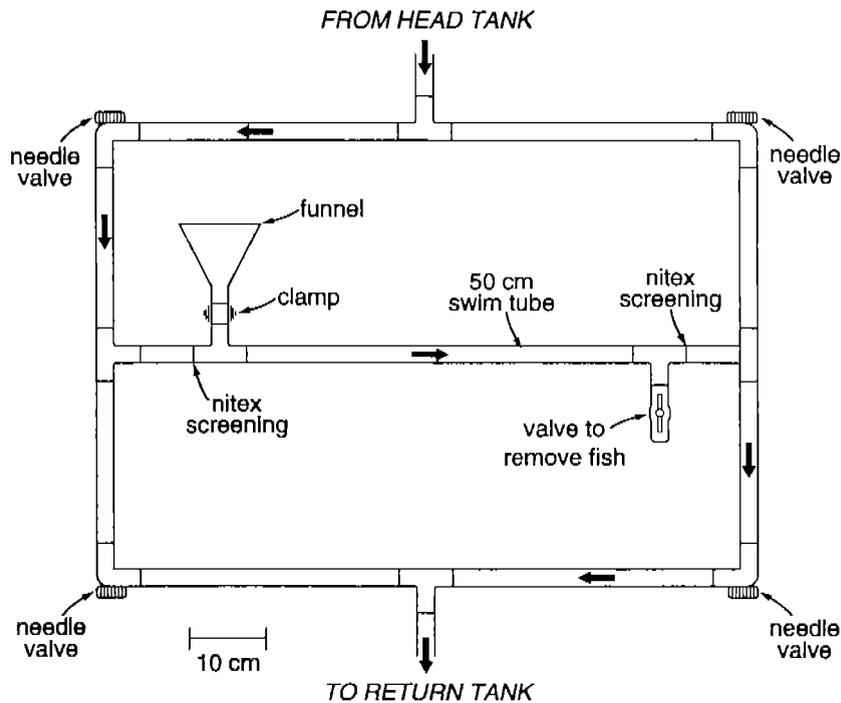


FIGURE 1.—Apparatus used to test swimming ability of striped bass larvae. Arrows denote direction of water flow during swimming tests. Swim tube (50 cm long) is clear; remainder of apparatus is opaque.

to the volume of water a larva is capable of searching for food.

Methods

Culture methods.—From April to June 1992, striped bass larvae from the California Department of Fish and Game Central Valley Hatchery were transferred to laboratory facilities at the University of California, Davis, 1–4 d after hatching. I reared the larvae in 32-L circular tanks in a flow-through system held at 17°C and 3‰ salinity. Fish were maintained at a density of 8/L and in a 12 h light : 12 h dark photoperiod. *Artemia* sp. nauplii were maintained at a nominal concentration of 100/L during daylight hours by aliquot sampling 2–3 times per day.

Experimental design.—Experiments were designed to determine failure velocity (the current velocity at which 50% of the larvae fail to sustain swimming speeds) in 1-h tests. Current velocities tested were 0.5–4.5 cm/s in 0.5 cm/s increments. Older larvae had a wider range of swimming ability and were tested at more velocities than 6-mm larvae. I tested 6-mm larvae at six velocities, 0.5–3.0 cm/s; 7-mm larvae at seven velocities, 1.0–4.0 cm/s; and 8-mm larvae at seven velocities,

1.5–4.5 cm/s. Ten fish in each size-class were tested individually at each velocity. I began testing fish 8 d posthatch.

Swimming apparatus.—The swimming apparatus followed the design of Bishai (1960) and Houde (1969). A rectangle was assembled from 19-mm PVC (polyvinyl chloride) pipe. Four 13-mm nalgene needle valves, one at each corner, regulated the water flow (Figure 1). Fish were tested in a clear tube (50 cm long) that ran across the middle of the PVC rectangle. Gravity-induced current flowed in either direction, and both current direction and velocity were controlled by valve adjustment. Air bubbles were bled out of the apparatus. Nitex fabric screening (900- μ m mesh) prevented the fish from moving out of the swimming tube and may have helped create a laminar flow. I measured current velocities by timing the passage of dye through the tube. Ten velocity-calibration tests were made for each velocity, and the mean valve setting was determined. Water was supplied to the device from the culture system head tank, in which temperature and salinity were constant.

Experimental protocol.—A larva was introduced into the water-filled funnel of the swimming

TABLE 1.—Current velocities (calculated from probit analysis) at which 50% of striped bass larvae in three size-classes failed to remain in a swimming tube for 1 h (1-h FV50) at 17°C. Also given are confidence limits for 1-h FV50 for each size-class. BL is body length.

Size-class (mm)	1-h FV50	
	Median velocity	95% confidence limits
Velocities in cm/s		
6.0–6.9	1.7	$1.3 \leq \text{FV50} \leq 2.1$
7.0–7.9	2.1	$1.6 \leq \text{FV50} \leq 2.5$
8.0–8.9	3.0	$2.6 \leq \text{FV50} \leq 3.4$
Velocities in BL/s		
6.0–6.9	2.8	$2.2 \leq \text{FV50} \leq 3.5$
7.0–7.9	3.0	$2.3 \leq \text{FV50} \leq 3.6$
8.0–8.9	3.8	$3.3 \leq \text{FV50} \leq 4.3$

device with a plastic spoon. Release of the clamp below the funnel washed the larva into the swimming tube. The current was immediately shut off, and the larva was allowed 10 min to acclimate to the tube. I increased the current gradually up to test velocity. Because most fish larvae are phototactic (Corazza and Nickum 1981) as well as rheotactic (Blaxter 1969), an incandescent light source at the upstream end of the tube provided the larva with an additional orientation cue. I observed the larva carefully during the acclimation period and the first 5 min of the test. If there was any evidence of damage to a larva from handling or if it did not swim for 5 min, the test was terminated.

I scored a larva as "passed" if it remained in the 50 cm swimming tube for 1 h. If the larva was washed downstream and impinged on the Nitex screening in less than 1 h, it was scored as "failed." Occasionally a larva would lie on the bottom of the tube where the current was minimal because of hydrodynamic drag. If a larva "rested" for more than 5 min, it was scored as failed. The fish was removed from the tube after the swimming test and held in a beaker. After being observed in the beaker for at least 1 h, the fish was measured (standard length), and the presence or absence of an inflated swim bladder was recorded.

Observations were recorded on fish activity at 15-min intervals throughout the swimming test. I recorded position of the larvae in the tube (cross-sectional and lengthwise) as well as tail-beat frequency (slow or fast).

Statistical analysis.—I used probit analysis, which is based on the linear transformation of a sigmoid-type curve (Hubert 1984), to analyze the swimming data. Determination of swimming abil-

ity can be viewed as a bioassay experiment (Brett 1967; Houde 1969). Current velocities are dose rates, and the velocity at which 50% of the larvae fail (FV50) is analogous to the dose at which 50% of test organisms die (LD50). I used the SAS probit procedure (SAS Institute 1990) to calculate FV50 and confidence limits for each size-class. I used a chi-square test of independence for a two-way contingency table (Sokal and Rohlf 1981) to test for differences in swimming ability attributable to swim bladder inflation.

Results

Failure velocities (FV50) increased with size for striped bass larvae and were 1.7, 2.1, and 3.0 cm/s for 6-, 7-, and 8-mm larvae, respectively (Table 1). Lack-of-fit tests (Pearson chi-square) for each successive size-class showed that the fraction failing to swim for 1 h at each velocity fit the probit model ($P = 0.14, 0.43, \text{ and } 0.89$), and confidence limits were calculated (Table 1). Fish tended to either swim for 1 h or fail within 15 min; intermediate swim times were less common (Figure 2).

Larval behavior differed in the velocities tested. After being washed into the tube and in the absence of a current, larvae explored the tube unless they were damaged. Damaged larvae lay on the bottom and were removed. When the current was turned on, larvae immediately swam into it and oriented themselves facing the upstream end of the tube and near the light. At higher velocities larvae maintained a constant position in the top half of the tube, where the velocities were expected to be near the mean value in the cross section of the tube. At lower velocities the fish did not maintain a constant position and tended to move about the tube, alternately losing and gaining position in reference to the upstream end near the light. Whenever a larva approached the darkness of the downstream end of the tube it swam vigorously upstream. At failure velocities, larvae tended to lose tube position incrementally and spent several minutes at the downstream end fighting to stay in the lit portion of the tube. Failure was more unpredictable at lower velocities; at low velocities, a larva could be swept away (or swim downstream or simply stop swimming) from any position in the tube. The fraction of older larvae completing the 1-h tests was more predictable and more closely related to velocity than that of 6- and 7-mm larvae (Figure 3).

Failure to sustain swimming in the current was not permanently debilitating. All larvae survived

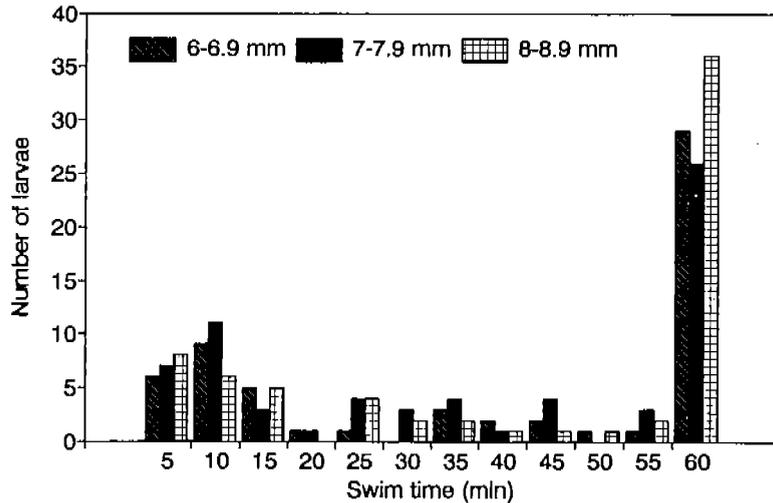


FIGURE 2.—Duration of sustained swimming (min) by striped bass larvae of three size-classes in a laboratory swim chamber, all velocities combined.

the tests and swam normally in beakers for at least 1 h after being removed from the tube.

There was no difference in sustained swimming ability between the larvae due to the presence or absence of an inflated swim bladder ($P = 0.20$, 0.70 , and 0.35 for 6-, 7-, and 8-mm larvae, respectively). Observations during the swim test suggested that larvae with uninflated swim bladders swam with greater tail beat frequency.

Discussion

Striped bass larvae of 6–9 mm approach the upper range of sustainable swimming speeds that have been determined for larvae of other perciform fishes in this size range (Table 2). The speeds (BL/s) I calculated for striped bass larvae are slightly lower than those of Doyle et al. (1984), but our methods differed and the larvae in my study were smaller. Doyle et al. (1984) began their experiments with 9–11.9-mm larvae and tested 10 fish at a time at three velocities: 3.0 cm/s, 6.0 cm/s, and 18 cm/s. All 9–11.9-mm larvae failed at 18 cm/s. Neither water temperature nor number of replicates were specified by Doyle et al. (1984). In addition, because 10 fish were tested at the same time, there may have been a schooling effect. Striped bass larvae from both studies, however, were able to attain 3–4 BL/s (Table 2).

Cruising speeds become asymptotic at 3–4 BL/s for many species of adult fish (Bainbridge 1960). I did not reach the asymptote in my study, but my objective was to study swimming speeds of the youngest larvae at the age that they are switch-

ing to exogenous foods. Doyle et al. (1984) recorded speeds of 10 BL/s for 12–20-mm larvae, but Doyle et al. included fish that occupied areas of reduced flow along the edges of the flume. Critical swimming speeds, the maximum velocity fish can maintain for a precise time period (Beamish 1978), of 3–4 BL/s have been measured for striped bass juveniles (Young and Cech, in press); adults reach critical swimming speeds of 2.9–3.3 BL/s (Freadman 1979). Sisson and Sidell (1987) reported sustainable swimming speeds of 1.8–2.4 BL/s for striped bass adults by measuring the speed

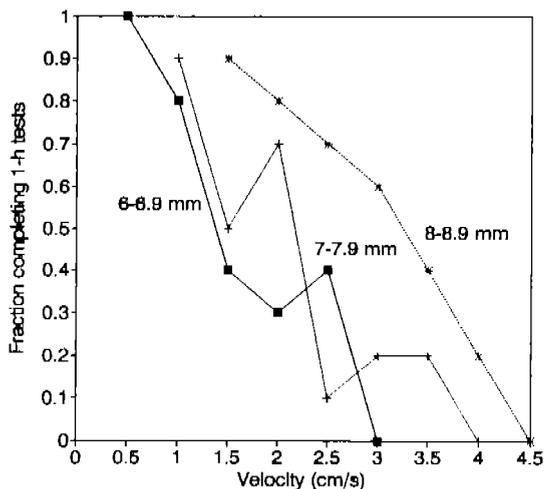


FIGURE 3.—Fraction of striped bass larvae of each size-class that continued to swim for 1 h in laboratory swimming tests as a function of water velocity.

TABLE 2.—Average sustainable swimming speeds for selected fish larvae (standard length 5–10 mm). BL is body length.

Species	Temperature (°C)	Speed (BL/s)	Study method	Reference
Pacific herring ^a	10	0.83	Film	Rosenthal and Hempel (1970)
	10	1.3	Videotape	Batty (1984)
Northern anchovy ^b	17	1.7	Film	Hunter (1972)
Striped bass		3–4	Flume	Doyle et al. (1984)
	17	2.8–3.8	Flume	This study
Largemouth bass	19	4–5	Flume	Laurence (1972)
Yellow perch ^c	13	2.8	Flume	Houde (1969)
Walleye ^d	13	1.5	Flume	Houde (1969)

^a *Clupea harengus*.

^b *Engraulis mordax*.

^c *Perca flavescens*.

^d *Stizostedion vitreum*.

at which white muscle fiber was recruited. Swimming performance, expressed in BL/s, favors smaller individuals due to reduced hydrodynamic drag (Beamish 1978), and this may explain why the developing larvae were able to reach adult speeds according to this measure.

Swimming in a current flume may produce higher speeds than would normal feeding activity in a rearing tank. The forced swimming speeds did not appear to be overly stressful because all fish in my study swam normally for at least 1 h after testing and did not appear otherwise stressed. Fish that completed the 1-h tests remained in the upstream end of the tube and had to be maneuvered out the tube after an hour, suggesting that the speeds reached could be sustained for longer than the test period.

Striped bass larvae in this study showed variable swimming ability. The ability of younger larvae to sustain swimming for 1 h was less closely related to velocity than that of 8-mm larvae (Figure 3). The more variable swimming ability in relation to velocity among the youngest fish may indicate a general improvement in swimming performance with age. The greatest variability in velocity-related swimming performance occurred in 7-mm larvae (Figure 3) and may indicate a transition period in swimming ability.

Methods for measuring swimming speeds of lar-

val fish fall into two categories: observation, including the use of film or videotape, or testing swimming ability against a current in a flume. Observation techniques tend to restrict fish to smaller containers suitable for photographic purposes and may explain, in part, the lower velocities attained in observation studies (Table 2).

The development of swimming ability is species specific, and differences in swimming speeds for 5–10 mm larvae (Table 2) may represent different stages of development or swimming modes. Walleye larvae are relatively poor swimmers at 7–9 mm (Table 2) due to large yolk sacs and slow development of fins, but swimming speeds double as yolk is absorbed (Houde 1969). Swimming modes based on anatomical differences (Webb and Weihs 1986) also affect larval swimming speeds. The eel-like larvae of Pacific herring swim in a slow undulating fashion (Rosenthal and Hempel 1970; Batty 1984) whereas northern anchovy (Hunter 1972) achieve intermediate speeds with "beat-and-glide" swimming (Table 2). Chub mackerel reach high speeds with continuous tail beats (Hunter and Kimbrell 1980).

Swimming modes and consequent foraging ability are based on energetic tradeoffs (Hunter 1981). Swim bladder inflation achieves neutral buoyancy, increases swimming efficiency (Doroshov et al. 1981), and might be expected to aid sustained swimming. In my study, however, I found no difference in 1-h sustainable swimming speeds due to the presence or absence of an inflated swim bladder. Fish without inflated swim bladders swam with greater tail beat frequencies. Chub mackerel larvae attained high speeds with rapid tail beat frequencies, which overcame negative buoyancy (Beamish 1978), but the larvae paid a high metabolic price (Hunter and Kimbrell 1980). Rapid tail beats and fast swimming help to increase search area but are not as energetically favorable as beat-and-glide swimming used by larvae with inflated swim bladders (Webb and Weihs 1986). Rapid tail beat frequency becomes increasingly unfavorable as larvae grow and Reynold's number and inertial forces increase. Striped bass larvae with uninflated swim bladders have poorer feeding success and survival rates than their counterparts (Doroshov et al. 1981; Meng and Orsi 1991).

Swimming speeds are important to feeding models because speeds determine how much area larvae are capable of searching for food (Hunter 1981; Dabrowski et al. 1988). Reactive distance, the distance at which prey is perceived, is com-

bined with swimming speed to determine the volume of water a larva is capable of searching (Blaxter 1986). Swimming speeds reached by striped bass in this study suggest that the larvae may be capable of searching greater volumes than previously believed. Reported search volumes range from 0.1 L/h to 1.8 L/h for 6–10-mm fish larvae (Hunter 1981). Assuming a half-circle perceptible area and a 5-mm reactive distance similar to other larval fishes (Hunter 1981), striped bass larvae may be capable of searching 4 L/h. This searching ability suggests the larvae may be able to grow and survive at prey densities observed in the field.

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References

- Bainbridge, R. 1960. Speed and stamina in three fish. *Journal of Experimental Biology* 37:129–153.
- Batty, R. S. 1984. Development of swimming movements and musculature of larval herring (*Clupea harengus*). *Journal of Experimental Biology* 110:217–227.
- Beamish, F. W. H. 1978. Swimming capacity. Pages 101–189 in W. S. Hoar and D. J. Randall, editors. *Fish physiology*, volume 7. Academic Press, New York.
- Bishai, H. M. 1960. The effects of water currents on the survival and distribution of fish larvae. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 25:135–146.
- Blaxter, J. H. S. 1969. Development: eggs and larvae. Pages 178–252 in W. S. Hoar and D. J. Randall, editors. *Fish physiology*, volume 3. Academic Press, New York.
- Blaxter, J. H. S. 1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society* 115:98–114.
- Boreman, J., and H. M. Austin. 1985. Production and harvest of anadromous striped bass stocks along the Atlantic coast. *Transactions of the American Fisheries Society* 114:3–11.
- Brett, J. R. 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. *Journal of the Fisheries Research Board of Canada* 24:1731–1741.
- Chesney, E. J. 1989. Estimating food requirements of striped bass larvae *Morone saxatilis*: effects of light, turbidity and turbulence. *Marine Ecology Progress Series* 53:191–200.
- Corazza, L., and J. G. Nickum. 1981. Positive phototaxis during initial feeding stages of walleye larvae. *Rapports et Procès-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer* 178:492–494.
- Dabrowski, K., F. Takashima, and Y. K. Law. 1988. Bioenergetic model of planktivorous fish feeding, growth and metabolism: theoretical optimum swimming speed of fish larvae. *Journal of Fish Biology* 32:443–458.
- Daniel, D. A. 1976. A laboratory study to define the relationship between survival of young striped bass (*Morone saxatilis*) and their food supply. California Department of Fish and Game, Administrative Report 76-1, Sacramento.
- Doroshov, S. I., J. W. Cornacchia, and K. Hogan. 1981. Initial swim bladder inflation in the larvae of physoclistous fishes and its importance for larval culture. *Rapports et Procès-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer* 178:495–500.
- Doyle, R. T., D. N. Wallace, R. K. Dias, and J. V. Merriner. 1984. Laboratory study of the swimming ability and behavior of fish larvae. *New York Fish and Game Journal* 31:196–216.
- Eldridge, M. B., J. A. Whipple, and M. J. Bowers. 1982. Bioenergetics and growth of striped bass, *Morone saxatilis*, embryos and larvae. *U.S. National Marine Fisheries Service Fishery Bulletin* 80:461–474.
- Eldridge, M. B., J. A. Whipple, D. Eng, M. J. Bowers, and B. M. Jarvis. 1981. Effects of food and feeding factors on laboratory-reared striped bass. *Transactions of the American Fisheries Society* 110:112–120.
- Freadman, M. A. 1979. Swimming energetics of striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*): gill ventilation and swimming metabolism. *Journal of Experimental Biology* 83:217–230.
- Houde, E. D. 1969. Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). *Journal of the Fisheries Research Board of Canada* 26:1647–1659.
- Houde, E. D., and L. Lubbers, III. 1986. Survival and growth of striped bass, *Morone saxatilis*, and *Morone* hybrid larvae: laboratory and pond enclosure experiments. *U.S. National Marine Fisheries Service Fishery Bulletin* 84:904–914.
- Hubert, J. J. 1984. Bioassay. Kendall/Hunt, Dubuque, Iowa.
- Hunter, J. R. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. *U.S. National Marine Fisheries Service Fishery Bulletin* 70:821–838.
- Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. Pages 34–77 in R. Lasker, editor. *Marine fish larvae*. Washington Sea Grant Program, University of Washington, Seattle.
- Hunter, J. R., and C. A. Kimbrell. 1980. Early life history of Pacific mackerel, *Scomber japonicus*. *U.S.*

- National Marine Fisheries Service Fishery Bulletin 78:89-101.
- Hunter, J. R., and G. L. Thomas. 1974. Effect of prey distribution and density on the searching and feeding behavior of larval anchovy *Engraulis mordax*. Pages 315-334 in J. H. S. Blaxter, editor. The early life history of fish. Springer-Verlag, Berlin.
- Laurence, G. C. 1972. Comparative swimming abilities of fed and starved larval largemouth bass (*Micropterus salmoides*). Journal of Fish Biology 4:73-78.
- Meng, L. 1993. Estimating food requirements of striped bass larvae: an energetics approach. Transactions of the American Fisheries Society 122:244-251.
- Meng, L., and J. J. Orsi. 1991. Selective predation by larval striped bass on native and introduced copepods. Transactions of the American Fisheries Society 120:187-192.
- Miller, P. E. 1976. Experimental study and modelling of striped bass egg and larval mortality. Doctoral dissertation. John Hopkins University, Baltimore, Maryland.
- Miller, T. L., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657-1670.
- Munk, P., and T. Kiorboe. 1985. Feeding behavior and swimming activity of larval herring (*Clupea harengus*) in relation to density of copepod nauplii. Marine Ecology Progress Series 24:5-21.
- Rosenthal, H., and H. Hempel. 1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus*). Pages 344-363 in J. H. Steele, editor. Marine food chains. University of California, Berkeley.
- SAS Institute. 1990. SAS user's guide, volume 2, version 6 edition. SAS Institute, Cary, North Carolina.
- Sisson, J. E., III, and B. D. Sidell. 1987. Effect of thermal acclimation on muscle fiber recruitment of swimming striped bass (*Morone saxatilis*). Physiological Zoology 60:310-320.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Freeman, New York.
- Stevens, D. E. 1977. Striped bass (*Morone saxatilis*) year class strength in relation to river flow in the Sacramento-San Joaquin estuary, California. Transactions of the American Fisheries Society 106:34-42.
- Stevens, D. E., D. W. Kohlhorst, and L. W. Miller. 1985. The decline of striped bass in the Sacramento-San Joaquin estuary, California. Transactions of the American Fisheries Society 114:12-30.
- Theilacker, G. H., and K. Dorsey. 1980. Larval fish diversity, a summary of laboratory and field research. Pages 105-142 in Workshop on the effects of environmental variation on the survival of larval pelagic fishes. Food and Agriculture Organization of the United Nations, Intergovernmental Oceanographic Commission Report 28, Rome.
- Tsai, C. 1991. Prey density requirements of the striped bass, *Morone saxatilis* (Walbaum), larvae. Estuaries 14:207-217.
- Webb, P. W., and D. Weihs. 1986. Functional locomotor morphology of early life history stages of fishes. Transactions of the American Fisheries Society 115:115-127.
- Young, P. S., and J. J. Cech, Jr. In press. Improved growth, swimming performance and muscular development in exercise-conditioned young-of-year striped bass. Canadian Journal of Fisheries and Aquatic Sciences.

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