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Arthur W. Kendall, Jr.

Washington Sea Grant Program
Division of Marine Resources
University of Washington HG-30
Seattle, Washington 98195

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ABOUT THE AUTHOR: Dr. Arthur W. Kendall, Jr., is with the Northwest and Alaska Fisheries Center, National Marine Fisheries Service.

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The distribution and abundance of fish eggs and larvae have been used in many parts of the world to estimate various population parameters such as year-class strength and spawning biomass. Early life history studies of marine fishes of the eastern North Pacific have lagged behind those in other major fisheries areas (e.g., North Sea, western North Atlantic, California Current). The life history modes of many fishes of the eastern North Pacific are different from those in other areas. I contend this has placed certain constraints on the research that can be done profitably in this area. I will discuss the life history patterns of North Pacific fishes, the constraints on fisheries investigations imposed by these patterns, and offer some suggestions for further studies.

Life History Modes

Embryonic development among the different species of teleosts takes place in a variety of environments (Figure 1). The site of development relates to the amount of parental investment given to each embryo, and to the developmental state of the embryo when it becomes free-living. There is a concomitant decrease in fecundity with an increase in parental investment to individual progeny. The most fecund fish species which provide the least parental care are those that spawn free-floating pelagic eggs. At the other extreme are viviparous fishes such as the poeciliids and embiotocids. In species with pelagic eggs, parental care is limited to investing the eggs with a certain amount of yolk, and assuring that the eggs are spawned, fertilized, and hatched in an area suitable for larval development. Because cannibalism by adults on their pelagic young is widespread, it is not always obvious that spawning locations are areas with conditions conducive to larval survival. Pelagic fish eggs of most species are only about 1 mm in diameter, which reflects the low parental investment to individual progeny. This reproductive mode has apparently evolved to take care of all eventualities in a spatially and temporally heterogeneous (patchy) environment. Among eastern North Pacific fish this pattern is demonstrated mainly by *Theragra chalcogramma*, most pleuronectids, and most oceanic fishes, whereas in other marine areas it is the dominant pattern.

Fishes that lay demersal eggs provide a better chance for survival of individual young in several ways. The embryos are subject to less extreme and more stable environmental conditions on the bottom than they would be at the surface of the sea. Through adult behavior associated with spawning demersal eggs, fertilization can

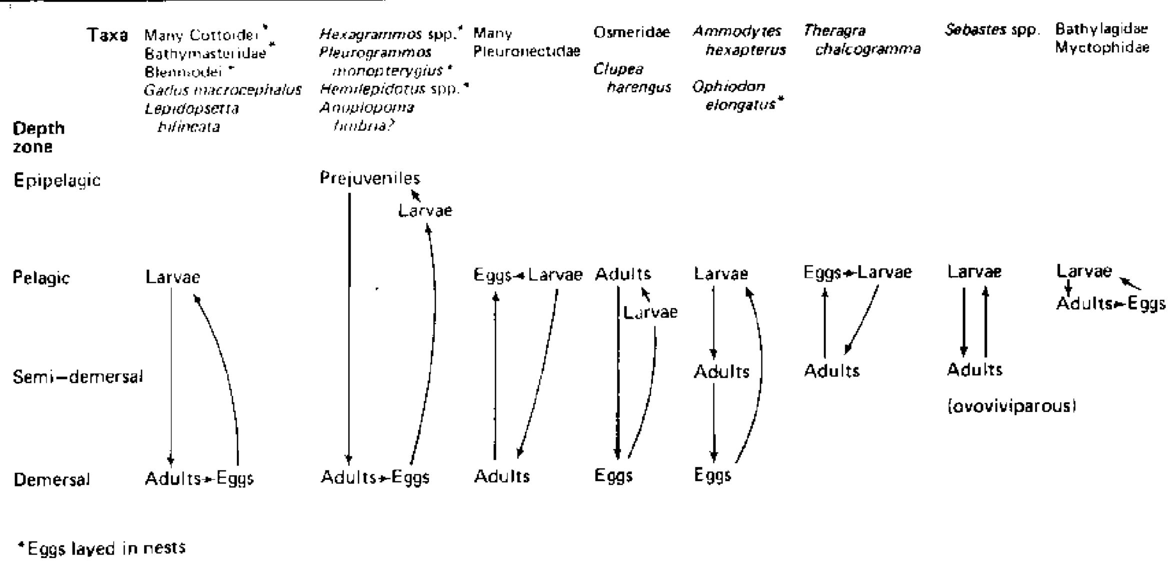


Figure 1. Representative life history modes of eastern North Pacific fishes.

Table 1. Taxonomic distribution of eastern North Pacific fishes in relation to their early life history modes[1]

Orders (29)	Sex product[2]	Families (16%) world	Families (16%) N.E. Pacific	Species (3%) marine	Species (3%) Fresh water	Species (3%) N.E. Pacific	% marine species in N.E. Pacific
Clupeiformes	P/D	4	2	267	25	3	
Anguilliformes	P	22	2	603	0	4	
Notacanthiformes	P	3	1	24	0	1	
Salmoniformes	P/D	24	11	428	80	34	8
Myctophiformes	P	16	6	390	0	17	4
Gadiformes	P/D/V	10	5	679	5	34	5
Lophiiformes	P	15	1	215	0	5	
Atheriniformes	P/D/V	16	2	327	500	2	
Lampridiformes	P	10	2	35	0	2	
Beryciformes	P	15	1	143	0	2	
Zeiformes	P/D	6	1	50	0	1	
Syngnathiformes	D	6	1	198	2	1	
Gasterosteiformes	P/D	2	2	7	3	3	
Scorpaeniformes	P/D/V	21	6	900	100	148	16
Perciformes	P/D/V	147	19	5,930	950	53	<1
Gobiesociformes	D	3	1	142	2	2	
Pleuronectiformes	P/D	6	2	117	3	22	19
Tetraodontiformes	P/D	8	1	312	8	1	
		334	66	10,767	1,678	335	

[1]The Oregonian and Aleutian regions of Briggs (1974). The numbers of fish are from Hart (1973) and a checklist of fishes of Alaskan waters (Quast and Hall 1972). The types of sex products are largely from Breder and Rosen (1966).

[2]P = pelagic eggs, D = demersal eggs, V = viviparity

also be better assured. Additionally the eggs will not drift away from favorable nursery areas. *Gadus macrocephalus* and *Lepidopsetta bilineata* exhibit this pattern. *Ammodytes hexapterus* and *Mallotus villosus* bury demersal eggs, another way to enhance survival. *Clupea harengus pallasi* deposits adhesive demersal eggs on kelp and other hard substratum.

A widespread life history pattern is to lay demersal eggs in masses or nests attached to a substratum. In many fishes such nests are guarded by one or both parents. These demersal eggs are usually larger than the 1 mm diameter seen in planktonic eggs, allowing the larvae to be larger and more advanced at hatching. This is a very widespread pattern among eastern North Pacific fishes, used by most of the speciose scorpaeniformes and blennioids.

Salmonids exhibit an even greater development of parental care in their anadromous habits and deposition of large eggs. The ovoviviparous pattern of *Sebastes* enhances survival by eliminating the pelagic egg and assuring fertilization. The fecundity of *Sebastes* is still rather high though, so the larvae must not have a much better chance to survive than those from pelagic eggs. Syngnathid males incubate eggs in a brood pouch, providing a high degree of parental care.

Parental care reaches its extreme among eastern North Pacific fishes in the viviparous embiotocids. These have very low fecundities and long gestation periods, during which the egg, larval, and juvenile stages remain within the body of the female while she supplies nourishment through a placenta-like structure.

There is a disproportionate number of fishes with some advanced form of parental care in the eastern North Pacific. There are 29 orders in 409 families of teleost fishes (Nelson, 1976). Sixty-six families, 16% of the total, are represented in the Northeast Pacific (Table 1). Of the 10,900 marine species worldwide there are 335 in this area (3%). Orders with more than 3% of their species in the North Pacific are several with demersal eggs or some form of viviparity. Particularly noteworthy are the scorpaeniformes. The perciformes, most of which have pelagic eggs, are not well represented in the North Pacific. The myctophiformes are represented in this area by widespread oceanic species. Pleuronectiformes are an exception in that they are well represented and all but one species have pelagic eggs.

Another comparison can be made between rank abundance of larvae in different areas and whether or not they developed from pelagic eggs (Figure 2). In the California

Current the more abundant larvae (except those of *Sebastes*) are derived from pelagic eggs. In the Middle Atlantic Bight the most abundant species without pelagic eggs ranks 13th and makes up only 2% of the catch. In contrast, off Kodiak Island nearly all the abundant larvae originate from species with demersal eggs.

Several reasons have been advanced for the low number of pelagic-egg producing species in the North Pacific. In dealing with the pleuronectids that lay demersal eggs, Pearcy (1962) considered important the advantages of staying at the spawning site, without drifting into fresh, cold surface water. Marshall (1953) noted the increased size and yolk of eggs of fishes of high latitude and those of the deep sea. He considered the advantages that a larger hatching size affords the larva in these conditions.

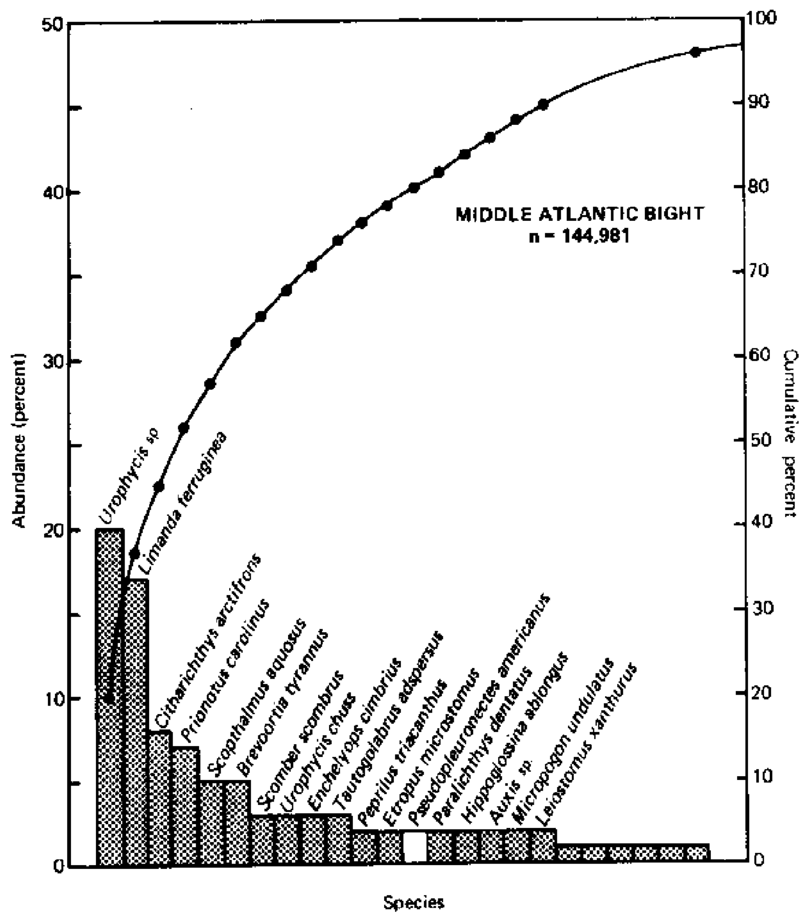
Apparently, pelagic eggs larger than 1 mm are selected against, so larger eggs are demersal. Some factors that are advantageous to larger larvae at hatching are: 1) they have relatively lower food requirements; 2) they have better swimming ability; 3) they have less intraspecific competition, since there are fewer of them; 4) they hatch at a more advanced stage. All these advantages may have been important selective pressures favoring larger eggs at higher latitudes. The greater seasonal differences in productivity at high latitudes result from the seasonal differences in sunlight. The fish probably favor producing fewer larger eggs during a short spawning season, because there would be little value in spreading egg production over a long season.

Constraints on Fisheries Investigations Imposed by Life History Patterns

Ahlstrom (1965) has given three reasons for conducting ichthyoplankton research:

1) To determine the present size of the adult population from the abundance of pelagic eggs.

Figure 2. Relative abundance of fish larvae from surveys in the Middle Atlantic Bight (from Berrien et al. [1978]), California Current (from Ahlstrom [1965]), and Gulf of Alaska, Kodiak (from Kendall, unpubl.). Shaded bars represent species producing pelagic eggs.

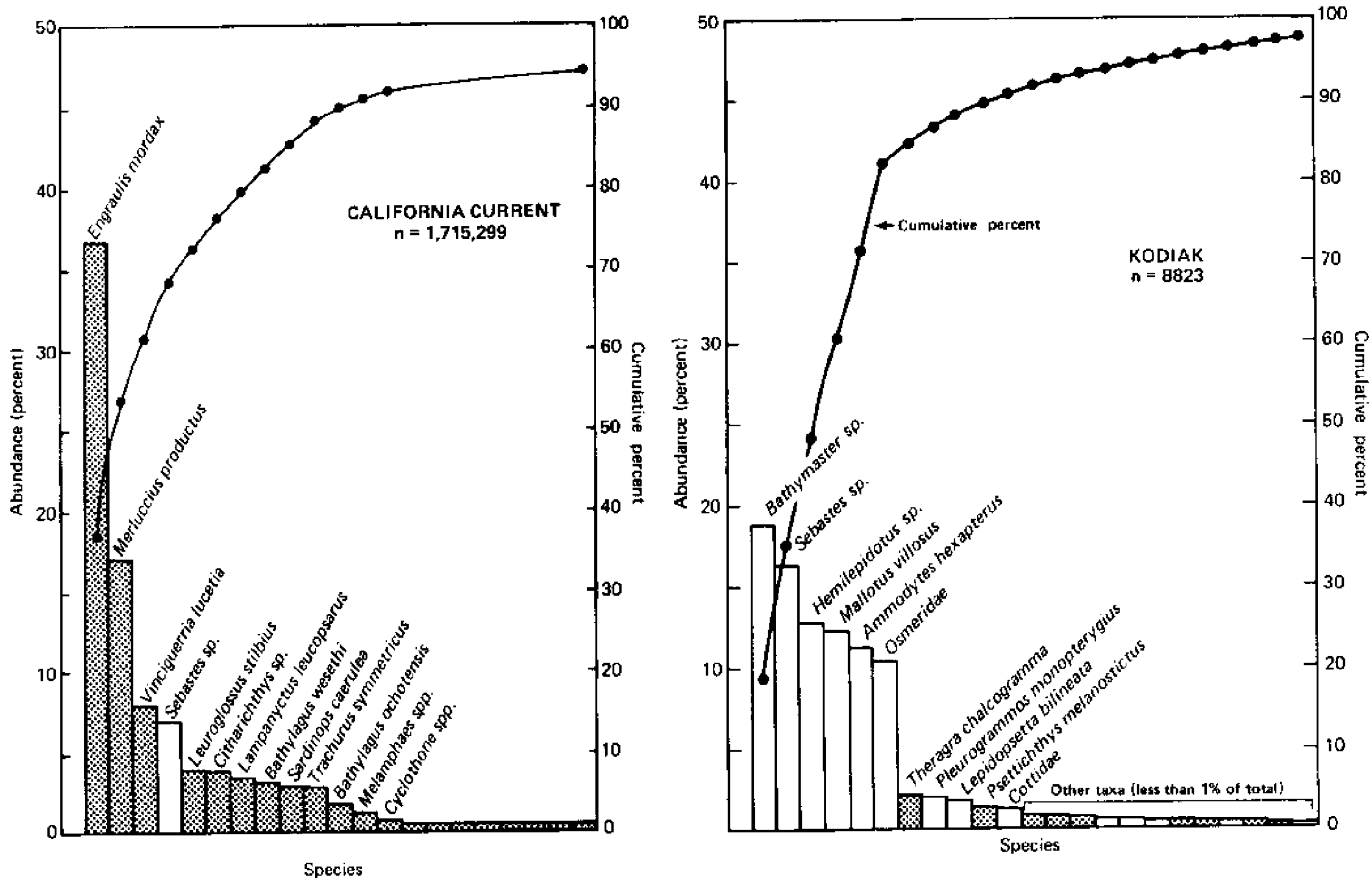


2) To determine by sampling larvae the strength of the year class resulting from a year's spawning.

3) To determine the distribution and abundance of all fish, exploited and unexploited, in the area.

An additional reason is that biologists are finding eggs and larvae of fish interesting physiological, morphological, behavioral, and systematic objects of study. The sensitivity of these stages to pollutants makes them useful organisms for environmental impact studies. The early life history modes of eastern North Pacific fishes influence studies in each of these research areas.

In order to assess the size of the spawning stock from egg and larval surveys, the youngest stages need to be sampled. In this way effects of mortality, particularly mortality that might vary from place to place or year to year, are minimized. Planktonic eggs are the best materials for this type of estimate (e.g., see Houde, 1977). Mortality of pelagic eggs is primarily from predation since mechanical damage from storms is not expected (Pommeranz, 1974). Because the eggs rely on yolk for nourishment they are not subject to variation in extraneous food supply. Eggs have the added advantage of having a simpler spatial distribution than other life history stages. Their distribution is determined by the spawning distribution of the adults and the dispersive influence of water movements. They do not swim or school. Most fishes seem to spawn on a diel cycle (Ferraro, 1980). Thus in any plankton tow, eggs of a species occur in developmental batches that represent the products of several days' spawning in the area. When the eggs in each batch in a sample can be separated and counted, the intensity of spawning for several days, as well as egg mortality, can be estimated. The number of batches at any one time is about equal to the number of days it takes the eggs to hatch. In warmer water, such as off California or in the Middle Atlantic Bight in summer, eggs have a short incubation time of about 2-7 days. In the cooler waters of the eastern North



Pacific, incubation times extend to a few weeks. Thus in this area the separation of batches is more difficult. The assumptions are tenuous that would allow a mortality rate to be determined from decreases in numbers as development proceeds. During the longer incubation period the eggs could drift further from the area where they were spawned.

From these considerations I conclude that pelagic eggs of cold water species are not as valuable for census as those from warmer waters. Few eastern North Pacific fishes have pelagic eggs anyway, so this technique to census spawning biomass has further limited potential here (although it could be applied to the pleuronectids and *Theragra chalcogramma*). Use of early larvae for census studies, particularly of species with demersal eggs, requires further assumptions that decrease the accuracy of the estimate. Use of demersal eggs for such censuses have been attempted for such species as herring which spawn over fairly large areas (Gjøsaeter and Saetre, 1974). However, considering the nesting habits of so many eastern North Pacific fishes this technique is not feasible.

Information on the spawning behavior of the target species is needed to interpret egg abundance in plankton tows. Much of this is not available for fish of the eastern North Pacific. Some of the needed population parameters are: age-specific fecundity, age composition of the population, geographic range of the species and of spawning adults, seasonal timing of spawning and shape of the spawning curve, sex ratio, and population structure of the species.

There are also constraints on using ichthyoplankton surveys for year-class-strength measurements in the eastern North Pacific. For this type of estimate a census of late larvae is needed. Presumably these larvae have passed through all the critical gates that determine the differential survival of larvae in different years. Most fishes in the eastern North Pacific are relatively long-lived. This means that several year classes contribute to the population at any one time. Thus the influence of any one year class is not as great as in shorter-lived species. The effects of good and bad year classes are averaged. For such species a population model using an average recruitment value could be applied with less concern for error.

The fish stocks in the eastern North Pacific cover huge geographic areas. A particular year may be good for recruitment (i.e., larval mortality may be unusually low) in one part of the area but may be bad in other parts. Again this may lead to an averaging of good and bad years, when the entire biomass of the population is considered.

In fishes with diminished fecundity and increased parental care, several of the sources of mortality of egg and early larval stages are reduced or absent. The larger larvae have more food reserves, have a wider range of food sizes to choose from, are faster swimming, and are better developed so that they can capture food and avoid predators more effectively. All these factors, and others associated with increased parental care, may contribute to reduced variation in year-class strength that is caused by differential mortality of early stages.

The third reason for egg and larval research is to assess the latent resources of an area. As demonstrated by Ahlstrom (1965), the plankton net collects larvae of all marine-spawning species regardless of their habitat as adults. In order to apply this technique to determine the relative size of the various populations in an area, other population parameters, such as residence time in the plankton, growth rate of the larvae, length of spawning season, and fecundity must be known to "weight" the numbers of larvae of each species. In other words, one larva of a long-lived species with demersal guarded eggs may represent as many adults as several larvae of a short-lived species with planktonic eggs. With such diverse life history patterns as seen in eastern North Pacific fishes, interpretation of larval abundance data for latent stock evaluation is difficult.

How many latent stocks of marine fish are left which could be harvested? Many of the noneconomic species represented as larvae in plankton surveys are small as adults, cannot be harvested, or may not be palatable or marketable.

Other areas of research using early life history stages of fishes for a wide range of biological studies show as much promise in this part of the world as in others. Many studies rely on rearing marine fishes, and techniques learned elsewhere are being applied here. For systematic studies, the adult taxonomy of fishes of the area must be better known. Some gaps in this knowledge are presently hampering efforts in working with larvae from these waters. Interesting studies could be done using larvae to clarify taxonomic relationships between species, genera, and families.

Early Life History Stages in Fisheries Studies

The eastern North Pacific is an area with highly productive fisheries and an area, like others, where concerns about overfishing and environmental degradation are expressed. Studies using early life history stages can contribute to our understanding of these fisheries resources. The first steps involve identification, location, and timing of young stages of species. Large scale seasonal ichthyoplankton surveys are required to obtain this information. In the Bering Sea and the Gulf of Alaska (particularly near Kodiak Island) the annual cycle of occurrence of fish eggs and larvae is known in broad outline. From Southeastern Alaska to California, knowledge is not as great, but present studies are helping close this gap.

Walleye pollock (*Theragra chalcogramma*) is a good candidate for further detailed work, using its pelagic eggs and larvae. A major spawning occurs in the Bering Sea between Unimak Pass and the Pribilof Islands in spring. The pelagic eggs from this spawning could be used to estimate the size of the spawning stock and later larvae could be censused to estimate year-class strength. A new technique applying an "instantaneous" census of pelagic egg abundance and the proportion of recently spawning fish to estimate adult biomass (Parker, 1980) can be applied to this pollock population. Information is being collected that will be needed to complement such studies. Eventually it may be possible to relate environmental conditions to year-class size of this stock.

Rearing studies to develop reliable, repeatable culture techniques for larval fishes are needed so that these life history stages will be available for physiological studies. Fish eggs and larvae have been found to be particularly sensitive to a number of pollutants. The effects of pollutants on these life forms must be considered in evaluating the impact of man's activities on the ecology of an area. Such effects can best be determined using laboratory-reared eggs and larvae.

Taxonomic studies involving early life history stages need to be an important facet of research in the eastern North Pacific. The identity of larvae of many fishes is not known or is poorly documented. Because adults of the area are incompletely known, research on the larvae will help solve taxonomic problems encountered with the adults.

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