A Review of Survival Rates of Fish Eggs and Larvae in Relation to Impact Assessments

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Introduction

Pursuant to promulgation of the Federal Water Pollution Control Act Amendments of 1972, Section 316b, electric generating stations are required to demonstrate that cooling water intake structures reflect the best technology available for minimizing adverse environmental

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impact. The primary types of impact are impingement of fish on the intake screens and entrainment of smaller fish and eggs into the cooling system. The size of the intake screen mesh, usually ⅜ inch, and size of fish determine whether the fish are entrained or impinged. The impingement problem was reviewed by Hanson et al. (1977). The few published studies on entrainment of fish show that millions of larvae are sometimes entrained daily by a plant during the period of peak abundance (Edsall, 1975). Impact of entrainment or other perturbations may be assessed by translation of egg and larval losses to the potential number of adults they represent in the absence of entrainment. This is compared with a reference such as stock size or commercial catch. Implementation of models requires information on natural survival rates of the species of concern, or at a minimum, what survival rates may be expected among the various groups of fishes.

ABSTRACT—Enormous fecundities of fishes are balanced by high egg and larval mortalities resulting from natural interacting environmental stresses. Survival rates generally increased inconsistently with age of eggs and larvae. Few published studies provided the data needed to compare relative mortality among the three major developmental stages. Mortality was greatest during the egg stage in the walleye and striped bass, but during the postlarval stage in some marine species. Wide ranges of egg survival for Atlantic herring, northern pike, rainbow smelt, and walleye depend on whether egg production is based on fecundity or field counts, and whether survival is measured to a stage of drifting larvae or late eggs.

Among freshwater species, hatching success was low in unprotected eggs and high in species which exhibit parental care, construct nests, but do not exhibit parental care, have special protective mechanisms (yellow perch), and apparently in species which deposit eggs in vegetation. Among anadromous species, egg survival in striped bass was particularly low in comparison to that in salmon. In the sea, hatching success of demersal eggs was much higher than in pelagic eggs. Survival of yolk-sac larvae was generally higher in marine and freshwater species than in anadromous species. Survival of postlarvae was highest in freshwater species in relation to high daily survival rates and short developmental periods.

The occurrence of brief critical periods of high mortality was generally not supported when data were corrected for larval extrusion. The potential for high mortality to be offset by compensatory mechanisms is supported by literature. A direct relationship of survival rates and development time suggested that high mortality rates were an expected mechanism for regulation of populations having short developmental periods. The availability and applicability of survival data to modeling of impact is assessed. Many environmental factors should be considered when extrapolating survival data from one site to another.

This paper represents a compilation of available fish egg and larval natural survival rates and discusses problems associated with interpretation and use of survival data, major sources of mortality, survival rates associated with various reproductive strategies, and the critical period concept. Effects of human perturbations and fish culture on survival rates are not considered.

Interpretation of Survival Data

Since survival data are of little value for modeling unless they are available for each of the developmental stages (Table 1), it was necessary to construct survival curves and designate times of transition to subsequent stages (Fig. 1-4) when adequate data were available. Stages are classified as eggs, yolk-sac larvae (from hatching to complete absorption of yolk-sac), and postlarvae (from yolk-sac absorption to demersal or fully developed juvenile).The survival curves are also necessary to examine the critical period concept, which is dependent on differences of slope within a curve rather than absolute rates of mortality (Pearcy, 1962). Representative survival data are presented, either by selection of data which appears to be typical of different years of study or by averaging data for more than 1 year as described in the footnotes. However, it is not possible at this time to quantitatively account for all errors which may result from bias in sampling methodology.

Complete data on postlarvae are available for relatively few species because avoidance of plankton nets increases with size of larvae. It was neccessary to assume that postlarval survival rate was constant in order to complete the postlarval survival curves for Pacific sardine[1] and yellow perch, as described in Table 1. This avoidance problem may be resolved by collection of postlarvae or juveniles with trawls, as in studies of walleye (Forney, 1976), winter founder (Pearcy 1962), and Atlantic herring (Graham et al., 1972), or with trap nets, as in northern pike studies (Forney, 1968).

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[1]Scientific names follow Bailey et al. (1970) except foreign names as listed in Table 4.

Figure 1.—Survival curves for eggs and larvae of plaice during abnormal (P-AY) and typical (P-TY) years. Atlantic mackerel (AM), Japanese sardine (JS), jack mackerel (JM), Japanese anchovy (JA), and Black Sea anchovy (BSA). Incomplete segments are indicated by arrows. Yolk-sac stages indicated by parenthesis. See Tables 1 and 2 for sources.
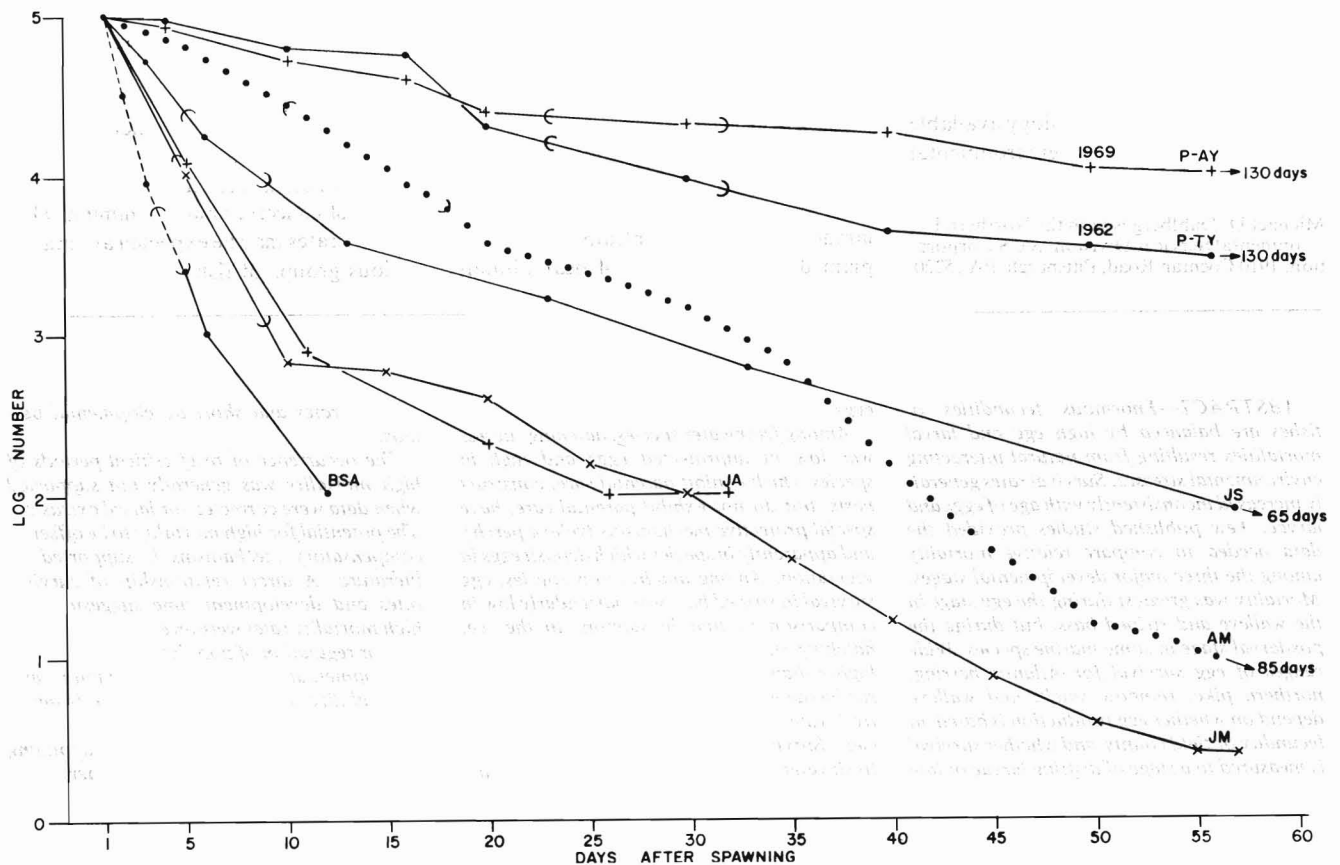
Determination of survival of yolk-sac larvae generally required interpolation between the egg and fully vulnerable yolk-sac stages. This approach is necessary because the smallest larvae are generally extruded through nets in the sea and are not fully planktonic in freshwater. This approach results in a constant survival rate for smaller larvae instead of a more probable tendency for survival to increase during this period.

Egg production was indicated by numbers of 5-day-old eggs in plaice (Bannister et al., 1974) and 1.8-day-old eggs in jack mackerel (Farris, 1961). Actual egg production was estimated by extrapolation to the spawning date, assuming a constant survival rate among the early egg stages.

The use of age-related fecundity data to calculate egg production is a possible source of error in the survival data for northern pike (Forney, 1968), walleye (Forney, 1976), yellow perch (Clady, 1976) and Atlantic herring off Norway (Dragesund and Nakken, 1973). This may result in high estimates of egg production if fertilization is not complete, egg extrusion is incomplete as in salmon (Johnson, 1965), or there are non-spawning adults as in walleye (Forney, 1976) and salmon (Johnson, 1965). Clady (1975) indicated that the ratio of eggs deposited (based on field counts) and potential egg deposition (based on fecundity) was low (15-34 percent) in a smallmouth bass population. However, this was possibly a result of egg predation

by red water mites before the eggs were sampled. Comparisons of egg production based on fecundity, and water body sampling yielded differences varying by a factor of 2.7 in striped bass (Polgar, 1977) and 3-34 in Clyde herring (Saville et al., 1974). However, these discrepancies were thought to be a result of inadequate egg sampling rather than incomplete egg production.

Major Factors Which Influence Mortality Rates

The applicability of data from one region for another will depend on how similar the environmental conditions are during the developmental periods. A number of the major factors which should be considered are discussed

Figure 2.—Survival curves for eggs and larvae of northern pike (NP), yellow perch (YP), walleye (W), Pacific sardine (PS), Black Sea mackerel (BSM), Atlantic herring in Norway (AH-N), round herring (RH), Atlantic thread herring (ATH), and scaled sardine (SS). Yolk-sac stages indicated by parenthesis. See Tables 1 and 2 for sources.
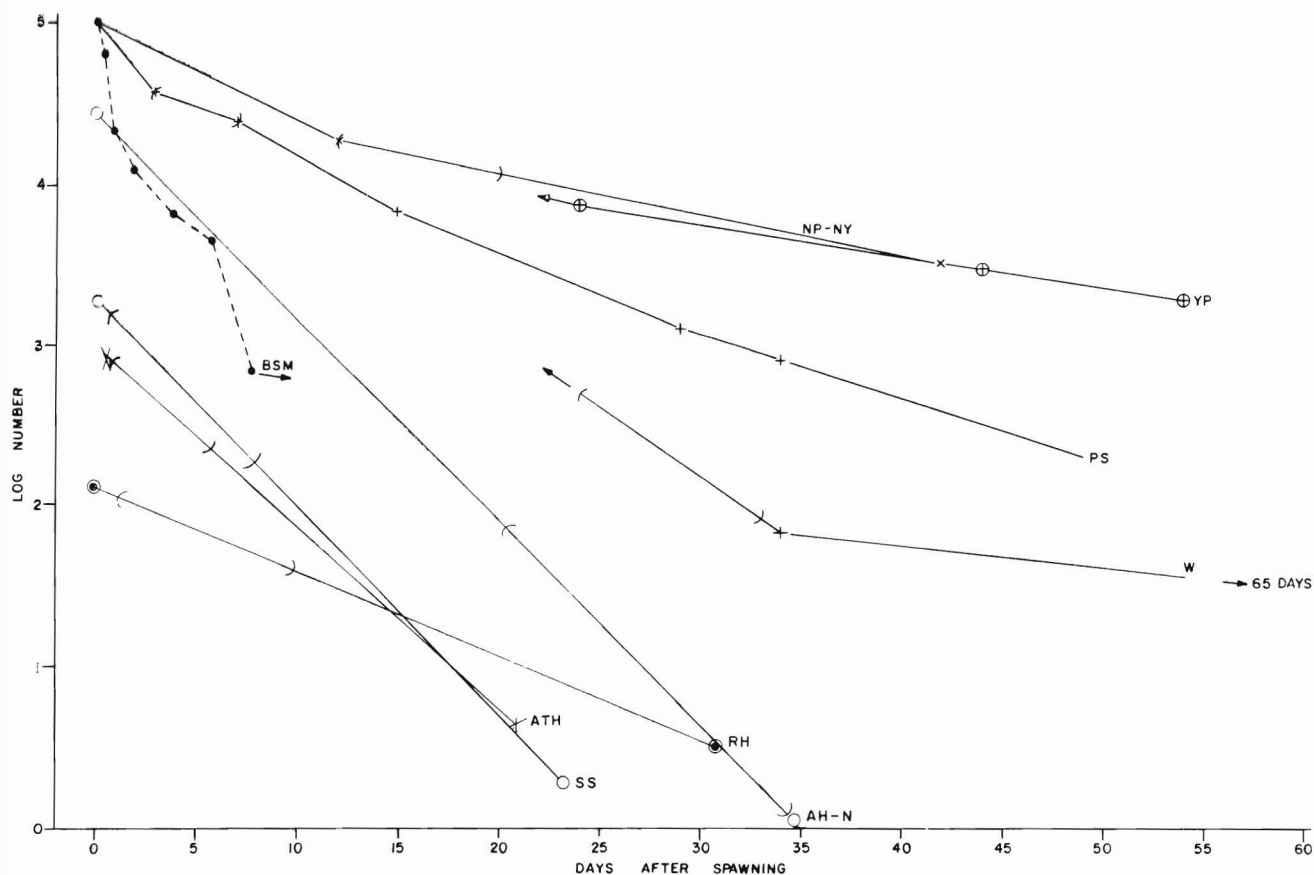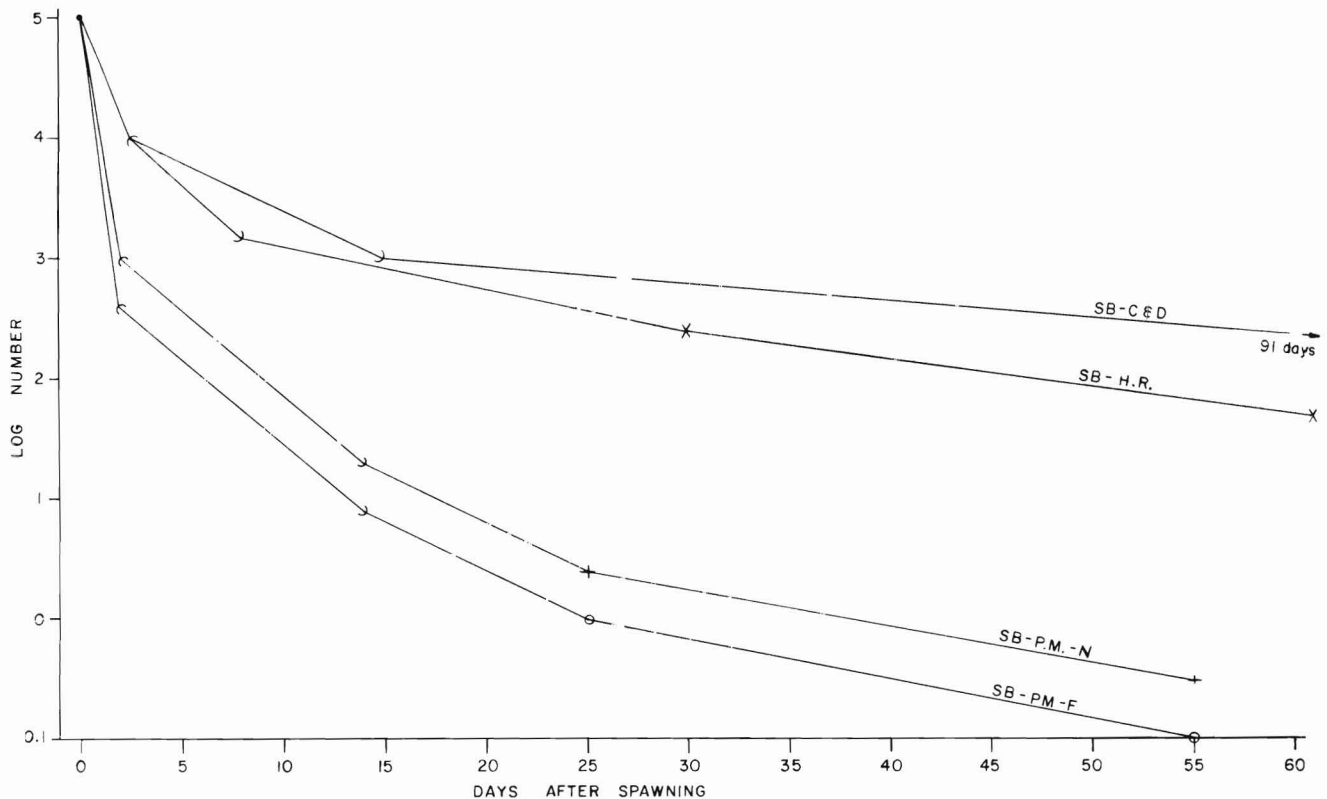
Figure 3.—Survival curves for eggs and larvae of striped bass in Potomac River based entirely on net samples (SB-PM-N), in Potomac River with egg densities based on fecundity-at-age data (SB-PM-F), in Chesapeake and Delaware Canal (SB-C & D), and in Hudson River (SB-HR). Yolk-sac stages indicated by parenthesis. See Table 1 for sources.

below. Further quantification would lend more predictive value to this information. However, this would be rather academic for predictive purposes since extent of mortality is a function of intensity as well as type of perturbation. Quantitative estimates of the magnitude of mortality due to some factors such as predation and starvation are almost totally lacking (May, 1974).

Substrate characteristics influenced egg survival in salmon (Larkin, 1977), brook trout (Hausle and Coble, 1976), walleye (Johnson, 1961), and herring (Galkina, 1971). Siltation was a source of mortality in eggs of smallmouth bass (Latta, 1975), lake trout (Youngs and Oglesby, 1972), salmon (McNeil, 1966) and Pacific herring (Galkina, 1971). Survival of Pacific herring eggs in subtidal water was about 100 percent

when eggs were deposited on high vegetation and free from silt (Galkina, 1971).

Low flow or low water levels were detrimental to survival of eggs of salmon (Warner, 1963; McNeil, 1966), rainbow smelt (Rupp, 1965) and Pacific herring (Soin, 1971), and larvae of northern pike (Hassler, 1970) and striped bass (Stevens, 1977). Mortality often resulted from stranding of the eggs. Mortality of Pacific herring eggs from desiccation increased from 30 to 100 percent from the lower to the upper intertidal zone, and total mortality was 5 percent or less in subtidal areas (Soin, 1971).

Reduction of oxygen to a critical level can cause mortality, e.g., salmon eggs (McNeil, 1966), brook trout eggs (Hausle and Coble, 1976), carp eggs (Nikolskii, 1969), and Baltic cod larvae (Grauman,

1973). Lethal dissolved oxygen levels were caused by high egg concentrations in Atlantic herring (Jones and Hall, 1974), Pacific herring (Hempel, 1971), rainbow smelt (McKenzie, 1947), and salmon (Johnson, 1965).

Adverse effects of low water temperature on eggs have been shown with smallmouth bass (Kramer and Smith, 1962), rainbow smelt (Rothschild, 1961), and northern pike (Hassler, 1970). Low water temperatures apparently reduced the rate of larval development and caused prolonged exposure to predation in plaice (Bannister et al., 1974), Pacific sardine (Murphy, 1961), Atlantic herring (Graham et al., 1972), northern anchovy (O'Connell and Raymond, 1970), and walleye (Busch et al., 1975). Colton (1959) reported mass mortality of marine fish larvae due to natural warming. A
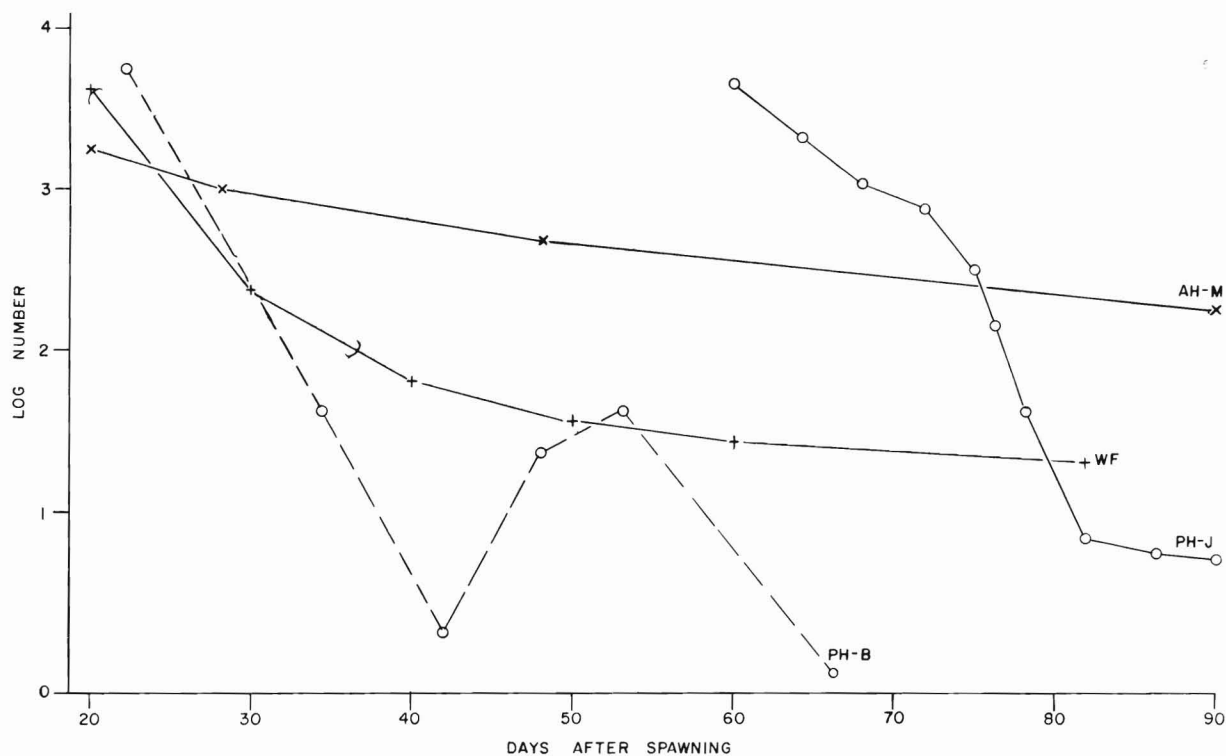
Figure 4.—Partial survival curves for larvae of winter flounder (WF), Atlantic herring off Maine (AH-M), Pacific herring off Japan (PH-J), and Pacific herring off British Columbia (PH-B). Approximate days after spawning are indicated. See Tables 1 and 2 for sources.

rapid rise in water temperature adversely affected embryonic and larval survival in herring (Rannak, 1971).

Storms and wave action caused mortality of herring larvae (Wiborg, 1976) and cod eggs (Rollefsen, 1930). Wave action caused stranding of 1 percent of the yellow perch eggs in a lake (Clady, 1976) and along with low temperature was responsible for failure of largemouth bass nests (Kramer and Smith, 1962).

Egg loss from nonfertilization is generally minimal and has been reported as about 1 percent in salmonids (Warner, 1963) and 0.2-0.4 percent in Baltic herring (Rannak, 1971). Egg loss from predation has been reported in many species, including Atlantic herring (Dragesund and Nakken, 1973), Pacific herring (Soin, 1971), smallmouth bass (Latta, 1975), and rainbow smelt (Rothschild, 1961). Predation and cannibalism were significant sources of larval mortality in

Black Sea anchovy (Dekhnik et al., 1970), Black Sea mackerel (Dekhnik, 1964), Japanese anchovy (Nakai et al., 1955), Pacific sardine (Murphy, 1961), northern anchovy (O'Connell and Raymond, 1970), winter flounder (Pearcy, 1962), walleye (Forney, 1976), yellow perch (Tarby, 1974), northern pike (Forney, 1968), pink salmon (Johnson, 1965), and sockeye salmon (Hartman et al., 1962). Occasional high rates of predation on eggs and larvae of roach, rainbow trout, and other freshwater species were noted by Paling (1971).

The hypothesis that lack of food causes larval mortality (Hjort, 1914) has been supported by studies of Atlantic mackerel (Sette, 1943), plaice (Bannister et al., 1974), Japanese sardine (Nakai and Hattori, 1962), Atlantic herring (Graham et al., 1972), pilchard (Karlovac, 1967), and Japanese anchovy (Nakai et al.,

1955). Dekhnik et al. (1970) noted that postlarvae survive 10-18 days without food and concluded that "...the food factor cannot be considered a cause of the mortality of fish larvae in the Black Sea." However, inadequate food increases vulnerability to other stresses and its effect on survival is mainly indirect (Nikolskii, 1969).

Relationship of Survival Rates to Reproductive Strategies

In addition to specific environmental factors cited above, it is possible to make some generalizations regarding the survival rates of fish eggs and larvae in relation to different reproductive strategies and habitats.

Survival of Fish Eggs

Hatching success of eggs is often low in freshwater species which do not guard the demersal eggs. As little as 3 percent survival from egg to migrant larvae has

been reported for the white sucker (Scott and Crossman, 1973). Forney (1976) noted less than 1 percent walleye survival through the swim-up stage in Oneida Lake, with most of the loss probably in the egg stage. Walleye survival from recently spawned eggs to a prehatching "eyed" stage was 2.4-25 percent on various natural substrates (Johnson, 1961). High egg mortality also occurs in the rainbow smelt: Rothschild (1961) reported 24 percent egg survival (to 1-15 days before hatching) and 0.5 percent survival to the drifting yolk-sac stage; McKenzie (1947) found that the hatching rate was usually 0.8-1.8 percent; and Rupp (1965) reported a mean hatch of 1.1 percent in lakeshore spawners of this species.

Egg survival was generally high in freshwater species exhibiting parental care (Breder and Rosen, 1966) and in freshwater and anadromous salmonids which cover the eggs with gravel (Table 3). Parental care was a factor in the 49-94 percent survival of white crappie eggs (Siefert, 1968), 26-33 percent survival to emergence in smallmouth bass (Clady, 1975; Latta, 1975), and 94 percent survival of smallmouth bass eggs in a stream (Pflieger, 1966). However, only 44-55 percent of smallmouth bass nests produced fry in large natural lakes (Latta, 1975).

High egg survival has been reported in three freshwater species which spawn in vegetation: 60-95 percent for northern pike (Franklin and Smith, 1963), 80-94 percent at high oxygen concentrations for carp (Nikolskii, 1969), and 34-90 percent for carp-bream (Nikolskii, 1969). Forney (1968) reported 77 percent viability of northern pike eggs in a regulated marsh but found that recruitment to pelagic yolk-sac larvae was only 16-19 percent. Protection afforded by the unique egg mass envelopes contributes to high survival of yellow perch eggs: Clady (1975) observed that viability was generally over 95 percent.

Survival of unguarded demersal eggs of three marine species (Atlantic herring, Pacific herring, and capelin) was generally considered to be over 90 percent (Baxter, 1971; Soin, 1971; Rannak, 1971; Gjøsaeter and Saetre,

Table 1.—Survival rates of eggs and larvae of marine, freshwater, and anadromous fishes. Footnotes are cross-referenced to Figures 1-5.

Fishes	Eggs			Yolk sac larvae			Postlarvae			Total		
	Survival	Days	Survival per day	Survival	Days	Survival per day	Survival	Days	Survival per day	Survival	Days	Survival per day
Marine												
Atlantic herring[1]	0.030	21	0.846	0.175	14	0.884	0.050000	90	0.967	0.000263	125	0.936
Atlantic mackerel[2]	0.300	9	0.875	0.200	8	0.818	0.000067	60	0.852	0.000004	77	0.851
Atlantic thread herring[3]	0.660	0.8	0.595	0.400	4.9	0.830						
Black sea anchovy[4]	0.060	2.5	0.325	0.383	1.5	0.527						
Jack mackerel[5]	0.132	3.5	0.560	0.100	4.5	0.600	0.002182	49	0.885	0.000024	57	0.830
Japanese sardine[6]	0.270	4	0.721	0.333	4	0.760	0.003333	62	0.913	0.000300	70	0.893
Pacific sardine[7]	0.360	3	0.712	0.667	4	0.904	0.008333	43	0.896	0.002000	50	0.883
Plaice[8]	0.118	22	0.907	0.678	9	0.958	0.000125	99	0.914	0.000010	130	0.915
Round herring[9]	0.380	2	0.616	0.250	8	0.841						
Scaled sardine[10]	0.120	0.8	0.071	0.106	7.5	0.742						
Freshwater												
Northern pike[11]	0.180	13	0.880	0.572	8	0.931	0.291262	22	0.945	0.030000	43	0.922
Walleye[12]	0.005	24	0.800	0.132	9	0.800	0.333333	31	0.965	0.000060	64	0.859
Yellow perch[13]							0.259740	30	0.956	0.020000	55	0.931
Anadromous												
Striped bass[14]	0.009	2	0.095		12	0.726	0.014000	41	0.901	0.000003	55	0.793
Striped bass[15]	0.003	2	0.055	0.021	12	0.726	0.014000	41	0.901	0.000001	55	0.778
Striped bass[16]	0.100	2.5	0.398	0.100	12.5	0.832	0.100000	75	0.970	0.001000	90	0.926
Striped bass[17]	0.100	2.25	0.360	0.150	6	0.728	0.030000	52	0.935	0.000450	60	0.879

[1]Dragesund and Nakken (1973). Means of egg survival (0.01-0.05) and yolk-sac larva survival (0.05-0.30). Egg survival based on fecundity-at-age data. (Fig. 2). Postlarva data from Cushing (1974). Average values for 6-year study, limited to first 90 days (Fig. 4)

[2]Sette (1943). Planktonic survival was 1×10^{-6} to 1×10^{-5}, but 4×10^{-6} in his Figure 17. Apparent net avoidance in older larvae. (Fig. 1)

[3]Houde (1977b). Means of survival to 5.5 mm yolk-sac larvae and 15.5 mm early postlarvae. (Fig. 2)

[4]Dekhnik (1963), Nikolskii (1969). Egg survival also given as 58 percent (Dekhnik, 1960) and 19-40 percent (Pavlovskaia, 1955). (Fig. 1)

[5]Farris (1961). Means of data for 3 years. Survival for first month was approximately 0 1 percent all 3 years. Eight day period of yolk nutrition (Farris, 1960). (Fig. 1)

[6]Nakai and Hattori (1962, Table 6). Means of data for 3 years (Fig. 1)

[7]Lenarz (1972) for abundance by length and Ahlstrom (1954) for age-length relationship. Samples collected at night and corrected for extrusion (Lenarz, 1972). Egg survival (0.36) from Smith (1973). Four-day yolk-sac larva period (Ahlstrom, 1954). Daily survival rate for days 30-35 assumed to be constant through day 50. (Fig. 2)

[8]Bannister et al. (1974). Data for typical year (1962). Yolk-sac larva period follows Ryland (1966). (Fig. 1)

[9]Houde (1977a). Means of survival to 5.5-mm yolk-sac larvae and 15.5-mm early postlarvae. (Fig. 2)

[10]Houde (1977c). Means of survival to 5.5-mm prolarvae and 15.5-mm early postlarvae. (Fig. 2)

[11]Forney (1968). Means of data for 2 years. Assume transformation to juvenile at 35 mm and 43 days after spawning (Franklin and Smith, 1963). Actual egg survival was between the observed 77 percent viability and 18 percent survival to pelagic yolk-sac larvae. (Fig. 2)

[12]Forney (1976). Mean values for 3 years in which cohorts which were not augmented with yolk-sac larvae. Survivorship of yolk-sac larvae (13.2 percent) estimated from relative numbers of 1- to 3-day-old larvae and 10-day-old larvae by assuming that differences in numbers of 10-day-old larvae in augmented and unstocked cohorts resulted from stocking. Egg production based on fecundity. Trawled juvenile data used to complete the postlarvae survival segment (Fig. 2)

[13]Noble (1975). Survival values for days 25 to 45 in 3 years, assumed to be constant to demersal age (55 days). Survival and duration of earlier stages from Clady (1975). (Fig. 2)

[14]Polgar (1977, Table 2) Assumed exponential age distribution. Net samples only, through post-finfold (late postlarva) stage. (Fig. 3)

[15]Polgar (1977). As above, but with egg production based on fecundity-at-age data. (Fig. 3)

[16]Portner (1975). Assumed 0.100 survival for each stage. (Fig 3)

[17]LMS (1975), Swartzman et al. (1977) Net samples only, through juvenile I (late postlarva) stage. (Fig. 3)

1974). Lower survival from spawning on less suitable substrates or from dense packing of eggs has been reported, but this is probably of little consequence in comparison to predation on eggs (Hempel, 1971). Dragesund and Nakken (1973) concluded that egg loss from predation was 15-40 percent, and mortality from hatching to recruitment into the plankton was 83-95 percent in one herring population. An assumed 10 percent hatch of demersal winter flounder eggs (Hess et al., 1975) has not been verified.

Data in Table 1 indicate that survival of pelagic eggs in the sea was relatively low (6-66 percent, mean 26 percent) although Murphy (1977) concluded that demersal eggs were more vulnerable to predation. However, survival of Black Sea anchovy eggs has also been reported as 58 percent (Dekhnik, 1960) and 19-40 percent (Pavlovskaia, 1955). Survival of pelagic Japanese anchovy eggs was 70 percent (Hayasi, 1967). Survival of pelagic sole eggs was 0.05 percent and 4.35 percent at two locations off England (Riley, 1974).

Survival of pelagic cunner eggs was estimated as 5 percent by Williams et al. (1973). Survival of pelagic Baltic (Atlantic) cod eggs varied from 1 to 21 percent in relation to dissolved oxygen, buoyancy (resulting from salinity) and egg quality (based on size and fat content) (Grauman, 1973). Survival of pelagic Argentinean anchovy eggs was 7-13 percent (Ciechomski and Capezzani, 1973). There are additional observations on viability of pelagic eggs, which probably exceed actual survival rates, e.g., viability of pelagic pilchard eggs was 50 percent off England and 48-87 percent in other studies (Southward and Demir, 1974). Very low survival (0.3-10 percent) was also reported for the semibuoyant eggs of anadromous striped bass (Table 1).

Survival of Yolk-Sac Larvae

Survival of yolk-sac larvae ranged from 2.3 percent (winter flounder) to 68 percent (plaice) in marine species, 13 to 57 percent in two freshwater species, and 2.1 to 15.0 percent in striped

bass (Tables 1-3). Daily survival rates were 53-96 percent, 80-93 percent, and 73-83 percent, respectively. Survival of yolk-sac larvae of Danubian shad was less than 10 percent (Dekhnik et al., 1970). Thus, there are no obvious differences in survival rates among the groups with the possible exception of low survival in the anadromous species.

Survival of Postlarvae

Postlarval survival (Table 1) was considerably higher in the three

Table 3.—Survival rates of salmonids from egg to hatching and emergence in nature.

Species	Hatching	Egg to emergence
Atlantic salmon [1]	0.93	0.92
Brook trout	[2]0.80-0.93, [3]0.84	[3]0.59, [4]0.79
Brown trout rainbow trout and chinook salmon [5]	0.71-0.97	0.91
Brown trout	[6]0.89, [7]0.98	
Chum salmon [8]	Over 0.80	0.01-0.25
Coho salmon	[9]0.35-0.85, [10]0.85	[11]0.26-0.54, [12]0.14-0.54
Cutthroat trout [13]	0.25-0.40	
Lake whitefish [14]		Less than 0.13
Pink salmon	Over [15]0.80	[16]0.03-0.21, [17]0.01-0.25
Rainbow trout		[18]0.42-0.92
Sockeye	[19]0-0.79	[20]0.20, [21]0.085
Steelhead	[22]0.86	[23]0.40

[1]Warner (1963). Survival to late eyed stage and emergence.
[2]Shetter (1961). Typical range.
[3]Hausle and Coble (1976).
[4]Brasch (1949). Upwelling favorable to survival.
[5]Hobbs (1940). New Zealand.
[6]Allen (1951) and Braum (1971).
[7]Kramer and Smith (1965).
[8]McNeil (1966). Typical emergence values.
[9]Cloern (1976). Typical range, but 0-0.014 in Wisconsin.
[10]Briggs (1953).
[11]Moring and Lantz (1975).
[12]Koski (1966).
[13]Ball and Cope (1961).
[14]Van Oosten (1956).
[15]McNeil (1966).
[16]Hanavan and Skud (1954). Tidal waters.
[17]McNeil (1966). Typical values.
[18]Bjorn (1966). Planted eggs.
[19]Krogius (1951).
[20]Johnson (1965). Survival to entry into nursery ground
[21]Hartman et al. (1962). Survival to fry outmigration.
[22]Briggs (1953).
[23]Coble (1961).

Table 2.—Survival rates of fish larvae and various larva and egg combinations not shown in Tables 1 and 3. Footnotes cross-referenced to Figures 1-5.

Species	Stage	Survival	Days	Survival per day
Winter flounder [1]	Yolk-sac larvae	0.023	17	0.800
	Postlarvae	0.319	28	0.960
Pacific herring [2]	10-15 mm postlarvae	0.120	14	0.860
	15-18 mm postlarvae	0.017	8	0.601
	18-28 mm postlarvae	0.500	19	0.964
	10-28 mm postlarvae	0.0009	40	0.839
Pacific herring [3]	Postlarvae	0.0005	20	0.684
	Postlarvae	0.025	11	0.715
Pilchard [4]	2-20 mm larvae	0.004		
Northern anchovy [5]	3-16 mm larvae	0.007		
Chub mackerel [6]	Eggs and larvae	0.005	23	0.721
Japanese anchovy [7]	Eggs and larvae	0.0009	31	0.799
Black sea mackerel [8]	Eggs	0.207	1.1	0.239
	Yolk-sac larvae	0.056	6	0.618
Smallmouth bass [9]	Eggs to fry emergence	0.286	10	0.882
Smallmouth bass [10]	Eggs to fry emergence	0.941	10	0.994

[1]Pearcy (1962). Data excludes 2.3-3.5 mm larvae. Translocation was minor component of total losses. Survival curve extrapolated to complete transformation age in Figure 4.
[2]Iizuka (1966). Data for postlarvae in 1959, representing three distinct survival slopes. Complete recruitment at 60 days after spawning. (Fig. 4)
[3]Stevenson (1962). Bimodal curve represents two broods of larvae. (Fig. 4)
[4]Karlovac (1967). 2-20 mm larvae (Fig. 5).
[5]Lenarz (1972). 3-16 mm larvae. Night samples corrected for losses through 0.55-mm mesh. (Fig. 5).
[6]Watanabe (1970). Spawning to day 23. Also called Japanese common mackerel
[7]Nakai et al. (1955). Survival from spawning to day 31. Mean of 3 years. (Fig. 1).
[8]Dekhnik (1964). From his table 3. (Fig. 2).
[9]Clady (1975). Data for 3 years. Ten-day duration from Allan and Romero (1975). Survival also reported as 27.6 percent (Latta, 1963).
[10]Pflieger (1966). Stream population. Duration from Allen and Romero (1975).

Table 4.—List of common and scientific names of foreign fishes cited in this paper.

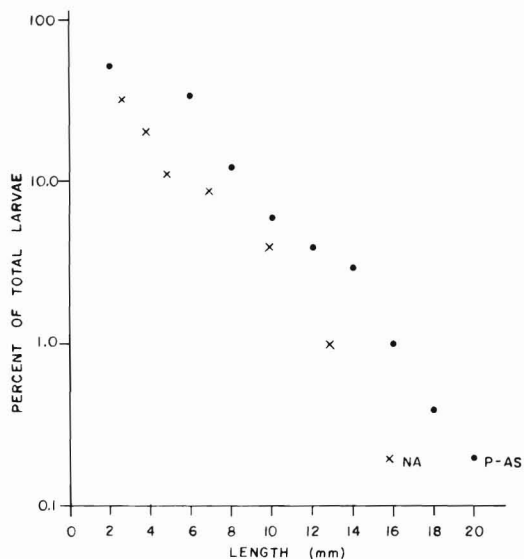| Common name	Scientific name
Argentinean anchovy	Engraulis anchoita
Black sea anchovy	Engraulis encrasicholus
Black sea mackerel	Trachurus mediterraneus
Carp-bream	Abramis brama
Danubian shad	Alosa alosa
Japanese anchovy	Engraulis japonica
Japanese sardine	Sardinops melanosticta
Pilchard	Sardina pilchardus
Roach	Rutilus rutilus
Sole	Solea solea

Figure 5.—Partial larval survival curves of Adriatic Sea pilchard (P-AS) and northern anchovy (NA) in terms of percent of total larvae VS length. See Table 2 for sources.

days (10-12 mm) (Dragesund and Nakken, 1971, May 1974) and 70-95 percent in 14 days (9-13 mm) (Dragesund and Nakken, 1973). The delay of a high mortality period (98 percent in 8 days) to a size range of 15-18 mm in Pacific herring postlarvae in Japanese waters (Iizuka, 1966) may be attributable to their retention in a bay. The relatively constant survival rate of yolk-sac and postlarval Atlantic herring in the Gulf of Maine (Graham et al., 1972 as modified by Cushing, 1974) suggests that observation of high mortality in other populations of herring may result from offshore drift or errors caused by net avoidance. Offshore drift as a major cause of death was postulated for Pacific herring in British Columbia (Stevenson, 1962) although the extent of mortality at sea was not determined.

Observations representing catastrophic mortality may be confused with critical periods. Catastrophic mortality in the early larval stages of herring was documented by Soleim (1942). Marr (1956) and May (1974) suggested that the net in this study was contaminated with herring larvae of previous hauls. Wiborg (1976) and Nikolskii (1969) cited evidence that such mass mortalities result from storms.

The occurrence of a critical period in Adriatic pilchard (Karlovac, 1967; May, 1974) is not strongly supported by Karlovac's data. Samples were collected at monthly intervals during the spawning seasons, and larval densities were tabulated by size. A plot of larval numbers as percent of total larvae VS lengths (Fig. 5) following the procedure of Lenarz (1972), does not provide any evidence of a critical period. However, no correction for variation in growth rate was made.

Data on striped bass of the Potomac River, Chesapeake and Delaware Canal, and Hudson River (Table 1, Fig. 3) reveal very high mortality of eggs (90-99.7 percent). Highest egg mortality of Potomac River striped bass is apparent when egg production is based on fecundity-at-age data. The marked differences in the striped bass survival curves for the three study areas are influenced by the use of hypothetical survival rates for the Chesapeake and

freshwater species (26-33 percent) than in the 10 examples of marine species (0.01-31.9 percent, mean 4.09 percent). This may be attributable to higher daily survival rates and shorter postlarval periods (22-31 days). An intermediate rate of survival is apparent for the 41-75 day postlarval periods in the striped bass.

Observations on Possible Critical Periods

Enormous fecundities of fishes are balanced by high mortality rates. The occurrence of most mortality during a short period in early development is the critical period concept. Total losses are undoubtedly highest during egg or yolk-sac larva stages (Farris, 1960, Dekhnik et al., 1970). If a critical period can be identified, then it is likely that the consequences of human perturbations would be much greater if they occurred after the critical period rather than before.

Critical period may also be viewed in terms of relative survival rates among the developmental stages. Data in Tables 1

and 2 indicate that mortality is greatest in the postlarval stages of the marine species and also in the Hudson River striped bass. Therefore, the environmental conditions existing during the relatively long postlarval periods may be more critical to the determination of year-class strength than the egg and yolk-sac larva environments.

Critical periods have been postulated for many species. Larval survival curves, presented as percent of larvae VS length, for Pacific hake, jack mackerel, Pacific sardine, and northern anchovy (Lenarz, 1973) revealed some evidence for early critical periods, but there was also some degree of extrusion through the 0.55-mm mesh net. Survival curves of pacific sardine (Fig. 2) and northern anchovy larvae (Fig. 5) did not provide any evidence of a critical period when densities were corrected for loss of small larvae through the mesh (Lenarz, 1972).

Survival curves of herring larvae do not follow a consistent pattern (Fig. 2, 4). Mortality rates of Norwegian herring larvae were estimated at 94 percent in 6
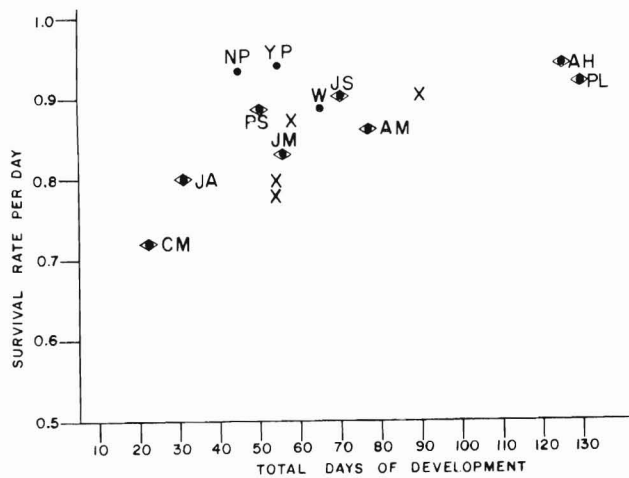
Figure 6.—Relationship of daily survival rates and lengths of developmental period in striped bass (X), chub mackerel (CM), Japanese anchovy (JA), northern pike (NP), Pacific sardine (PS), yellow perch (YP), jack mackerel (JM), walleye (W), Japanese sardine (JS), Atlantic mackerel (AM), plaice (PL), and Atlantic herring (AH). Diamond figure indicates marine species. See Tables 1 and 2 for sources.

Delaware Canal population, and by differences in sampling and/or data interpretations, and therefore do not provide strong evidence for a critical period.

Maintenance of stock size depends largely on egg production and rate of survival through egg and larval stages. It follows that species having short periods of egg and larval development will exhibit higher daily mortality rates which may be interpreted as critical periods. To investigate the relationship of daily egg and larval survival rates with total time of egg and larval development, these data (Tables 1, 2) were plotted for species represented by relatively complete survival data (Fig. 6). Daily survival rates ranged from 72 percent in chub mackerel to 94 percent in Atlantic herring and a general correlation is apparent. However, the low survival rates of chub mackerel and Japanese anchovy are strongly influenced by the absence of larger larvae. A trend of increasing survival with time of development is apparent with the remaining marine species. Higher daily survival rates apparently represent a

compensatory mechanism, functioning to maintain egg and larval populations through longer developmental periods in marine fish. Limited data make a similar assessment with freshwater or anadromous fishes difficult. However, data on chinook salmon (Johnson, 1965) support the hypothesis. A daily survival rate of 99 percent was calculated for a possible 9-month development period

The critical period is a relative concept and depends more on the differences of slope in a survival curve rather than absolute rates of mortality. Pearcy (1962) concluded that this concept has limited usefulness, particularly if compensatory mechanisms actively respond to periods of high mortality. The prevalence of compensation in fishes was reviewed by McFadden (1977)

Discussion

Current federal regulations often necessitate entrainment impact modeling in the absence of complete or site-specific data. In the simplistic equivalent adults model (Horst, 1975), larva to adult survival is estimated from data on fecundity, annual survival rates, and egg

to larva survival. Other models require additional data on survival rates of larvae and juveniles, population size, larval production, compensatory reserve, etc. Such information is available for a very limited number of species and must be used cautiously in predictive modeling.

Data collected at one site may not be applicable to another if there are differences in natural factors, such as substrate characteristics, disease, water level, dissolved oxygen, water temperature, wave action, predation, cannibalism, food supply, carrying capacity, and condition of spawners. Interaction of more than one stress has been frequently observed. It has been proposed that low water temperatures significantly prolong development and exposure to predation. several stresses may act simultaneously as in smallmouth bass (Latta, 1975), yellow perch (Clady, 1976), salmon (Johnson, 1965), and marine fishes (May, 1974). Skud (1973) concluded that environmental factors had a "random influence" in pink salmon since egg and larval survival was highest when the spawners were large and spawned early. First year survival of smallmouth bass was probably determined by carrying capacity in a stream (Pflieger, 1975).

Natural stresses cause high mortality of eggs in those freshwater species which broadcast the eggs and have no special protective mechanisms. This strategy points to predation as a chronic source of the high mortality in walleye and rainbow smelt. The importance of predation by invertebrates, considered to be the main predators on fish eggs and larvae (Nikolskii, 1969), has received little attention. Larval and nymphal insects and leeches feed on rainbow smelt eggs (Rothschild, 1961).

High egg survival has been reported in freshwater species which cover the nested eggs with gravel (salmonids), deposit eggs in vegetation (carpbream, carp, northern pike), have unique egg mass envelopes (yellow perch) or guard the nests (centrarchids) Many studies have shown over 90 percent survival of demersal eggs of marine species which broadcast the eggs and have no protective mechanisms However most of these studies probably did not account

for predation which resulted in 15-40 percent mortality in one herring study (Dragesund and Nakken, 1973). The ratio of swim-up larvae and deposited eggs does not provide a reliable measure of egg survival because mortality during the period of hatching and recruitment into the plankton may be high (Forney, 1968; Dragesund and Nakken, 1973). Furthermore, the youngest yolk-sac larvae often associate with the bottom and are not fully vulnerable to plankton sampling gear in freshwaters. Mortality of pelagic eggs has been determined from ratios of various egg stages, but this is tenuous when of short duration such as 1 or 2 days. Polgar (1977) indicated that striped bass eggs were not adequately sampled during the daytime because this species spawns at night. The semibuoyant nature of the eggs may also result in low estimates when sampled with plankton gear. Selection of representative egg survival values is particularly important in the equivalent adults model because of the proportional inverse relationship with the projected adult loss. Because of the sampling problems and natural variability, application of a possible range of survival values is recommended.

Yolk-sac larvae are the most difficult of the three developmental stages to sample because they are frequently extruded through the net in marine studies and are in a transition between a demersal and pelagic existence in most freshwater species. Thus, survival of yolk-sac larvae is generally based on survival curves which exclude data for the smallest larvae or have incorporated correction factors (Lenarz, 1972). Earlier observations of possible critical periods in marine fishes generally reflect this sampling error. Such data gaps do not preclude impact modeling and may represent a minor factor in relation to the various assumptions that are required and the minimal information available on compensatory reserve in fishes.

Development of survival data is lagging far behind the modeling state-of-the-art in impact assessment. As a result, important decisions are being made from incomplete data. A need for further evaluation of models is also evident in the literature. As an example, a series of

models for entrainment of striped bass in the Hudson River yielded conflicting results. Major differences in predictions were related to definition of life stages, whether fishing mortality and mortality of larvae and juveniles were density-dependent or density-independent, method of computing recruitment of young-of-the-year fish, and major differences in values of parameters such as egg production, population size, and survival probabilities (Swartzman et al., 1977).

Acknowledgments

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