AN APPROACH TO RECRUITMENT RESEARCH IN INSULAR ECOSYSTEMS

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ABSTRACT: Population maintenance of species with pelagic larvae in island systems is poorly understood, but general agreement has emerged in recent years that processes in the plankton are responsible for recruitment variability. An initial, multi-disciplinary approach is suggested to examine questions of population maintenance with special attention to retention of larval forms around islands. Intensive but directed studies of physical and biological oceanography in waters surrounding an island and studies of fish populations, including recruitment patterns on the island, are proposed. A rationale is developed for the initial study to be conducted at an isolated, oceanic island to simplify the survey work and interpretation of results. Such a study could lead to new insights on the planktonic processes which affect recruitment variablity and would be invaluable to the design of similar studies in more complicated archipelagic or tropical coastal systems.

1. INTRODUCTION

Marine organisms which inhabit isolated islands or seamounts are faced with limited adult habitat and with ocean currents which advect larvae away from the source population; some species have probably developed mechanisms for population maintenance, but these remain largely unknown at the present time. Thus the problems of recruitment of island and seamount resources differ significantly from those of species associated with continental shelf and slope regions, regardless if in boreal, temperate, or tropical regions. In this paper I consider some of the questions which must be addressed if we are to better understand the process of recruitment in island and seamount ecosystems.

The vast majority of tropical marine species, particularly those of commercial importance, are characterized by a life history with a pelagic larval stage. While early studies typically suggested that these stages were adaptive for dispersal (Ekman,1953), an alternate view was developed by Johannes (1978), who argued that pelagic larvae were an adaptation to minimize predation of the vulnerable larval stages. Still, other scientists hold to the concept that dispersal remains the selective advantage of a pelagic stage (Barlow, 1981).

To understand recruitment in insular ecosystems, the above issue is important but the fact remains that pelagic larvae must return to replenish the source population. Several early studies of reef fish ecology held that space, rather than recruitment, was the limiting factor to these populations (Smith and Tyler 1972, 1975), inferring that a large pool of potential recruits could fill space on the reef at any time. If this were indeed the case, fishery exploitation of a given population size could possibly be maintained at a higher level than if recruitment were variable and the limiting factor. Unfortunately, more detailed study has shown that recruitment is highly variable within species. On a short time scale, Victor (1982) has shown sporadic recruitment despite continuous spawning in the labrid Thalassoma bifasciatum. Other studies have further demonstrated that recruitment is one of the most important factors in the population dynamics of reef fishes (Doherty, 1983; Williams, 1983; Sale and Douglas 1984). The temporal component of recruitment variability is probably the most important, with interannual differences of at least an order of magnitude (Shulman 1985). Spatial variations, at least on the scales examined, would appear to be less important. Similar recruitment patterns may occur over scales of 1 km (Shulman, 1985) to 50 km, the latter apparently after mixing of cohorts in the plankton (Victor, 1984). Eckert (1984), however, noted little similarity in spatial recruitment patterns in a series of reefs in the Great Barrier Reef system, and Sale et al. (1984) suggested that spatial variability on this scale is as important as variability in year class strength. The question of spatial variations and its relationship with temporal variability needs more work.

Since the source of variability in recruitment occurs in the planktonic stage (Victor, 1983; Warner, 1984) this is an important place to begin investigations. The important processes to address initially must be whether variability in recruitment is under physical or biotic control. If the pelagic larval stage is an adaptation to reduce predation as suggested by Johannes (1978), then biotic effects in the planktonic environment may not result in a strong component of interannual variability. Planktonic prey of fish larvae may be enhanced on the mesoscale by the "island mass effect" (Gilmartin and Relevante, 1974) and the associated higher standing stocks of plankton near islands (Jones, 1962). Physical factors, on the other hand, may play a more important role in recruitment variability. Physical oceanography around islands is complex and variable (Barkley, 1972; Hogg et al., 1978; Pingree and Maddock, 1980, 1985) and advection likely plays the dominant role in variability in recruitment strength in tropical island species. In the life history, biotic factors may play the dominant role after settlement.

2. MECHANISMS OF POPULATION MAINTENANCE

The physical mechanisms important in larval retention around islands, banks, or seamounts have been discussed by Bakun (this volume) and I will not elaborate on them here. The physical processes alone, however, are not likely to result in retention of larvae; related biological processes, such as temporal spawning activity by adults and behavioral attributes of the planktonic stages, doubtless interact with the physical mechanisms to result in retention and ultimate recruitment (Lobel and Robinson, 1983). While flow patterns may result in significant aggregation of planktonic organisms under certain situations (Hamner and Hauri, 1981), insular holoplanktonic assemblages distinct from oceanic assemblages occur around islands and patterns of convergences may maintain such populations (Boden, 1952). Peterson et al. (1979) described a similar mechanism for maintenance of a copepod population in an upwelling area, but invoked a behavioral mechanism to explain differential utilization of current patterns. Larvae are capable of significant behavioral responses to physical factors which may result in alterations in the distribution pattern (Boehlert and Mundy, 1986).

Eddies and gyres which form around islands and seamounts may act to trap waters for significant periods of time (Pingree and Maddock, 1980; Wolanski et al. 1984). Sale (1970), Emery (1972), and Shomura and Barkley (1979) suggested that such eddies were important in retaining planktonic stages. Further conceptual development of this idea has been provided by Lobel and Robinson (1983); data supporting the role of eddies in population maintenance exist for the continental shelf off Norway (Sundby, 1984), Rockall Bank (Dooley, 1984), and George's Bank (Smith and Morse, 1985). Understanding the physical and temporal attributes of such eddies will be necessary to show their importance in a recruitment mechanism.

3. CURRENT RESEARCH APPROACHES

The study of recruitment has historically taken indirect approaches which look at the final result, including age distributions, year class strengths, and, in the case of reef fishes, temporal and spatial recruitment patterns, looking at the results of the process of recruitment rather than the mechanism. Many of the recent studies outlined above demonstrate significant temporal variability in recruitment, including interannual variability, despite a relatively stable spawning stock. The work of Victor (1983, 1984), in particular, points to processes in the plankton which determine the timing and strength of recruitment in tropical systems (Warner, 1984). The northern anchovy in the California Current system was studied for many years as part of the CalCOFI program and this historical data base on larval distribution and abundance has been critical to further work; the greatest advances in understanding causes of recruitment success or failure, however, have been made in the last decade by determining the role of physical (storms, turbulence) and biotic (prey microdistribution) factors (Lasker 1975, 1978) and their effects on mortality in the field. This approach has allowed generalities to be drawn about similar ecosystems (Bakun, 1985). A comparative approach could also be profitable in tropical systems.

Much of the research on recruitment in tropical fishes has addressed the issue of the high diversity of reef fishes (Sale, 1982), but recent studies on recruitment have directed more researchers to look to processes in the plankton as determinants of recruitment (Helfman, 1978; Doherty et al. 1985; McFarland and Ogden, 1985). Studies on the reef have documented spawning activity and recruitment patterns, but little research has been done on the intervening pelagic stage (McFarland and Ogden, 1985). Still, research on the growth patterns of recruits has resulted in a greater understanding of the timing and variability of recruitment. Use of daily growth increments on new recruits and the ability to detect "recruitment marks" on older ones (Ralston, 1975; Brothers and McFarland 1979) has led to inferences regarding age at recruitment for many species (Brothers and Thresher, 1985; Brothers et al. 1983). Application of this technique to a single species has shown a high degree of spatial coherence in recruitment pattern over a scale of 50 km in the Caribbean (Victor, 1984); this study was significant in that the ages within groups recruiting at the same time were mixed, suggesting that cohorts spawned at different times were mixed in the plankton. These studies are important and allow us to draw inferences about processes occurring in the planktonic environment.

There have been fewer studies in the pelagic environment in tropical ecosystems which relate to recruitment. Distributional studies have typically lacked the detailed physical measurements necessary to understand the meaning of observed patterns. Several intriguing results nonetheless exist. Miller (1974), for example, noted differences in abundance of fish larvae upstream, downstream, and in the reef waters of Molokini, a small islet near Maui in Hawaii; larval fish in reef waters and downstream were typically smaller than in upstream waters, but were 26 and 4 times as abundant, respectively. It is known that areas of stagnant water may be held in the lee of islands in response to a current (Pingree and Maddock, 1980; Wolanski et al. 1984) and that zooplankton may swarm or form aggregations in such locations (Hamner and Hauri, 1981). An interesting point of Miller's study, however, was that densities of passively transported tunicate eggs did not differ among the three areas, suggesting that larval behavior was an important feature of the observed distributional patterns. Other studies in Hawaii have documented differences in distributional patterns among different groups of ichthyoplankton (Leis and Miller, 1976; Leis 1982b); Leis (1982a) has also used eggs and larvae of nearshore species as tracers of coastal water but later suggested that "the assumption that larvae of reef fishes are passive particles to be treated as conservative properties of water parcels is unjustified without much more information than is currently available on larval behavior" (Leis and Goldman,1984). While these studies provide intriguing results, they lack the concurrent physical data necessary for firm interpretation. More recent studies on small reefs within the Great Barrier Reef have included physical measurements (Leis and Goldman, 1983, 1984; Williams et al. 1984).

4. AN APPROACH TO UNDERSTANDING INSULAR RECRUITMENT MECHANISMS

Components of a fairly comprehensive program addressing insular recruitment in the Caribbean were discussed in Richards (1982) and included studies of physical oceanography, larval distribution, planktology, primary productivity, and fisheries data analysis. In this paper I recommend a more modest approach for an initial but intensive study. If we agree that processes in the plankton are the major source of variability in recruitment, then we narrow the primary sources of this variability to either physical (advection) or biotic (predation, prey availability) factors (Hunter,1976). While the biotic factors doubtless play a role, study of predation- or starvation-induced mortalities may be premature in tropical ecosystems, mainly because our understanding of distributional patterns is somewhat rudimentary and abundances of shore-fish larvae are quite low (Leis and Miller, 1976). Reef fishes typically have extended spawning seasons and apparently use a planktonic stage to reduce predation on the reef (Johannes, 1978; Thresher and Brothers, 1985); also, species with planktonic eggs may spawn in a manner which minimizes temporal and spatial overlap with predators (Frank and Leggett, 1985). Although predation may be an important source of interannual variability in mortality of larval stages, it will be difficult to study without knowledge of distribution. Advection and other physical factors may initially be a more tractable problem for study and clearly play an important role in recruitment variability in tropical island ecosystems. While not intensively studying prey and predator distribution, an initial study of advection, distribution, and retention mechanisms would provide preliminary distributional data which could later be used to design studies of prey microscale distribution (Owen, 1981) or predation and starvation (Hewitt et al. 1985).

Another way to simplify an initial tropical recruitment experiment would be to conduct the work around an isolated, oceanic island. This provides two advantages. First, the complexities in physical oceanography inherent in archipelagic systems, including eddies and downstream effects, will be minimized (Barkley, 1972). Secondly, it avoids the problem of an unknown source population. Early larvae and the vast majority of recruits of shore fishes captured near an isolated oceanic island were likely spawned there. Shore-based studies of recruitment (Victor, 1982, 1984; McFarland et al. 1985; Shulman, 1985) have typically not addressed the problem of the source of recruits. With a pelagic duration of 20-50 days (Brothers and Thresher, 1985), recruits could come from a wide geographic area. Remaining in an isolated system for an initial experiment thus has the advantage of providing a better understanding of the primary mechanisms involved in larval retention and recruitment which may then be applied to more complicated systems; it also will address the question of locally recruiting populations proposed by Bakun (this volume). Another advantage is that the populations may be unexploited and thus population characteristics such as age distribution and natural mortality can be determined from sampling and age analysis.

The proposed study would involve physical and biological components. The physical oceanographic component would involve primarily measurements of mesoscale phenomena, first looking at the general geostrophic flow component and its variability and studying the effects of the island on flow, including both local and downstream effects. Specifically, the physical retention mechanisms considered in Bakun (this volume) must be evaluated to assess their ability to retain larvae and juveniles in the region of the island. In the initial, intensive studies, special consideration should be given to developing simpler means of determining flow patterns, including use of XBT data, perhaps in conjunction with objective analysis models (Mooers and Robinson, 1984), should they prove reliable in waters around islands. Special attention should also be paid to remote sensing methods. Surface thermal images in the tropics may not be of great value, but ocean color analysis can be used to detect variations in chlorophyll which might be related to island effects (Dandonneau and Charpy, 1985). Similarly, satellite altimetry could potentially be used for detection of eddies or current patterns and may facilitate subsequent detection of the appropriate signals.

The biological program in offshore waters will be primarily shipboard sampling and should concentrate on local island species. Sampling for variability in abundance and microdistribution of prey, primary productivity, and other trophic factors would be minimized in this initial study. Patterns of chlorophyll distribution, however, should be taken to ground-truth remote sensing proposed for the physical component. Initially, a large scale spatial study of larval and juvenile fish distribution will be necessary, including upstream/downstream sampling and intensive sampling in the island wake region and nearshore waters. As an example, preliminary data on horizontal ichthyoplankton abundance around Johnston Island (Figure 1) demonstrate that larval abundance in downstream waters may be several times higher than in upstream waters; the increases are explained by increases of shore-fish larvae as opposed to midwater or noninsular forms. Unfortunately, concurrent physical data are unavailable from this study to test the retention mechanisms proposed by Bakun (this volume). Limited sampling should also be conducted in the shallows or lagoon waters, but these have not typically been shown to be important nurseries for most species (Leis, 1981; Leis and Goldman 1983). The ichthyoplankton sampling should be conducted with high resolution in the vertical plane, with concurrent sampling of physical factors (depth, temperature, salinity) as is done with the MOCNESS or BIONESS nets. Scoping studies should be done to determine the depths of residence of shore fish larvae and these depths should be studied intensively to minimize the needed sampling; typically, the upper mixed layer is where the majority of shore fish larvae will be found in tropical systems, as shown for waters off Hawaii (Figure 2). Studies of the relationship of larval distribution to physical and diel factors can then be used to infer behavioral patterns and their role in the physical retention mechanisms.

Larger volume sampling techniques, particularly midwater trawls, should be used to define the horizontal patterns of larger larvae and transformed juveniles which are rare or undersampled by the plankton gear; to maximize the use of shiptime, large nets as described in Pearcy (1980) which are semi-quantitative and have uniform mesh, should be used. Such large sampling gear was used by Sale (1970), who observed overall densities of juvenile convict surgeonfish, _Acanthurus triostegus_, of 0.0017 per 1000 m^3. Although these densities are low, such nets may sample 100 m^3 per second when towed at 2 kt and thus detect areas of moderate density with reasonable sampling times.

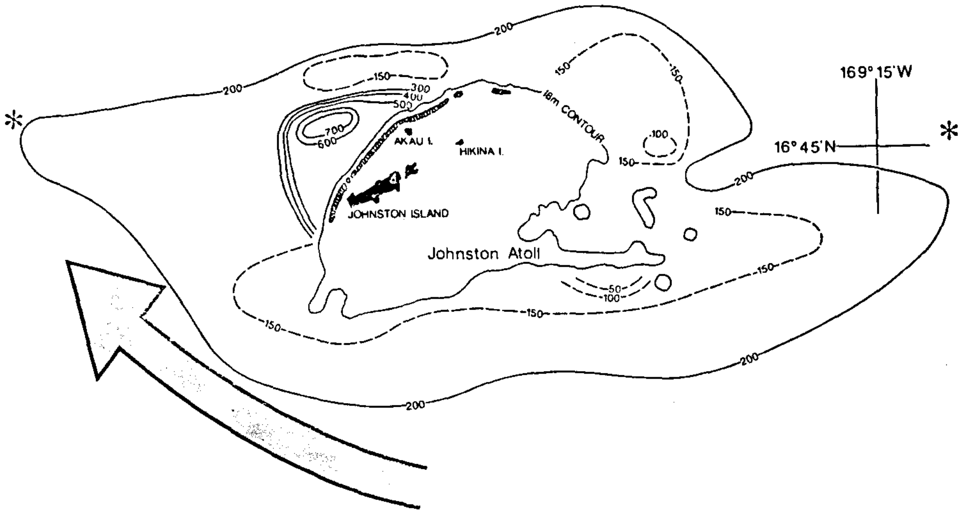

FIGURE 1. Distribution of ichthyoplankton around Johnston Island in November, 1984 collected from the Townsend Cromwell with a 1 m^2 opening-closing Tucker trawl. Densities refer to numbers of larvae per 10^3 m^3 in the 50-100 m depth stratum. The arrow represents surface current deduced from drogues deployed a month earlier (P. S. Lobel, personal communication). Note the high density of larvae on the downstream side of the island. Data from Boehlert (unpublished). Asterisks indicate that collections were made at greater distances east and west of the atoll.

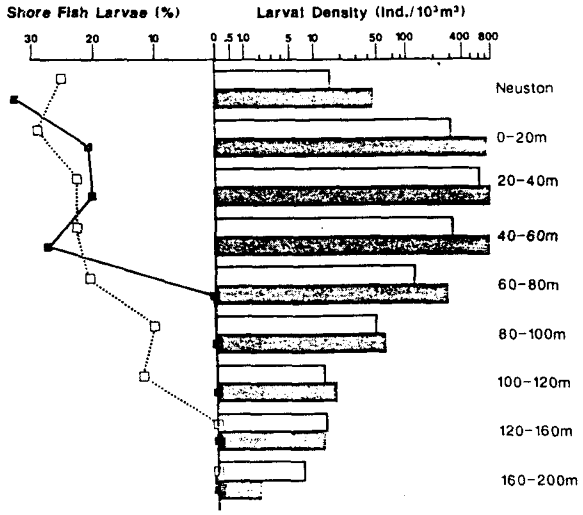

FIGURE 2. Larval densities (log scale) as a function of depth at both day and night at a station 5 nmi off the leeward coast of Oahu, Hawaii (lat. 21°21' N., long. 158°13.3' W.) taken in September, 1985. Each value represents a single haul. Clear bars represent day densities, cross-hatched bars represent night densities. The neuston samples are from the surface to 70 cm. On the left of the figure, the percentage of shore fish larvae (as opposed to pelagic or midwater fishes) is shown, with closed squares representing night, open squares day samples. Data from Boehlert and Mundy (unpublished).

A nearshore biological component of this study should be developed to sample all life stages from new recruits to adults. The age structure of adult populations should be determined with sufficient numbers to allow both estimation of mortality rates and variability in year class strength. These should be combined with length-based methodologies to streamline subsequent sampling. Sampling of new recruits should be undertaken during and after the main offshore sampling. This part of the study should at least include surveys to assess the densities of recruits and otolith studies to determine the birthdate and settlement date distribution of recruits. This will provide both the planktonic duration and the success of cohorts sampled during earlier offshore work. The latter work would be particularly important to correlate with physical oceanography and the distribution and abundance of earlier life stages in the pelagic environment.

From a temporal standpoint, the intensive study should be conducted during the season which coincides with the spawning peaks of most reef species, but preferably for a longer period in the first year to assess seasonal variability. The duration of the intensive offshore study should be at least one month, which will allow the distributional and physical analysis as well as coinciding with the approximate pelagic duration of many fish species (Brothers and Thresher, 1985). This type of study should be conducted over a period of two or three years (with more precise and therefore less intensive sampling each year) to assess interannual variability. If remote sensing methods prove useful, relevant data could be collected throughout the year.

This study should concentrate on any insular species to allow flexibility. Target species attributes should include known life histories (identified larvae, juvenile stages and habitats), sufficient larval and juvenile abundance to statistically assess distributional patterns and recruitment, and a large enough adult population to allow repeated sampling and estimation of population age structure. As with any ichthyoplankton program, however, the proposed research should consider the suite of species captured in the study to evaluate species associations.

If framed as a two to three year study, this research could provide answers to many unanswered questions about recruitment in tropical insular ecosystems. The study of an isolated island ecosystem would provide focused hypotheses which could then be tested in the more complicated archipelagic and island group systems where fisheries for a variety of species with pelagic eggs and larvae exist. To achieve these objectives, however, an intensive and interdisciplinary approach will be necessary.

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