REEF FISHES AT SEA: OCEAN CURRENTS AND THE ADVECTION OF LARVAE

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ABSTRACT

This paper presents an overview of an interdisciplinary study of the kinematics and dynamics of reef fish larvae in offshore currents, especially mesoscale quasigeostrophic eddies. We develop herein the conceptual framework and background information for our on-going studies, the preliminary results of which will be presented at the 1983 ASZ meetings. The focus of this research has been to define the appropriate scales in ocean circulation relative to the developmental biology and reproductive ecology of coastal marine fishes whose larvae are planktonic.

INTRODUCTION

Interest in the topic of larval dispersal by ocean currents has been longstanding and its broad implications to ecology, evolution and fisheries are well known. Yet, the factors that ultimately limit the distribution of oceanic planktonic organisms have not been clearly specified (Wiebe 1976). The constraints upon the transport of planktonic larvae along coasts and across oceans are few. Only the direction and velocity of the prevailing currents, the timing of reproduction, and the length of the planktonic stage place limits upon where, when and how far species are transported (Scheltema 1972, 1977). One critical variable in the survival of certain shore-dwelling species may be the phase and quantity of larvae of one species relative to the phasing and quantity of another in contest for spaces sporadically open to occupancy (Sale 1977, 1978).

Determining the fate of fish larvae as plankton in open ocean currents is not just interesting with regard to the life cycle of fishes. It is also crucial to the resolution of key ecological hypotheses concerning species distributions and diversity in reef and shore communities (Helfman 1978, McFarland 1982). Furthermore, resolution of these important questions leads directly into a discussion about the evolutionary strategies of island species, one notable feature of which is the origin and maintenance of endemic species. Other aspects of this work are basic to applied fisheries and the development of effective fisheries management plans, since a majority of food, game and aquarium fishes possess planktonic larvae and/or may seek larval fishes as food (e.g., Huntsman at &J. 1982).

The following discussion highlights the key questions and outlines significant results and references pertaining to the study of planktonic larvae of coastal marine fishes.

An overall approach for the study of physical oceanic processes affecting ichthyoplankton distributions ideally would include: 1) mapping current patterns and confirming the appropriate scales of variability, 2) strategic sampling of plankton in and out of specified currents, 3) relating the time scales of current variability to the duration of pelagic lifespans of larvae by aging techniques (especially otolith ring counts), 4) monitoring spawning and recruitment of shore fishes in relation to the dynamics of the offshore current field. Some other aspects for such an interdisciplinary study also have been discussed by Richards (1982).

OCEAN EDDIES AND PLANKTON

Mesoscale eddies, in general, are the features of ocean circulation which most likely entrain planktonic organisms, thereby affecting their transport (Wiebe et al. 1976, Cox and Wiebe 1979, Angel and Fasham, 1983). In particular, recent findings on the variable nature of ocean circulation around islands and along coasts (for review see Chopra 1973, Hogg et al. 1978) and the increasing understanding of eddy entrainment and advective processes provide a potential solution to the anomolous spawning seasons of tropical marine fishes at some locations. The variable occurrence of mesoscale ocean eddies (on the order of monthly and perhaps seasonal periods) and the peak reproductive season of coastal marine animals (with planktonic larvae) may be synoptic. We are studying such a case in the Hawaiian Islands.

We will discuss the potential role of eddies in marine biology as a general phenomenon. Among the specific details yet to be carefully considered are any potential differences that may exist according to the type of eddy involved (Angel and Fashman 1983). Two types of eddies are known: warm-core or anticyclonic eddies and cold-core or cyclonic eddies. In the northern hemisphere anticyclonic eddies rotate clockwise and cyclonic eddies rotate counterclockwise. Eddies develop by a variety of physical mechanisms including wake phenomena in the lee of islands and by extreme meanders of a strong stream current. Whether or not the way in which an eddy is generated has a subsequent impact on its biological function is unknown. Robinson (1983) recently has compiled a comprehensive review of the role of eddies in marine science.

A more general physical feature relating to the distribution of pelagic fishes and ichthyoplankton are thermal fronts. Thermal fronts are sharp gradients of temperature with distance. The expression of fronts can result from several sources, including the edges of eddies, upwellings, current shears, convergence and divergence zones, jet streams and, vertically, at the thermocline. To what degree pelagic larvae of shore fishes are able to select locations within currents by temperature or other cues is unknown. The overall correlation of fish distributions across fronts in general has yet to be determined. The possibility also exists that various fronts may differ in some physical way that is detectable by fishes but which we have not yet recognized. There are, however, good examples of the distribution of myctophid fishes consistent with thermal patterns across fronts and eddies (Brandt 1981, 1983; Brandt and Wadley 1981). Myctophids are mesopelagic fishes whose entire lifespans are spent in the open sea.

It is not our intent here to review past works on plankton communities. The open ocean dynamics of plankton migrations and global distributions are well known and have been extensively discussed by others (e.g., Reid et al. 1978, Wiebe et al. 1976, Cox and Wiebe 1979, Wiebe and Boyd 1978, Boyd et al. 1978). Among the remaining questions is how the physical dynamics interact with the biological dynamics (e.g., reproductive patterns, swimming and energetic abilities of the plankton,etc.) to form and maintain a "patch" (Haury et al. 1978). Evidence for the role of ocean eddies in trapping planktonic organisms can be obtained by sampling zooplankton densities inside and outside of eddies. In the few cases where such discrete sampling has been done, the general result has shown higher abundances of zooplankton in eddies than in surrounding waters (Uda 1957, Uda and Ishino 1958, Wiebe et al. 1976, Ortner et al. 1978). Other planktonic populations can become trapped inside eddies and transported out of the species' normal range as the eddies move (Wiebe et al. 1976, Ortner et al. 1978, Boyd et al. 1978, Wiebe and Boyd 1979, Cox and Wiebe 1979). Loeb (1979) presented data on larvae and mesopelagic fishes which accumulate inside the North Pacific Gyre (also, Reid et al. 1978).

REEF FISHES SPAWNING STRATEGIES

The longstanding belief that tropical marine animals spawn continuously throughout the year without seasonal variation no longer appears generally valid. Distinct peaks of reproduction have now been documented for marine fishes in several tropical localities (Munro et al. 1973, Watson and Leis 1974, Johannes 1978, Lobel 1978, Nzioka 1979). In the absence of strong and recognizable seasonal fluctuations characteristic of the temperate latitudes, annual periods of peak reproduction by tropical coastal marine species are difficult to explain.

We have collected data and examined evidence which suggests that seasonal reproduction by certain tropical species may be in phase with variable offshore quasigeostrophic mesoscale circulation. This circulation is a major environmental factor determining the fate of the planktonic larvae of coastal species. The model species is one which lives its adult life in coastal marine habitats but whose larvae are planktonic in offshore waters. This is typical for a majority of reef fishes. Such species may spawn seasonally in response to natural selection acting on the survival of planktonic offspring. These offspring float with ocean currents which advect and disperse them.

Past emphasis has been on the idea that widespread transport of planktonic larvae across long distances is an evolutionary adaptation reducing the susceptibility of a population or lineage to extinction by local catastrophes (Vermeij 1978). The ecology of some shore fishes, however, suggests the possibility that transport of offspring far from the site of origin or native habitat may not always be favored by Natural Selection. The "lottery" hypothesis, described by Sale (1977, 1978; 1982), is based on experimental field evidence showing that the availability of living sites limits the numbers of pomacentrid fishes and that similar species utilize the same kind of space. Priority of arrival as recruits, rather than subtle differences in ecological requirements or competitive abilities as adults, appears to determine which species occupy each site (Sale 1978). Thus, Natural Selection should favor those individuals of a species who maximize the return of their offspring to home reefs. Sale's lottery hypothesis has stirred considerable debate (Smith 1978, Dale 1978, Anderson et al. 1981). It is clear that the resolution of whether to accept or reject it as a viable hypothesis lies, in part, in determining the fate of the planktonic larvae in the ocean currents (Helfman 1978, McFarland 1982).

Even though an extensive literature deals with the genetics and evolutionary consequences of dispersing offspring (Gadgil 1971), little strategic sampling has been done to ascertain the frequence of dispersal in natural animal populations in general, and in marine populations in particular (Leis 1983). Recent advances in knowledge of the ocean circulation make this just now a feasible scientific undertaking.

The Hawaiian fauna has a high percentage of endemic species, emphasizing that many species have clearly delineated and limited distributions. Conversely, the life history strategy of some species may be to colonize distant habitats. A mechanism whereby such larvae are transported en masse would increase the chance of successful colonization elsewhere. Hawaiian eddies appear to remain stationary near the islands up until several months and then, perhaps, to move off into the open ocean. Thus, eddy mechanisms could be responsible for transporting fish larvae through the open ocean as well as maintaining populations near shore. Any feature of the ocean circulation which would accumulate larvae is likely to accumulate other planktonic particles also. Larvae in eddies are transported in microcosm ecological communities (Wiebe et al. 1976, Wiebe 1976, Ortner et al. 1978). The duration of existence and extent of movements of eddies are important factors determining whether or not eddies function to retain plankton near islands or to transport plankton away. An especially important relationship which needs to be examined is the comparative lifetimes of mesoscale eddies and the planktonic phase of shore fishes.

FISH LARVAE IN EDDIES

We have investigated whether or not offshore ocean eddies near Hawaii play a key role in the life cycle of coastal marine species by functioning to retain planktonic larvae near the islands until such larvae metamorphosize and return to inshore habitats. In general, the peak period of eddy formation and movement appears to coincide with the peak season of reproduction by Hawaiian shore fishes. In the following sections we will develop the ideas, discuss the mechanisms related to the prototype model, and present relevant biological and physical evidence. We will present preliminary results of our field investigations at the December 1983 meeting of the ASZ.

The possibility that ocean eddies near islands might function as reservoirs for planktonic larvae of coastal species was indicated early by Boden (1952). He commented that animals in Bermuda breed during months when wind driven circulation is at a minimum. At this time, a convergence between warm and cold water currents occur, and anticyclonic eddies form. Boden discovered that plankton accumulated in this region of the convergence. Emery (1972) reported a similar situation for the island of Barbados, West Indies, and provided evidence for the existence of eddies in the island's lee. Planktonic larvae in these eddies ostensibly avoid being swept away from the island (Emery 1972). Eddies discovered in Hawaiian waters have been similarly implicated by Jones (1968). Evidence for the function of eddies in preventing loss of larvae from Hawaiian waters and maintaining fish larvae of the family Acanthuridae near shores was later obtained by Sale (1970). He presented data suggesting that the surface eddies were effective in trapping planktonic larvae which then were revolved past the island of Oahu (about 25 to 50km from shore) every five to six days (see also Leis and Miller 1976). A key feature of the Hawaiian eddies is that some remain in the vicinity of the islands for at least 65 days, (Patzert 1967, Lobel and Robinson, in prep.), which is sufficient time for development of some larvae into a stage capable of migrating back to the inshore habitat (eg., Acanthurus triostegus sandvicensus, Randall, 1961; Chaetodon milaris, Ralston 1976).

The biological importance of retaining planktonic eggs and larvae near shore to the maintenance of island populations is obvious. However, the behavioral and physical mechanisms by which planktonic larval fishes return have not been elucidated and the potential role of eddies has not been widely recognized.

It is well known, for example, that the larvae of fishes which dominate Hawaiian inshore habitats (e.g., labrids, scarids, acanthurids, and chaetodontids) are nearly absent from inshore waters, but instead are found offshore many kilometers away (Miller 1973). Many Hawaiian fishes display a collective spawning peak in the spring (Watson and Leis 1974, Lobel 1978). Watson and Leis (1974) suggested that the spring spawning peak was an adaptation to local currents. A general shift in the prevailing large scale currents around the Hawaiian Islands occurs in late spring and again in the fall (Barkley et al. 1964). Watson and Leis (1974) proposed "These shifts, which should be associated with weaker currents, occur with spring and fall spawning peaks. Synchronization of spawning with periods of reduced current flow would allow development and metamorphosis of the pelagic larvae before they were swept out to sea" (see also Johannes 1978). Additional evidence suggests that it is not the shifts in prevailing currents, per se, but the offshore eddies and other variable mesoscale currents which form during those times which may be the important factor involved (Lobel 1978).

We have suggested a relationship between the occurrence of ocean eddies and the distribution and abundance of coastal marine larvae. If this relationship is approximately true, then we expect the following, given two alternative environmental circumstances:

I. If ocean eddies or other currents acting to reduce dispersal are predictable in time and space and meet other basic criteria (i.e., the eddies persist at least 2.5 months and remain near islands) then:

   A. Spawning of coastal marine species with planktonic larvae is expected to be synoptic with the time that eddies are most probably present.

   B. Recruitment of pre-juveniles to the reef also will be concurrent with eddies in time and space.

II. If eddies occur but are unpredictable, dissolve sooner than 2.5 months, or move far away, then:

A. Spawning will be independent of eddy occurrence.

B. Recruitment probably will be greatest when eddies occur near shore but also will be unpredictable.

The complex process of offshore transport and return of larvae to coasts involves quasi-continuous exchange of recently spawned eggs being swept offshore and older larvae being brought back. Ocean currents affecting the transportation of larvae must not only bring fish to hospitable coasts but also must do so within time scales appropriate to larval developmental periods. Larvae must not merely be brought back nearshore but must be returned at a time when they can undergo metamorphosis and settle onto reefs. Among the significant questions remaining are: What is the mechanism by which larvae return to coastal habitats? Are pre- juveniles (post-larvae) able to "home-in" on some cue and actively swim some distance from sea to shore or is passive drift the sole mechanism?

A CONCEPTUAL MODEL FOR THE EFFECT OF MESOSCALE OCEAN CURRENTS ON THE LIFE CYCLE OF REEF FISHES

Our research to date has led us to formulate a working conceptual model for the processes discussed above. In summary, reproduction and recruitment of coastal fishes occurs to some degree all year but with peaks during the spring-summer months in Hawaii, with a phase lag of a few months between first reproduction and first recruitment. The offshore currents are variable in both space and time (fairly rapid to quasi-steady), and typically consist of one or more eddies and/or fronts and currents. These mesoscale features will, in certain places, make contact with sections of coasts on islands in the Hawaiian Archipelago. This creates locations where offshore water is swept onto the reef and locations where water is swept off. Thus, reef habitats may be either near the source of steady incoming offshore water or be situated further down stream along the same path. While an eddy is quasistationary in adjacent offshore waters, all nearby coastal currents are dominated by the eddy flow field, and drifting particles are likely to be entrained. At other places or times, the mesoscale features are absent, the currents are weak and simple tidal oscillations occur (except during episodes of occasional oceanic events, e.g., storms, tsunamis, errant eddies, etc.). Under these conditions, oceanic and coastal waters mix mainly in regions of flood divergence and ebb convergence flows associated with tidal processes. The overall picture will change with time and location especially when a large eddy is present and moves along or away from the coast. An eddy is expected to act as a major entrapment and near-island retention mechanism. Thus, depending on the location of a reef relative to offshore mesoscale features the larvae produced by the residing fauna may be swept over stretches of reef before moving offshore, move quickly offshore, or be trapped nearshore. Once offshore larvae may be carried out to sea and lost or trapped in an eddy which, if it remains near an island, will enable larvae to return to suitable adult habitats. Recruitment may depend, in part, on those mesoscale eddies and currents bringing larvae near to shore. If the seasonality of such currents is predictable in time and space, then potential exists for species to adapt by developing a peak in reproduction at times when the offshore mesoscale field most favors nearshore retention of larvae.

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