ICHTHYOPLANKTON ASSEMBLAGES AT SEAMOUNTS AND OCEANIC ISLANDS

G. W. Boehlert and B. C. Mundy

ABSTRACT

Seamounts and oceanic islands support demersal or neritic fish populations and are lo-calized sources of eggs and larvae added to a background of oceanic ichthyoplankton. As-sociated larval fish assemblages, however, have been identified in few studies, and most have been based on subjective classifications of species by reproductive characteristics. At sea-mounts, little evidence exists that ichthyoplankton assemblages differ from the background field despite physical mechanisms proposed to maintain planktonic forms. Larvae of bottom-associated species are notably rare in samples taken in these regions. In contrast, characteristic ichthyoplankton assemblages have been described at oceanic islands. Unique assemblages may exist in embayments and lagoons, but they are not well described. Nearshore assemblages (0 to 0.5 km offshore) are dominated by larvae of small species with demersal eggs; neritic assemblages (0.5 to 5 km offshore) include inshore species with demersal and planktonic eggs mixed with larvae of certain species that are usually oceanic as adults. Although larvae of some inshore species with pelagic eggs are found offshore in oceanic assemblages (beyond 3 to 5 km), assemblages there are poorly described. Spatial and seasonal spawning behavior of adults plays the key role in formation of ichthyoplankton assemblages. Mechanisms that may maintain ichthyoplankton assemblages at islands include boundary layers, small scale frontal dynamics, tidal currents, topographically produced eddies, seasonally reduced or variable currents, and regions of no or returning flow. Behavior of larvae, particularly that affecting vertical distribution, can modify the influences of these mechanisms. The integrity of assem-blages can be disrupted by both biotic and abiotic factors.

Seamounts and isolated oceanic islands are habitats for demersal and pelagic fish communities not found in the open ocean. These communities are point sources of eggs and larvae that contribute to ichthyoplankton assemblages of the surrounding oceanic waters. Recruitment back to seamounts and islands depends upon the fate of the egg and larval stages and thus, to some extent, upon their retention near these habitats. Distance from these isolated habitats is therefore an important variable in consideration of such assemblages.

The unique problem that seamounts and oceanic islands pose to the recruitment of fishes was first stated by Gosline and Brock (1960): ". . . the possibility presents itself that variations in the normal pattern of oceanic currents around the islands may sweep a variable number of these young fish with their relatively feeble swimming abilities beyond the point of no return." They also suggested, "This argues that the migratory pattern of these fishes is uniquely adapted to best assure their return to the inshore habitat at the proper time." Their suggestions have since formed the basis of the hypotheses investigated by most studies of ichthyo-plankton in island areas.

The factors affecting the existence of ichthyoplankton assemblages may be con-veniently classified into those influencing formation, maintenance, or disruption (Table 1). The formation of assemblages is influenced not only by adult spawning patterns, but also by current-topography interactions that may accumulate buoy-ant plankton (Miller, 1974; Wolanski et al., 1989; Black and Moran 1991). Op-timal physical and biotic conditions may also lead to species associations (e.g., "ecological safe sites"; Frank and Leggett, 1983). Maintenance of larval fish as-semblages involves an increasing role of larval fish behavior, including seeking specific environmental features (Sulkin, 1986; Olla and Davis, 1990), and prey-

Table 1. Factors of potential importance in the formation, maintenance, and disruption of ichthyoplankton assemblages around islands and seamounts

Type of factor	Influencing formation[*]	Influencing maintenance[†]	Influencing disruption[‡]
Adult behavior	Spawning location Spawning time (tidal, diel, lunar, seasonal)	None	Predation (cannibalism) Influences on settlement
Egg development	Buoyancy (demersal vs. pelagic eggs, egg density) Incubation time Hatching location Hatching time	None	None
Larval behavior	Buoyancy at hatching Swimming ability at hatching	Habitat preference (temperature, salinity, light, depth) Vertical migration	Ontogenetic changes in vertical distribution Metamorphosis (settlement, schooling)
Biotic environment	Predation (absence will create "ecological safe sites")	Prey presence	Predation Prey absence (starvation)
Abiotic environment	Convergences Fronts	Eddies (Taylor Columns) Upwelling Downwelling Internal waves Convergences Fronts	Diffusion Mixing Advection

[*] Factors promoting spatial and temporal co-occurrence.
[†] Factors promoting integrity of assemblages over time.
[‡] Factors causing eventual breakdown of assemblage structure.

searching behavior (Hunter and Thomas, 1974; Doherty et al., 1985). Behavioral interaction with hydrography may result in dramatic accumulations of larvae into very localized assemblages (Kingsford, 1990). Because islands and seamounts may also be the loci of enhanced primary productivity (Doty and Oguri, 1956; Genin and Boehlert, 1985), retention near these areas may confer an advantage in survival.

In opposition to the factors forming and maintaining ichthyoplankton assemblages are those disrupting them. Mixing from turbulent flow, wind events, or other features will disrupt assemblages and dilute them over time. Advection may retain an assemblage intact, but can alter its position relative to a fixed sampling point, and thus its detection. Changes in larval behavior with ontogeny may alter the assemblage composition over time. Finally, the end of participation in an assemblage may be considered the point at which juveniles leave the environment occupied by larvae.

Investigations of ichthyoplankton assemblages at oceanic islands are still at the stage of describing general patterns (Boehlert et al., 1992; Leis, 1991), and those at seamounts are even less detailed. In this paper, we review the available information on 1) ichthyoplankton distributions at isolated seamounts and oceanic islands as they relate to spatial assemblages, 2) evidence that larvae of topographically associated species are maintained locally, and 3) the physical and biological mechanisms that may form, maintain, or disrupt assemblages near each type of topographic feature.

SEAMOUNTS

Physical Mechanisms. —Local recruitment by retention of larvae above a seamount is an attractive hypothesis, but one not easily visualized in the face of diffusive and advective forces. Potential mechanisms retaining larvae must be characterized by specific time and space scales. The time scales most pertinent to the formation and maintenance of larval fish assemblages are on the order of weeks to months, involving spawning and egg and larval development. We consider two spatial scales pertinent to larval assemblages: the near-field area around small seamounts (<ca. 10 km summit diameter) and the far-field area surrounding seamount chains, very large banks, or seamount complexes.

Current-topography interactions on both scales at seamounts have received a great deal of attention from physical oceanographers. Perhaps most interesting is the generation of semi-stationary eddies (Taylor columns) above seamounts. Other oceanographic complexities are present at seamounts, however, including internal wave reflection (Eriksen, 1982), tidally induced currents and eddies (Meincke, 1971), trapped waves (Brink, 1989), and eddies shed downstream (Royer, 1978). To examine their potential role in maintenance of biological populations, one must consider the speed and temporal variability of impinging currents, the temporal stability of topographic effects, and the size and shape of the seamount of interest.

Taylor columns are characterized as closed-streamline anticyclonic vortices above topographic obstacles in an impinging flow (Fig. 1A). They have been predicted theoretically, demonstrated experimentally in the laboratory (Taylor, 1917; Huppert and Bryan, 1976), and observed in the field (Owens and Hogg, 1980; Dooley, 1984). They can extend from the seamount summit to the ocean surface or, in the case of a stratified ocean, to the bottom of the pycnocline (Bakun, 1988). Development of Taylor columns frequently involves upwelling along the seamount flanks (Bezrukov and Natarov, 1976). Shomura and Barkley (1980) first speculated that Taylor columns may maintain planktonic stages and facilitate recruitment, and suggested that differences in the biota and productivity among seamounts might be attributed to variability in the occurrence and intensity of Taylor columns. For small seamounts, the temporal persistence of trapped vortices is a key question. Development of a Taylor column is based upon seamount morphology, current speed, water column stratification, and the Coriolis parameter. At a given seamount, temporal variations in the impinging current flow (including tidal factors and other time-variant flows) and stratification are the causes of temporal variations in vortex development. Decreased current speeds can result in the breakdown of the vortex, whereas excessive speeds can result in eddies being shed downstream (Hogg, 1980). Under certain circumstances, tidal currents may generate similar vortices above seamounts; Meincke (1971) observed an anticyclonic vortex trapped above Meteor Seamount, and concluded that it was driven by tidal influences.

The persistence of Taylor columns relative to biological time scales is poorly known. Existing evidence at smaller seamounts does not support physical time scales that match the requisite biological time scales. Genin and Boehlert (1985) noted uplifted isotherms and higher chlorophyll levels over a small seamount and suggested the presence of a Taylor column with a likely residence time of a few days; it was not present 2 and 17 days later. Darnitsky et al. (1984) observed upwelling only twice over Wanganella Bank during six cruises in 4 years. Although longer periods of Taylor-column persistence (on the order of several months) were inferred from hydrographic and Eulerian current measurements above a deep
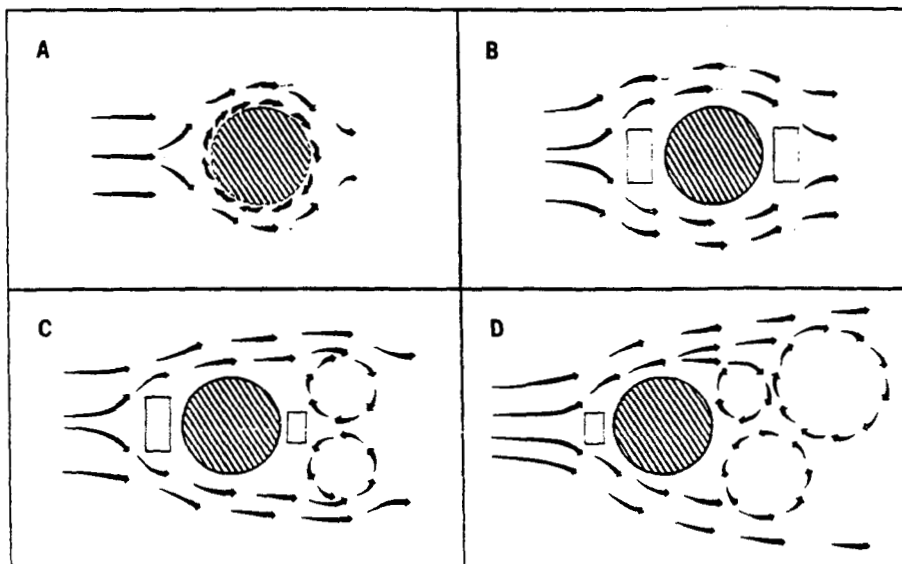
Figure 1. Variations in current-topography interactions. A. Interaction of flow with a seamount may lead to an eddy-like Taylor column remaining stationary over the summit (after Hogg, 1980). B–D. Interactions of a cylindrical island in a unidirectional current flow (after Hamner and Hauri, 1981). Slow current speeds result in laminar flow (B); increasing current leads to turbulent flow with down-stream, contra-rotating eddies (C). Further increases lead to eddy shedding downstream (D). Stippled areas indicate stagnation points in the flow.

seamount in the North Atlantic (Owens and Hogg, 1980), the area was charac-terized by steady flow not commonly observed at shallow (<200 m) depths where most fish larvae occur.

At greater spatial scales (beyond the immediate area of the seamount summit), however, time scales may be appropriate for formation and maintenance of ich-thyoplankton assemblages. Anticyclonic eddies shed from seamounts or seamount chains may remain in the general vicinity, as shown by Lagrangian current ob-servations from satellite-tracked drifters (Cheney et al., 1980); retention of ich-thyoplankton in the general region of seamounts may occur within such eddies for periods up to several weeks. These eddies can cause physical and biological variability in downstream waters (Royer, 1978; Genin et al., 1988), but detection of a biological signal (or larval fish assemblage) attributable to a seamount effect would require detailed biological and physical sampling as well as knowledge of the history of the water parcel.

At very large banks, some observations support the presence of quasi-stagnant water masses that may retain larvae. Eide (1979) observed this over a bank off the coast of Norway and found it consistent with the Taylor-column theory. Similar suggestions have been proposed for Rockall Bank, where Dooley (1984) noted episodic breakdowns of the gyral structure and suggested that these could have effects on variability in year-class strength of commercial fishes because of inconsistency in larval fish retention. Loder et al. (1988) characterized the ocean-ography at four large banks in the northwestern Atlantic, all of which have residual circulation indicative of anticyclonic motions around the bank. By considering the overall physical oceanography in light of time and space scales of water

exchange in the around-bank, cross-bank, and vertical directions, they reduced highly complex flow patterns to more understandable terms relative to biological time and space scales. Of the four banks, only Georges Bank appeared to have water residence times approximately equal to or greater than the recirculation time of the gyre; it was thus the best candidate for consistent retention of larval stages and possibly assemblages.

Seamount Ichthyoplankton.—The first study of ichthyoplankton at a seamount was at the Great Meteor Seamount off North Africa in 1970 (Nellen, 1973, 1974). This seamount was not deemed to be conducive to the spawning and early survival of fishes but instead acted as a disturbance to the surrounding pelagic ecosystem. Larvae of oceanic species were reduced in numbers and diversity over the seamount summit. Nellen (1973, 1974) suggested that predation or physical damage during diel descent to the seamount plateau increased the mortality of vertically migrating oceanic species. In contrast, larvae of two topographically associated species were more abundant at the summit than in the surrounding ocean. From this, he suggested that non-migrating larvae of species spawning over the seamount were maintained by currents. Larvae of euneustonic species were neither more abundant nor subject to increased mortality at the seamount. Nellen (1973) suggested two influential hypotheses: hydrography may maintain larvae of species spawning over seamount summits: and predation and exclusion of migrators reduce the abundance of oceanic larvae over seamounts.

These hypotheses are neither entirely supported nor refuted by other studies. Later sampling at the Great Meteor Seamount failed to find concentrations of topographically associated species (Belyanina, 1984). No evidence of retention of larvae was found at seamounts in the Indian Ocean (Belyanina, 1985). Conflicting results were obtained from samples taken within and between seasons at a seamount in the central North Pacific Ocean (Boehlert and Genin, 1987: Boehlert, 1988). In summer, larval fish densities were not different above and away from the summit during the day in three of the four depth strata sampled, but were more abundant away from the summit at all depths at night. In winter, larvae were more abundant over the summit than away from it at all depths during day and night (Boehlert and Genin, 1987). Boehlert (1988) suggested an interaction of three factors to explain the biological observations: first, semi-stationary eddies could maintain larval fish populations over the summit: second, vertically migrating taxa would be excluded from the summit's region by its physical presence: and third, predation at the summit would reduce the abundance of oceanic taxa. He concluded that none of the factors alone could explain the observations, but their interaction probably increased biological variability in the ocean above and downstream from the seamount.

There have been no studies explicitly identifying ichthyoplankton assemblages at seamounts. Three generalities about groups of fish larvae found at seamounts may be extracted from published studies: 1) the dominant larvae at most seamounts are widespread oceanic species (typically oceanic species of the Myctophidae and the Stomiiformes); 2) larvae of topographically associated species are rare at all but shallow seamounts; and 3) the abundance of larvae of topographically associated species often decreases with increasing distance of seamounts from larger land masses.

Surprisingly few studies have found larvae of topographically associated species to be more abundant at seamounts than in the surrounding ocean. Larvae of benthic species were found to be dominant in only one study (Robertson and Mito, 1979), a gadiform, *Gaidropsarus novaezealandiae,* and a bovichtid, *Bovich-*
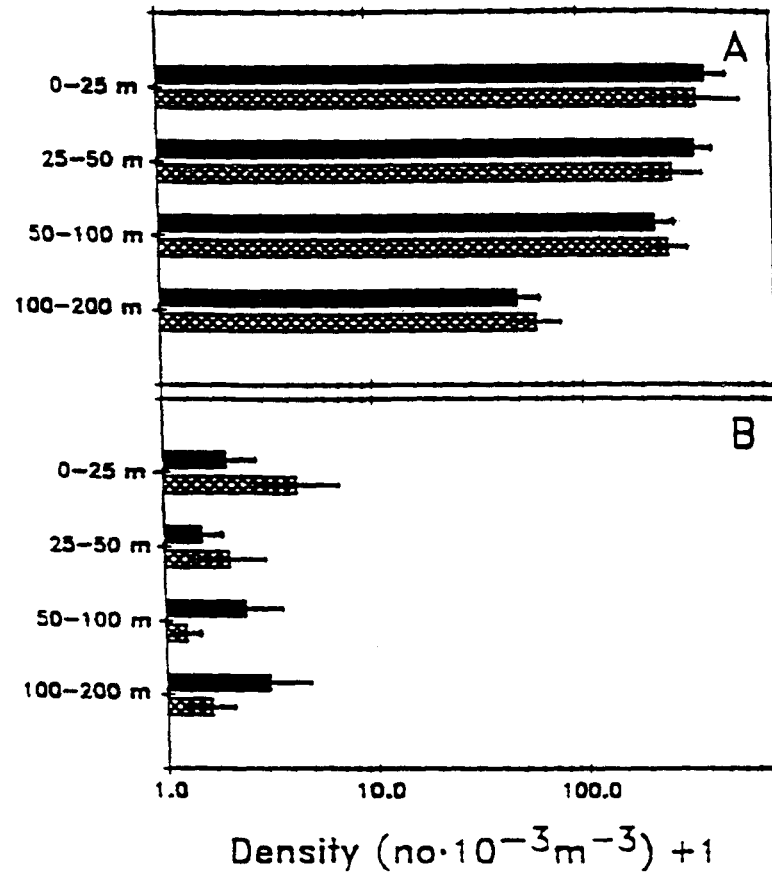
Figure 2. Densities of oceanic larvae (A) and seamount-associated (demersal or benthopelagic) larvae
(B) at Southeast Hancock Seamount in July 1984 (summer) and February 1985 (winter) with replicate
samples during day and night at four discrete depths (from Boehlert and Mundy, unpubl.). Solid bars
indicate densities over the seamount summit: cross-hatched bars indicate densities at a station 20 km
west of the summit. Error bars indicate ±1 SE.

tus variegatus, at banks off New Zealand. Larvae of seamount-associated species
were notably rare in studies at the Hancock Seamount in the central North Pacific
Ocean (Boehlert, 1988). On average, they were at least one hundred times less
abundant than oceanic species (Fig. 2). The rarity of larvae of topographically
associated species at this seamount is unexpected, because it supports large pop-
ulations of demersal fishes (Sasaki, 1986).

   Detailed examination of the distribution of larvae at Southeast Hancock Sea-
mount provides further evidence that larvae of most species were not retained
over the seamount summit. Sampling consisted of two cruises (July 1984 and
February 1985) with stations above and 20 km to the west of the seamount summit
in each cruise: samples at both stations were taken in four discrete depth strata
(Boehlert and Genin, 1987; Boehlert, 1988; Fig. 2). Additional samples were taken
in the neuston (0 to 1 m) in winter. Seamount taxa at 0 to 50 m were most

abundant away from the seamount (Fig. 2). The dominant species in these strata was *Beryx splendens*, collected only in summer (Mundy, 1990). Only in the two deepest strata (50 to 200 m) were larvae of seamount taxa more abundant over the seamount summit than away from it (Fig. 2). These were almost all *Maurolicus muelleri*, which were collected only in winter (Boehlert and Mundy, unpubl.). Larvae and small juveniles of *Pseudopentaceros wheeleri*, the dominant species in samples of adult fishes at this seamount, were only collected in neuston tows. Dispersal of *P. wheeleri* away from seamounts may actually be enhanced by the exclusive occurrence of their larvae in the neuston (Boehlert and Sasaki, 1988), where wind-driven advection will rapidly disperse the larvae away from their source. Thus, evidence exists for greater abundance of larvae of only one species, *M. muelleri*, over Southeast Hancock Seamount. Demonstrating retention of larvae at the seamount, however, will require more detailed information on ocean currents and the distribution of late larval stages.

The frequency of occurrence and abundance of larvae of topographically associated species decrease with increasing distance of seamounts from larger land masses and increasing summit depth. Nellen (1973, 1974) suggested that although the neritic species with abundant larvae were spawning at the Great Meteor Seamount, reproduction there was unlikely to sustain populations. Such "dependent populations" have also been noted at seamounts in the central North Pacific (Belyayev, 1990). In the Indian Ocean, larvae of shallow water fishes were absent from two seamounts isolated from continental areas and present at two seamounts closer to shelf areas (Belyanina, 1985). A similar pattern was found in a more intensive study of one deep (182 m) and three shallow (10 m) seamounts in the same region (Gordina and Bladimirtsev, 1987). In the latter study, larvae of neritic species were most abundant at shallow seamounts.

Several sampling problems are apparent with existing surveys of ichthyoplankton around small seamounts. First, temporal sampling patterns have been inadequate to detect seasonal peaks of larval abundance for certain species. Second, spatial sampling in the studies identified above is typically restricted to stations above the summit and at some distance away from the summit. Thus, analysis of the spatial distributions of larvae was often based upon paired comparisons, as opposed to a broader geographic analysis and consideration of variables such as current direction. A related problem is that almost no studies have reported measurements of currents simultaneous with ichthyoplankton collections. Gordina and Bladimirtsev (1987) found that larvae of neritic species were concentrated in eddies downstream of shallow (10 m) seamounts, rather than directly above the summit centers. Oceanic larvae dominated in upstream areas. The distribution of neritic larvae was given as evidence that such larvae may be advected from their source but retained in the vicinity of shallow seamounts by eddies.

The problems of spatial sampling and oceanographic measurements have been better addressed at certain large banks. Rockall Bank (Dooley, 1984), Georges Bank (Smith and Morse, 1985), and Browns Bank (Campana et al., 1989) show characteristic eddies that have been proposed to maintain eggs and larvae through the planktonic stages to promote local recruitment. Even so, Campana et al. (1989) suggested, the Browns Bank mechanism was a "leaky gyre," and cohorts of larval haddock, *Melanogrammus aeglefinis*, were split into retained and vagrant groups. Above some threshold size, banks may have self-sustaining populations, but typically with species characteristic of adjacent continental shelves or slopes. The processes described in Loder et al. (1988) seem to be applicable in such cases.

To summarize, seamount ichthyoplankton assemblages containing topographically associated species have been most frequently identified near shallow (<200

m) summits which are near larger land masses. There is little evidence that persistent ichthyoplankton assemblages, distinct from those in the surrounding ocean, exist near deeper, more isolated seamounts. The physical interference of seamounts with vertical migration and the high predation rates at seamount flanks and summits generally act to increase variability in plankton at seamounts and downstream therefrom (Genin et al., 1988). Thus, fish that spawn at seamounts may be subject to extreme variability in recruitment due to dispersal of larvae away from adult habitats. Recruitment to seamounts may depend more upon occasional events than it does at oceanic islands. Recruitment of many species at seamounts may also include major input from populations at larger land masses (Nellen, 1973; Vasilenko and Sokolovskaya, 1989). The combination of highly variable and occasionally allochthonous recruitment may help explain several features of fish populations at seamounts, including the lower than expected rate of endemism (Wilson and Kaufman, 1987), susceptibility of seamount populations to recruitment overfishing (Sasaki, 1986), and unpredictable recovery after overfishing (Lutjeharms and Heydorn, 1981).

OCEANIC ISLANDS

An early hypothesis about the distribution of larval fishes at oceanic islands suggested that larval Acanthuridae might be retained in their vicinity by small eddy systems (Randall, 1961). Sale (1970) found larval acanthurids to be more abundant offshore (48 to 58 km) than near Oahu, Hawaii (4.8 to 8.0 km), and also proposed that eddies returned these larvae to the island. These suggestions have been generalized to other families of fishes (Johannes, 1978). Prior to the publications of Miller (1974) and Watson and Leis (1974), however, there was almost no empirical information on the distribution of ichthyoplankton near oceanic islands to allow informed speculation about these ideas.

Early surveys off Oahu suggested that fish larvae were not distributed near islands as if they had passively diffused from the island source (Miller, 1974). Distinct differences in the distributions of taxa indicated the influence of behavioral differences (Watson and Leis, 1974). Larvae of certain highly visible reef families, including the Acanthuridae, Chaetodontidae, Labridae, and Scaridae, were rare in nearshore samples (Miller, 1974; Leis, 1978). The early suggestion that some types of larvae occur far from shore (Sale, 1970) has been verified. Larvae of labrids and pomacentrids, for example, have been found 370 to 1200 km from the nearest adult habitat (Leis, 1983; Victor, 1987). The occasional occurrence of such larvae at extreme distances does not mean that they are most abundant away from land; several taxa often considered to have widely dispersed larvae are actually most abundant at intermediate distances from shore (Wyatt, 1982; Young et al., 1986; Leis, 1989; Clarke, 1991).

The planktonic habitat near oceanic islands is occupied preferentially not only by larvae of topographically associated fishes, but also by larvae of certain oceanic fishes (Miller, 1979; Leis et al., 1991). The importance of this habitat to these oceanic species is unknown. As an example, the increased nearshore abundance of tuna larvae in the genus *Thunnus* (Fig. 3) may simply be a result of the higher abundance of spawning adults near islands. Tunas typically aggregate near islands and banks for feeding (Uda and Ishino, 1958), but larvae are not regularly concentrated in other areas of adult occurrence, such as fronts. An alternate hypothesis is that waters around islands are more suitable for survival of early larvae, perhaps through improved feeding conditions. Primary productivity around islands, may be higher than in the open ocean (the "island mass" effect), particularly around
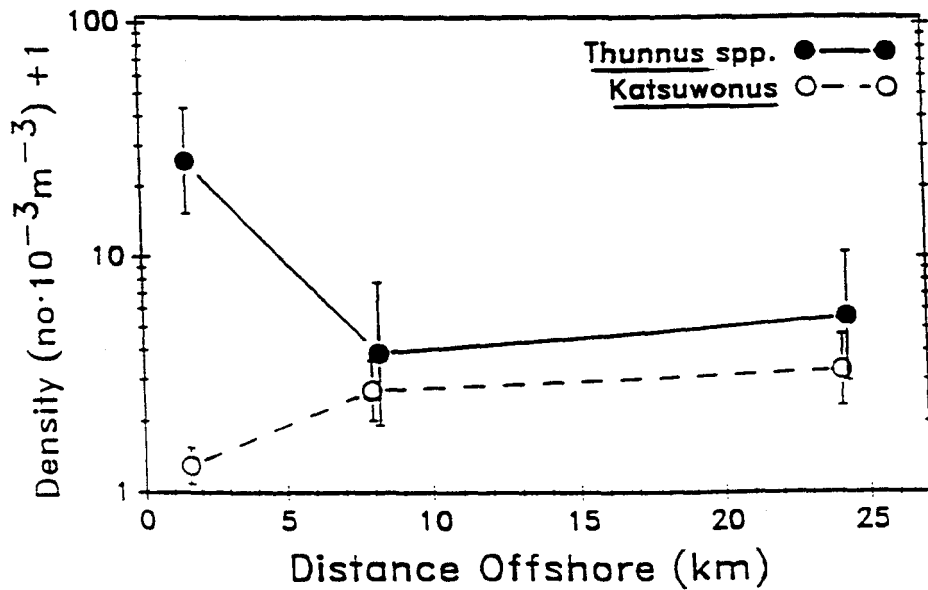
Figure 3. Onshore-offshore patterns of distribution of *Thunnus* spp. and *Katsuwonus pelamis* collected during June 1986 off the leeward coast of Oahu, Hawaii. Values are means from discrete-depth samples taken in the upper 40 m for *Thunnus* spp. (N = 10 nearshore station, N = 6 at each offshore station) and the upper 80 m for *K. pelamis* (N = 16 nearshore station, N = 10 at each offshore station). Error bars indicate ±1 SE.

high islands, such as Oahu (Gilmartin and Revelante, 1974; Dandonneau and Charpy, 1985). Waters near islands in tropical and subtropical areas may also be characterized by increased zooplankton abundance, often of species uncommon in offshore waters (Jones, 1962; Hernandez-Leon, 1988, 1991). Thus, greater availability of prey in nearshore waters could result in higher survival rates for early larvae during the stage when prey density requirements are highest (Hunter and Kimbrell, 1980). In the case of *Thunnus* spp., Higgins (1970) noted a threefold higher abundance of juveniles at stations 56 km. as opposed to 7 km. offshore of Oahu. Such oceanic larvae may thus disperse from nearshore areas with increasing age as their prey-searching capabilities improve. The case is made, however, for possible enhanced survival for larvae developing in waters around islands.

Sampling Problems. —Description of the distributions of larvae of many island-associated fishes has been hampered by their low abundance in the plankton. Larvae of one of the most visible coral reef families, the Chaetodontidae, comprise <0.5% of the total larvae in ichthyoplankton surveys (Leis, 1989). Clarke (1991) noted that the average densities of many taxa 13 km off Oahu, including those previously described as rare inshore, typically range from 0.0001 to 0.01 · 1,000 m⁻³. He pointed out that it is necessary to sample water volumes >1,000 m³ to describe the distributions of most island-associated species. This has not been done in most studies. The sampling problems of accurately describing the distributions of naturally sparse fish larvae enhance the utility of examining larval fish assemblages. Patterns may be detected in assemblages that are obscured by the patchy distribution or low sample sizes of individual taxa.

Spatial and temporal scales of sampling have often been insufficient to identify

the spatial extent or temporal persistence of assemblages. The time and space scales pertinent to larval fish assemblages around islands vary with island size but are ill-defined for virtually all islands. The biological time scales are on the order of weeks to months, the characteristic time scale for the pelagic period prior to recruitment to the juvenile or adult habitat (Thresher and Brothers, 1989). Spatial scales of biological interest are dependent upon the habitat type used by the species of fish (demersal or pelagic), the spawning type (pelagic or demersal egg), and perhaps the distances characterizing diffusive and advective processes over the relevant time scale. Most studies of island ichthyoplankton have conducted onshore-offshore transects to analyze patterns of larval fish distribution. Because spatial sampling has largely ignored the larger scale of distribution around islands, spatial variation in assemblage distribution is poorly known. Thus, discussion of physical mechanisms relative to larval fish distribution around islands has been largely speculative.

Early Evidence for Assemblages in Island Systems. —The first suggestions that different assemblages of larvae exist at oceanic islands came from studies off Oahu. Miller (1974) noted that fish larvae were more concentrated in nearshore (<10 m depth) than offshore (>10 m depth) areas, larvae of certain offshore species were abundant inshore, and the abundance of larvae from demersal eggs was inversely correlated with the abundance of larvae of mesopelagic species. Watson and Leis (1974) found that larvae of pelagic bay species with pelagic eggs and reef species with demersal eggs were abundant within an embayment on Oahu. Larvae of oceanic species and reef species with pelagic eggs were rare in the bay; Watson and Leis (1974) suggested that these larvae completed their planktonic life in offshore waters. From this series of studies, Leis and Miller (1976) concluded that larvae of insular species from demersal eggs occur more frequently in a nearshore assemblage, while those from pelagic eggs are more frequent offshore.

The assemblages identified at Oahu form the basis for almost all subsequent work around islands. Evidence for at least four larval fish assemblages can be found in studies of ichthyoplankton distributions around islands subsequent to Leis and Miller's (1976) work: 1) assemblages unique to embayments and lagoons, 2) extreme nearshore assemblages, 3) intermediate nearshore assemblages, and 4) offshore assemblages. The latter three will be referred to as the "nearshore," "neritic," and "oceanic" assemblages, following Leis (1978).

Embayment Assemblages. —The presence of distinct assemblages in embayments and lagoons of oceanic islands (referred to as "embayment assemblages," for brevity) has not been investigated in detail. Although Leis (1981) did not observe a nursery function in a small reef lagoon within the Great Barrier Reef, larger lagoons and embayments on certain oceanic islands may differ in this respect. Preliminary results of studies at oceanic atolls in the Coral Sea (Leis, 1986a) and at French Polynesia (Leis, 1991) suggest that larval fish assemblages there consist of species not found in abundance outside of lagoons. The Gobiidae, Apogonidae, Pomacentridae, and Blenniidae are the dominant families in these assemblages. The initial suggestion that an embayment at Oahu had a unique assemblage of larvae (Watson and Leis, 1974) was corroborated by Leis and Miller (1976), Miller et al. (1979), and Kobayashi (1989: Table 2).

Recent collections within the lagoon of Palmyra Atoll, Line Islands, contained mostly larvae that were not found in samples outside of the reef, including many samples taken within 0.5 km of the atoll (Boehlert and Mundy, unpubl.). These lagoonal collections were also composed almost entirely of larval Gobiidae, Apogonidae, Pomacentridae, and Blenniidae. Thus, larval fish assemblages in enclosed

Table 2. Selected taxa included in larval fish assemblages proposed in studies at tropical and subtropical islands. The assemblages are those found in embayments (estuaries, lagoons, and other semi-enclosed areas), nearshore waters (0 to 0.5 km offshore), neritic waters (0.5 to 3–5 km offshore), and oceanic waters (3–5 to 600 km offshore). Egg types are noted because some assemblages were suggested to be dominated by larvae from either pelagic or demersal (including brooded or viviparous) eggs. Ubiquitous pelagic species are excluded because they form the background field of larvae to which island taxa are added

Taxon	Assemblage	Reference	Egg type
Engraulididae	neritic	12	pelagic
Encrasicholina purpurea	embayment	6, 13	pelagic
E. punctifer	neritic?	7	pelagic
	oceanic	2, 5	pelagic
Clupeidae			
Jenkinsia sp.	nearshore	17, 20	unknown
Spratelloides delicatulus	nearshore	7	demersal?
Myctophidae			
Benthosema fibulatum	neritic	1	pelagic
Lampadena urophaos	nearshore	7	pelagic
	neritic	1, 7	pelagic
Synodontidae	nearshore	20	pelagic
	neritic	3	pelagic
	oceanic	4	pelagic
Ophidiidae	nearshore	20	pelagic?
Bythitidae	nearshore	2	livebearer
Exocoetidae	neritic	13	pelagic
Holocentridae	neritic?	4	pelagic
Pegasidae	oceanic	5	unknown
Syngnathidae	nearshore	20	brooded
Scorpaenidae	neritic	12	pelagic
Symphysanodontidae	oceanic	4	pelagic
Serranidae	oceanic	4, 13	pelagic
Apogonidae	embayment	2, 6, 10, 13	brooded
	nearshore	12	brooded
	neritic	12, 13	brooded
	oceanic	13	brooded
Epigonidae	neritic	3, 7	pelagic
	oceanic	3	pelagic
Lutjanidae	neritic?	4	pelagic
Mullidae	nearshore	10, 12	pelagic
	neritic	13	pelagic
Haemulidae	nearshore	20	pelagic
Pempherididae	nearshore	20	pelagic
Sciaenidae			
Pareques iwamotoi	nearshore	18	pelagic
Chaetodontidae	oceanic	3, 7, 11, 15	pelagic
	neritic	3, 11	pelagic
Pomacanthidae	oceanic	4	pelagic
Carangidae	embayment	13	pelagic
	neritic	13	pelagic
	oceanic	4	pelagic
Gnathanodon speciosus	embayment	2	pelagic
Pomacentridae	embayment	13	demersal
	nearshore	7, 10, 12	demersal
	neritic	12, 13	demersal
	oceanic	13	demersal
Abudefduf abdominalis	neritic	7, 8	demersal
Stegastes sp.	oceanic	21	demersal
Labridae	neritic	3, 12	pelagic
	oceanic	4, 7, 13, 15, 21	pelagic
Thalassoma sp.	oceanic	9, 21	pelagic

Table 2. Continued

Taxon	Assemblage	Reference	Egg type
Scaridae	neritic	3	pelagic
	oceanic	3, 7, 15	pelagic
Gobiesocidae	nearshore	2, 20	demersal
Callionymidae	neritic	12	pelagic
	oceanic	4	pelagic
Pinguipedidae	neritic	3	pelagic
	oceanic	4	pelagic
Creediidae	neritic	3	pelagic
Blenniidae	embayment	10, 13	demersal
	nearshore	7, 12	demersal
	neritic	3, 13	demersal
	oceanic	13	demersal
Exallias brevis	neritic	7, 8	demersal
Tripterygiidae	nearshore	2, 7, 8, 10, 12	demersal
Gobioidei	embayment	6, 13	demersal
	nearshore	2, 7	demersal
	neritic	7, 8, 12, 13	demersal
	oceanic	4	demersal
Amblygobius sp., others	embayment	2	demersal
Eviota epiphanes	neritic	1, 3, 7, 8	demersal
Schindleriidae (larvae and adults)			
Schindleria pietschmanni	nearshore	7	demersal?
	neritic	3	demersal?
Schindleria praematura	embayment	2	demersal?
	neritic	7, 8	demersal?
Acanthuridae	oceanic	4, 7, 13, 15, 19	pelagic
Scombridae	neritic	13, 14	pelagic
Thunnus albacares	nearshore	7	pelagic
	neritic	1, 16	pelagic
Bothidae	neritic	3	pelagic
	oceanic	13	pelagic
Molidae	neritic	13	pelagic
	oceanic	13	pelagic

1. Boehlert and Mundy (unpubl. data, Oahu); 2. Boehlert and Mundy (unpubl. data, Palmyra Atoll); 3. Boehlert et al. (1992); 4. Clarke (1991); 5. Hirota et al. (1980); 6. Kobayashi (1989); 7. Leis (1978); 8. Leis (1982); 9. Leis (1983); 10. Leis (1986b); 11. Leis (1989); 12. Leis and Goldman (1987); 13. Leis and Miller (1976); 14. Leis et al. (1991); 15. Miller (1974); 16. Miller (1979); 17. Powles (1977); 18. Powles and Burgess (1978); 19. Sale (1970); 20. Smith et al. (1987); 21. Victor (1987)

waters of oceanic islands may be qualitatively very different from those in enclosed lagoons of continental islands and tropical coasts (Table 2).

Nearshore Assemblages. — There is increasing evidence that some fish species have larvae found primarily at distances of 0 to 500 m from substrates (Barnett et al., 1984: Powles et al., 1984; Marliave, 1986; Jahn and Lavenberg, 1986). Leis (1978) described the assemblage at 200 m off leeward Oahu (Table 2). In a discussion of fish larvae at the Great Barrier Reef, which is not an island environment, Leis (1986a) noted that tripterygiids were among a special assemblage of larvae that could be frequently found ". . . in waters immediately to windward of coral reefs . . ." but which were ". . . found in high numbers nowhere else." This pattern was also found in a study at Palmyra Atoll, where the dominant larvae in samples collected <500 m from shore were tripterygiids, bythitids, gobiesocids, and certain gobiids, with this assemblage particularly abundant in a restricted portion of the island's circumference (Boehlert and Mundy, unpubl.). A comparison of larval densities north and south of the island in samples taken along the 100-m isobath, for example, shows dramatic differences (Fig. 4), with the greatest abundance on
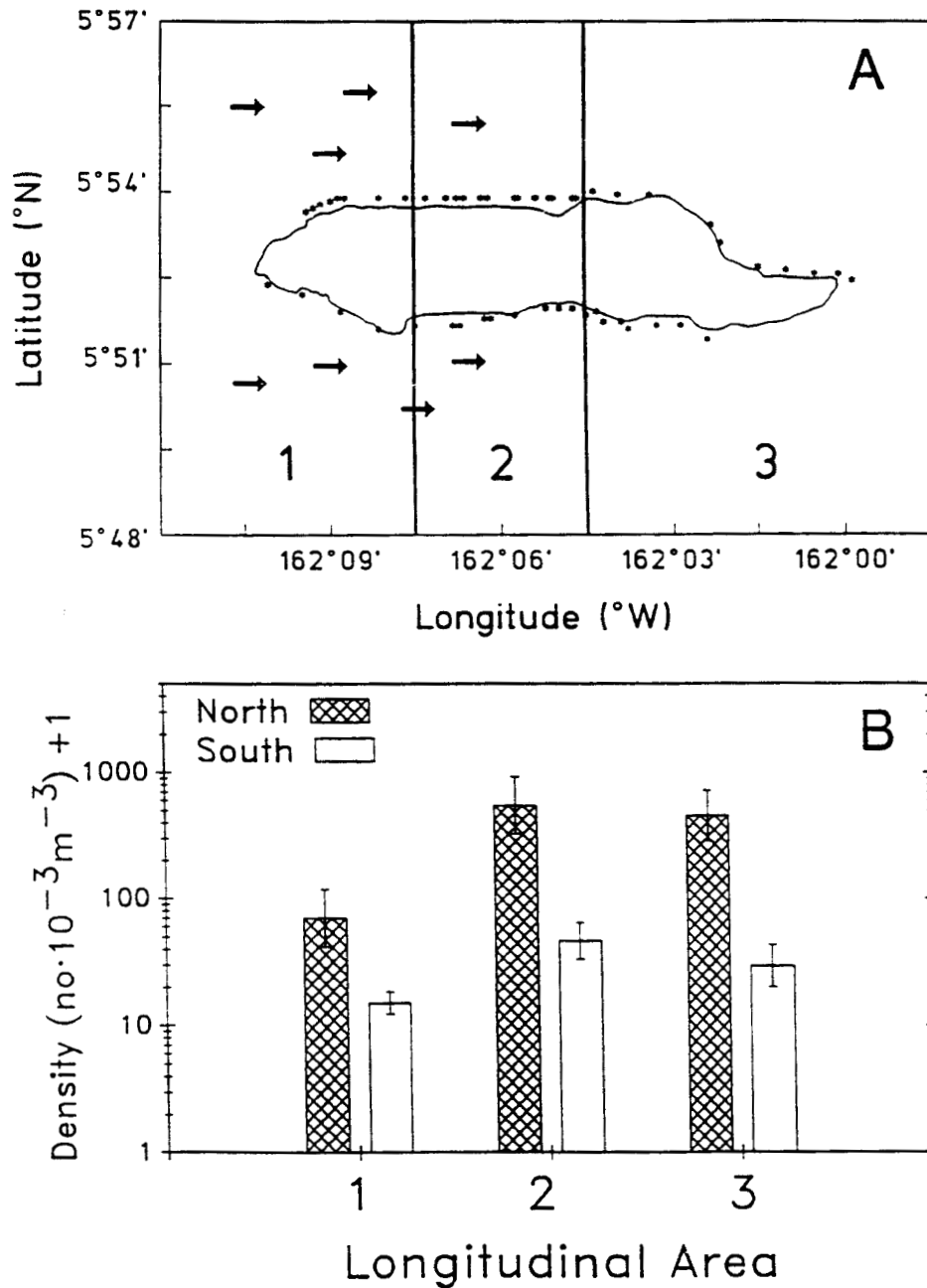
Figure 4. Larval fish distributions surrounding Palmyra Atoll in the central equatorial Pacific (Boeh-
lert and Mundy, unpubl.). A. Outline of the 10-m isobath surrounding the island, with the sampling
stations indicated by asterisks. All samples were taken during daylight hours with a 1-m² MOCNESS
in the upper 50 m. Data are divided into three longitudinal strata. General current direction is indicated
by arrows. B. Mean larval fish densities by longitudinal stratum, divided to north and south sides of
the island.

the northern side of the island. Thus, although the taxonomic composition of nearshore assemblages varies between studies, there is increasing evidence that such assemblages predictably occur near islands.

Within the nearshore assemblage, other types of larvae may have even more restricted distributions (Table 2). Larvae of the clupeid genus *Jenkinsia* (Powles, 1977) and of the sciaenid *Pareques iwamotoi* (Powles and Burgess, 1978; Miller and Woods, 1988) were found extremely close to the bottom (<2 m) near coral heads. In the Virgin Islands, Caribbean Sea, larvae that were rare in towed net samples were taken near reefs and at the lights of an undersea habitat (Smith et al., 1987). In Kaneohe Bay, Oahu. Hawaii. larvae of two gobiid species also were found to be most abundant within a few meters of coral reef heads (Kobayashi, 1989). These may be tropical, insular examples of larvae that are restricted in distribution to within a few meters of a substrate (Marliave, 1986). This near bottom habitat is sorely undersampled in island waters, as elsewhere.

Neritic Assemblage. — Most studies of larval fish distributions around islands have found evidence for an assemblage of larvae distributed in a band of approximately 0.5 to about 3 to 5 km from shore. but these distances may vary around different parts of islands. depending upon current strength and island morphology. The neritic assemblage is typically dominated by insular taxa with demersal eggs and a few oceanic taxa (Table 2). The contribution of insular taxa with planktonic eggs to this assemblage is not yet resolved. with more investigation being clearly required (Clarke. 1991). Components of the neritic assemblage off leeward Oahu vary between studies because of different analysis techniques. Leis (1978, 1982) identified an assemblage from an analysis of absolute abundances. while Leis and Miller (1976) used relative densities of larvae. Miller et al. (1979) combined the nearshore and neritic assemblages in their analysis.

A neritic assemblage similar to that off Oahu was found close to the lee of Johnston Island. an isolated atoll several hundred kilometers southwest of Hawaii (Boehlert et al., 1992). That study sampled a grid around the island on a scale pertinent to the neritic assemblage. An assemblage consisting of three groups of strictly island-related species was noted (Table 3). Two of the groups were small. with two and three taxa that were fairly rare but most abundant in the 50- to 100-m depth stratum. The largest group was composed of highly abundant taxa present in areas beyond the neritic area and throughout the upper 200 m but clearly most abundant in neritic waters in the 50- to 100-m stratum (Boehlert et al., 1992). The scale of the areas of high abundance for this assemblage relative to the island. however. was markedly greater than the distances normally seen in neritic assemblages and encompassed distances of ≤10 km downstream of the island. whereas the assemblage was rare upstream of the island. as would be expected (Fig. 5A). Similar upstream/downstream differences in larval fish abundance were noted at this scale at Jamaica (Wyatt. 1982).

The oceanic species found in neritic larval fish assemblages include three components: species associated with topography as adults, within families usually considered mesopelagic: widely distributed species with larvae abundant in all regions: and those with larvae concentrated in neritic regions. Examples of topographically associated species with larvae found in the neritic assemblage include *Lampadena urophaos* (Leis. 1978) and *Benthosema fibulatum* (Boehlert and Mundy, unpubl.) off Oahu. and *Scopelosaurus gibbsi* off Muraroa (Bourret et al., 1979). Widely distributed species with widely distributed larvae include *Ceratoscopelus warmingi* (Leis, 1978). A group of ubiquitous larvae that acted as a background field contributing to neritic and oceanic assemblages at Johnston Atoll included nine species that were present in over 66% of all samples (Table 3).

Table 3. Larval assemblages identified from an ichthyoplankton survey surrounding Johnston Island in the central tropical Pacific Ocean. Depths sampled included 0–50 m, 50–100 m, and 100–200 m. The species groups within assemblages were determined with a two-way synthesis table technique. Several other abundant species were not characterized by distributions coherent with other groups (from Boehlert et al., 1992)

Neritic Larval Assemblage

Eviota epiphanes. Salariini, Limnichthys donaldsoni. Parapercis sp., *Schindleria pietschmanni.* Labridae (present in nearly all depths and habitats, but most abundant in neritic area at 50–100 m)

Selar crumenophthalmus. Tetraodontidae, *Apogonichthys perdix* (greatest abundance in neritic area at 50–100 m)

Synodus spp., Bothidae (greatest abundance in neritic area at 50–100 m depth)

Mixed Neritic and Oceanic Larval Assemblage

Epigonus sp., Scaridae. Chaetodontidae, *Nealotus tripes* (greatest abundance in neritic and offshore areas. 0–50 m depth strata)

Oceanic Larval Assemblage

Lestidium spp., *Diaphus pacificus. Sudis atrox, Evermannella* sp. (present in nearly all depths and habitats, but greatest abundance in 50–200 m, both neritic and offshore areas)

Coryphaena hippurus. Cubiceps caeruleus. Bathophilis sp., *Caulophyrne* sp. (greatest abundance in offshore area. 0–50 m depth stratum)

Melamphaes spp., *Bregmaceros* sp., *Howella* sp., *Hygophum reinhardti* (greatest abundance in offshore area. 50–200 m depth)

Idiacanthus sp., *Gonostoma atlanticum. Gonostoma* spp. (present neritic and oceanic areas, most abundant at 100–200 m)

Scopelosaurus spp., *Gonostoma elongatum. Scopelarchus* spp. (present oceanic areas, most abundant at 100–200 m)

Ubiquitous Larval Taxa

Ceratoscopelus warmingi, Vinciguerria nimbaria. Diaphus spp., *Cyclothone* spp., *Lampanyctus nobilis. Bolinichthys* spp., *Symbolophorus evermanni. Hygophum proximum. Lampadena urophaos*

(present in more than two-thirds of all samples in the study, not included in the analytic procedure for defining assemblages)

These were not included in the assemblage analysis by Boehlert et al. (1992). Three of five assemblages of rarer oceanic taxa were less abundant in the neritic region. suggesting the possibility of exclusion from neritic waters, whereas two others were ubiquitous across areas. Examples of widely distributed taxa with larvae concentrated in neritic areas include *Thunnus albacares* (Fig. 3; Miller, 1979; Leis et al., 1991; Boehlert and Mundy, 1991) and the Istiophoridae (Leis et al., 1987).

Oceanic Assemblage. — The inshore limit of the oceanic assemblage around islands is found 2 to 5 km offshore; the seaward limit of this assemblage is poorly known (Leis and Miller, 1976). Note that "oceanic" in this context does not refer to an assemblage consisting only of larvae of oceanic species; rather, it refers to the assemblage containing larvae of insular taxa found at the greatest distance from an island in oceanic waters (Table 2).

The inshore distance for the transition between oceanic and neritic assemblages is most probably an artifact of sampling effort; identification of the true distance and its variability will depend upon continuous sampling in offshore transects covering different regions of an island. The offshore extent of oceanic assemblages is unknown largely because of limited sampling. Larvae of island-associated taxa have been found at great distances from the nearest adult habitat (Leis, 1983;
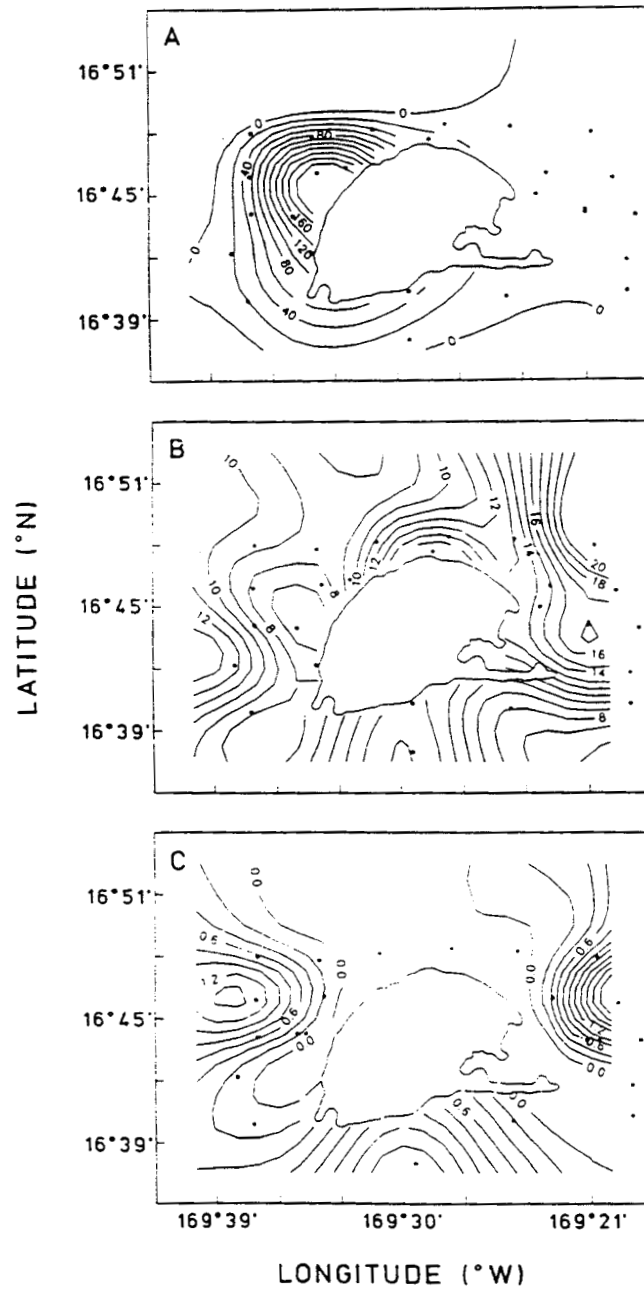
Figure 5. Distribution of ichthyoplankton around Johnston Island: the outline surrounding the island represents the 18-m isobath (data from Boehlert et al., 1992). General current flow in the region is from east to west with a moderately stagnant area downstream of the island where the highest densities in 5A occur. All density notations are in larvae per 1,000 m³. 5A. Distribution of the combined densities of species included in the first neritic assemblage (Table 3: assemblage A, dominated by *Eviota epiphanes*) in the 50 to 100 m depth stratum. 5B. Distribution of the second oceanic assemblage (Table 3: oceanic assemblage B, with *Coryphaena hippurus*) in the 0 to 50 m depth stratum. 5C. Distribution of the ubiquitous mesopelagic species *Vinciguerria nimbaria* in the 50 to 100 m depth stratum.

Victor, 1987), but are probably not frequent or abundant components of larval fish assemblages at these distances (Leis, 1984; Clarke, 1991). Regional differences may exist, however, and the presence of island-associated taxa extends to a radius of 100 to 300 km from islands in the Pacific Ocean and 300 to 600 km in the Indian Ocean (Fedoryako, 1989). Aoki and Ueyanagi (1989) suggested that *Coryphaena hippurus* occurred in association with oceanic islands, whereas its congener *C. equiselis* was distributed throughout oceanic waters. *Coryphaena hippurus* was included in one of the groups within the oceanic assemblage around Johnston Island (Table 3: Boehlert et al., 1992). The distribution of this assemblage around the island, however, was regionally variable (Fig. 5B); it occurred in very low densities near the island and increased in density with distance offshore. *Vinciguerria nimbaria*, a species ubiquitous in distribution, also had lower densities near the island than offshore (Fig. 5C). This species and the oceanic assemblage (Fig. 5B) were least abundant in the area where the dominant neritic assemblage was found in highest abundance (Fig. 5A). This suggests that maintenance of locally spawned species occurred, as opposed to concentration of all species. The role of behavior in maintaining this distribution pattern is unknown.

Following Leis and Miller (1976), most studies have included larvae of insular species with planktonic eggs in oceanic assemblages, along with the widely distributed, truly oceanic species (Leis 1978, 1982; Miller et al.. 1979). Similar results can be found in studies of larvae from Australia, a continental rather than insular system (Young et al.. 1986; Leis and Goldman, 1987). It is interesting to note, however, that the only assemblage at Johnston Island with a mix of oceanic and island-related taxa included the Chaetodontidae and Scaridae, with a distribution pattern showing abundance in both neritic and oceanic waters (Table 3). Investigations are thus demonstrating that not all families, or even all taxa within families with pelagic eggs, are as widely dispersed in oceanic assemblages as previously thought (Leis. 1987. 1989; Boehlert et al.. 1992). Resolution of these patterns will require more investigation with techniques that overcome the sampling problems noted by Clarke (1991).

Physical and Behavioral Mechanisms. —That islands, particularly in tropical regions, are areas of relatively high productivity seems to be related to vertical mixing and upwelling associated with current-topography interactions (Heywood et al.. 1990). These interactions are different from those around seamounts and will not be reviewed in detail here. Instead, the focus is how these interactions relate to the formation, maintenance, and breakdown of larval fish assemblages. [For a more comprehensive background on island-current effects, see reviews in Hogg (1980), Hamner and Hauri (1981), and Wolanski and Hamner (1988).]

Formation and maintenance of embayment assemblages probably depend upon a combination of boundary-layer effects, longer retention times for water, and behavior of larvae. Retention of larvae may be proportional to flushing times (Sammarco and Andrews. 1989), and larger, deeper lagoons typically have longer flushing times; moreover, wind-driven, two-layered circulation patterns exist in atoll lagoons (Atkinson et al., 1981). It is thus possible that larvae can behaviorally alter horizontal distribution with vertical movements (Doherty et al., 1985). Boundary mixing in coral reef lagoons is responsible for virtually all of the vertical mixing (Wolanski, 1987), but there is some evidence that the magnitude of mixing is sufficiently low in embayments and lagoons to allow larvae to maintain position. Kobayashi (1989), for example, observed consistent patterns of larval fish distributions at differing distances from patch reefs, suggesting visually mediated behavior in this fine-scale distribution. Epibenthic behavior of postflexion larvae

has been suggested to maintain larvae in specific areas (Leis et al., 1989; Breitburg, 1989); this presumably involves visual behavior and orientation to both the bottom and, in the case of schooling, to other individuals.

Physical mechanisms important for nearshore assemblages are similar but probably more varied. Localized benthic boundary layers may exist in certain areas with reduced flow, allowing aggregations of larvae (Hamner and Hauri. 1981). In contrast. highly turbulent mixing in surf zones would preclude position maintenance by larvae (Bakun, 1988). The larval fishes that have been observed in surf zones are typically later-stage larvae over relatively smooth bottoms (Senta and Kinoshita, 1985). Larger-scale interactions of currents and islands come into play as well for the nearshore assemblage. Laminar flow occurs at certain combinations of current speeds and island diameters: in laminar flow. the impinging current separates around the island and its entrained boundary layer. Thus, in gentle flows. there may be a boundary layer with little movement of water and moderately sized areas of very limited water movement ("stagnation points") both upstream and downstream (Hamner and Hauri. 1981; Fig. 1B). With increasing current flow. the thickness of this boundary layer decreases until a critical point is reached at which flow becomes turbulent. As a result. the distribution of nearshore assemblages around islands is not expected to be uniform. Regional differences in species composition (Leis. 1986b: Boehlert et al.. 1992) may be a result. Thus. current speed, proximity to bottom boundaries. bottom type or roughness. and island morphology may all affect the maintenance of nearshore assemblages.

Factors important in the formation of neritic assemblages include attributes of adult spawning, passive aggregation of positively buoyant eggs, and behavior of larvae (Table 1). Fish eggs may be advected to localized areas, providing an aggregation mechanism from more spatially dispersed spawning (see summary in Shapiro et al., 1988). Passive concentration of positively buoyant eggs into windrows may later result in concentrations of larvae. This is best demonstrated for the buoyant eggs of corals (Wolanski et al.. 1989: Black et al.. 1990) but is not well documented for fish eggs. The distribution of fish eggs in the downstream. neritic region around Johnston Island (Boehlert et al.. 1992). however. suggests that it may occur. Egg abundance in the upper 50 m of the water column showed highest densities downstream of the island (and in particular at a single station) in a moderately high background density (nearly 200 eggs·1.000 m^{-3}). At 50 to 100 m depth. egg abundances were high immediately downstream of the island (Fig. 6). but were nearly zero at greater distances. This suggests either that certain species spawn in deeper water near the island or that vertical mixing occurs. In the former case. the egg abundance may be due solely to spawning distribution. whereas in the latter case. passive accumulation may form and maintain the observed distribution. It is interesting to note the similarity of the egg distribution in Figure 6 to that of the neritic assemblage in Figure 5A. The dominant species (*Eviota epiphanes*) in that assemblage (Table 3) has demersal eggs, while some of the other species have pelagic eggs. Although physical mechanisms resulting in passive accumulation are not unique to oceanic islands, they may play an important role in the formation of spatially restricted neritic assemblages.

Current-topography interactions are important to neritic assemblages of larvae. Theory holds that with increases in current speed. flow becomes turbulent and a stable eddy pair can become entrained in the downstream area; upstream and downstream stagnation points may remain (Fig. 1C). The scale of the eddy pair is on the order of an island diameter. With further increases in current speed. one of the two eddies will increase in size and vorticity until it is shed downstream, followed by buildup and eventual shedding of the other eddy (Fig. 1D). Larvae
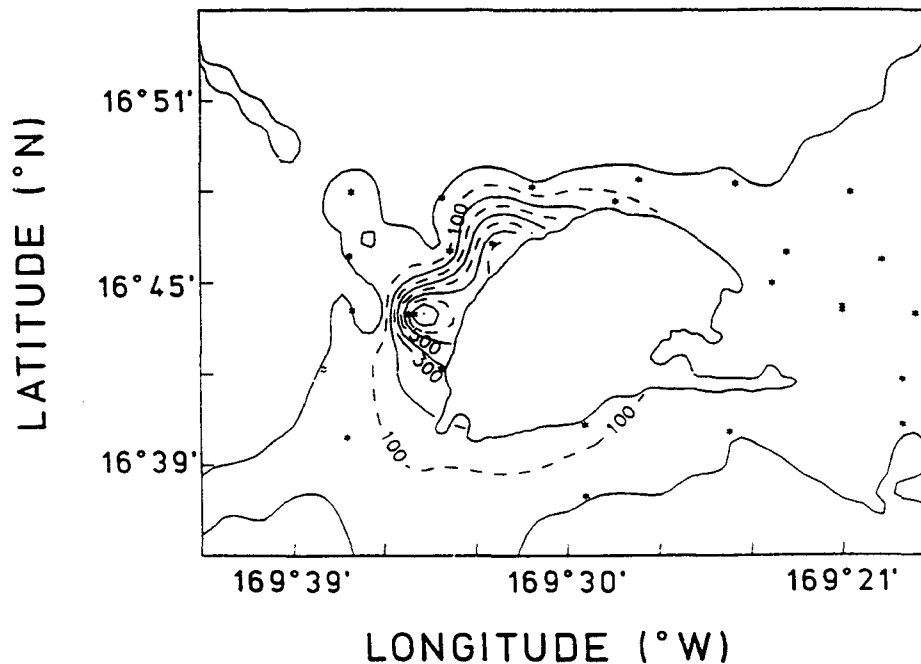
Figure 6. Distribution of fish eggs in the 50 to 100 m depth stratum around Johnston Island: the outline surrounding the island represents the 18-m isobath (from Boehlert et al.. 1992). Density notations are eggs per 1.000 m³.

may be retained in areas of limited water motion or in the entrained eddies. Larvae present in shed eddies will be advected from islands. Both physical and biological processes involved require more research. but they may affect the integrity and distribution of neritic assemblages.

Another theoretical mechanism that is pertinent to islands in tidally driven currents is rotary flow (Pingree and Maddock. 1985a). Observations at islands. however. are relatively limited: Pingree and Maddock (1985b) described movements of a drogue in waters surrounding a small island. Its behavior supported the predictions. with several clockwise loops around the island over a 3-day period. The relevance of this pattern to retention and maintenance of larval fish assemblages. however, is difficult to evaluate: little information was provided on the time scale of formation or retention of water masses around islands. Tidally generated eddies, however, are unlikely to remain near an island on the time scale important to recruitment (Wolanski and Hamner, 1988), and oceanic islands are typically less subject to tidal mixing and flow reversal as compared to islands on continental shelves (Bakun. 1988). The approach of Loder et al. (1988) could be beneficially applied in this situation. That is, analysis of time scales of water exchange in directions around an island (radially outward, rotary motions tangential to bathymetry, and in the vertical) would simplify highly complex flow patterns to allow interpretation of their role in biological phenomena.

The time scale of eddy retention is important to consider relative to assemblages. Downstream eddies with identifiable biological characteristics have been seen in several studies, but estimated time scales of water retention vary. Heywood and

Priddle (1987) estimate a minimum retention time of 11 days for an eddy characterized by high phytoplankton biomass observed downstream of King George Island in the Southern Ocean. Through downstream measurements of phytoplankton biomass, they suggested that only 50% of the phytoplankton was retained within the eddy during its residence at the island. Heywood et al. (1990) observed very distinct physical and biological features characterizing a trapped eddy downstream of Aldabra Atoll in the Indian Ocean, but it was absent 1 month later in slower flow conditions.

Upwelling in the lee of an island, as noted by Heywood et al. (1990), as well as along the flanks can interact with behavior to result in retention of larvae. Leis (1986b) suggested a related mechanism in the maintenance of larvae upstream of an island by upward swimming to maintain position in a downwelling feature. This is similar to proposed mechanisms of planktonic population maintenance through "winter cascading" off Bermuda (Boden and Kampa, 1953). The role of "linear oceanographic features" (Kingsford, 1990) may take many forms but, with appropriate behavior of the animals, can aggregate and potentially orient larval and juvenile fishes (Kingsford and Choat, 1986) in a landward direction. Tidally induced fronts may extend some distance (on the order of 2 km) from islands or reefs, thereby increasing the "effective size" of an island system (Kingsford et al., 1991).

Relatively little can be said about the nature of formation and maintenance of the oceanic assemblage. Eddy shedding from an island in a unidirectional current may develop a von Karman vortex street of eddies in downstream waters as observed by Barkley (1972) for Johnston Island. He suggested this wake would be detectable some 600 km downstream of that island. While this process would advect larval fish assemblages entrained in the eddy (presumably with species from the neritic and oceanic assemblages) far downstream, eddies from upstream along with their biological communities may be "trapped" by islands (Heywood and Priddle, 1987; Atkinson et al., 1990). Similarly, Dehknik et al. (1966) proposed that eddies transported oceanic larvae to the island of Cuba, as opposed to retaining larvae of nearshore species near the island.

Interrelations Among Assemblages: Questions of Scale. —As discussed above, the temporal and spatial bounds of ichthyoplankton assemblages around oceanic islands are poorly defined. Thus, it is difficult to evaluate the possible interrelationships among the four types of assemblages. Of the four, the spatial boundaries of the embayment and lagoon assemblage are best defined, yet little research exists on ichthyoplankton in these areas, unlike that in continental shelf islands (Leis, 1981, 1986a) or estuarine systems (Boehlert and Mundy, 1988). It is likely, however, that this assemblage has the best potential to maintain its integrity given the relative stability of the habitat and the microscale consistency of occurrence of certain species (Kobayashi, 1989). Similarly, the nearshore assemblage as defined by Leis (1978) may retain its integrity, possibly through visual orientation (i.e., bottom-oriented behavior) and use of microscale hydrographic features that may protect larvae from advection.

The neritic assemblages may be dependent upon small to mesoscale hydrographic processes and may thus be characterized by greater "leakiness" to the oceanic assemblage. Leis (1982) suggested that the neritic assemblage off Oahu may have been maintained by a small (ca. 3 km) tidally generated eddy with more stability than ocean current-generated eddies. Lobel and Robinson (1986, 1988), however, considered larger mesoscale eddies generated by local winds off the island of Hawaii as serving the same function. The scale, at some 50 to 150 km, clearly

exceeds the bounds of the neritic zones as defined above, yet the dominant species observed by Lobel and Robinson (1988) are characterized as neritic in other studies (Table 2). Lobel and Robinson (1988) suggested that larvae could complete their development during the period in which the eddy remained near the island. That these eddies expand and move off to oceanic waters periodically (Patzert, 1969), however, suggests that they may carry away significant components of the neritic assemblage, which will dissipate with time into the ocean assemblage.

It would be difficult to determine the real offshore extent of the oceanic assemblage because of the rarity of larvae. Certainly larvae of shorefishes taken at vast distances from land (Victor, 1987) have a poor chance at settlement in an appropriate habitat. Given the nature of the problem and the costs of sampling on this scale. it is doubtful that significant progress will soon be made in greater definition of this assemblage.

SUMMARY AND CONCLUSIONS

Evidence for the presence of unique ichthyoplankton assemblages is weak at best for small seamounts and equivocal at larger banks and seamounts. Some species seem to be adapted for transport of larvae away from these habitats. Seamounts may serve to disrupt oceanic ichthyoplankton assemblages through physical and biological interactions. Oceanic islands. on the other hand. have characteristic ichthyoplankton assemblages that have been described as embayment, nearshore. neritic. and oceanic. Even here. however. definition of the spatial and temporal dimensions of assemblages will require further work. The lack of identification of the assemblages by quantitative. replicated techniques means that they may only be considered as hypotheses of ecological associations. The absence of such investigations leads us to conclude our discussion of ichthyoplankton assemblages at seamounts and oceanic islands with two questions. First, "Do the proposed assemblages of fish larvae at seamounts and islands have ecological meaning?" The relationship to physical and biological factors. and the temporal and spatial robustness of island assemblages. require further attention before this can be answered. Second. "What role do these assemblages play in the maintenance of potential recruits in the two habitats?" Understanding this role may lead to improvements in our approach to dealing with questions of settlement and recruitment in seamount and oceanic island ecosystems.

ACKNOWLEDGMENTS

LITERATURE CITED

Aoki. M. and S. Ueyanagi. 1989. Larval morphology and distribution of the dolphin-fishes, *Coryphaena hippurus* and *C. equiselis* (Coryphaenidae). Tokai University Proceedings, Oceanography Section, 28: 157–174. [In Japanese. English translation by W. G. Van Campen. National Marine Fisheries Service. SW Fish. Sci. Cen. Honolulu. Laboratory translation no. 138.]

Atkinson. A.. P. Ward. J. M. Peck and A. W. A. Murray. 1990. Mesoscale distribution of zooplankton around South-Georgia. Deep-Sea Res. 37A: 1213–1227.

Atkinson. M.. S. V. Smith and E. D. Stroup. 1981. Circulation in Enewetak Atoll lagoon. Limnol. Oceanog. 26: 1074–1083.

Bakun. A. 1988. Local retention of planktonic early life stages in tropical reef/bank demersal systems: the role of vertically-structured hydrodynamic processes. Pages 15–22 *in* D. Pauly and A. Yañez-

Arancibia, eds. IOC Workshop Report no. 44 (Supplement), UNESCO, Paris. Papers submitted to the IREP (OSLR) Workshop on Recruitment in Tropical Coastal Demersal Communities. Ciudad del Carmen, Mexico, April 1986.

Barkley, R. A. 1972. Johnston Atoll's wake. J. Mar. Res. 30: 201–216.

Barnett, A. M., A. E. Jahn, P. D. Sertic and W. Watson. 1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow waters. Fish. Bull. U.S. 82: 97–111.

Belyanina, T. N. 1984. Observations on the ichthyofauna in the open waters of the Atlantic near the Great-Meteor Seamount. J. Ichthy. 24: 127–129.

————. 1985. Preliminary data on ichthyoplankton near seamounts of the northwest Indian Ocean. Oceanol. 25: 778–780.

Belyayev, V. A. 1990. Formation of new elements in the structure of the range of epipelagic fishes in the area of the Kuroshio Current. J. Ichthy. 30: 90–100.

Bezrukov, Yu. F. and V. V. Natarov. 1976. Formation of abiotic conditions over underwater elevations of some areas of the Pacific Ocean. Izvestiya TINRO 100: 93–99.

Black, K. P. and P. J. Moran. 1991. Influence of hydrodynamics on the passive dispersal and initial recruitment of larvae of Acanthaster planci (Echinodermata: Asteroidea) on the Great Barrier Reef. Mar. Ecol. Prog. Ser. 69: 55–65.

————, S. L. Gray and J. C. Andrews. 1990. Residence times of neutrally-bouyant matter such as larvae, sewage or nutrients on coral reefs. Coral Reefs 9: 105–114.

Boden, B. P. and E. M. Kampa. 1953. Winter cascading from an oceanic island and its biological implication. Nature 171: 426.

Boehlert, G. W. 1988. Current-topography interactions at mid-ocean seamounts and the impact on pelagic ecosystems. GeoJournal 16: 45–62.

———— and A. Genin. 1987. A review of the effects of seamounts on biological processes. Pages 319–334 in B. H. Keating, P. Fryer, R. Batiza and G. W. Boehlert, eds. Seamounts, islands, and atolls. Am. Geophy. Union. Geophys. Monogr. no. 43.

———— and B. C. Mundy. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Am. Fish. Soc. Symp. 3: 51–67.

———— and ————. 1991. Vertical and onshore-offshore distribution of tuna larvae (Pisces, Scombridae) off Oahu, Hawaii. SW Fish. Sci. C. Admin. Rep. H-91-11. 40 pp.

———— and T. Sasaki. 1988. Pelagic biogeography of the armorhead, Pseudopentaceros wheeleri, and recruitment to isolated seamounts in the North Pacific Ocean. Fish. Bull. U.S. 86: 453–465.

————, W. Watson and L. C. Sun. 1992. Horizontal and vertical distributions of larval fishes around an isolated oceanic island in the tropical Pacific. Deep-Sea Res. 39:439–466.

Bourret, P., D. Binet, C. Hoffschir, J. Rivaton and H. Velayoudon. 1979. Evaluation de "l'effet d'ile" d'un atoll: plancton et micronecton au large de Mururoa (Tuamotus). Office de la Recherche Scientifique et Technique Outre-Mer. Centre de Noumea. Nouvelle-Caledonie. 124 pp.

Breitburg, D. L. 1989. Demersal schooling prior to settlement by larvae of the naked goby. Environ. Biol. Fish. 26: 97–103.

Brink, K. H. 1989. The effect of stratification on seamount-trapped waves. Deep-Sea Res. 36: 825–844.

Campana, S. E., S. J. Smith, and P. C. F. Hurley. 1989. A drift retention dichotomy for larval haddock (Melanogrammus aeglefinus) spawned on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 93–102.

Cheney, R. E., P. L. Richardson and K. Nagasaka. 1980. Tracing a Kuroshio ring with a free drifting buoy. Deep-Sea Res. 27: 641–654.

Clarke, T. A. 1991. Larvae of nearshore fishes in oceanic waters near Oahu, Hawaii. NOAA Tech. Rep. NMFS 101: 1–19.

Dandonneau, Y. and L. Charpy. 1985. An empirical approach to the island mass effect in the south tropical Pacific based on sea surface chlorophyll concentrations. Deep-Sea Res. 32: 707–721.

Darnitsky, V. B., N. I. Zigel'man and S. A. Shakhunova. 1984. Variability of the levels of nutrient content in the boundary layer of Wangenella Bank. Pages 107–116 in Problems of the oceanography of the Pacific Ocean and Far Eastern seas. Gidrometeoizdat. no. 111, Leningrad: [In Russian. English translation by W. V. Van Campen. National Marine Fisheries Service, SW Fish. Cen., Honolulu. Laboratory translation no. 123]

Dehknik, T. V., M. Juarez and D. Salabria. 1966. Distribution of pelagic fish eggs and larvae in Cuban waters. Pages 131–170 in Issledonvaniya Tsentral'no-amrikanskih Morei. Naukova Dumka, Kiev. [Partial English translation by W. L. Klawe. Inter-American Tropical Tuna Commission, La Jolla, California.]

Doherty, P. J., D. Williams and P. F. Sale. 1985. The adaptive significance of larval dispersal in coral reef fishes. Environ. Biol. Fish. 12: 81–90.

Dooley, H. D. 1984. Aspects of oceanographic variability on Scottish fishing grounds. Ph.D. Thesis. University of Aberdeen, Aberdeen, Scotland. 154 pp.

Doty, M. S. and M. Oguri. 1956. The island mass effect. J. Cons. 22: 33–37.

Eide, L. I. 1979. Evidence of a topographically trapped vortex on the Norwegian continental shelf. Deep-Sea Res. 26: 601–621.

Eriksen, C. C. 1982. Observations of internal wave reflection off sloping bottoms. J. Geophy. Res. 87: 525–538.

Fedoryako, B. I. 1989. The influence of the vicinity of islands and continental shelf on the ichthyofauna of the upper epipelagial in the equatorial zones of the Indian Ocean and the western Pacific. J. Ichthy. 29: 30–35.

Frank, K. T. and W. C. Leggett. 1983. Multispecies larval fish associations: accident or adaptation? Can. J. Fish. Aquat. Sci. 40: 754–762.

Genin, A. and G. W. Boehlert. 1985. Dynamics of temperature and chlorophyll structures above a seamount: an oceanic experiment. J. Mar. Res. 28: 907–924.

————, L. Haury and P. Greenblatt. 1988. Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. Deep-Sea Res. 35: 151–175.

Gilmartin, M. and N. Revelante. 1974. The "island mass" effect on the phytoplankton and primary production of the Hawaiian Islands. J. Exper. Mar. Biol. Ecol. 16: 181–204.

Gordina, A. D. and V. B. Bladimirtsev. 1987. Distribution of ichthyoplankton in the regions of bottom elevations in the tropical part of the Indian Ocean. J. Ichthy. 27: 79–84.

Gosline, W. A. and V. E. Brock. 1960. Handbook of Hawaiian fishes. University of Hawaii Press. Honolulu. 372 pp.

Hamner, W. M. and K. R. Hauri. 1981. Effects of island mass: water flow and plankton pattern around a reef in the Great Barrier Reef Lagoon. Australia. Limnol. Oceanogr. 26: 1084–1103.

Hernandez-Leon, S. 1988. Gradients of mesozooplankton biomass and ETS activity in the wind-shear area as evidence of an island mass effect in the Canary Island waters. J. Plankton Res. 10: 1141–1154.

————. 1991. Accumulation of mesozooplankton in a wake area as a causative mechanism of the "island-mass effect." Mar. Biol. 109: 141–147.

Heywood, K. J., E. D. Barton, and J. H. Simpson. 1990. The effects of flow disturbance by an oceanic island. J. Mar. Res. 48: 55–73.

Heywood, R. B. and J. Priddle. 1987. Retention of phytoplankton by an eddy. Cont. Shelf Res. 7: 937–955.

Higgins, B. E. 1970. Juvenile tunas collected by midwater trawling in Hawaiian waters, July–September 1967. Trans. Am. Fish. Soc. 99: 60–69.

Hirota, J., S. Taguchi, R. F. Shuman and A. E. Jahn. 1980. Distributions of plankton stocks. productivity, and potential fishery yield in Hawaiian waters. Pages 191–203 in R. W. Grigg and R. T. Pfund. eds. Proceedings of the symposium on status of resource investigations in the Northwestern Hawaiian Islands. University of Hawaii Sea Grant Miscellaneous Report UNIHI-SEAGRANT-MR-80-04. Honolulu. Hawaii.

Hogg, N. G. 1980. Effects of bottom topography on ocean currents. Pages 167–205 in R. Hide and P. White. eds. Orographic effects in planetary flows. Global Atmospheric Research Program (GARP) Publication Series 23. World Meteorological Organization—International Council of Scientific Unions (WMO-ICSU). Geneva.

Hunter, J. R. and C. A. Kimbrell. 1980. Early life history of Pacific mackerel. Scomber japonicus. Fish. Bull. U.S. 78: 89–101.

———— and G. L. Thomas. 1974. Effect of prey distribution and density on the searching and feeding behavior of larval anchovy Engraulis mordax Girard. Pages 559–574 in J. H. S. Blaxter. ed. The early life history of fish. Springer-Verlag. New York. 765 pp.

Huppert, H. E. and K. Bryan. 1976. Topographically generated eddies. Deep-Sea Res. 23: 655–679.

Jahn, A. E. and R. J. Lavenberg. 1986. Fine-scale distribution of near-shore, suprabenthic fish larvae. Mar. Ecol. Prog. Ser. 31: 223–231.

Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Envir. Biol. Fish. 3: 65–84.

Jones, E. C. 1962. Evidence of an island effect upon the standing crop of zooplankton near the Marquesas Island, central Pacific. J. Cons. 27: 223–231.

Kingsford, M. J. 1990. Linear oceanographic features: a focus for research on recruitment processes. Aust. J. Ecol. 15: 391–401.

———— and J. H. Choat. 1986. Influence of surface slicks on the distribution and onshore movement of small fish. Mar. Biol. 91: 161–172.

————. E. Wolanski and J. H. Choat. 1991. Influence of tidally induced fronts and Langmuir circulations on distribution and movements of presettlement fishes around a coral reef. Mar. Biol. 109: 167–180.

Kobayashi, D. R. 1989. Fine-scale distribution of larval fishes: patterns and processes adjacent to coral reefs in Kaneohe Bay, Hawaii. Mar. Biol. 100: 285–293.

Leis, J. M. 1978. Distributional ecology of ichthyoplankton and invertebrate macrozooplankton in the vicinity of a Hawaiian coastal power plant. Ph.D. Thesis, University of Hawaii, Honolulu. 317 pp.

———. 1981. Distribution of fish larvae around Lizard Island, Great Barrier Reef: coral reef lagoon as refuge? Pages 471–477 in E. D. Gomez et al. Proceedings of the Fourth International Coral Reef Symposium. Marine Science Center, University of the Philippines, Quezon City.

———. 1982. Nearshore distributional gradients of larval fish (15 taxa) and planktonic crustaceans (6 taxa) in Hawaii. Mar. Biol. 72: 89–97.

———. 1983. Coral reef fish larvae (Labridae) in the East Pacific Barrier. Copeia 1983: 826–828.

———. 1984. Larval fish dispersal and the East Pacific Barrier. Oceanog. Trop. 19: 181–192.

———. 1986a. Ecological requirements of Indo-Pacific larval fishes: a neglected zoogeographic factor. Pages 759–766 in Indo-Pacific Fish Biology: Proceedings of the 2nd International Conference on Indo-Pacific Fishes. Ichthyological Society of Japan, Tokyo, Japan.

———. 1986b. Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. Mar. Biol. 90: 505–516.

———. 1987. Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae). Pages 189–238 in J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers. Biology and fisheries management. Westview Press, Boulder.

———. 1989. Larval biology of butterflyfishes (Pisces, Chaetodontidae): what do we really know? Environ. Biol. Fish. 25: 87–100.

———. 1991. The pelagic stage of reef fishes: The larval biology of coral reef fishes. Pages 183–230 in P. F. Sale, ed. The ecology of fishes on coral reefs. Academic Press, San Diego. 754 pp.

——— and B. Goldman. 1987. Composition and distribution of larval fish assemblages in the Great Barrier Reef Lagoon, near Lizard Island, Australia. Aust. J. Mar. Freshwater Res. 38: 211–223.

——— and J. M. Miller. 1976. Offshore distributional patterns of Hawaiian fish larvae. Mar. Biol. 36: 359–367.

———, B. Goldman and S. E. Reader. 1989. Epibenthic fish larvae in the Great Barrier Reef Lagoon near Lizard Island, Australia. Jap. J. Ichthy. 35: 428–433.

———, ——— and S. Ueyanagi. 1987. Distribution and abundance of billfish larvae (Pisces: Istiophoridae) in the Great Barrier Reef Lagoon and Coral Sea near Lizard Island, Australia. Fish. Bull. U.S. 85: 757–765.

———, T. Trnski, M. Harmelin-Vivien, J.-P. Renon, V. Dufour, M. K. El Moudni and R. Galzin. 1991. High concentrations of tuna larvae (Pisces: Scombridae) in near-reef waters of French Polynesia (Society and Tuamotu Islands). Bull. Mar. Sci. 48: 150–158.

Lobel, P. S. and A. R. Robinson. 1986. Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. Deep-Sea Res. 33: 483–500.

——— and ———. 1988. Larval fishes and zooplankton in a cyclonic eddy in Hawaiian waters. J. Plankton Res. 10: 1209–1223.

Loder, J. W., C. K. Ross and P. C. Smith. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic continental shelf. Can. J. Fish. Aquat. Sci. 45: 1860–1885.

Lutjeharms, J. R. E. and A. E. F. Heydorn. 1981. Recruitment of rock lobster on Vema Seamount from the islands of Tristan da Cunha. Deep-Sea Res. 28A: 1237.

Marliave, J. B. 1986. Lack of planktonic dispersal of rocky intertidal fish larvae. Trans. Am. Fish. Soc. 115: 149–154.

Meincke, J. 1971. Observations of an anticyclonic vortex trapped above a seamount. J. Geophys. Res. 76: 7432–7440.

Miller, G. C. and L. P. Woods. 1988. A new species of sciaenid fish, Pareques iwamotoi, from the western Atlantic, with color descriptions of prejuvenile and juvenile Pareques acuminatus and Pareques umbrosus. Bull. Mar. Sci. 43: 88–92.

Miller, J. M. 1974. Nearshore distribution of Hawaiian marine fish larvae: effects of water quality, turbidity and currents. Pages 217–231 in J. H. S. Blaxter, ed. The early life history of fish. Springer-Verlag, New York.

———. 1979. Nearshore abundance of tuna (Pisces: Scombridae) larvae in the Hawaiian Islands. Bull. Mar. Sci. 29: 19–26.

———, W. Watson and J. M. Leis. 1979. An atlas of common nearshore marine fish larvae of the Hawaiian Islands. University of Hawaii Sea Grant. Miscell. Rep. UNIHI-SEAGRANT-MR-80-02. Honolulu. 179 pp.

Mundy, B. C. 1990. Development of larvae and juveniles of the alfonsins, Beryx splendens and B. decadactylus (Berycidae, Beryciformes). Bull. Mar. Sci. 46: 257–273.

Nellen, W. 1973. Untersuchungen zür Verteilung von Fischlarven und Plankton im Gebiet der Grossen Meteorbank. "Meteor" Forschungs-Ergebnisse 13: 47–69.

————. 1974. Investigations on the distribution of fish larvae and plankton near and above the Great Meteor Seamount. *In* J. H. S. Blaxter, ed. The early life history of fish. Springer-Verlag, New York.

Olla, B. L. and M. W. Davis. 1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser. 63: 105–112.

Owens, W. B. and N. G. Hogg. 1980. Oceanic observations of stratified Taylor columns near a bump. Deep-Sea Res. 27: 1029–1045.

Patzert, W. D. 1969. Eddies in Hawaiian waters. Hawaii Inst. Geoph. Rep. 69-8: 1–51.

Pingree, R. D. and L. Maddock. 1985a. Rotary currents and residual circulation around banks and islands. Deep-Sea Res. 32: 929–947.

———— and ————. 1985b. Stokes, Euler and Lagrangian aspects of residual tidal transports in the English Channel and the southern bight of the North Sea. J. Mar. Biol. Assoc. U.K. 65: 969–982.

Powles. H. 1977. Description of larval *Jenkinsia lamprotaenia* (Clupeidae, Dussumieriinae) and their distribution off Barbados. West Indies. Bull. Mar. Sci. 27: 788–801.

———— and W. E. Burgess. 1978. Observations on benthic larvae of *Pareques* (Sciaenidae). Copeia 1978: 169–172.

————. F. Auger and G. J. FitzGerald. 1984. Nearshore ichthyoplankton of a north temperate estuary. Can. J. Fish. Aquat. Sci. 41: 1653–1663.

Randall, J. E. 1961. A contribution to the biology of the convict surgeonfish of the Hawaiian Islands. *Acanthurus triostegus sandvicensis*. Pac. Sci. 15: 215–272.

Robertson, D. A. and S. Mito. 1979. Sea surface ichthyoplankton off southeastern New Zealand. summer 1977–1978. N.Z. J. Mar. Freshwater Res. 13: 415–424.

Royer, T. C. 1978. Ocean eddies generated by seamounts in the North Pacific. Science 199: 1063–1064.

Sale, P. F. 1970. Distribution of larval Acanthuridae off Hawaii. Copeia 1970: 765–766.

Sammarco, P. W. and J. C. Andrews. 1989. The Helix experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals. Limnol. Oceanog. 34: 896–912.

Sasaki, T. 1986. Development and present status of Japanese trawl fisheries in the vicinity of seamounts. Pages 21–30 *in* R. N. Uchida, S. Hayashi and G. W. Boehlert, eds. Environment and resources of seamounts in the North Pacific. NOAA Tech. Rep. NMFS 43.

Senta, T. and I. Kinoshita. 1985. Larval and juvenile fishes occurring in surf zones of western Japan. Trans. Am. Fish. Soc. 114: 609–618.

Shapiro, D. Y., D. A. Hensley and R. S. Appeldoorn. 1988. Pelagic spawning and egg transport in the coral-reef fishes: a skeptical overview. Environ. Biol. Fish. 22: 3–14.

Shomura, R. S. and R. A. Barkley. 1980. Ecosystem dynamics of seamounts—a working hypothesis. Pages 789–790 *in* The Kuroshio IV. Proceedings of the Fourth Symposium for the Cooperative Study of the Kuroshio and Adjacent Regions. the Japanese Academy, Tokyo, Japan. 14–17 February 1979. Saikon Publisher, Tokyo.

Smith, W. G. and W. W. Morse. 1985. Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region. a gyre-influenced spawning area. Mar. Ecol. Prog. Ser. 24: 1–13.

Smith, C. L., J. C. Tyler and L. Stillman. 1987. Inshore ichthyoplankton: a distinctive assemblage. Bull. Mar. Sci. 41: 432–440.

Sulkin, S. 1986. Application of laboratory studies of larval behavior to fisheries problems. Can. J. Fish. Aquat. Sci. 43: 2184–2188.

Taylor, G. I. 1917. Motions of solids in fluids when the flow is not irrotational. Proc. Royal Soc. London. A 93: 99–113.

Thresher, R. E. and E. B. Brothers. 1989. Evidence of intra-oceanic and inter-oceanic regional differences in the early life history of reef-associated fishes. Mar. Ecol. Prog. Ser. 57: 187–205.

Uda, M. and M. Ishino. 1958. Enrichment pattern resulting from eddy systems in relation to fishing grounds. J. Tokyo U. Fish. 44: 105–129.

Vasilenko, A. V. and T. G. Sokolovskaya. 1989. On mass penetrations of the Japanese horsemackerel, *Trachurus japonicus*, and the black filefish, *Navodon modestus*, into the open waters of the Northwestern Pacific Ocean. J. Ichthy. 29: 99–102.

Victor, B. C. 1987. Growth, dispersal, and identification of planktonic labrid and pomacentrid reef-fish larvae in the eastern Pacific Ocean. Mar. Biol. 95: 145–152.

Watson, W. and J. M. Leis. 1974. Ichthyoplankton of Kaneohe Bay, Hawaii. A one-year study of fish eggs and larvae. U. Hawaii Sea Grant. Tech. Rep. UNIHI-SEAGRANT-TR-75-01, Honolulu, Hawaii. 178 pp.

Wilson, R. R., Jr. and R. S. Kaufman. 1987. Seamount biota and biogeography. Pages 355–377 *in* B. H. Keating, P. Fryer, R. Batiza and G. W. Boehlert, eds. Seamounts, islands, and atolls. Am. Geophy. Union. Geophy. Mono. no. 43.

Wolanski, E. 1987. Some evidence for boundary mixing near coral reefs. Limnol. Oceanog. 32: 735–739.
————— and W. M. Hamner. 1988. Topographically controlled fronts in the ocean and their biological influence. Science 241: 177–181.
—————. D. Burrage and B. King. 1989. Trapping and dispersion of coral eggs around Bowden Reef, Great Barrier Reef, following mass coral spawning. Cont. Shelf Res. 9: 479–496.
Wyatt, J. R. 1982. The distribution, abundance and development of young Jamaican reef fishes. Scientific report of the U.W.I.-O.D.A. fisheries ecology research project 1974–1979. Res. Rep. Zool. Depart. University of the West Ind. no. 63 (part 1, section 1: 1–40, section 2): 1–112.
Young, P. C., J. M. Leis and H. F. Hausfield. 1986. Seasonal and spatial distribution of fish larvae in waters over the north west continental shelf of western Australia. Mar. Ecol. Progr. Ser. 31: 209–222.

ADDRESSES: (G.W.B., B.C.M.) Honolulu Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, Hawaii 96822-2396; PRESENT ADDRESS: (G.W.B.) Pacific Fisheries Environmental Group, P.O. Box 831, Monterey, California 93942.