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OVERVIEW

SYSTEMATICS AND DEVELOPMENT OF EARLY LIFE HISTORY STAGES OF MARINE FISHES: ACHIEVEMENTS DURING THE PAST CENTURY, PRESENT STATUS AND SUGGESTIONS FOR THE FUTURE

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The overview of the field of Systematics and Development that we prepared for the meetings was a more extensive version than the present account. In this condensed version we will still attempt to deal with the basic questions asked in the initial version: How did our discipline develop? Where are we now? What about the future?

HISTORICAL BACKGROUND

In 1865 G. O. Sars, the eminent Norwegian planktonologist, observed that the cod had pelagic eggs and larvae. However, it was not until 1879, just a century ago, that Sars published his impressive, milestone epoch-making investigation on the cod fisheries of the Lofoten Islands reporting on the complete life history of the cod, from pelagic eggs and pelagic larvae to juvenile and adult stages.

Sars' work on cod stimulated interest in pelagic fish eggs and larvae, in general, and it was soon found that most of the species of commercial interest had floating eggs and larvae. The initial impetus was in rearing fish eggs and larvae to determine characters that would permit their identification in plankton collections. During the last two decades of the 19th Century prodigious research activity centered in England, Italy and Germany. Notable among the early enthusiastic workers in Great Britain were J. T. Cunningham, E. W. L. Holt, W. C. McIntosh, E. E. Prince, and A. T. Masterman; who worked mainly between 1885 and 1900. Simultaneously in Italy, a triad of scientists were conducting pioneering investigations; C. Emery, L. Facciola, and F. Raffaele, who published in the years between 1878 to 1900. Other early workers of consequence include Alexander Agassiz from the USA and E. Ehrenbaum and Fr. Heinicke in Germany.

The rationale for conducting ichthyoplankton surveys was well-stated by Johan Hjort (Murray and Hjort, 1912) in "The Depth of the Oceans."

> "This power of distinguishing the different species in early stages has been of great advantage to oceanography. By securing the eggs and larvae floating in the surface waters, we can decide what species spawn in a definite area. We capture in our silk nets a profusion of different eggs and larvae, and can with certain limitations separate them as belonging to various species, just as we assort the catches of adult fishes from a haul with the trawl. The spawning area of a species can thus be determined by merely taking numerous tow-nettings and ascertaining the presence or absence of the eggs belonging to the species in question."

In 1900, the Norwegians activated a research vessel, the "Michael Sars," for open sea work; and in 1901, Hjort conducted an ichthyoplankton survey off northern Norway where he succeeded in finding areas of abundant cod spawning. At the time, there was no fishery for cod in the area, but his discovery stimulated a fishery that soon took some millions of cod. Hjort described the research:

> "Stimulated by this experience I advised the International Council for the Study (sic) of the Sea to effect a systematic survey of the spawning areas of the cod family. My proposals were adopted and an

> enormous amount of material relating to the natural history of the cod family was accumulated, thanks to the exertions of those on board the Danish, Belgian, English, Scottish, Dutch, Norwegian, Swedish and German investigation steamers.
>
> "The Danish steamer, "Thor," under the leadership of Schmidt, investigated certain parts of the Atlantic and the waters round Iceland. The Norwegian steamer, "Michael Sars," examined the Norwegian Sea and the northern portion of the North Sea, while the steamers of the other countries worked mainly in the North Sea."

This joint investigation conducted in 1901 was one of ICES earliest undertakings in obtaining a wealth of information about the spawning areas and biology of the various gadoids. More importantly, they stimulated research on ichthyoplankton in a number of countries.

Collections obtained during this cooperative research venture from the Danish research steamer, "Thor," in 1903 and 1904 were to be worked up into classic papers by C. G. J. Petersen and J. Schmidt. Petersen devoted much of his research efforts to obtaining complete life history series of flatfishes, while Schmidt's main early thrust was with gadoid life history series. Between 1905 and 1907, Schmidt published six contributions dealing with gadoid larvae. Altogether, Schmidt described life history series for 17 kinds of gadoids. His contributions are landmarks, that set high standards of quality for establishing and presenting life history series that have challenged all subsequent workers.

Schmidt is perhaps best known for his work locating the breeding ground of the European eel (*Anguilla vulgaris*), by studying the distribution of its leptocephali in the North Atlantic. The eel research furnished impetus for the Dana Round the World Expedition of 1928–30.

Because space limitations do not permit a more extended discussion of the historical background, we have prepared a summary table listing some of the more important contributions to deal with early life history series of marine teleost fishes (Table 1).

PRESENT STATUS

We next wish to address the question — where are we now? Since the end of World War II, we have witnessed major advances in our knowledge of fish eggs and larvae on a worldwide scale and major advances in the quality of the papers being published. Our discipline, on the whole, is in a healthy state.

There are two basic ways to establish life history series of eggs and larvae. One rears eggs and larvae to determine their characters; or one uses ichthyoplankton collections to construct series working backwards from juveniles to larvae and eggs. The rearing approach using eggs and milt of known adults can be carried out most successfully with inshore fishes, or with commercial species that are fished throughout the year. Few of the offshore epipelagic species and none of the mesopelagic or bathypelagic species have been reared from artificially fertilized eggs. Although it is preferable to begin with eggs of known parents, much recent work utilizes live eggs obtained from plankton hauls for rearing. With improvement in rearing techniques, this method has

Table 1. Some of the more important contributions dealing with early life history series of marine teleost fishes (see also Table 2).

Scientist	Date	No. contri-butions	Group dealt with	Source: Field coll.	Source: Rear-ing	Stages: Egg	Stages: Larvae	Stages: Juv. Ad.	Area
Petersen, C. G. J.	1904–09	3	Flatfishes	X	—	—	all	some	E. North Atlantic
Schmidt, J.	1905–07	6	Gadoid	X	—	—	all	some	E. North Atlantic
Schmidt, J.	1908–32	ca. 44	Eels, Mar. teleosts	X	—	—	all	some	N. Atl. — Worldwide
Ehrenbaum, E.	1905–09	book	Mar. teleosts	X	X	some	all	some	E. North Atlantic
Sanzo, L.	1905–40	ca. 65	Mar. teleosts	X	X	some	all	some	Mediterranean
Kyle, H. M.	1913	1	Flatfishes	X	—	—	all	some	Medit. — adj. N. Atl.
Fage, L.	1918	1	Shorefishes	X	—	—	most	some	Medit. — adj. N. Atl.
Tåning, A. V.	1918	1	Myctophids	X	—	—	all	all	Medit. — adj. N. Atl.
Jespersen and Tåning	1919–26	2	Sternoptychids	X	—	some	all	some	Medit. and E. North Atl.
Delsman, H. C.	1921–38	24	Mar. teleosts	X	X	some	most	some	Indo Pacific
Hildebrand and Cable	1930–38	3	Shore-Bay fishes	X	X	most	all	most	W. North Atlantic
D'Ancona et al.	1931–56	4 parts	Mar. teleosts	X	X	many	most	some	Mediterranean
Uchida et al.	1958	1	Mar. teleosts	X	X	some	all	some	Off Japan
Mito, S.	1960–63	12	Pelagic fish eggs	X	X	all	all	–	Off Japan
Castle, P. H. J.	1959 to date	many	Eels	X	X	some	all	some	Off N. Z. -- also worldwide
Dekhnik, T. V.	1973	1	Ichthyoplankton	X	X	most	most	—	Black Sea

proven very useful for constructing life history series. The advantage of rearing is that complete larval series in prime condition can often be obtained and identified as post-larvae or juveniles.

Two technical advances have greatly aided studies of early life history series of fishes. The more important for larval studies are the techniques for clearing and staining specimens in order to follow sequence of ossification as well as to make precise counts of meristic characters. The other involves use of x-rays for making radiographs for determining internal osteological features.

Internal characters that can be studied on cleared and stained specimens are becoming increasingly important in identification of larvae. Among the internal characters are those associated with the vertebral column, with supporting bones for fins, with head bones, etc. For example, the character of pterygiophores and their arrangement in relation to vertebral spines can be quite useful, or the number and arrangement of pre-dorsal bones or the supporting bones for the caudal fin, etc. (Potthoff, 1974; Ahlstrom et al., 1976). One of our contributions introduced the dynamic approach for larval descriptions (Ahlstrom and Ball, 1954). In this approach the sequence of changes occurring during the larval period are treated character by character.

During the present decade we have given seven concentrated courses on the identification of fish eggs and larvae and one of the by-products of this has been the challenge to assemble characters of both adults and larvae that will permit the investigator to assign specimens to order or suborder as the first step in identification. The basic characters that the larval fish taxonomist has to work with are fourfold: (1) body shape (morphometrics); (2) pigment patterns; (3) countable structures (meristics); and (4) characters that are strictly larval. We give meristic characters more emphasis than morphometric because complete counts of fin rays, vertebrae, branchiostegal rays, etc. are usually obtained during the larval period, whereas body shape, while sometimes helpful, can change markedly between the larval and later life stages. Pigment patterns are of most use in distinguishing among species within a genus or between genera within a family, but seldom at higher taxonomic levels. Characters that are exclusively larval can be very useful in identification to the family level and sometimes to genus or species. We have found that the only convenient way of assembling such a mass of data is in tables. A set of such tables was included in our contribution given at the 2nd Ichthyological Congress in Paris (Ahlstrom and Moser, 1976).

For what portion of marine fish do we have early life history series? In "Fishes of the World" Nelson (1976), 450 familes of fishes are recognized. Of these, about 300 families fall into our area of interest; i. e., marine fishes that have pelagic eggs and/or pelagic larvae that can be captured by plankton net.

In our concentrated courses of identification of fish eggs and larvae, we study over 200 life history series representing 100 fish families. The course covers eggs and/or larvae of about 1/3 of the families that comprise the marine fish fauna. Eggs and/or larvae are known for about 110 additional marine families, hence early life history stages are known for over 2/3 of the families. What about the families whose eggs and larvae are not known yet? These are mostly small families, or those with bathypelagic distributions.

POTENTIAL FUTURE DIRECTIONS

The literature provides the basis for identifying the majority of marine fish larvae to family, genus or species, even in previously unsurveyed waters. Nearshore species and speciose tropical faunas have been particularly difficult to identify and are a challenge for the future. Our ability to solve difficult identification problems can be enhanced in several ways — by improving the quality of the specimens, by critically evaluating the characters we now use, and by discovering new characters.

Proper preservation of ichthyoplankton has always been a problem and each of us has had the experience of trying to identify poorly preserved material. The problem is particularly apparent when working with early larval stages and with material collected in the tropics. Research is needed on shipboard handling and preservation techniques, and advances in these areas could improve the effectiveness of ichthyoplankton surveys. Research is also needed in the area of long-term storage of specimens, particularly to solve such problems as fading of pigment characters, leaching of calcium from bony structures, and deterioration of tissues.

Identification of ichthyoplankton could be enhanced by a critical evaluation of the characters that are presently in use. Character variability has rarely been treated adequately and is an area of potentially valuable research. First on the list of variation studies is melanistic pigmentation. We need to know more about variation in number and morphological appearance of melanophores. What is the variability within broods, populations, and species? The shape or form of certain melanophores is often used in descriptions and identifications. How does this vary among individuals, particularly in relation to time of day or depth of capture? Melanophore pattern and number is such an important character for ichthyoplankton identification, especially for embryonic and early larval stages, that we could benefit greatly from research into the nature of these characters. Similarly, more information is needed on variation in morphometric and meristic characters. What are the limits of variability of body measurements and proportions that we use to distinguish species and higher taxa? Variation in countable characters is sometimes well known for juveniles and adults, but is seldom treated in larval descriptions. Do larvae show a greater variability in meristic characters than adults?

The search for new characters is never ending and certainly many remain to be discovered for fish eggs and larvae. Internal characters have received more attention in recent years. Developmental osteology has become a field in its own right and increased knowledge there has helped greatly in solving difficult taxonomic problems. With the advent of cartilage stains, the potential for solving difficult diagnostic problems is expanded further. Internal soft structures, especially those of the digestive tract, offer similar potential for solving special problem identifications or even in routine identification.

The elucidation of fine surface structures by scanning electromicroscopy (SEM) has potential for solving special taxonomic problems. For example, Sumida et al. (1979) used scanning electromicrographs to distinguish differences between chorion structure of *Pleuronichthys* and *Synodus* eggs. These differences were not apparent at lower magnification under a stereomicroscope but, once demonstrated by use of the SEM, they could be seen by careful study under a stereomicroscope. Similar application of the SEM may be useful in determining differences in spination, scale structure, or skin surface pattern of closely related larval species.

As mentioned in the historical review, rearing of fish larvae had a central role in the beginning of ichthyoplankton research. In the past, technical requirements for rearing marine fishes have limited its use in identification of eggs and larvae. Recent advances in the culture of food organisms (e.g., dinoflagellates, rotifers and copepods) and the increased availability of rearing facilities permit more widespread use of this valuable approach. For some difficult taxonomic problems involving large numbers of closely related species, such as in the scorpaenid genus *Sebastes* which contains about 100 species, rearing provides the only hope for differentiating the large residue of unidentified species. In addition to providing larval series preserved in prime condition and at desired ontogenetic stages, rearing offers the opportunity to study the effect of diet and environmental conditions, such as light and temperature, on character variability.

The use of developmental stages to gain insights into systematic relationships and to make phylogenetic inferences has a long history in vertebrate biology. This approach is especially useful when the larval stages have undergone an adaptive radiation that is separate from the juveniles and adults, as in anurans and teleosts. It is clear that for some groups of marine fishes the larval and adult worlds are distinctly separate evolutionary realms and, as a result, a rich array of larval characters may be added to the list of adult characters for systematic analysis.

Bertelsen's (1951) monograph on deep-sea anglerfishes was the first to utilize the characters of larvae in a comprehensive revision of a major group of marine fishes. By using a combination of ontogenetic and adult characters he was able to solve the major problems surrounding sexual dimorphism, species diagnosis, and higher relationships within this confusing group. Other workers have recognized the value of larval characters in elucidating systematic relationships and have used these characters to varying extents in taxonomic papers (Table 2). This approach has been particularly useful in treating myctophiform families, but recent studies on scorpaeniform, pleuronectiform, and perciform families suggest that larval characters may have wide application among higher teleosts.

At present, many ichthyologists recognize the potential for using larval characters in systematic revisions and it has become standard practice to attempt to locate and borrow larval material for such studies. With the growth of ichthyoplankton studies and the increased availability of larval material, we look forward to more frequent inclusion of early life history stages in systematic revisions of fishes.

The use of computers in phylogenetic studies of teleosts is widespread, however, larval characters have not yet been included in these analyses. In groups with highly evolved larval stages it would be interesting to compare the results of numerical analyses run on larvae and adults. The addition of larval characters to those of the adults in cladistic analysis is promising. Another potential use of computers is as a substitute for taxonomic keys. Dichotomous keys are difficult or impossible to construct for larvae since the essence of ontogenetic characters is change. A broad array of characters covering meristics, morphometry, pigmentation, distribution, season of occurrence, and relative abundance could be assembled and programmed to sort an unknown specimen down to the most likely species or group of species.

To conclude, our discipline has a distinguished past, and has become increasingly sophisticated in recent years, but many challenging problems remain for future research.

Table 2. Some contributions in which ontogenetic characters are used to clarify systematic relationships.

Scientists	Date	No. contributions	Group dealt with	Stages: Egg	Stages: Larvae	Stages: Juv. Ad.	Larval characters showing relationships: Among species	Among genera	Among subfam. or families	Among orders
Ege, Vilh.	1931–57	3	Paralepididae	—	+	±	X	X		
Bertelsen, E.	1951	1	Ceratioidei	—	+	+	X	X	X	
Bertelsen and Marshall	1956	1	Miripinnati	—	+	±	X	X	X	
Pertseva-Ostroumova, T. A.	1961	1	Pleuronectidae	+	+	±	X	X		
Pertseva-Ostroumova, T. A.	1965	1	Myctophidae	—	+	—	X	X		
Berry, F.	1964	1	Mar. teleosts	—	+	—				X
Moser and Ahlstrom	1970–74	3	Myctophidae	—	+	±	X	X	X	
Gutherz, E. J.	1970	1	Bothidae	—	+	—		X		
Mead, G. W.	1972	1	Bramidae	—	+	+	X	X		
Ahlstrom, E. H.	1974	1	Sternoptychidae	—	+	±	X	X		
Johnson, R. K.	1974	1	Scopelarchidae	—	+	+	X	X		
Okiyama, M.	1974	1	Myctophiformes	—	+	—		X	X	
Potthoff, T.	1974	1	Scombridae	—	+	+	X			
Richards and Potthoff	1974	1	Scombridae	—	+	±	X			
Aboussouan, A.	1975	1	Carangidae	—	+	—	X	X		
Ahlstrom, Butler and Sumida	1976	1	Stromateoidei	±	+	±	X	X	X	
Ahlstrom, Moser and O'Toole	1976	1	Myctophidae	—	+	+		X		
Bertelsen, Krefft and Marshall	1976	1	Notosudidae	—	+	±	X	X		
Ahlstrom and Moser	1976	1	Mar. teleosts	+	+	+				X
Moser, Ahlstrom and Sandknop	1977	1	Scorpaenidae	—	+	±	X	X	X	
Futch, C. R.	1977	1	Bothidae	—	+	—		X	X	
Powles and Stender	1978	1	Sciaenidae	—	+	±		X		
Richardson, S.	Symp. contri.	1	Cottidae	—	+	+		X		
Okiyama and Ueyanagi	1978	1	Scombridae	—	+	—		X	X	
Kendall, A.	1979	1	Serranidae	—	+	+		X	X	

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