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LARVAL FISH ASSEMBLAGES AND OCEANIC BOUNDARIES

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Knowledge of ichthyoplankton assemblages has its origins in the fisheries research and oceanographic expeditions of the late nineteenth century. Early ichthyoplankton studies focused on the geography and timing of spawning and the survival of the young of commercially important species, while the collections of far ranging oceanographic expeditions provided a global view of ichthyoplankton diversity and distribution patterns. The utility of ichthyoplankton approaches in fisheries research has increased in response to an increasing need for fishery-independent stock assessment, the subject of the companion symposium in this volume. With fisheries science now moving beyond single-species concepts, ichthyoplankton research has a key role in our understanding of the ecology and evolution of fish faunas and their constituent populations. The need to focus on ichthyoplankton assemblages as an integral part of their environment is central to this understanding and is the basis for this symposium.

One objective of the symposium is to review what is known about the composition and structure of larval fish assemblages in the world ocean and present the results of current research on these assemblages. The focus here is on larvae rather than total ichthyoplankton since fish eggs still are poorly known and incompletely identified in most ichthyoplankton collections. Also, many species have demersal or internally brooded eggs though their planktonic larvae are prominent members of ichthyoplankton assemblages. Taxonomic competence has advanced sufficiently over the past several decades to permit identification (at least to family) of most larvae taken in plankton survey tows (Fahay, 1983; Leis and Rennis, 1983; Leis and Trnski, 1989; Matarese et al., 1989; Miller et al., 1979; Moser et al., 1984; Jones et al., 1978, and subsequent volumes in the series; Okiyama, 1988; Olivar and Fortuño, 1991; Richards, 1985; Russell, 1976). The diversity encountered in ichthyoplankton samples places a premium on accurate identification of fish eggs and larvae. Progress in both fisheries and ecological applications of ichthyoplankton research is as dependent on advances in taxonomic competence as it is on sampling and analytical innovation.

Another central issue of the symposium is the relation of larval fish assemblages to the environment. Ichthyoplankton and associated hydrographic data accumulated over the past several decades provide a basis for addressing some fundamental questions. How are fish distributions delimited by hydrography? Does the limitation occur during early ontogeny, during the adult stage, or both? If both, what are the relative contributions of larval and adult stages? Are larval fish assemblages primarily a consequence of adult distributions or are they distinct evolutionary phenomena? Is there adaptive commonality or complementarity among component taxa of an assemblage? What can we say about the fine scale horizontal and vertical structure of assemblages and what is the relation of this structure to physico-chemical boundaries? What role do the latter play in the formation and maintenance of larval fish assemblages?

Knowledge of the physiological characteristics and energetic requirements of fish larvae is basic to the investigation of these questions. Over the past several decades, such information has accrued steadily from field and laboratory studies. Often, important advances were presented in the series of international early life history symposia which began at Lake Arrowhead, California in 1963 (Lasker, 1965). The contribution of Houde and Zastrow, the lead paper in this symposium, represents such an advance. Here, for the first time, growth, mortality, metabolic rates, stage durations, and growth and assimilation efficiencies of marine and freshwater fish larvae are summarized by ecosystem and ordinal taxonomic category. Ecosystem- and taxon-specific energy budgets derived from these calculations form the basis for an initial estimation and discussion of broad scale trophic requirements of fish larvae and lay a foundation for the papers that follow.

The papers are arranged regionally, beginning with the Central Pacific and Indo-Pacific, followed sequentially by the Antarctic, South Atlantic, western North Atlantic region, and North Pacific. Boehlert and Mundy begin this section with a survey of larval fish assemblages associated with seamounts and oceanic islands, primarily drawing from their studies in the central Pacific. They found little evidence that ichthyoplankton assemblages at seamounts differ from the background field despite the presence of physical mechanisms proposed in the literature to retain planktonic larvae at such features. This is in contrast to distinct nearshore, neritic, and oceanic assemblages described for islands. Boehlert and Mundy's discussion of mechanisms that may maintain assemblages at islands (e.g., boundary layers, small scale frontal dynamics, tidal currents, and topographically produced eddies) points to future research paths.

Some of these issues are addressed in the paper by Leis on larval fish assemblages associated with Indo-Pacific coral reefs. An important finding was that larval fish assemblages associated with coral reefs have distinct spatial structure that varies vertically and horizontally. Vertical patterns result from larval behavior and break down at night. Horizontal patterns are dependent on habitat and topography with most variation in the on/offshore dimension. Leis found that the decline in abundance of shorefish larvae with increasing distance from the reef varied markedly among taxa. This points to the importance of larval behavior in determining assemblage composition and structure, as does the fact that habitat changes, particularly those in close proximity to the reef, can result in striking changes in assemblages.

The paper by Kingsford further emphasizes the potential role of behavior of early life-history stages and environmental structure as a determinant of assemblage pattern. The recent work of the author and others suggests that the spatial scale of abiotic and biotic structures in the pelagic environment may range more than a thousandfold and that survival of larval and juvenile fishes of a wide array of taxa may depend on associations with these structures. Moreover, the effect of these structures may be accentuated by their accumulation at fronts. The author documents potential associations of 72 fish families with large pelagic structures (drift algae, gelatinous zooplankton, flotsam) and discusses the role that small scale structure (e.g., cell aggregations, marine snow) may play in modifying the trophic environment and affecting survival of fish larvae.

In our view, future investigations of the role of structure in the pelagic environment and its relation to the early stages of fishes must ultimately address the more general subject of zooplankton contagion and the adaptations that larval fish have evolved to find and exploit food patches resulting from contagious distribution. These structures, essentially invisible to net sampling, must play a key role in early survival since integrated measures of larval fish prey from net samples indicate that average concentrations are typically below the minimum threshold for first-feeding larval fishes.

The summary of Antarctic larval fish assemblages by Loeb, Kellerman, North, White, and Koubbi is comprehensive and timely. The endemic and specialized Antarctic fauna is highly vulnerable to exploitation and habitat degradation and many species have experienced dramatic declines over the recent past. The shorefish fauna is dominated by demersal or benthopelagic notothenioids whose early life histories are characterized by large egg size, morphologically advanced hatchlings, and an extended pelagic pre-settlement phase. Bounded by the Antarctic Polar Front, the Southern Ocean is a habitat dominated by strong currents and gyres, complex topography (basins, ridges, islands, and ice shelves), and a highly seasonal production cycle that is closely linked with a distinct seasonal hatching sequence for components of the ichthyofauna. Initial analyses of Antarctic and Sub-Antarctic larval fish assemblages indicate a finely tuned and highly integrated system reflective of a unique evolutionary history and a complex and demanding environment.

Olivar and Shelton describe the larval fish assemblages of the Benguela Current region of South Africa and Namibia. Like other eastern boundary current systems, it is driven by a cold subpolar current, experiences strong coastal upwelling and high seasonal productivity, and is a region of striking oceanographic complexity where vastly different fish faunas merge at water mass boundaries. Another feature shared with other eastern boundary regions is a highly productive fishery dominated by resident species (or populations) of *Sardinops, Engraulis, Trachurus,* and *Merluccius.* Variations in the upwelling regime strongly affect (and may control) assemblage composition and the abundance of component taxa.

The papers on the western North Atlantic region describe the composition and dynamics of larval fish assemblages on a wide range of scales. The paper by Richards, McGowan, Leming, Lamkin, and Kelley provides a fine scale view of assemblages across regions of the Loop Current, the dominant hydrographic feature of the Gulf of Mexico. The assemblages are strikingly diverse, reflective of extensive tropical oceanic and mesopelagic elements augmented by a highly diverse tropical shelf fauna at the Loop Current front. Principal components analysis revealed distinct assemblages on the oceanic and shelf sides of the front and demonstrated the role of the front in delimiting assemblage boundaries. Although no distinct frontal assemblage was apparent, larvae of scombrids and carangids were closely associated with the front (usually the oceanic side) and frontal mixing and dynamics may be important in their distribution and survival.

Govoni describes the distributions of larva assemblage indicator species at the Mississippi River plume front and Gulf Stream front off the South Atlantic Bight (SAB) in relation to hydrographic features, and postulates physical mechanisms that may result in flux of larvae across fronts. The early life histories of gulf and Atlantic menhaden (*Brevoortia patronus, B. tyrannus*) and spot (*Leiostomus xanthurus*) are closely tied to these frontal regions. Their larvae are concentrated in these regions by entrainment through frontal convergence and possibly by migration and selective spawning behavior of the adults. Presumably elevated productivity associated with frontal dynamics (e.g., upwelling, shear) provides a propitious trophic environment, while larvae are confined within the appropriate water mass by frontal boundaries. Shelf-break fronts contribute to the complexity of both of these frontal systems. Displacement of larger larvae to nursery areas requires flux across frontal boundaries and the author explores the potential means by which advection may occur. Dynamic processes (e.g., filament, eddy, meander formation) in conjunction with specific behavior patterns may be involved in translocation of larvae, although evidence for these or other mechanisms has yet to be revealed.

The processes are further addressed by Cowen, Hare, and Fahey in relation to larval fish assemblages of the New York Bight. They described five distinct assemblages whose membership and boundaries varied over the summer. Assemblages of the New York Bight and the Middle Atlantic Bight (MAB) are a mixture of year-round resident species and species from the south, derived either from northward migration of spawners or from larvae advected northward from the SAB. The authors propose that larvae spawned in the SAB and entrained along the inner boundary of the Gulf Stream may be translocated shoreward by a combination of dynamic processes (e.g., warm-core rings spun off the Gulf Stream, mesoscale eddies associated with the shelf/slope front, sub-surface intrusions of slope water associated with the pycnocline). They present evidence that stage-specific behavior may play an important part in shoreward movement of larvae. Some species migrate downward to the zone of cross-shelf intrusion and others may actively migrate shoreward after reaching an advanced larval stage.

Doyle, Morse, and Kendall describe and compare the larval fish assemblages off the northeastern and northwestern coasts of the U.S.A. in an effort to identify mechanisms involved in the evolution of these assemblages. Description of the east coast assemblages is based on MARMAP, a comprehensive fishery ecosystem study that occupied nearly 11,000 ichthyoplankton/oceanographic stations between Cape Hatteras and Nova Scotia from 1977 to 1987. West coast assemblages are described from a series of 10 ichthyoplankton surveys conducted off the coasts of Washington, Oregon, and Northern California from 1980 to 1987. Georges Bank and the Gulf of Maine have distinct assemblages that are contained within semi-isolated circulation systems. Shelf and Slope/Oceanic assemblages of the MAB result from interaction between seasonal cycles (temperature, production, and spawning) and the complex MAB recirculation system. In contrast, assemblages off the west coast have evolved in relation to two dominant environmental features, the California Current and its associated seasonal upwelling cycle. Spawning of taxa that contribute to shelf and slope assemblages appears to be correlated more closely with the onshore/offshore shift in Ekman transport than with production cycles.

Moser and Smith described the larval fish assemblages of the California Current region based on the 30-year time series of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and show how vertical and horizontal distributions of component taxa change across a front. Three major assemblages (Northern Complex, Southern Complex, and Southern Coastal Complex) are apparent from analyses based on occurrence and abundance of larvae. Groups within the Northern and Southern Complexes are closely associated with the distinct water masses of the region (Subarctic, Transitional, Eastern Tropical Pacific, Central). The CalCOFI station grid is adequate to define assemblage distributions; however, identification of variables that may be important in delimiting assemblage boundaries requires fine scale horizontal and vertical sampling. Moser and Smith report the results of a cruise conducted off Ensenada, Mexico, where a semi-permanent front separates cold eutrophic water to the north from warm oligotrophic water to the south. The study demonstrated the transition from Subarctic-Transitional to Eastern Tropical Pacific fauna and showed a marked change in vertical distributions for taxa occurring on both sides of the front. The authors suggest that this shift in vertical distribution may be related to trophic conditions and larval feeding behavior, factors which also may play key roles in the evolution of larval fish assemblages.

McGowen's study on nearshore larval fish assemblages of the Southern California Bight (SCB) identified six assemblages that were related to seasonality and cross-shelf distribution. The major assemblages were a winter-spring shelf, a summer shelf, and an offshore assemblage that was similar to the principal assemblage of Moser and Smith's Northern Complex. Longshore variation in assemblage structure was not evident in the SCB; however, there was some evidence that semi-isolated habitats off rocky headlands may have assemblages that are distinct from those of the open coast. Life-history strategies of SCB taxa are characterized by mechanisms which retain larvae near shore; however, recruitment of some populations of shorefish taxa larvae are dependent on larvae entering the SCB gyre (Southern California Eddy).

These symposium contributions have accomplished the primary goal of bringing together and summarizing what is known about larval fish assemblages. The 12 papers reveal a large and growing information base for most regions of the world ocean and indicate that we can begin to address some fundamental questions pertaining to larval fish assemblages. The basis for the taxonomic composition of larval fish assemblages is one such issue and it is clear that adult distributions and spawning seasonality are principal causal factors. It is also apparent that these are not the only causal factors since most assemblages include taxa that are geographically and/or temporally separated from adult spawners. Just as the basis for assemblages is heterogeneous, so is spatial distribution among assemblage members. Our appreciation of fine scale horizontal and vertical pattern within assemblages has grown considerably with the advent of discrete multiple samplers; however, this field of study is just beginning and it is obvious that much more emphasis must be placed here if we are to progress in our understanding of assemblage dynamics.

The taxa that make up these assemblages of larvae are characterized by a great diversity of size, stage duration, morphology, and pigmentation. A reasonable assumption is that these reflect: 1) an equally great diversity of adaptations for survival in the planktonic environment and 2) on a larger scale, a diverse constellation of successful early life-history strategies. In contrast, Houde and Zastrow show a general homogeneity in temperature-adjusted rates for growth, ingestion, mortalilty, and metabolism across broad taxonomic categories and ecosystems. Moreover, these authors indicate that the most striking difference found in their survey—the lower metabolic and mortality rates of freshwater larvae—can be ascribed to greater weight at hatching compared with marine larvae. We suggest that these findings and those of other symposium contributors point to the importance of behavior in concert with morphological and pigment specializations as prime factors in adaptation and survival of larvae.

We can hope that information on rates and energetics of the great mesopelagic and oceanic larval fish assemblages can be added to that amassed and synthesized by Houde and Zastrow. Likewise, we must increase our knowledge of vital rates and processes of later life-history stages. Ichthyoplankton surveys have been used widely to estimate fish biomass because they are a comprehensive and relatively inexpensive fishery-independent method. The accuracy and precision of these estimates depends on the competency of the plankton work and on the state of knowledge of the reproductive biology and demography of the subject populations. Reproductive and demographic information is scanty for all but a few fish species and this precludes the application of ichthyoplankton methods to multi-species fishery management problems, as well as to ecological and community research. For some species, such as the northern anchovy (*Engraulis mordax*) and the herring (*Clupea harengus*), we can estimate fairly accurately the juvenile and adult biomass represented by a planktonic egg or larva (Lasker, 1985; Heath, this volume). Much research effort is needed if we are to extend this competence beyond a few high profile coastal species. We are just beginning to appreciate the diversity of reproductive and demographic patterns of mesopelagic (e.g., Childress et al., 1980; Gjøsaeter and Kawaguchi, 1980; Miya and Nemoto, 1991) and oceanic fishes (e.g., Davis et al., 1991; Jenkins et al., 1991; Richards, 1991). Small additions to our knowledge of reproduction and demography of these faunas will immediately increase the usefulness of ichthyoplankton surveys and set us on the road toward multispecies and ecosystem studies.

The relation of larval fish assemblages to hydrography was treated extensively in this symposium and it is clear that fronts and other dynamic features as well as water-mass properties play important roles in the regulation of assemblages and, ultimately, in the regulation of parent fish populations. Just as was suggested for the study of pattern within assemblages, advances in our knowledge of assemblages at their boundaries will require fine scale, three-dimensional collection of fish larvae and the principal elements of their biotic and abiotic environment. Many of the contributions indicated strong interplay between frontal features and larvae of coastal fish populations. Frontal systems, especially those that include currents, are characterized by elevated productivity and by an array of dynamic features with potential for advection and translocation of early life-history stages. The role of such systems in the generation of assemblages may be as important as their role in maintaining assemblage boundaries.

A final consideration is whether larval fish assemblages have an intrinsic adaptive function as has been suggested by Frank and Leggett (1983). Are larval fish assemblages, each derived from highly diverse phylogenetic lineages and adult habitats, anything more than the result of convergent evolution of life-history strategies? Detection of an intrinsic adaptive function for these assemblages is daunting, given our limited understanding of structure and process in pelagic communities, in general. Multispecies approaches to the study of fish populations are just emerging, as are comprehensive studies of plankton communities; larval fish assemblages are subsets of these. Doyle et al. (this volume) note McGowan and Miller's (1980) emphasis on the relative rarity of fish larvae compared with other plankters and aptly suggest that, "It may be necessary to focus on the zooplankton assemblage in its entirety . . . to understand fully the multispecies spatial patterns that prevail among larval fishes." Extending this further, we suggest that it is necessary to consider the abundance of later ontogenetic stages of species that make up a larval fish assemblage. The impact of planktivorous juveniles and adults of the major larval fish groups (coastal pelagic, oceanic, and mesopelagic species) on the biomass and species structure of zooplankton populations may be far greater than what can be inferred from numerical dominance of major crustacean groups over larval fishes. The point is that population regulation may occur over all scales and ontogenetic stages and one could not expect to gain insight into the dynamics of larval fish assemblages without making progress in understanding the systems in which they are embedded. In this context larval fish assemblages may be opportune windows into the communities to which they contribute.

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