Status of early life history descriptions of marine teleosts

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Abstract.—Use of early life history stages of fish in systematic and ecological studies has increased in recent years. It is now recognized that eggs and larvae present a wide array of characters suitable for systematic analysis that are largely independent of adult characters. Fisheries recruitment studies focus on survival of eggs and larvae as the most important factor influencing variations in population abundance. A requisite to these studies is detailed information on the appearance of fish eggs and larvae in order to identify them in plankton samples. This paper reviews the proportions of fish species for which at least illustrations of eggs and larvae, sufficient to permit their identification in plankton samples, have been published worldwide and by geographic region. Factors which may influence differences in proportion of identifiable eggs and larvae by region are discussed. Factors considered important include species diversity, a history of important commercial fisheries, research emphasis, and interests of individual scientists in various regions. We conclude that although eggs and larvae of most species can now be identified in some regions of the world, there are still gaps in our knowledge that prevent realizing the full potential of ichthyoplankton studies in systematic and fisheries research. Filling these gaps will require continued traditional morphological research as well as application of biochemical genetic and rearing techniques.

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Fish eggs and larvae collected in plankton samples are becoming increasingly important to the study of fisheries, oceanography, and systematics (e.g. Moser et al., 1984; Rothschild, 1986). Accurate identification of early life history stages of fish is a requisite for studies in these fields. Several kinds of publications assist researchers in identifying fish eggs and larvae: 1) some revisions of primarily oceanic groups include descriptions of larvae (e.g. ceratioids [Bertelsen, 1951], bregmacerotids [D'Ancona and Cavinato, 1965], and scopelarchids [Johnson, 1974]); 2) detailed descriptions of the development of a species based on reared or plankton-caught individuals or on a combination of both are common (e.g. Ahlstrom and Ball, 1954; Potthoff et al., 1980; Ditty and Shaw, 1992); and 3) descriptions of several species of a genus or family are also available (e.g. Ahlstrom et al., 1976; Belyanina, 1984; Kendall and Vinter, 1984; Baldwin, 1990).

While these detailed accounts are essential for systematic studies, publications that describe species by geographic region rather than by systematic group are more useful for identification of eggs and larvae from plankton samples. Agassiz (1882), Ehrenbaum (1905, 1909), and D'Ancona et al. (1931–56) are early examples of such publications, and several others have been published recently (e.g. Miller et al., 1979; Auer, 1982; Fahay, 1983; Leis and Rennis, 1983; Wang, 1986; Okiyama, 1988; Leis and Trnski, 1989; Matarese et al., 1989; Olivar and Fortuño, 1991). Besides assisting researchers in identifying fish eggs and larvae in plankton collections, these publications facilitate evaluation of descriptive developmental information available for fishes of a particular region.

In this paper we 1) evaluate the degree to which descriptions of the early life history stages of marine fish are available on the basis of recently published early life history guides, 2) compare our current level of knowledge of fish egg and larva identification by geographic region throughout the world, and 3) discuss potential reasons for regional differences in our level of knowledge.

Methods

We collected information on the status of early life history descriptions primarily from recently published guides on development of fishes in marine waters of seven specific regions of the world (Fig. 1): Northeast Atlantic (Russell, 1976); Northwest Atlantic (Mid-Atlantic Bight) (Fahay, 1983; supplemented by Fahay, 1993); Indo-Pacific (Leis and Rennis, 1983; Leis and Trnski, 1989); Japan (Okiyama, 1988; supplemented by Ozawa, 1986); Antarctica (Kellerman, 1989); Northeast Pacific (Matarese et al., 1989); and Southeast Atlantic (Olivar and Fortuño, 1991). We also used publications that summarized available descriptive early life history information for two additional geographic regions: the Mediterranean Sea (Aboussouan, 1989) and the west central Atlantic (Richards, 1990). Publications summarizing development of fishes in other major geographic regions (e.g. Southeast Pacific) are not available. We compiled data from the published guides as well as from the more recent, but restricted, publications on the basis of the illustrations of eggs and larvae they contained and then compared our results with those of Richards (1985) who summarized early life history information available at that time based on the work of Moser et al. (1984). We employed six early life history stages (egg, yolk sac, preflexion, flexion, postflexion, and transforming) and considered a particular stage of a species as known if an illustration of that stage had been published. The quality of egg and larval illustrations varies, and we subjectively excluded those that we thought would be inadequate for identifying plankton-collected specimens. Since accurate species lists were not always available in the guides, some subjectivity was involved in determining the number of species present in a region. In cases where the geographic regions covered by early life history guides were more restricted than those considered in regional species lists we used the lists found in the guides. Paxton et al. (1989) was also consulted for the number of species in several regions. Although information was available for eggs and juveniles in some regions, data on larvae were generally used for comparisons because they were more widely available.

To assess the impact of particular scientists on the availability of early life history information on fish for a geographic region, we developed a key author index based on references in Moser et al. (1984). Moser et al. (1984) summarized available early life history information for all fishes, so its bibliography provides an indicator of the contributions of individuals up to about 1982. Key authors were identified as having four or more publications describing the early life history of marine fishes, or as having published a regional compilation of early life history information. The key author index was calculated by dividing the number of publications by key authors by the number of species in a region. Since our purpose here was to indicate the relative amount of research on larval fish taxonomy in various regions, the number of publications was tabulated rather than the number of taxa described. To give a historical perspective, this index was calculated separately for papers published before and after 1950; 1950 was chosen arbitrarily but coincides roughly with increased worldwide harvest of fish following World War II (the world fish catch doubled between 1952 and 1965 [Schaefer and Alverson, 1968]). In the Discussion section we also refer to work done before and after 1900 (as did Ahlstrom and Moser [1981]) to highlight the roots of ichthyoplankton research since the International Council for the Exploration of the Sea was founded in 1898 and since it began field work on fish eggs and larvae in 1901.

To investigate the relationship between commercial fishing activity and the status of early life history information on a regional basis, we compiled regional commerical catch data (Fig. 1) for 10-year intervals between 1938 and 1988 (Food and Agriculture Organization [FAO] 1965, 1974, 1979, 1984, 1991, 1992). The first year that such statistics were available was 1938; so compiling data in 10-year increments should document changes in the regional contribution to the world catch which could be related to changes in early life history information. The reported catches include organisms other than marine fish (e.g. molluscs, crustaceans, and seaweeds), but they are a rather uniform fraction of the total catch, and marine fish represent more than 80% of the total catch. Regional catches in 1938 and 1948 were averaged to represent conditions before 1950, and regional catches in 1958, 1968, 1978, and 1988 were averaged to represent conditions after 1950. The three Antarctic regions (48, 58, 88) used by FAO were combined for our analysis. Catches in the Indian Ocean (51, 57), east central Pacific (77), and west central Pacific (71) were combined to be comparable to the Indo-Pacific region considered by Leis and Rennis (1983) and Leis and Trnski (1989), although the FAO areas included temperate waters not included in Leis and Rennis (1983) and Leis and Trnski (1989). Other FAO regions do not correspond exactly to the regions included in early life history guides (Fig. 1), but at the level of resolution used here such differences are probably insignificant.

To indicate families with the greatest need for additional larval fish taxonomic research, we calculated the ratio of the number of species for which larvae had been described over the number of species present by family for the nine geographic regions for which data were available. It was not possible to calculate this ratio with the data in Aboussouan (1989) or Okiyama (1988). Among those above the median of this ratio, up to 10 per region, families in each region for which this ratio was >0.5, were then ranked on the basis of the number of species they contained.

Results

On a worldwide basis, Richards (1985) concluded that 20,423 fish species were included in the material summarized in Moser et al. (1984). Of these species,

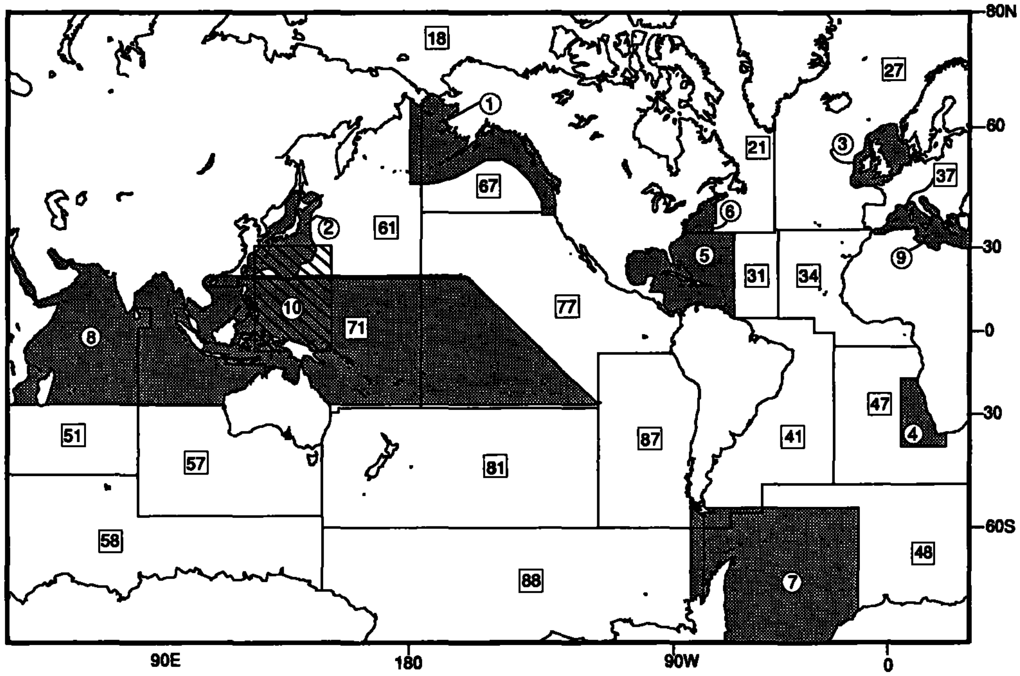

Figure 1

FAO fishing areas (numbers in squares) and areas included in early life history guides (shaded, numbers in circles which are keyed to references in Table 2, except for 10 which refers to Ozawa, 1986). Early life history guides in Indo-Pacific area 8 deal with reef and shore fishes in that area, although oceanic areas are also shaded on the map.

the eggs of 726+ (4%) were known, and larvae of 1,932+ (10%) were known. At a higher taxonomic level, however, larvae of representative species from about two-thirds of the families of marine fishes are known (Ahlstrom and Moser, 1981). Richards (1985) did not subdivide the larval stage as we have (yolk-sac, preflexion, flexion, and postflexion), but most of the illustrations in Moser et al. (1984) are of flexion and postflexion larvae. Although not specifically intended to provide original information for specific identification of fish larvae, Moser et al. (1984) presented many original illustrations.

Regional guides to early life history stages of fishes are now available for nine large areas of the world ocean (Fig. 1). Such guides for both coasts of South America are noticeably lacking, as are guides to most oceanic regions. Some species described in the guides are also found outside the areas specifically covered in these guides; therefore identification of eggs and larvae collected elsewhere is also facilitated by the use of these guides. Some recent guides partially overlap the geographic regions addressed in earlier guides (e.g. Brownell [1979] studied fishes from the Cape of Good Hope, an area that was included in Olivar and Fortuño [1991]; Miller et al. [1979] studied Hawaiian fishes, and their research was included in Leis and Rennis [1983] and Leis and Trnski [1989]; Ozawa [1986] studied oceanic fishes in the areas included in the works of Okiyama [1988], Leis and Rennis [1983], and Leis and Trnski [1989]; and Fritzsche [1978], Hardy [1978, a and b], Johnson [1978], Jones et al. [1978], and Martin and Drewry [1978] studied a portion of the Northwest Atlantic that was included in Fahay [1983]).

We selected the Northeast Pacific as addressed in Matarese et al. (1989) (i.e. the Pacific Ocean and Bering Sea within 200 nautical miles of the coast between lat. 38°N and 66°N and west to long. 180°) for detailed evaluation of the taxonomic composition and available early life history information of the ichthyofauna (Table 1). A total of 627 species of fishes are found in the region, and 592 are thought to spawn in marine waters there (Matarese et al., 1989). These species represent 22 orders and 94 families. The most speciose orders are the Scorpaeniformes (272 species) and Perciformes (140 species). The most speciose families in the Scorpaeniformes are the Cottidae, Cyclopteridae, and Scorpaenidae, and in the Perciformes, the Zoarcidae. While most of the fishes in the Northeast Pacific are oviparous, only about 252 species

(43%) of them are expected to spawn pelagic eggs. Among the Scorpaeniformes, only *Anoplopoma fimbria* is known to have pelagic eggs.

Eggs have been illustrated for only 44 (less than 10%) of the species in the Northeast Pacific, and 8 of these species produce demersal eggs. Eggs are known for 16 of the 31 species of Pleuronectiformes with pelagic eggs (36% of all described eggs). Yolk-sac larvae are known for 90 species of fishes, including 32 species of the viviparous scorpaenid genus *Sebastes* and 18 species of Pleuronectiformes. Preflexion larvae are known for 165 species, flexion larvae for 169 species, postflexion larvae for 217 species, and transforming larvae for 150 species. Some pelagic juveniles are included in the count for transforming larvae, particularly those of the genus *Sebastes*. At least one illustration of an early life history stage is available for 263 species in the Northeast Pacific (44% of the total). To give an indication of the rate of advances in knowledge of the ichthyofauna and its early life history in the Northeast Pacific, since publication of Matarese et al. (1989), one new species has been described (Yabe, 1991), and descriptions of the larvae of seven additional species have become available (Maeda and Amaoka, 1988; Matsui, 1991; Busby and Ambrose, 1993).

The percentage of fishes with descriptive information available on early life history stages varies considerably in various regions of the world (Table 2). Compared with the Northeast Pacific where the eggs of 14% of the species with pelagic eggs are known, only 5% of such species in the western central Atlantic have been identified, whereas the eggs of about 70% of such species are known in the Northeast Atlantic.

Compared with the Northeast Pacific, where the larvae of 44% of the species are known, larvae are known for 34% of the species found in waters around Japan, for 27% of the species in the western central Atlantic, and for only 10% of the species in the Indo-Pacific (Table 2). However, larval illustrations are available for more than half of the species in several geographic regions: Northwest Atlantic, Mediterranean Sea, Southeast Atlantic, Northeast Atlantic, and the Antarctic (Table 2).

Based on early life history guides, the number of species for which early life history information is lacking varies by family and by region (Table 3). Among the families which have larvae described for fewer

Table 1

Taxonomic composition and status of early life history descriptions of northeast Pacific fishes based on Matarese et al. (1989).

Order	Families present	Species present	Number of species illustrated: Eggs	Larval stage: Yolk-sac	Preflexion	Flexion	Postflexion	Transforming	Species with at least one illustration
Notacanthiformes	1	2	0	0	0	0	0	0	0
Anguilliformes	8	10	0	0	2	2	6	0	6
Clupeiformes	2	5	3	2	3	3	3	2	3
Salmoniformes	7	50	6	2	7	6	12	5	12
Stomiiformes	6	23	2	1	4	10	17	9	18
Aulopiformes	7	10	0	1	4	5	7	5	10
Myctophiformes	2	22	0	2	11	10	15	10	15
Gadiformes	5	19	2	5	7	8	10	7	10
Ophidiiformes	3	10	0	0	3	2	2	0	3
Batrachoidiformes	1	1	0	0	0	0	0	0	0
Lophiiformes	2	7	0	0	0	2	2	2	2
Gobiesociformes	1	2	0	1	2	1	1	1	2
Beloniformes	1	1	1	1	1	1	1	1	1
Atheriniformes	1	2	2	0	2	2	2	0	2
Lampriformes	2	2	1	0	2	0	2	1	2
Beryciformes	5	11	0	0	1	1	2	1	2
Zeiformes	1	1	0	0	0	0	0	0	0
Gasterosteiformes	3	4	0	0	1	1	1	1	1
Scorpaeniformes	6	272	4	46	65	68	79	75	103
Perciformes	26	140	6	11	24	24	36	13	42
Pleuronectiformes	3	32	17	18	25	23	18	16	28
Tetraodontiformes	1	1	0	0	1	0	1	1	1
Totals	94	627	44	90	165	169	217	150	263
Percent of total species			7.0	14.4	26.3	27.0	34.6	23.9	41.9

Table 2

Comparison by geographic region of the number of species with egg and larval illustrations available, key author index, and rank of commercial catches.

Geographic region (FAO areas)	Species present	Number illustrated		Percent known		Source	Key author index		Rank of catches	
		Eggs	Larvae	Eggs	Larvae		<1950	>1950	<1950	>1950
Northeast Pacific (1:67)	592		263	14	44	Matarese et al., 1989	0.000	0.039	—[1]	7
Japan (Northwest Pacific) (2:61)	3500		1181		34	Ozawa, 1986; Okiyama, 1988	0.001	0.042	3	1
Northeast Atlantic (3:27)	131	91	108	70	82	Russell, 1976	0.298	0.008	1	3
Southeast Atlantic (4:47)	239	48	141	20	59	Olivar and Fortuño, 1991	0.017	0.050[2]	8	6
Western Central Atlantic (5:31)	1803	97	486	5	27	Richards, 1990	0.003	0.003	5	9
Northwest Atlantic (6:21)	317	135	222	43	71	Fahay, 1993[3]	0.063	0.146	4	5
Antarctic (7:48,58,88)	158		80		51	Kellerman, 1989	0.000	0.044	12	13
Indo-Pacific (8:51, 57, 71, 77)	3921		394		10	Leis and Rennis, 1983; Leis and Trnski, 1989	0.006	0.007	2	2
Mediterranean Sea (9:37)	569		360		63	Aboussouan, 1989	0.111	0.035	6	10
World	20423	726	1932	4	10	Richards, 1985				

[1] North Pacific not divided into east and west regions.
[2] Olivar and coauthors have published at least nine descriptive papers since 1986 (see Olivar and Fortuño, 1991) that if included here would raise the value to 0.088.
[3] M. P. Fahay (NOAA, Sandy Hook Laboratory, Highlands, NJ 07732, pers. comm. Sept. 1993) indicated that data for the New Jersey area reported here are representative of the Northwest Atlantic.

than half of the species present in several regions are Scorpaenidae, Macrouridae, and Bothidae. Besides these widely distributed families, large proportions of species of families with more restricted ranges are undescribed as larvae, such as the Cottidae in the Northeast Pacific. More species in oceanic families are poorly known as larvae than are indicated in Table 3, because only Ozawa (1986) deals exclusively with that fauna.

Discussion

Factors contributing to variations in the amount of early life history information available among geographic regions include the history of fisheries in the region, the presence of key researchers, and the taxonomic diversity and scientific interest in each region.

History of the fisheries

Generally the geographic regions where larvae of the majority of species are known have had long histories of important fisheries. Studies on fish eggs and larvae were pioneered in the late 1800's by countries that engaged in the fisheries of the Northeast Atlantic (see Hempel, 1979; Ahlstrom and Moser, 1981). Work before 1900 consisted mainly of basic biological studies, sampling eggs and larvae at sea, and rearing eggs and yolk-sac larvae following artificial fertilization for release at sea. Similar studies were initiated concurrently off the east coast of North America. Although during this period the identity of the eggs and larvae of many species was established and knowledge of oceanography of the regions was expanded greatly, these early studies resulted in ill-fated mass releases of young larvae reared in hatcheries on both sides of the North Atlantic (Shelbourne, 1965).

From 1900 to 1950, most early life history studies were conducted on North Atlantic fishes, expanding beyond descriptive work, rearing experiments, and release of young larvae (see Ahlstrom and Moser, 1981). The amount of such research was related to harvest by region. Based on catches in 1938 and 1948,

Table 3

Ranks, by numbers of species, of families with more than half of the species having undescribed larvae, by region.

	Reference and region											
	(Olivar and Fortuño, 1991)	(Leis and Rennis, 1983)	(Leis and Trnski, 1989)	(Fahay, 1993)	(Russell, 1976)	(Kellerman, 1989)	(Richards, 1990)	(Matarese et al., 1989)	(Ozawa, 1986)			
	Southeast Atlantic	Indo-Pacific Reef	Indo-Pacific Shore	Northwest Atlantic	Northeast Atlantic	Antarctic	Western Central Atlantic	Northeast Pacific	Oceanic West Pacific	Number of times mentioned	Avg. rank	Number of times mentioned *(10–rank)
Families with >50% of species with undescribed larvae in at least two regions												
Scorpaenidae	5	4		1			9	4		5	4.6	27
Macrouridae	1					3	7	6		4	4.3	23
Bothidae			2				6		2	3	3.3	20
Gobiidae		1					1			2	1.0	18
Cyclopteridae						1		2		2	1.5	17
Myctophidae						2			1	2	1.5	17
Sciaenidae			3				3			2	3.0	14
Blenniidae	4	3								2	3.5	13
Serranidae		6					2			2	4.0	12
Cynoglossidae			6	2						2	4.0	12
Ophidiidae	7						4	9		3	6.7	10
Gonostomatidae								8	3	2	5.5	9
Mugilidae			10		2					2	6.0	8
Engraulidae			4				10			2	7.0	6
Apogonidae	10	5								2	7.5	5
Chaetodontidae		10		10						2	10.0	0
Families with >50% of species with undescribed larvae in only one region, followed by ranks in parentheses												
	Centrolophidae (2)	Labridae (2)	Soleidae (1)	Balistidae (3)	Triglidae (1)		Labrisomidae (5)	Cottidae (1)	Melanostomiidae (4)			
	Sparidae (3)	Pomacentridae (7)	Carangidae (5)	Gerreidae (4)			Chaenopsidae (8)	Zoarcidae (3)				
	Gobiesocidae (6)	Callionymidae (8)	Clupeidae (7)	Tetraodontidae (5)				Stichaeidae (5)				
	Moridae (8)	Lutjanidae (9)	Hemiramphidae (8)	Syngnathidae (6)				Pholidae (7)				
	Argentinidae (9)		Opisthognathidae (9)	Echeneidae (7)				Alepocephalidae (10)				
				Ostraciidae (8)								
				Diodontidae (9)								

the total world catch of all marine species at this time was less than 200 million metric tons (t). Among regions, the Northeast Atlantic ranked first in catches, followed by the western central Pacific, the Northwest Pacific, the Northwest Atlantic, and the western central Atlantic, which together accounted for over 75% of the total catch (Table 2). With the goal of understanding stock fluctuations of Northeast Atlantic fishes, ichthyoplankton studies were conducted largely under the auspices of the International Council for the Exploration of the Sea and this effort is reflected in the state of knowledge for that region. About the same time, similar research was beginning in the Northwest Atlantic. Equally productive research, following work that began in the late 1800's, was being conducted on fishes of the Mediterranean Sea. Early life history studies were also emerging in Japan (where local fisheries have always been vital) with ichthyoplankton surveys beginning in 1938. Work that included descriptions of fish eggs and larvae was also being conducted in India. The western central Pacific and Atlantic contributed significantly to the world catch, and in spite of the immense numbers of species in these regions, progress was made in describing larval fishes there. Larvae of many groups of oceanic fishes were described based largely on collections of the worldwide Dana expeditions and published as Dana Reports. This work resulted partially from interest in the far-reaching early life history of freshwater eels, *Anguilla* spp., which were important to the economy of northern Europe.

Since 1950, early life history knowledge has increased significantly in several regions and is still roughly in proportion to the activity of the fisheries in the regions and countries involved. The total world catch during this period increased to over 800 million t, and the Northwest Pacific replaced the Northeast Atlantic as the most productive region (Table 2). The Southeast Pacific moved from a rank of 11 to 4 among the 14 regions. Earlier, the North Pacific was not divided into east and west portions, but since 1950 the Northeast Pacific was ranked 7, although the catch here was only 15% of that in the Northwest Pacific. Since 1950, Russian scientists have documented early life histories of a wide variety of fishes worldwide as a result of the activity of their distant-water fishing and research fleets. During this time, many fish eggs and larvae from the Northwest Pacific, particularly from waters around Japan, were described. Larvae of most of the fishes of the depauperate Antarctic fauna have been identified as a result of scientific interest and developing international fisheries in the region, although the catches in this region are still insignificant when compared with other regions. Ichthyoplankton studies in the Northeast Pacific initially concentrated on a few commercially important species (e.g. *Sardinops sagax*, *Scomber japonicus*, and *Hippoglossus stenolepis*). The creation of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) in 1947, which targeted research on the Pacific sardine, *Sardinops sagax*, was an important step for egg and larval identification in the California Current region of the Northeast Pacific. Although only 3% of marine species worldwide are expected to spawn in the Northeast Pacific, some species there are very abundant and support large commercial fisheries. Except for the speciose genus *Sebastes*, early life history stages of most commercially important fishes in the region are now well known. Recent catches in the Southeast Pacific ranked fourth among FAO regions worldwide; however, little early life history work has been conducted in this region and larvae of most fishes remain undescribed.

Key researchers

Our use of the bibliography in Moser et al. (1984) to develop a key author index means that some important scientists may not have been included. However, based on the key author index we developed, the contributions of authors who produced multiple descriptions of eggs and larvae of marine fishes have influenced the early life history knowledge of particular geographic regions in terms of the proportion of species whose larvae are known. The key author index for papers produced prior to 1950 is highest (>0.06) in regions where the percent larvae known is also highest (Table 2): Northeast Atlantic (82%), Northwest Atlantic (71%), and Mediterranean (63%). Researchers on eggs and larvae before 1950 in the Northeast Atlantic included Ehrenbaum, Holt, McIntosh, Schmidt, and Petersen (Table 4). In the Northwest Atlantic, early researchers included Agassiz, Breder, Kuntz, and Hildebrand. The Mediterranean has a long history of early life history research where eight key authors including D'Ancona, Padoa, Sanzo, and Sparta were identified for publications before 1950.

Since 1950, the only region with a key author index >0.05 is the Northwest Atlantic, although the index may be inflated because the number of species in the region is probably underestimated. Active researchers in the Northwest Atlantic since 1950 include Eldred, Evseenko, Houde, Leiby, and Smith (Table 4). Other regions where key authors have made notable contributions since 1950 are Japan, the Southeast Atlantic, Northeast Pacific, and the Antarctic. The relatively high taxonomic diversity of

Table 4

Senior authors of four or more publications with original early life history descriptions, or of regional compilations of early life history descriptions based on citations in Moser et al. (1984).

Region	Senior author	Total no. papers	<1950	>1950
Oceanic and >1 region	Belyanina, T. N.	7		7
	Bertelsen, E.	13		13
	Castle, P. H. J.	6		6
	Dekhnik, T. V.	4		4
	Efremenko, V. N.	4		4
	Ege, V.	5	2	3
	Gorbunova, N. N.	7		7
	Pertseva-Ostroumova, T. A.	11		11
	Rass, T. S.	4	1	3
Totals		61	3	58
Mediterranean	Bertolini, F.	2	2	
	D'Ancona, U.	8	7	1
	Fage, L.	2	2	
	Padoa, E.	12	1	11
	Raffaele, F.	1	1	
	Roule, L.	2	2	
	Sanzo, L.	29	28	1
	Sparta, A.	27	20	7
Totals		83	63	20
Number of species		569		
Key author index		0.146	0.111	0.035
Percent larvae known		63		
NE Atlantic	Clark, R. S.	2	2	
	Cunningham, J. T.	3	3	
	Ehrenbaum, E.	5	5	
	Holt, E. W. L.	4	4	
	Lebour, M. V.	3	3	
	McIntosh, W. C.	4	4	
	Petersen, C. G. J.	6	6	
	Russell, F. S.	1		1
	Schmidt, J.	12	12	
Totals		40	39	1
Number of species		131		
Key author index		0.305	0.298	0.008
Percent larvae known		82		
NW Atlantic	Agassiz, A.	2	2	
	Breder, C. M., Jr.	7	6	1
	Dannevig, A.	1	1	
	Eldred, B.	6		6
	Evseenko, S. A.	5		5
	Fahay, M. P.	3		3
	Hildebrand, S. F.	3	3	
	Houde, E. D.	7		7
	Kuntz, A.	4	4	
	Leiby, M. M.	6		6
	Smith, D. G.	9		9
Totals		53	16	37
Number of species		317		
Key author index		0.167	0.050	0.117
Percent larvae known		64		
NE Pacific	Ahlstrom, E. H.	8		8
	Moser, H. G.	8		8
	Richardson, S. L.	7		7
Totals		23	0	23
Number of species		592		
Key author index		0.039	0.000	0.039
Percent larvae known		44		
Japan	Amaoka, K.	10		10
	Dotsu, Y.	11		11
	Fugita, S.	14		14
	Kobayashi, K.	7		7
	Minami, T.	5		5
	Mito, S.	20		20
	Okiyama, M.	18		18
	Shiogaki, M.	13		13
	Suzuki, K.	9		9
	Takita, T.	7		7
	Uchida, K.	4	2	2
	Yusa, T.	9		9
Totals		127	2	125
Number of species		3,500		
Key author index		0.036	0.001	0.036
Percent larvae known		37		
Indo-Pacific	Delsman, H. C.	22	22	
	Fourmanoir, P.	5		5
	Jones, S.	9	2	7
	Leis, J. M.	7		7
	Miller, J. M.	2		2
	Robertson, D. A.	6		6
Totals		51	24	27
Number of species		3,921		
Key author index		0.013	0.006	0.007
Percent larvae known		10		
WC Atlantic	Beebe, W.	5	5	
	Richards, W. J.	5		5
Totals		10	5	5
Number of species		1,803		
Key author index		0.006	0.003	0.003
Percent larvae known		27		
SE Atlantic	Aboussouan, A.	11		11
	Brownell, C. L.	1		1
	Gilchrist, J. D. F.	4	4	
Totals		16	4	12
Number of species		239		
Key author index		0.067	0.017	0.050
Percent larvae known		59		
SW Atlantic	de Ciechomski, J. D.	8		8
Antarctic	Yefremenko, V. N.	7		7
Number of species		158		
Key author index		0.044	0.000	0.044
Percent larvae known		51		

fishes in Japanese waters accounts for its low key author index (0.036), but the Japanese probably have been the most prolific scientists working on early life history descriptions since 1950; 125 papers by Japanese key authors were cited in Moser et al. (1984). Even so, Leis (1985) has indicated that the bibliography of Moser et al. (1984) underrepresents the contributions of Japanese scientists. Two early standouts among the Japanese were Uchida and Mito, but recent work by Dotsu, Yusa, Amaoka, Okiyama, Ozawa and Fujita has significantly increased the knowledge of the region. Relatively low taxonomic diversity and an abundance of recent work by Olivar, among others, published since 1986 contributes to a rather high (0.088) key author index for the Southeast Atlantic. In the California Current region the CalCOFI program stimulated early life history descriptions that resulted in many publications by Ahlstrom and Moser (1981) and their coauthors. The Russians, as a result of the activity of their far-reaching fishing efforts since 1950, have contributed to a more complete understanding of early life history of eggs and larvae in several regions through the work of key authors such as Belyanina, Deknik, Gorbunova, and Rass. Also, several Russians, such as Pertseva-Ostroumova as well as non-Russians such as Bertlesen, Castle, and Ege have published papers on early life histories of oceanic groups.

A graph of the cumulative key author index plotted against the percent of the number of species occurring in various regions whose larvae are known, indicates that in all regions where >60% of the larvae are known, the key author index is >0.1 (Fig. 2). Regions with low key author indices (Japan, western central Atlantic, and Indo-Pacific) also have low percentages of known larvae (<40%). However, these regions also have large numbers of species present (Table 2).

Scientific interest and taxonomic diversity

Richards (1985) points out that early life histories of commercially important groups (e.g. herrings, salmons [salmonids], tunas, flatfishes [pleuronectiforms], and cods) have been the subject of a disproportionately greater number of studies and are thus better known than groups that are not the objects of large commercial fisheries. Significant interest in the systematics of particular taxa (e.g. cods in the Northeast Pacific) or the recruitment of particular species (e.g. *Gadus morhua*, *Theragra chalcogramma*, *Clupea harengus*, and *Scomber scombrus*) can lead to increased knowledge of the general early

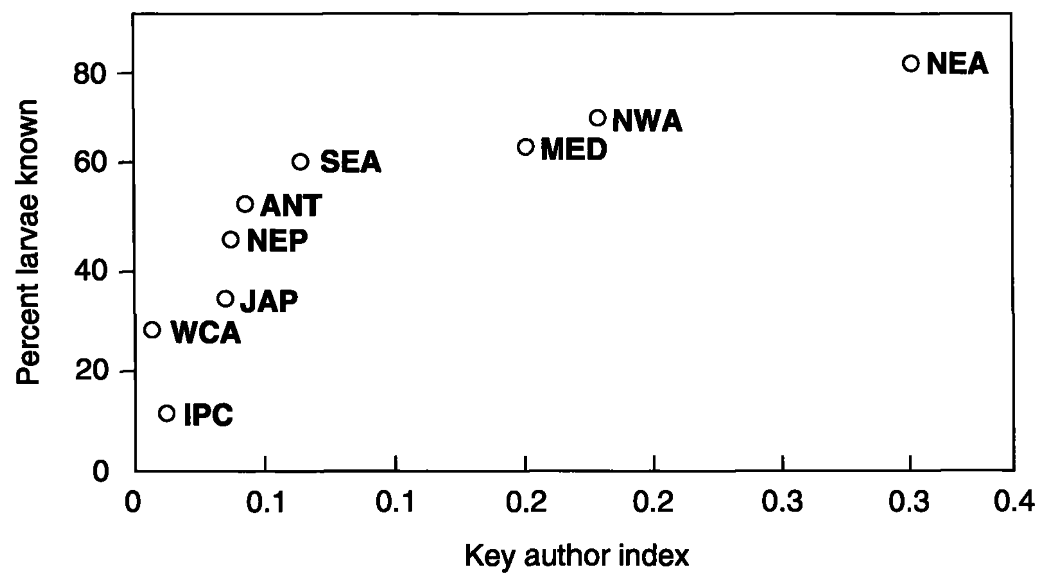

Figure 2

Key author index (see text) plotted against percent of species in geographic regions where larvae are known. ANT=Antarctic; IPC=Indo-Pacific; JAP=Japan; MED=Mediterranean; NEA=Northeast Atlantic; NWA=Northwest Atlantic; NEP=Northeast Pacific; SEA=Southeast Atlantic; WCA=western central Atlantic.

life history of fishes for a region.

The taxonomic diversity of Indo-Pacific coral reefs and Japanese waters is much greater than that found at higher latitudes, resulting in lower proportions of species with identified larvae in these and other low-latitude regions. Speciose perciform families present at lower latitudes contribute to the difficulty of identifying larvae in these regions. In other regions, taxonomic groups that have undergone extensive radiation complicate identification of larvae. For example, about 70 species of *Sebastes* are present in the Northeast Pacific and they cannot be identified routinely in plankton samples (Matarese et al., 1989). The larvae of some closely related taxa in commercially important groups in other regions have proven very difficult to identify (e.g. tunas [scombrids], some herrings [clupeids], and North Atlantic cods [gadids]).

Conclusions

In spite of the relatively large proportions of fishes in some regions for which some early life history stages have been illustrated, identification problems still limit the usefulness of ichthyoplankton studies. For example, in the Northeast Pacific where identification is possible only to family or genus for several groups (e.g. *Sebastes* spp., cottids, agonids, and stichaeids), more descriptive work remains to be done. It is ironic that some groups containing some of the world's most important fisheries (e.g. tunas, cods, and herrings) also pose some of the more difficult problems regarding egg and larval identification. Research involving field studies of fish eggs and larvae in several parts of the world is now concentrating on recruitment dynamics of commercially important species, whose early stages are well described.

Two of the goals of the Ahlstrom Symposium held in 1983 were to accumulate information on fish development by taxa, and thus stimulate additional research on poorly known groups, and to highlight the potential usefulness of developmental information in systematic studies. Since the volume based on the Ahlstrom Symposium was published (Moser et al., 1984), many important original descriptive papers have appeared (e.g. Ditty, 1989; Fahay, 1992), but it does not seem that there has been a significant increase in the number of larvae known. Rather than an increase in original descriptions, the late 1980's saw the publication of several regional guides to fish early life history (see Table 2). While some recent systematic studies have considered larval as well as adult characters (e.g. Cohen, 1989; Baldwin, 1990; Baldwin and Johnson, 1993; Strauss, 1993), there are still unresolved theoretical problems with this approach. Some ichthyologists still do not want to deal with those "unidentifiable pinheads" (Winterbottom, 1986), and rigorous analysis of developmental, in addition to adult, characters can be a daunting task. According to Johnson (1993): "Almost 10 years after its [i.e. Moser et al., 1984] publication the historical separation between studies of early life history stages and 'mainstream' systematic ichthyology appears only slightly diminished. Most comparative osteological and phylogenetic studies of fishes do not incorporate development and thus ignore the potential for additional suites of characters and for testing homology."

A combination of rearing studies and developing series from plankton samples as well as more innovative techniques such as biochemical genetics (Seeb and Kendall, 1991) will be required to fill the gaps in our knowledge on the identification of early developmental stages of marine fishes. Although the value of egg and larval studies are recognized in fisheries science, their usefulness will probably remain limited without the continued efforts of scientists who often describe early life stages as ancillary but enjoyable endeavors.

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