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Horizontal and vertical distributions of larval fishes around an isolated oceanic island in the tropical Pacific

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Abstract—Ichthyoplankton and oceanographic sampling was conducted in November 1984 in waters surrounding Johnston Atoll (16°44′N, 169°32′W), a small, isolated atoll in the central Pacific Ocean. The typical flow pattern in this region is westward; the nearest island is in the Hawaiian Archipelago, 760 km away.

Most collections were dominated by oceanic taxa. In the 0–50 m stratum, larval densities were relatively uniform horizontally, but densities down-current of the island tended to be higher, and fish eggs were concentrated there. In the 50–100 m stratum, larval abundance on the down-current side of the island was markedly higher than either up-current or farther down-current. Oceanic taxa did not display this pattern, while marked areas of very high abundance characterized the island-related taxa, the most abundant including the gobiid *Eviota epiphanes* and the apogonid *Pseudamiops* sp. Estimates of geostrophic flow indicate that the region down-current of the atoll was one of return flow associated with apparent mesoscale eddies or meanders north and west of the island. This region may serve as a down-current retention area for the pelagic larvae of island-related taxa and may facilitate recruitment back to the source populations.

INTRODUCTION

THE mechanism of population maintenance in the marine fauna of islands is an important question in population biology (EHRLICH, 1975; DOHERTY and WILLIAMS, 1988). Lacking an upstream source population, island species with small, pelagic larval stages must rely on local recruitment to maintain their populations despite often unidirectional ocean currents that can advect larvae away. Peculiar distributional features of larvae near islands and coral reefs have been documented in a variety of studies (LEIS and MILLER, 1976; LEIS, 1982b; SMITH *et al.*, 1987; KOBAYASHI, 1989). Several mechanisms have been proposed for the maintenance of plankton and fish larvae near islands: "winter cascading" (BODEN and KAMPA, 1953), retention in eddies remaining near islands (SALE, 1970; EMERY, 1972), flow–topography interactions and tidal features (HAMNER and HAURI, 1981; WOLANSKI and

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Hamner, 1988) and behavioral patterns such as ontogenetic migration or epibenthic schooling (Leis *et al.*, 1989).

The adaptive significance of pelagic larvae in tropical waters historically has been thought to be related to long-distance dispersal (Barlow, 1981). An alternate view is that a pelagic phase with young, vulnerable life stages in offshore waters results in significantly reduced predation pressure compared to reef waters (Johannes, 1978). This view assumes that mortality due to advection is more than offset by the lower predation pressure in offshore waters. While early studies of tropical reef populations suggested that space availability structured communities (Ehrlich, 1975), most recent papers have concluded that recruitment variability plays a major role in population dynamics, a role fundamentally similar in tropical and temperate systems (see review by Doherty and Williams, 1988). The spatial component of recruitment variability is relatively small compared with the large intra- and interannual component (Shulman, 1985). Choat *et al.* (1988) have suggested that the spatial variability may be a result of settlement and habitat selection, whereas temporal variability is related to specific, and often rare, oceanographic events that lead to strong recruitment for island fish fauna.

Obviously variability in advective processes is an important component of recruitment variability, particularly for maintaining a population at an isolated island. Johannes (1978) suggested that spawning during seasons of weakest prevailing currents and winds may help retain larvae in waters near the island, and Lobel (1989) suggested that spawning peaks coincide with the highest prevalence of mesoscale eddies. The evidence for concentrations of larval fish coinciding with eddies or other features needed to support these arguments is equivocal. In this paper, we examine the distribution of ichthyoplankton around an isolated oceanic island and assess the distributional patterns in light of physical oceanographic conditions.

MATERIALS AND METHODS

The study site was Johnston Atoll, located at 16°44′N, 169°32′W in the central Pacific Ocean, composed of a reef with four small islands in a lagoon approximately 20 km across the long axis of its 18 m isobath. The nearest land is French Frigate Shoals, a group of small islands in the Hawaiian Archipelago, some 760 km to the north. Surveys were conducted aboard the NOAA ship *Townsend Cromwell* during November 1984.

Environmental sampling was conducted with expendable bathythermograph (XBTs, Sippican T-4) and conductivity–temperature–depth (CTD) stations. A 93 km × 93 km grid, symmetrical around the island, was developed, and XBT and CTD stations were occupied in a regular pattern in this grid. The CTD data were processed following Roden and Irish (1975) using algorithms from Fofonoff and Millard (1983).

Ichthyoplankton was sampled at night with an opening–closing Tucker trawl (Clarke, 1969) with three nets and a double-release mechanism operated by messengers (Boehlert *et al.*, 1985). Each net was 0.333 mm mesh (Nitex) with a 1.4 m^2 mouth. Ship speed varied between 0.9 and 1.1 $m\ s^{-1}$ to maintain a wire angle of 45°. At this angle, the effective mouth area of the net is 1.0 m^2. Since no time–depth recorder was available, tow depths were estimated as a function of wire angle and meters of wire out.

Samples were taken to describe both the vertical and horizontal distributions of ichthyoplankton. Four nominal depth strata (0–25, 25–50, 50–100 and 100–200 m) were initially sampled at four stations to describe the pattern of vertical distribution. An uncontaminated, discrete-depth sample was collected in the second net by lowering the trawl with the first net open, opening the second net for the desired sampling time and then closing it. The two shallower strata were sampled in a single deployment by lowering the net to 50 m, opening the second net and then opening the third net at a depth of 25 m. For the two deeper strata, the second net was closed at the upper end of the stratum, and the trawl was retrieved with the third net open. Within each stratum, the net was fished in a stepped oblique fashion. Based upon a preliminary assessment of early sampling, larvae were most abundant in the 50–100 m stratum. Stations to determine the pattern of geographic distribution around the island were thus sampled at 0–50 and 50–100 m. The long axis of the station grid was oriented east–west in the general current flow pattern in this region (BARKLEY, 1972).

Tows were 12–24 min in duration. Water volumes filtered were estimated with a calibrated General Oceanics flowmeter mounted in the center of each net. Missing flowmeter readings were estimated using standard methods (SMITH and RICHARDSON, 1977). Plankton samples were preserved at sea in 10% buffered formalin. Displacement volumes of plankton were measured by the difference after straining plankton from a known total volume and measuring the water volume (OMORI and IKEDA, 1984).

Whole samples were sorted for fish eggs and larvae and squid larvae in the laboratory using a dissecting microscope. Larvae were identified to the lowest possible taxon following MILLER *et al.* (1979), MOSER *et al.* (1984), LEIS and RENNIS (1984) and several unpublished sources. Larvae were categorized as either yolk-sac, preflexion, flexion, postflexion, juvenile/adult or unclassified (damaged specimens that could not be classified). After analysis, specimens were stored in 5% buffered formalin.

Larvae were divided into three different types based upon the habitat occupied by the adults. "Island" larvae are taxa whose adult stages are found in association with the island. "Oceanic" larvae are those with adult stages in open ocean waters; examples are reef fishes and mesopelagic fishes, respectively. The third larval type consists of species whose adult affiliation with habitat is unclear, or are a combination of different taxa that renders the classification meaningless (e.g. categories "Anguilliformes" or "unidentified larvae").

Data analysis

Optimal estimation of ocean current field. Temperature profiles combined with mean temperature–salinity (T–S) relations from six CTD casts in the study area provided density profiles. Combining XBT observations with T–S relations yielded dynamic height profiles. Dynamic height was computed relative to 450 m.

The dynamic height data were interpolated objectively by a statistical procedure, "objective analysis", that is detailed elsewhere (GANDIN, 1965; BRETHERTON *et al.*, 1976; CARTER, 1983; SUN *et al.*, 1988). The correlation function needed by objective analysis was assumed to be in the form of

$$F(r) = \left(1 - \frac{r^2}{b^2}\right) \exp\left(-\frac{r^2}{2b^2}\right),$$

where r is the spatial interval and b is the spatial correlation scale, either a typical eddy or the first Rossby radius, R_i, in the study area (CARTER and ROBINSON, 1987). ROBINSON *et al.* (1986) determined the spatial correlation scale from dynamic height data observed in the

California Current region and fitted the correlation with the above formula. Due to the nature of our data, the determination of correlation scale from dynamic height data is not feasible. EMERY *et al.* (1984) calculated R_i from hydrocast data for 5° squares of the North Pacific. They found that the R_i values in an open ocean area near Johnston Atoll were approximately 75 km. Based upon their findings, we chose a typical correlation scale on the order of 75 km. The objectively interpolated dynamic height data were then smoothed by using a Shapiro filter of order 4 (SHAPIRO, 1970). Such filtering can remove unresolvable, small-scale features of two grid-point intervals.

Ichthyoplankton data. Egg and larval densities were standardized as number per 1000 m^3 of water filtered in each tow. Because of the non-normal distribution of ichthyoplankton data, pairwise comparisons of abundance in differing locations or depth strata were made using a randomization *t*-test (SOKAL and ROHLF, 1981) with 10,000 randomized iterations. This test requires no assumptions about the underlying distribution of the data. Geographic plots of larval abundance isopleths were made using Golden Graphics "Surfer" software; grids were developed by using kriging, and the resultant plots smoothed by cubic spline.

Assemblage groupings of fish larvae and habitats were determined with a Braun–Blanquet two-way synthesis table technique (MUELLER-DOMBOIS and BRIDGES, 1981) using the 1987 version of the COENOS program (CESKA and ROEMER, 1971). This program first rejects species with cosmopolitan distributions (those occurring in more than two-thirds of all samples). Similar species are then combined into groups based upon co-occurrence in the samples. Co-occurrence is defined by presence or absence, independent of abundance. A taxon was included in a group if the species occurred in at least 50% of the sites where that group occurred and in no more than 20% of the sites outside this group. Analysis was based upon all samples with a subset of 90 taxa, excluding very rare taxa and higher level taxa that comprise several species.

RESULTS

Oceanographic conditions

Thirty-four XBT and six CTD casts were taken over a 8650 km^2 domain (Fig. 1) during 11–12 November 1984 to describe the physical environment. Surface temperatures ranged from 27.2° to 27.6°C; a typical temperature profile (Fig. 2) was characterized by an isothermal mixed layer of approximately 100 m depth and declining temperature with depth below the mixed layer. The mixed layer depth (as judged by the 26.8°C isotherm) varied from 60 to 106 m, and the temperature range at 100 m was 24.5° to 27.2°C.

The estimated geostrophic current field at the surface is characterized by current speeds of up to about 30 cm s^{-1} (Fig. 3A). The pattern is similar at 100 m (Fig. 3B). The geostrophic flow pattern supports the general pattern of westward flow to the east of the island, characteristic of this latitude (BARKLEY, 1972), but complexities in flow suggest either eddies or meandering wave crests near the island. Flow was eastward to the north side of the island, with the suggestion of a mesoscale cyclonic eddy at the north end of the domain (Fig. 3). The eastward return flow on the west side of the island was associated with this supposed eddy and with a feature suggestive of a mesoscale anticyclonic eddy (or meander) east-southeast of the island. A stagnant region clearly seen just off the northwest coast of the island was associated with the region of eastward (return) flow.

Larval distribution

Ichthyoplankton sampling was conducted at 44 stations on the nights of 13–21 November 1984 to describe larval fish distribution (Fig. 4). Most stations were near the atoll, although some were as far away as 38.2 km east and 65.2 km west of the island. A

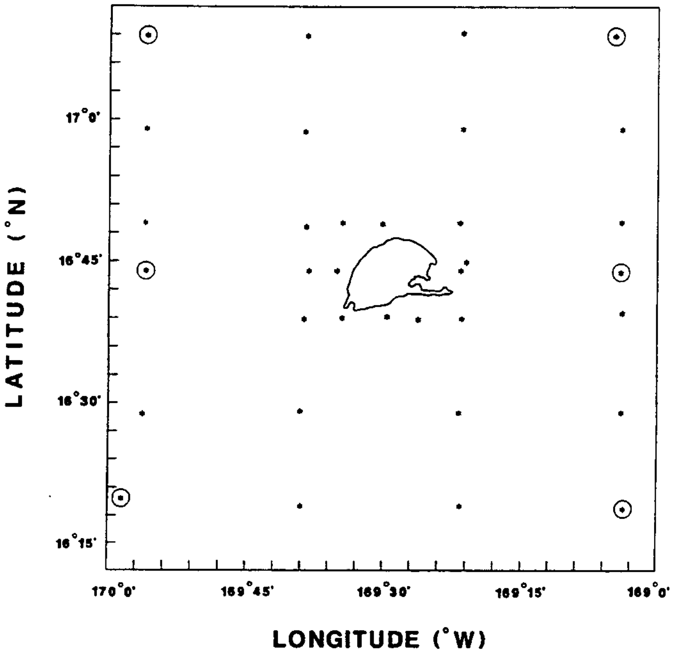

Fig. 1. Locations of 34 XBT stations (asterisks) and CTD stations (circles) around Johnston Atoll. The outline at the center indicates the 18 m isobath surrounding the atoll.

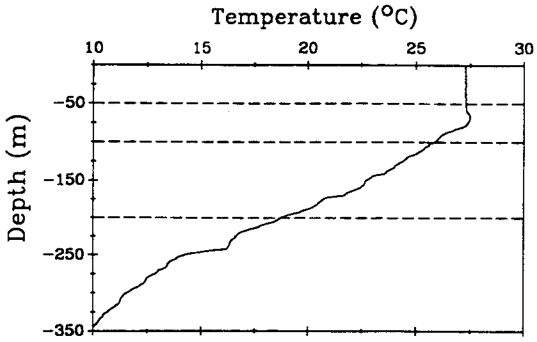

Fig. 2. Temperature profile of a typical XBT cast taken near Johnston Island. Note the extent of the isothermal mixed layer. Horizontal dashed lines indicate the boundaries of the major depth strata sampled for ichthyoplankton.

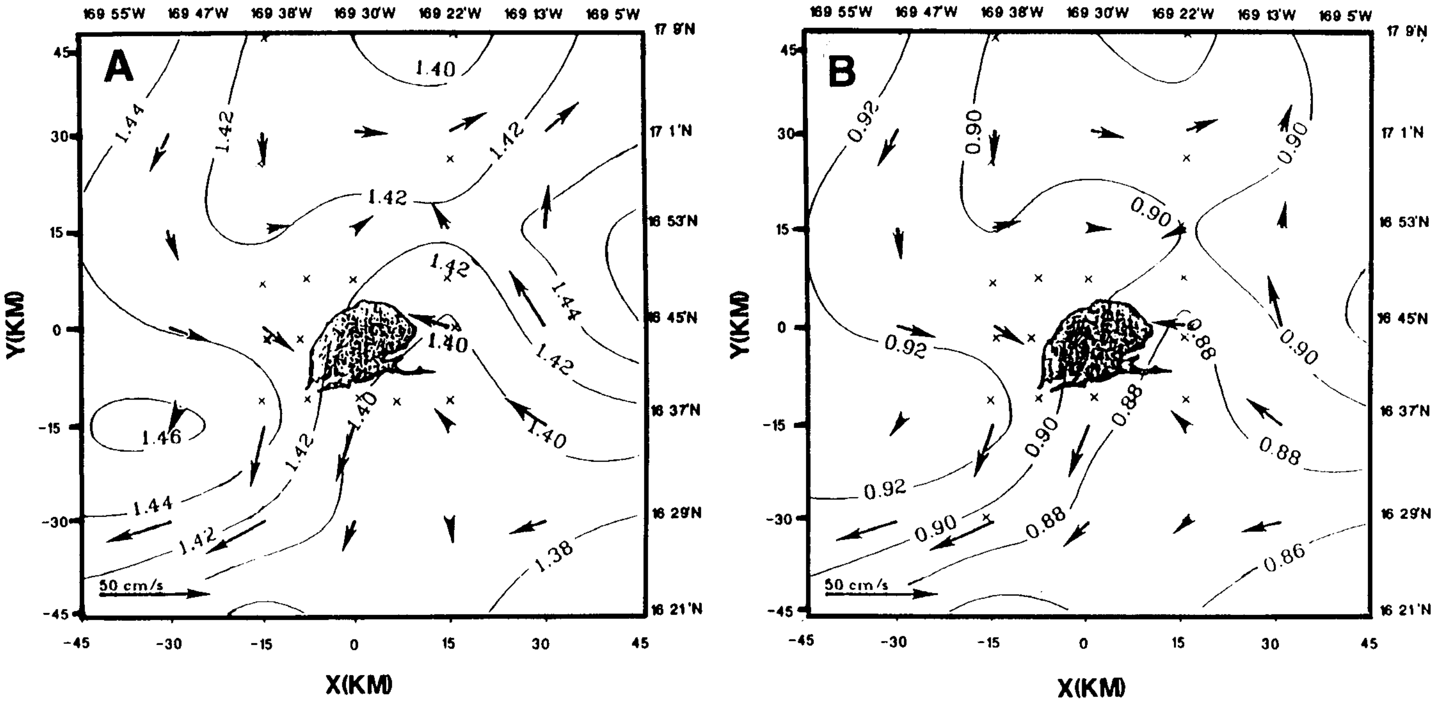

Fig. 3. Objective analysis-based quasi-geostrophic flow pattern at (A) the surface and (B) 100 m relative to 450 m. Contours are dynamic height in dyn. m. Arrows represent current vectors, arrow tails indicate the grid points where the geostrophic flows were actually computed, and their lengths represent current speed. Xs indicate XBT stations. Note that the extent of this domain is less than that in Fig. 1.

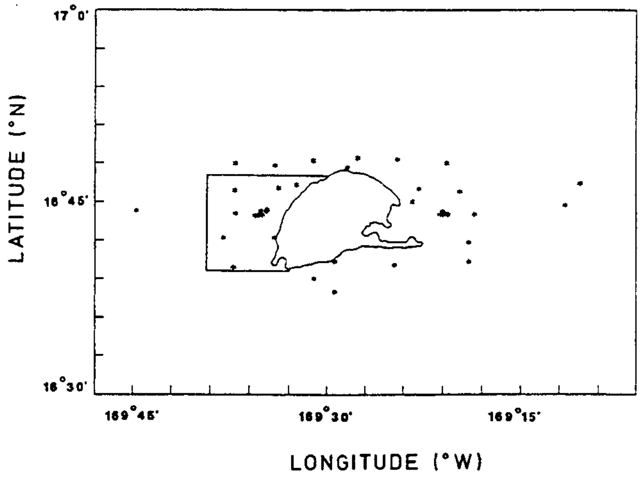

Fig. 4. Geographic locations of the 44 ichthyoplankton stations sampled around Johnston Atoll on the nights of 13–21 November 1984. In addition to those shown on the map, there are two stations farther to the west (at 16°44.0'N, 170°5.0'W and 16°44.4'N, 170°4.1'W) and two farther to the east (at 16°44.5'N, 169°52.5'W and 16°45.2'N, 169°50.5'W). The outline at the center indicates the 18 m isobath surrounding the atoll, and the box to the west of the island indicates the putative retention area used to contrast densities.

total of 8252 fish eggs, 12,777 fish larvae, 208 juvenile/adult fishes, 835 squid larvae and 2755 ml of plankton (displacement volume) were collected in 70 plankton samples. Volumes of water filtered ranged from 499 to 1477 m^3 per sample (mean, 1034 m^3). Fish larvae were identified to 322 taxa in 64 families and 15 orders. To facilitate analysis, these were reduced to a total of 145 taxa by combining rare or unidentified types (within families) to a higher level taxa. Numerically, the collections were dominated by myctophids (46.5% of the total; dominant species: *Bolinichthys* sp., *Ceratoscopelus warmingi* and *Diaphus* spp.), gobiids (19.0%; dominant species: *Eviota epiphanes* and *Gnatholepis anjerensis*), gonostomatids (6.0%; dominant species: *Cyclothone* spp. and *Gonostoma* spp.), photichthyids (4.7%; dominant species: *Vinciguerria nimbaria*), apogonids (4.4%; dominant species: *Pseudamiops* spp.) and paralepidids (2.8%; dominant species: *Lestidium* spp.). As a function of developmental stage, our collections took 34 yolk-sac, 6256 preflexion, 1675 flexion, 3834 postflexion, 208 juvenile/adult and 978 unclassified fishes.

Vertical distribution

Four complete stations at four depth strata (0–25, 25–50, 50–100 and 100–200 m) were occupied at two locations: about 9.5 km west (16°44'N, 169°35'W) and 16.7 km east (16°44'N, 165°21'W) of the center of the atoll. Because this early sampling revealed larvae most abundant in the 50–100 m stratum, sampling in the two shallower strata was discontinued and a single sample in the 0–50 m stratum was substituted. Later analysis of the vertical distributions in the four samples of the 0–25 and 25–50 m strata demonstrated only minor differences in the densities of larvae, specific taxa and combined categories of

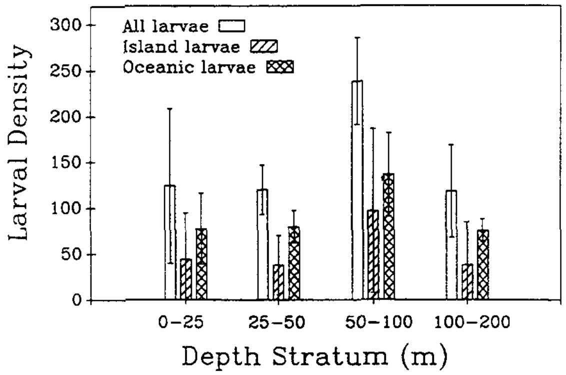

Fig. 5. Vertical distribution of larval fishes from the four stations where four depth strata were sampled. Each value of larval density (larvae 1000 m^{-3}) is the mean of four samples taken at different geographic locations. Error bars represent ±2 S.E.

larvae (Fig. 5). The two shallow strata had similar mean values for all larval classes, although variability was higher in the 0–25 m stratum. Densities were significantly higher in the 50–100 m stratum for all larvae and oceanic larvae (ANOVA, $P < 0.10$), but island larvae did not show significant differences among depths. Densities of all larval types decreased in the 100–200 m stratum to values similar to that in the shallowest stratum (Fig. 5). A more detailed analysis of vertical distribution is based upon three strata, 0–50, 50–100 and 100–200 m. The eight samples from 0–25 and 25–50 m were combined (by station) into four 0–50 m samples.

Fish larvae and eggs showed variable patterns of distribution among the depth strata (Table 1). Plankton displacement volume decreased with depth and, in the deepest stratum, was about half that of the shallowest stratum. Fish eggs and larvae are generally characterized by patchy distributions, and as expected, the variance of density was relatively high. Fish eggs were most abundant in the shallowest stratum, decreasing to about half in the 50–100 m stratum and to about 5% of the surface values in the deepest stratum. Total larval densities were similar in the two shallowest strata with slightly higher values in the 50–100 m stratum; densities in the deepest stratum were about half those in the two shallowest strata.

Mean densities of island larvae were highest in the 50–100 m stratum, but not significantly so (one-tailed randomization t-test, $P = 0.104$). Shallow and deep strata similarly did not differ. Densities of oceanic larvae in the upper two strata were similar and were significantly greater than in the deep stratum ($P < 0.001$). The variability in abundance of island larvae was much higher than that of oceanic larvae, with coefficients of variation of 1.51 and 0.30, respectively. This difference is probably due to the greater geographic variation in abundance of island larvae (see below).

The vertical distributions of individual species are characterized by differing depths of maximum density (Table 1); only the larger patterns and those for selected species will be described here. Highest densities of most gonostomatid species occurred in the deepest stratum, but *Cyclothone* spp. were most abundant in the two upper strata. Densities of most aulopiform taxa were highest in the 50–100 m stratum. The pattern for the myctophids differed by subfamily. Densities of myctophine taxa were generally highest in the

100–200 m stratum, but the two most abundant taxa (*Hygophum proximum* and *Symbolophorus evermanni*) were equally abundant in the 50–100 m stratum. Densities of most lampanyctine taxa, as exemplified by *Ceratoscopelus warmingi* and *Diaphus* spp., were highest in the 0–50 m stratum and lowest in the 100–200 m stratum.

Most island larval taxa are Perciformes, and the most frequent pattern for perciform taxa was greatest abundance in the 0–50 m stratum. The numerically dominant taxa (*Eviota epiphanes*, unidentified gobiids, *Pseudamiops* spp., *Parapercis* sp. and *Schindleria pietschmanni*), however, were most abundant in the 50–100 m stratum. Some island taxa from among several orders were most abundant in the 100–200 m stratum; these include Chlopsidae, *Apogonichthys perdix* and Callionymidae.

Vertical distribution within species varied with developmental stage. To determine these patterns, "early larvae" were defined as yolk-sac and preflexion larvae, and "late larvae" as flexion and postflexion larvae. Juvenile/adult and unclassified categories were not included in this analysis. Several species showed patterns of increasing percentages of early stage larvae with increasing water depth; examples were *Serrivomer* sp. (with only early stage larvae in deep water) and the paralepidid *Lestidium* spp. In the Myctophidae, opposite patterns were evident between the subfamilies Myctophinae and Lampanyctinae. The percentages of early stage *Symbolophorus evermanni* larvae increased significantly with depth (ANOVA on arcsin transformed data, $P < 0.001$), whereas the opposite was true for the lampanyctines *Ceratoscopelus warmingi* ($P = 0.001$) and *Diaphus* spp. ($P < 0.001$; Fig. 6A). In the Perciformes (and among island larvae in general), a pattern of decreasing percentages of early larvae with increasing depth was apparent (Fig. 6B); the

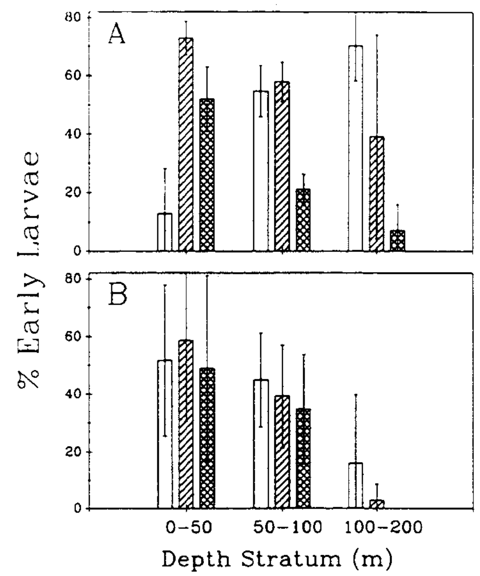

Fig. 6. Patterns of the vertical distribution of different developmental stages of six species. Per cent early larvae refers to the sum of yolk-sac and preflexion larvae as a percentage of early plus late larvae (where late refers to flexion and postflexion larvae). (A) □, *Symbolophorus evermanni*; ▨, *Ceratoscopelus warmingi*; ▩, *Diaphus* spp. (B) *Eviota epiphanes*, *Pseudamiops* sp. and *Limnichthys donaldsoni*, respectively. Error bars represent ±2 S.E.

Table 1. *Vertical distribution of fish larvae, fish eggs, squid larvae, and plankton displacement volume around Johnston Atoll. Densities (larvae* 1000 m^{-3}*) are mean values based upon* 29, 30 *and* 7 *samples in the* 0–50, 50–100 *and* 100–200 m *strata, respectively. Types of larvae refer to the habitat occupied by the adults, defined as island* (1), *oceanic* (2) *and other* (3). *Values associated with higher level taxonomic categories, such as family or higher indicate unidentified species in that category. Taxonomic categories generally follow* NELSON (1984)

		Larval density by stratum					
		0–50 m		50–100 m		100–200 m	
Taxon	Type	Mean	S.D.	Mean	S.D.	Mean	S.D.
Anguilliformes	3	0.095	(0.362)	0.600	(0.917)	0.359	(0.667)
Nemichthyidae	2	0.061	(0.329)	0.000	(0.000)	0.000	(0.000)
Chlopsidae	1	0.000	(0.000)	0.053	(0.290)	0.239	(0.631)
Muraenidae	1	0.078	(0.357)	0.031	(0.167)	0.000	(0.000)
Serrivomeridae							
Serrivomer sp.	1	1.295	(1.519)	1.393	(1.963)	0.553	(0.734)
Congridae	1	0.041	(0.160)	0.085	(0.259)	0.000	(0.000)
Ophichthidae	1	0.094	(0.378)	0.287	(0.645)	0.122	(0.324)
Derichthyidae							
Derichthys sp.	2	0.000	(0.000)	0.199	(0.662)	0.000	(0.000)
Stomiiformes							
Stomioidea	2	0.596	(1.151)	1.083	(1.178)	2.081	(1.052)
Gonostomatidae	2	0.057	(0.212)	0.057	(0.217)	0.113	(0.300)
Cyclothone spp.	2	11.617	(5.496)	9.017	(5.434)	1.106	(1.602)
Diplophos taenia	2	0.538	(1.270)	0.108	(0.281)	0.219	(0.374)
Gonostoma spp.	2	0.000	(0.000)	0.198	(0.481)	2.202	(0.973)
G. atlanticum	2	0.104	(0.378)	0.429	(0.826)	2.972	(2.092)
G. elongatum	2	0.000	(0.000)	0.084	(0.335)	1.750	(1.899)
Photichthyidae							
Ichthyococcus sp.	2	0.000	(0.000)	0.000	(0.000)	0.112	(0.297)
Vinciguerria nimbaria	2	5.767	(3.478)	11.770	(7.597)	4.344	(3.455)
Sternoptychidae							
Sternoptyx sp.	2	0.000	(0.000)	0.000	(0.000)	0.816	(0.810)
Valenciennellus tripunctulatus	2	0.000	(0.000)	0.000	(0.000)	0.232	(0.396)
Astronesthidae	2	0.424	(0.692)	0.156	(0.325)	0.000	(0.000)
Astronesthes spp.	2	0.089	(0.359)	0.168	(0.563)	0.245	(0.647)
Melanostomiidae							
Bathophilus sp.	2	0.164	(0.484)	0.000	(0.000)	0.000	(0.000)
Eustomias sp.	2	0.764	(1.341)	0.288	(0.527)	0.000	(0.000)
Leptostomias sp.	2	0.000	(0.000)	0.086	(0.263)	0.000	(0.000)
Photonectes sp.	2	0.015	(0.078)	0.217	(0.510)	0.000	(0.000)
Malacosteidae	2	0.028	(0.151)	0.000	(0.000)	0.000	(0.000)
Idiacanthidae							
Idiacanthus sp.	2	0.000	(0.000)	0.488	(0.843)	1.630	(1.601)
Aulopiformes							
Synodontidae							
Synodus spp.	1	0.014	(0.078)	0.242	(0.628)	0.000	(0.000)
Scopelarchidae	2	0.027	(0.147)	0.057	(0.314)	1.732	(1.753)
Benthalbella sp.	2	0.000	(0.000)	0.172	(0.679)	0.238	(0.631)
Scopelarchus spp.	2	0.000	(0.000)	0.000	(0.000)	0.551	(0.837)
Paralepididae	2	0.674	(1.308)	0.860	(1.083)	0.782	(0.909)
Lestidiini	2	0.249	(0.587)	0.657	(1.364)	0.000	(0.000)
Lestidiops spp.	2	1.564	(1.559)	0.825	(1.133)	0.119	(0.316)
Lestidium spp.	2	0.288	(0.564)	3.609	(3.545)	2.280	(2.654)

Table 1. *Continued*

		Larval density by stratum					
		0–50 m		50–100 m		100–200 m	
Taxon	Type	Mean	S.D.	Mean	S.D.	Mean	S.D.
Aulopiformes—*continued*							
Stemonosudis macrura	2	0.027	(0.147)	0.000	(0.000)	0.000	(0.000)
Sudis atrox	2	0.302	(0.591)	1.173	(1.330)	0.583	(0.925)
Notosudidae	2	0.000	(0.000)	0.027	(0.150)	0.000	(0.000)
Scopelosaurus spp.	2	0.199	(0.569)	0.735	(1.997)	1.673	(2.189)
Evermannellidae							
Evermannella sp.	2	1.011	(1.764)	1.021	(1.100)	0.590	(0.800)
Odontostomops normalops	2	0.015	(0.078)	0.237	(0.660)	0.000	(0.000)
Myctophiformes							
Myctophidae	2	4.647	(4.679)	1.614	(2.000)	1.149	(1.205)
Myctophinae	2	0.961	(2.476)	3.907	(2.946)	2.294	(2.460)
Electrona spp.	2	0.013	(0.070)	0.000	(0.000)	0.112	(0.297)
Gonichthys sp.	2	0.000	(0.000)	0.176	(0.433)	0.351	(0.651)
Hygophum proximum	2	1.016	(1.402)	10.766	(7.910)	11.725	(4.636)
H. reinhardti	2	0.063	(0.303)	0.412	(0.585)	0.590	(0.639)
Myctophum spp.	2	0.000	(0.000)	0.703	(1.415)	0.353	(0.652)
M. asperum	2	0.000	(0.000)	0.105	(0.343)	0.000	(0.000)
M. aurolanternatum	2	0.000	(0.000)	0.000	(0.000)	0.113	(0.300)
Protomyctophum sp.	2	0.223	(0.542)	0.353	(0.629)	0.464	(0.649)
Symbolophorus evermanni	2	0.877	(1.244)	8.157	(5.363)	7.317	(4.011)
Centrobranchus spp.	2	0.000	(0.000)	0.000	(0.000)	0.114	(0.303)
Benthosema spp.	2	0.000	(0.000)	0.089	(0.363)	0.000	(0.000)
Lampanyctinae	2	0.692	(1.309)	0.317	(0.511)	0.112	(0.297)
Bolinichthys spp.	2	5.623	(7.482)	4.614	(4.427)	1.136	(1.289)
Ceratoscopelus warmingi	2	69.253	(38.334)	39.178	(24.619)	4.903	(5.185)
Diaphus spp.	2	10.778	(8.945)	9.188	(5.337)	4.722	(2.890)
D. pacificus	2	0.445	(0.798)	2.271	(1.937)	1.626	(1.425)
Lampadena spp.	2	0.684	(1.401)	0.111	(0.287)	0.000	(0.000)
L. urophaos	2	2.820	(2.959)	1.875	(1.629)	0.113	(0.300)
Lampanyctus spp.	2	1.361	(2.102)	1.194	(1.030)	0.568	(0.581)
L. nobilis	2	4.417	(3.538)	3.072	(2.128)	0.811	(0.923)
L. steinbecki	2	0.777	(1.327)	1.093	(1.516)	0.652	(1.393)
Lobianchia sp.	2	0.000	(0.000)	0.000	(0.000)	0.239	(0.631)
Taaningichthys sp.	2	0.061	(0.330)	0.137	(0.376)	0.000	(0.000)
Triphoturus nigrescens	2	0.000	(0.000)	0.059	(0.224)	0.000	(0.000)
Gadiformes							
Bregmacerotidae							
Bregmaceros sp.	3	0.083	(0.348)	0.883	(1.093)	2.339	(3.108)
Ophidiiformes	3	0.000	(0.000)	0.109	(0.355)	0.000	(0.000)
Carapidae	1	0.000	(0.000)	0.063	(0.239)	0.000	(0.000)
Lophiiformes							
Antennariidae	1	0.014	(0.077)	0.000	(0.000)	0.113	(0.300)
Ceratioidei	2	0.000	(0.000)	0.051	(0.196)	0.000	(0.000)
Caulophrynidae							
Caulophryne sp.	2	0.181	(0.547)	0.000	(0.000)	0.000	(0.000)
Melanocetidae							
Melanocetus johnsoni	2	0.089	(0.357)	0.139	(0.377)	0.000	(0.000)

Table 1. *Continued*

		Larval density by stratum					
		0–50 m		50–100 m		100–200 m	
Taxon	Type	Mean	S.D.	Mean	S.D.	Mean	S.D.
Cyprinidontiformes							
Exocoetidae	2	0.107	(0.341)	0.031	(0.171)	0.000	(0.000)
Parexocoetus sp.	2	0.075	(0.335)	0.060	(0.228)	0.000	(0.000)
Hemiramphidae	3	0.121	(0.451)	0.000	(0.000)	0.000	(0.000)
Lampriformes							
Lampridae							
Lampris guttatus	2	0.000	(0.000)	0.028	(0.154)	0.000	(0.000)
Mirapinnidae							
Parataeniophorus sp.	2	0.028	(0.151)	0.000	(0.000)	0.000	(0.000)
Beryciformes							
Melamphaidae	2	0.000	(0.000)	0.028	(0.154)	0.112	(0.297)
Melamphaes spp.	2	0.061	(0.326)	1.254	(1.470)	0.925	(0.968)
Scopelogadus spp.	2	0.000	(0.000)	0.029	(0.157)	0.352	(0.652)
Holocentridae	1	1.021	(2.641)	0.000	(0.000)	0.000	(0.000)
Syngnathiformes							
Aulostomidae							
Aulostomus chinensis	1	0.199	(0.596)	0.000	(0.000)	0.000	(0.000)
Syngnathidae	1	0.015	(0.078)	0.150	(0.409)	0.000	(0.000)
Scorpaeniformes							
Scorpaenidae	1	0.151	(0.474)	0.237	(0.524)	0.000	(0.000)
Perciformes							
Percoidei	1	0.705	(1.259)	0.208	(0.503)	0.234	(0.399)
Incertae sedis							
Howella sp.	2	0.056	(0.302)	0.838	(1.202)	0.242	(0.412)
Serranidae	1	0.193	(0.579)	0.000	(0.000)	0.000	(0.000)
Pseudogramma polyacantha	1	0.000	(0.000)	0.031	(0.167)	0.000	(0.000)
Priacanthidae	1	0.029	(0.156)	0.000	(0.000)	0.000	(0.000)
Apogonidae	1	1.522	(2.224)	0.519	(0.917)	0.112	(0.297)
Apogoninae	1	1.169	(2.260)	0.991	(1.337)	0.332	(0.415)
Apogonichthys perdix	1	0.000	(0.000)	0.057	(0.219)	0.112	(0.297)
Epigoninae							
Epigonus sp.	3	1.071	(2.421)	0.246	(0.701)	0.000	(0.000)
Pseudamiinae	1	0.374	(1.055)	0.241	(0.584)	0.000	(0.000)
Pseudamiops spp.	1	4.764	(9.996)	6.463	(13.400)	2.063	(2.081)
Echeneididae	2	0.000	(0.000)	0.063	(0.343)	0.000	(0.000)
Carangidae							
Selar crumenophthalmus	1	0.094	(0.285)	0.046	(0.180)	0.000	(0.000)
Coryphaenidae							
Coryphaena hippurus	2	0.276	(0.640)	0.057	(0.217)	0.000	(0.000)
Bramidae							
Brama sp.	2	0.231	(0.610)	0.168	(0.344)	0.245	(0.647)
Mullidae	1	0.194	(0.503)	0.174	(0.474)	0.000	(0.000)
Chaetodontidae	1	0.662	(1.943)	0.000	(0.000)	0.000	(0.000)
Pomacanthidae	1	0.065	(0.352)	0.134	(0.430)	0.000	(0.000)
Pomacentridae	1	1.565	(2.759)	0.566	(1.216)	0.119	(0.316)
Chromis sp.	1	1.479	(2.605)	0.316	(0.527)	0.000	(0.000)

Table 1. *Continued*

		Larval density by stratum					
		0–50 m		50–100 m		100–200 m	
Taxon	Type	Mean	S.D.	Mean	S.D.	Mean	S.D.
Labridae	1	1.119	(2.664)	0.716	(1.051)	0.227	(0.387)
Scaridae	1	0.167	(0.482)	0.116	(0.303)	0.000	(0.000)
Chiasmodontidae	2	0.442	(0.772)	0.370	(0.659)	0.229	(0.392)
Kali sp.	2	0.042	(0.165)	0.083	(0.253)	0.000	(0.000)
Mugiloididae							
Parapercis sp.	1	0.361	(0.859)	3.272	(7.347)	1.253	(1.990)
Creediidae							
Limnichthys donaldsoni	1	1.243	(2.492)	1.950	(3.308)	1.145	(1.347)
Champsodontidae							
Champsodon sp.	1	0.000	(0.000)	0.057	(0.310)	0.000	(0.000)
Blenniidae							
Istiblennius gibbifrons	1	0.248	(0.592)	0.176	(0.550)	0.114	(0.303)
Salariini	1	4.234	(8.840)	2.936	(5.422)	0.119	(0.316)
Schindleriidae	1	0.197	(0.986)	0.295	(0.834)	0.113	(0.300)
Schindleria pietschmanni	1	0.978	(2.693)	2.852	(5.404)	0.465	(0.635)
S. praematura	1	1.447	(3.464)	0.808	(1.508)	0.122	(0.324)
Callionymidae	1	0.000	(0.000)	0.205	(0.447)	1.258	(1.941)
Gobiidae	1	8.688	(13.538)	20.944	(44.699)	4.534	(5.337)
Eviota epiphanes	1	8.885	(23.729)	35.334	(95.775)	12.502	(26.771)
Gnatholepis anjerensis	1	0.497	(1.858)	0.202	(0.593)	0.000	(0.000)
Acanthuridae	1	0.359	(1.021)	0.186	(0.414)	0.000	(0.000)
Scombroidei	2	0.095	(0.350)	0.186	(0.560)	0.000	(0.000)
Scombrolabracidae							
Scombrolabrax heterolepis	2	2.672	(2.742)	0.552	(0.900)	0.245	(0.647)
Gempylidae							
Gempylus serpens	2	1.307	(1.887)	0.708	(1.775)	0.226	(0.386)
Lepidocybium flavobrunneum	2	0.176	(0.734)	0.038	(0.161)	0.000	(0.000)
Nealotus tripes	2	0.208	(0.582)	0.031	(0.171)	0.000	(0.000)
Nesiarchus nasutus	2	0.213	(0.555)	0.188	(0.456)	0.000	(0.000)
Trichiuridae							
Lepidopus sp.	2	0.000	(0.000)	0.000	(0.000)	0.119	(0.316)
Scombridae	2	0.098	(0.340)	0.058	(0.223)	0.226	(0.386)
Katsuwonis pelamis	2	1.756	(1.692)	0.205	(0.805)	0.114	(0.303)
Scomber japonicus	2	0.042	(0.166)	0.000	(0.000)	0.000	(0.000)
Thunnus spp.	2	0.115	(0.390)	0.046	(0.183)	0.000	(0.000)
Istiophoridae	2	0.028	(0.151)	0.000	(0.000)	0.000	(0.000)
Nomeidae							
Cubiceps baxteri	2	0.206	(0.472)	0.069	(0.220)	0.000	(0.000)
C. pauciradiatus	2	0.105	(0.373)	0.141	(0.391)	0.000	(0.000)
Pleuronectiformes							
Bothidae	1	0.014	(0.078)	0.088	(0.362)	0.000	(0.000)
Tetraodontiformes							
Balistoidei	1	0.000	(0.000)	0.031	(0.172)	0.000	(0.000)
Monacanthidae	1	0.014	(0.078)	0.000	(0.000)	0.000	(0.000)
Ostraciidae	1	0.000	(0.000)	0.112	(0.362)	0.000	(0.000)
Tetraodontidae	1	0.014	(0.078)	0.113	(0.361)	0.000	(0.000)

Table 1. *Continued*

		Larval density by stratum					
		0–50 m		50–100 m		100–200 m	
Taxon	Type	Mean	S.D.	Mean	S.D.	Mean	S.D.
Unidentified larvae	3	2.884	(2.954)	3.378	(4.255)	1.049	(0.767)
Island larvae		42.911	(52.490)	81.280	(151.190)	25.299	(36.786)
Oceanic larvae		139.197	(56.525)	129.927	(40.956)	69.424	(11.837)
Total larvae		186.361	(77.521)	216.430	(151.870)	98.470	(43.262)
Fish eggs		180.224	(540.891)	93.047	(238.143)	8.700	(7.578)
Squid larvae		14.890	(7.042)	9.274	(7.203)	5.737	(4.432)
Plankton (ml 1000 m^{-3})		43.010	(11.805)	33.897	(10.028)	19.571	(5.041)

trend was significant for *Pseudamiops* sp. ($P = 0.05$) and *Limnichthys donaldsoni* ($P < 0.10$) but not for *Eviota epiphanes* ($P = 0.263$).

Geographic distribution

The results of the objective analysis suggested an area of return flow on the west-northwest side of the island; such an area might serve to retain island larvae for later recruitment. Indeed, certain categories of larvae were more abundant there. Sufficient samples existed in the 0–50 and 50–100 m strata to allow a geographic analysis of distribution. In the 0–50 m stratum, fish eggs were concentrated in this area (Fig. 7A), with the maximum recorded density more than five times that of the mean density (Table 1). Total fish larvae showed a pattern of slightly higher densities near this region as well as off the east-northeast side of the island (Fig. 7B). No clear pattern was discernible for oceanic larvae (Fig. 7C); island larvae, on the other hand, were concentrated in the return flow region but were in very low abundance elsewhere (Fig. 7D). Neither squid larvae nor plankton displacement volume increased in abundance in this region.

The patterns in the 50–100 m stratum (Fig. 8) were more pronounced than those in the shallower stratum. Mean densities of fish eggs were much lower in the 50–100 m stratum (Table 1), but densities in the area just downstream of the island were high, decreasing with increasing distance from the island to near zero (Fig. 8A). Superimposed upon a mean background density of about 150 larvae 1000 m^{-3}, total larval densities were also much greater in this area (Fig. 8B). Similar to the situation in the 0–50 m stratum, oceanic fish larvae were not concentrated in this area (Fig. 8C), but the island fish larvae were (Fig. 8D). Similar to the fish eggs at this depth (Fig. 8A), densities of island fish larvae were near zero in waters distant from the island (Fig. 8D).

To compare statistically densities in the putative downstream "retention area" with densities in other samples, an area was defined (shown bounded by the box in Fig. 4), and densities in that area were compared with densities from all other samples for selected taxa (Table 2). Fish larvae were significantly more abundant in this area ($P < 0.01$), as would be expected from Figs 7 and 8; the increase is attributable to island larvae. Fish eggs were significantly more abundant in this area in the deeper stratum ($P < 0.05$) but not in the shallow stratum, perhaps due to patchiness, as a single sample outside the area but near the

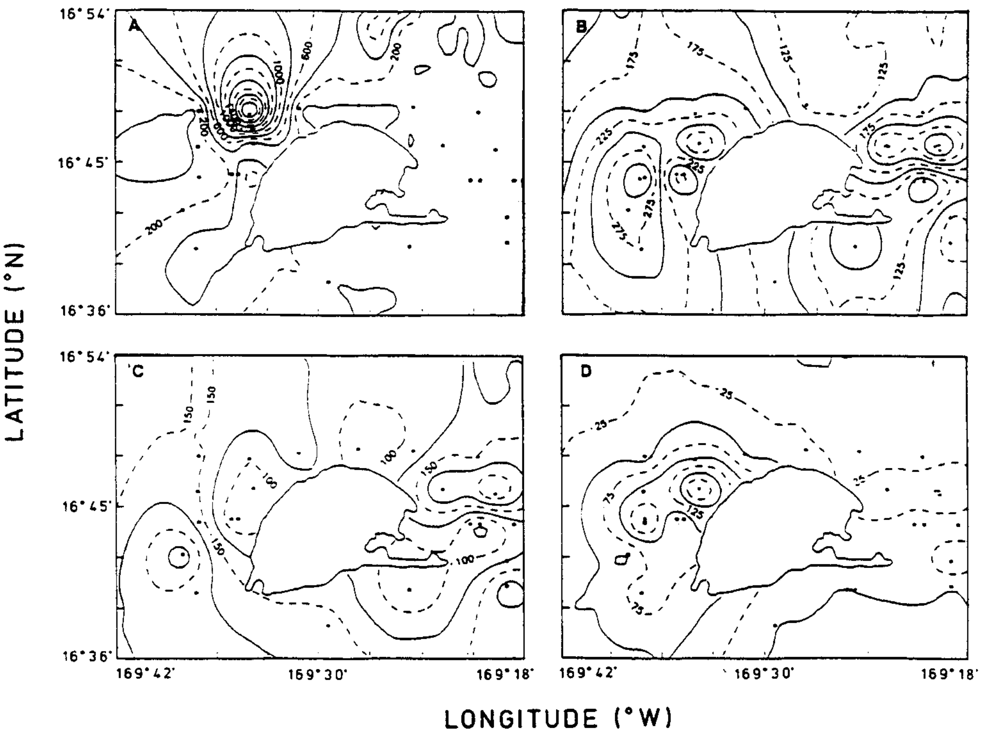

Fig. 7. Geographic patterns of density (nos 1000 m^{-3}) of (A) fish eggs, (B) total fish larvae, (C) oceanic fish larvae and (D) island fish larvae in the 0–50 m depth stratum. The outline area without contours represents the 18 m isobath surrounding Johnston Atoll.

island had 2823 fish eggs 1000 m^{-3}. Squid larvae were significantly more abundant outside the area in the shallow stratum ($P < 0.05$), and plankton displacement volume was significantly higher inside the area in the deeper stratum ($P < 0.05$).

A pattern of offshore distribution, with greater densities outside the area of return flow, was evident for many oceanic species, as exemplified by *Vinciguerria nimbaria* in both strata and *Hygophum proximum*, *Scombrolabrax heterolepis* and *Gempylus serpens* in the shallow stratum. *Scopelosaurus* spp., both species of evermannellids, *Brama* sp. and the other two gempylids also showed a trend toward greater densities outside the marked area. Among the myctophids, *Lampanyctus steinbecki* and *Lampanyctus* spp. demonstrated this offshore pattern in the deeper stratum, but the more abundant *L. nobilis* was distributed evenly. A similar discrepancy was also evident in the genus *Lampadena*, with a general trend of higher abundance outside the area but significantly higher abundance inside for *L. urophaos* in the deeper stratum ($P < 0.05$).

A trend of greater abundance of island larvae in the area of return flow is apparent, but many are not significantly more abundant because of low numbers or patchy distributions. The most abundant island taxa, however, generally were significantly more abundant in the retention area; specific cases are the Apogoninae, *Pseudamiops* spp., Labridae, *Parapercis* sp., *Limnichthys donaldsoni*, salariine blenniids, both schindleriid species,

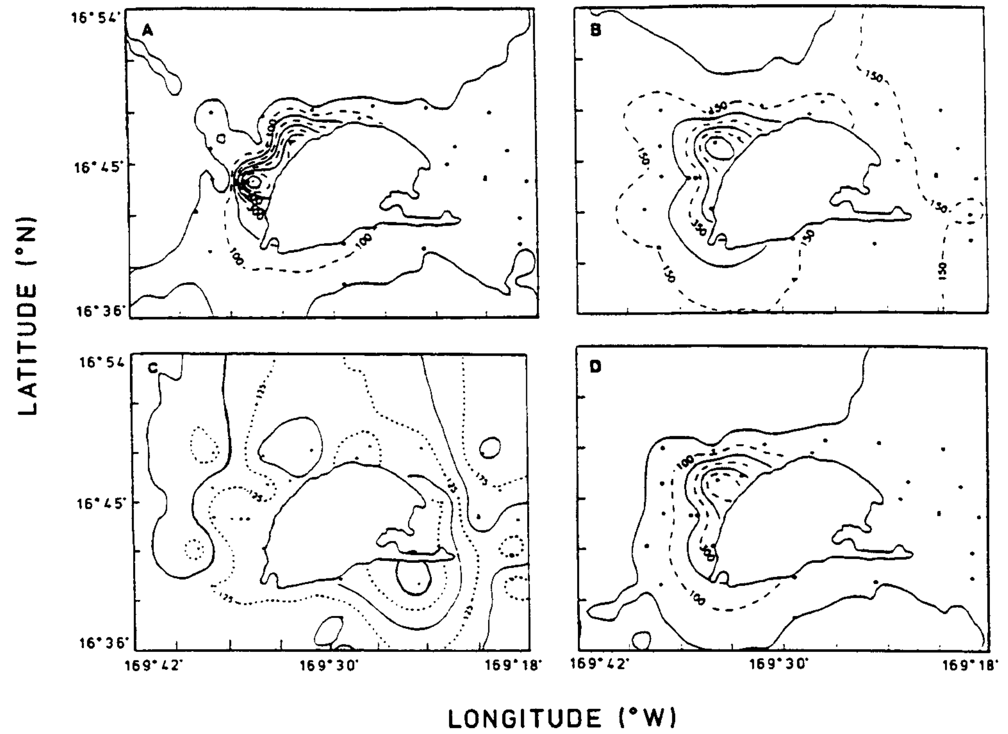

Fig. 8. Geographic patterns of densities (nos 1000 m^{-3}) of (A) fish eggs, (B) all fish larvae, (C) oceanic fish larvae and (D) island fish larvae in the 50–100 m depth stratum. The outline area without contours represents the 18 m isobath surrounding Johnston Atoll.

Eviota epiphanes and *Gnatholepis anjerensis*. The most abundant myctophid, *Ceratoscopelus warmingi*, was significantly more abundant in this area ($P < 0.05$), but only in the shallow stratum.

Species assemblages

Assemblage analysis using the two-way synthesis table defined nine assemblages of larvae with 33 taxa, of which 20 were oceanic (Table 3). These assemblages were associated with different habitats partitioned by depth and relation to the island retention area, and generally confirmed the island and oceanic groupings discussed earlier. Nine taxa were present in more than two-thirds of the samples and thus not included in the analysis; most other taxa, including both abundant and rare species, were not group members for lack of coherent distributional patterns. Group 1 comprised six island taxa abundant in all depths, but most abundant in the "island" area as opposed to the more distant samples. The occurrences of this group outside the "island" region were to the north and east in waters near the island. Group 2 comprised four abundant, oceanic, midwater taxa (two paralepidid genera, one evermannelid and one myctophid), with wide distributions but greater abundance in the two deeper strata. Taxa in these two groups

Table 2. *Mean densities (larvae* 1000 m^{-3}) *of selected taxa as a function of depth and location. Location* 1 *is bounded by the island platform to the east* (169°32.0′W) *to* 169°38.0′ *to the west, and by* 16°39.5′N *to* 16°46.5′N *as shown on Fig.* 4. *Types of larvae refer to the habitat occupied by the adults, defined as island* (1), *oceanic* (2) *and other* (3). *Values associated with higher level taxonomic categories, such as family or order, indicate unidentified species in that category. Densities of selected taxa were compared within depth zones if at least* 20 *larvae of that taxon were captured at that depth. Significantly higher densities are indicated (one-tailed randomization* t-*tests*; $^*P < 0.05$; $^{**}P < 0.01$; *not corrected for multiple testing)*

		Density at depth 0–50 m				Density at depth 50–100 m			
		Location 1		Location 2		Location 1		Location 2	
Taxon	Type	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Anguilliformes									
Serrivomeridae									
Serrivomer sp.	2	0.811	(1.018)	1.449	(1.636)	2.592*	(3.228)	0.879	(0.703)
Ophichthidae	1	0.120	(0.317)	0.086	(0.402)	0.473	(0.951)	0.207	(0.469)
Stomiiformes									
Gonostomatidae									
Cyclothone spp.	2	10.990	(5.591)	11.816	(5.583)	11.031	(5.271)	8.153	(5.393)
Diplophos taenia	2	0.119	(0.204)	0.671	(1.436)	0.177	(0.353)	0.078	(0.248)
Photichthyidae									
Vinciguerria nimbaria	2	3.083	(2.063)	6.621**	(3.427)	7.141	(5.134)	13.754**	(7.706)
Astronesthidae									
Astronesthes spp.	2	0.000	(0.000)	0.118	(0.411)	0.000	(0.000)	0.240	(0.664)
Melanostomatidae									
Eustomias sp.	2	0.778	(1.441)	0.760	(1.344)	0.289	(0.434)	0.288	(0.573)
Photonectes sp.	2	0.000	(0.000)	0.019	(0.090)	0.000	(0.000)	0.310	(0.588)
Idiacanthidae									
Idiacanthus sp.	2	0.000	(0.000)	0.000	(0.000)	0.293	(0.647)	0.571	(0.916)
Aulopiformes									
Synodontidae									
Synodus spp.	1	0.060	(0.159)	0.000	(0.000)	0.712	(0.992)	0.041	(0.188)
Paralepididae									
Lestidiini	2	0.000	(0.000)	0.328	(0.658)	1.397*	(2.185)	0.339	(0.660)
Lestidiops spp.	2	1.037	(1.147)	1.731	(1.656)	0.800	(1.163)	0.836	(1.148)
Lestidium spp.	2	0.560	(0.828)	0.201	(0.443)	4.216	(3.744)	3.348	(3.518)
Notosudidae									
Scopelosaurus spp.	2	0.000	(0.000)	0.263	(0.644)	0.000	(0.000)	1.050	(2.331)

Table 2. Continued

		Density at depth 0–50 m				Density at depth 50–100 m			
		Location 1		Location 2		Location 1		Location 2	
Taxon	Type	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Aulopiformes—*continued*									
Evermannellidae									
Evermannella sp.	2	0.311	(0.659)	1.234	(1.952)	0.733	(1.113)	1.144	(1.098)
Odontostomops normalops	2	0.000	(0.000)	0.019	(0.090)	0.000	(0.000)	0.338	(0.771)
Myctophiformes									
Myctophidae									
Myctophinae									
Hygophum proximum	2	0.119	(0.314)	1.302**	(1.496)	10.480	(9.454)	10.888	(7.411)
Symbolophorus evermanni	2	0.367	(0.679)	1.040	(1.348)	6.452	(4.561)	8.887	(5.614)
Lampanyctinae									
Ceratoscopelus warmingi	2	93.139*	(47.623)	61.653	(32.568)	39.323	(27.508)	39.116	(24.004)
Diaphus pacificus	2	0.000	(0.000)	0.586	(0.873)	1.696	(1.634)	2.518	(2.039)
Diaphus spp.	2	5.744	(5.078)	12.379*	(9.390)	9.084	(6.813)	9.233	(4.768)
Lampadena spp.	2	0.248	(0.657)	0.823	(1.553)	0.000	(0.000)	0.158	(0.334)
L. urophaos	2	1.967	(1.553)	3.092	(3.265)	2.901*	(1.606)	1.435	(1.463)
Lampanyctus spp.	2	0.556	(1.297)	1.617	(2.264)	0.665	(0.730)	1.421*	(1.071)
L. nobilis	2	3.567	(2.656)	4.687	(3.789)	3.060	(2.273)	3.077	(2.122)
L. steinbecki	2	0.323	(0.689)	0.922	(1.457)	0.386	(0.615)	1.396*	(1.691)
Beryciformes									
Holocentridae	1	0.745	(1.971)	1.109	(2.856)	0.000	(0.000)	0.000	(0.000)
Scorpaeniformes									
Scorpaenidae	1	0.368	(0.680)	0.082	(0.382)	0.000	(0.000)	0.338	(0.602)
Perciformes									
Incertae cedis									
Howella sp.	2	0.000	(0.000)	0.074	(0.346)	0.945	(1.388)	0.791	(1.148)
Priacanthidae	1	0.120	(0.317)	0.000	(0.000)	0.000	(0.000)	0.000	(0.000)
Apogonidae	1	1.915	(2.145)	1.397	(2.283)	0.739	(1.204)	0.424	(0.780)
Apogoninae	1	3.279**	(2.812)	0.497	(1.610)	1.841*	(1.822)	0.627	(0.894)
Apogonichthys perdix	1	0.000	(0.000)	0.000	(0.000)	0.192	(0.381)	0.000	(0.000)
Epigoninae									
Epigonus sp.	3	0.796	(1.417)	1.158	(2.685)	0.195	(0.389)	0.268	(0.807)

Table 2. Continued

Taxon	Type	Density at depth 0–50 m				Density at depth 50–100 m			
		Location 1		Location 2		Location 1		Location 2	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Apogonidae—*continued*									
Pseudamiinae									
Pseudamiops spp.	1	13.616**	(16.685)	1.947	(4.388)	16.930**	(21.425)	1.977	(2.512)
Coryphaenidae									
Coryphaena hippurus	2	0.248	(0.657)	0.285	(0.651)	0.000	(0.000)	0.081	(0.257)
Bramidae									
Brama sp.	2	0.000	(0.000)	0.305	(0.687)	0.000	(0.000)	0.240	(0.391)
Mullidae	1	0.000	(0.000)	0.256	(0.566)	0.294	(0.612)	0.123	(0.408)
Chaetodontidae	1	0.808	(1.341)	0.616	(2.123)	0.000	(0.000)	0.000	(0.000)
Pomacanthidae	1	0.000	(0.000)	0.086	(0.404)	0.083	(0.250)	0.156	(0.492)
Pomacentridae	1	2.128	(2.013)	1.386	(2.976)	1.034	(1.964)	0.366	(0.678)
Chromis sp.	1	1.446	(2.947)	1.490	(2.563)	0.298	(0.448)	0.324	(0.567)
Labridae	1	2.049	(4.507)	0.823	(1.811)	1.311*	(1.386)	0.461	(0.778)
Scaridae	1	0.427	(0.660)	0.084	(0.395)	0.292	(0.442)	0.041	(0.188)
Mugiloididae									
Parapercis sp.	1	0.619	(0.795)	0.279	(0.879)	8.575**	(12.030)	0.999	(1.515)
Creediidae									
Limnichthys donaldsoni	1	3.454**	(3.869)	0.539	(1.363)	3.950*	(5.120)	1.094	(1.677)
Champsodontidae									
Champsodon sp.	1	0.000	(0.000)	0.000	(0.000)	0.189	(0.566)	0.000	(0.000)
Blenniidae									
Istiblennius gibbifrons	1	0.743	(0.793)	0.090	(0.424)	0.587	(0.909)	0.000	(0.000)
Salariini	1	5.055	(3.268)	3.973	(10.042)	6.221*	(8.439)	1.528	(2.685)
Schindleriidae									
Schindleria pietschmanni	1	3.615**	(4.735)	0.139	(0.456)	7.926**	(7.772)	0.677	(1.273)
S. praematura	1	5.696**	(5.248)	0.095	(0.445)	2.267**	(2.107)	0.183	(0.390)
Gobiidae									
Eviota epiphanes	1	35.578**	(39.096)	0.393	(0.990)	103.523**	(159.507)	6.110	(11.596)
Gnatholepis anjerensis	1	2.058	(3.516)	0.000	(0.000)	0.293	(0.636)	0.163	(0.585)
Acanthuridae	1	0.000	(0.000)	0.474	(1.154)	0.174	(0.346)	0.191	(0.448)

Table 2. Continued

Taxon	Type	Density at depth 0–50 m				Density at depth 50–100 m			
		Location 1		Location 2		Location 1		Location 2	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Perciformes—*continued*									
Scombrolabracidae									
Scombrolabrax heterolepis	2	0.811	(0.895)	3.264**	(2.877)	0.568	(0.841)	0.546	(0.945)
Gempylidae									
Gempylus serpens	2	0.179	(0.330)	1.665*	(2.040)	0.480	(0.770)	0.806	(2.073)
Lepidocybium flavobrunneum	2	0.000	(0.000)	0.232	(0.839)	0.000	(0.000)	0.054	(0.192)
Nesiarchus nasutus	2	0.000	(0.000)	0.281	(0.626)	0.083	(0.250)	0.234	(0.519)
Scombridae									
Katsuwonis pelamis	2	1.763	(2.014)	1.754	(1.630)	0.000	(0.000)	0.294	(0.955)
Thunnus spp.	2	0.312	(0.661)	0.053	(0.248)	0.000	(0.000)	0.065	(0.218)
Pleuronectiformes									
Bothidae	1	0.060	(0.159)	0.000	(0.000)	0.295	(0.638)	0.000	(0.000)
Island larvae		110.387**	(57.711)	21.442	(26.862)	219.682**	(226.529)	21.976	(17.490)
Oceanic larvae		142.030	(60.229)	138.296	(56.746)	123.166	(29.007)	132.824	(45.456)
Total larvae		258.580**	(67.359)	163.380	(66.517)	348.496**	(225.529)	159.830	(44.462)
Fish eggs		261.329	(317.618)	154.418	(598.641)	250.456*	(399.914)	25.586	(48.284)
Squid larvae		11.000	(4.690)	16.132*	(7.286)	8.444	(6.226)	9.629	(7.547)
Plankton (ml 1000 m^{-3})		41.857	(16.112)	43.377	(10.538)	40.578*	(9.915)	31.033	(8.821)

Table 3. Per cent occurrence and abundance of species groups within selected depth strata and area. The species groups are those determined in the two-way synthesis table technique (see Materials and Methods). The first row of numbers in each group refers to the percentage of stations in the particular depth stratum and area in which the species assemblage occurred. The second and third rows refer to the mean and standard deviation of the combined densities (larvae 1000 m^{-3}) *of group taxa. Nine taxa* (Ceratoscopelus warmingi, Vinciguerria nimbaria, Diaphus *spp.*, Cyclothone *spp.*, Lampanyctus nobilis, Bolinichthys *spp.*, Symbolophorus evermanni, Hygophum proximum *and* Lampadena urophaos) *were present in more than two-thirds of the samples and thus not included in the analysis. Several other abundant species were not characterized by distributions coherent with other groups*

		0–50 m		50–100 m		100–200 m
Group no.	Species	Island	Other	Island	Other	All
1	*Eviota epiphanes*					
	Salarini	100.0	21.1	100.0	44.4	57.1
	Limnichthys donaldsoni	50.369	6.140	131.506	10.991	15.710
	Parapercis sp.	(37.564)	(12.160)	(172.870)	(12.379)	(28.781)
	Schindleria pietschmanni					
	Labridae					
2	*Lestidium* spp.					
	Diaphus pacificus	28.6	26.3	77.8	94.4	71.4
	Sudis atrox	1.182	2.372	7.570	8.284	5.080
	Evermanella sp.	(1.918)	(2.644)	(5.657)	(5.588)	(2.789)
3	*Epigonus* sp.					
	Scaridae	28.6	15.8	11.1	0.0	0.0
	Chaetodontidae	2.344	2.216	0.592	0.327	0.000
	Nealotus tripes	(3.034)	(5.497)	(0.929)	(0.874)	
4	*Coryphaena hippurus*					
	Cubiceps caeruleus	14.3	21.1	0.0	0.0	0.0
	Bathophilis sp.	0.497	1.016	0.000	0.187	0.000
	Caulophyrne sp.	(1.314)	(1.853)		(0.361)	
5	*Synodus* spp.	14.3	0.0	22.2	0.0	0.0
	Bothidae	0.120	0.000	1.007	0.048	0.000
		(0.317)		(1.228)	(0.203)	
6	*Selar crumenopthalmus*	14.3	0.0	22.2	5.6	0.0
	Tetraodontidae	0.180	0.042	0.473	0.094	0.112
	Apogonichthys perdix	(0.476)	(0.184)	(0.950)	(0.397)	(0.297)
7	*Melamphaes* spp.					
	Bregmaceros sp.	0.0	5.3	85.7	72.2	57.1
	Howella sp.	0.514	0.171	2.527	3.972	4.096
	Hygophum reinhardti	(0.879)	(0.745)	(2.123)	(2.847)	(4.160)
8	*Idiacanthus* sp.	0.0	0.0	22.2	22.2	100.0
	Gonostoma atlanticum	0.000	0.142	0.782	1.212	6.805
	Gonostoma spp.		(0.461)	(1.568)	(1.939)	(3.012)
9	*Scopelosaurus* spp.	0	0	0	5.6	42.9
	Gonostoma elongatum	0.000	0.142	0.000	0.634	3.974
	Scopelarchus spp.		(0.463)		(1.738)	3.232)

approached a ubiquitous distribution without exceeding the analytical procedure's rejection criterion applied to *Ceratoscopelus warmingi*, *Vinciguerria nimbaria* and the other seven excluded taxa. Group 3 comprised four species of mixed affinities (two island, one oceanic and one other) found in the upper two strata. Although the assemblage occurred most frequently in island waters, total densities were not higher there. Group 4 taxa were all oceanic but restricted mainly to the upper stratum, whereas group 5 comprised two island taxa restricted mainly to island waters in the upper 100 m. Rarer island taxa characterized group 6, including the carangid *Selar crumenophthalmus* and the apogonid *Apogonichthys perdix*. The last three groups, all oceanic taxa, were most abundant in deeper water, and group 8 was distinguished by its more widespread occurrence of taxa.

DISCUSSION

A variety of studies have documented that planktonic communities near oceanic islands differ from those in the open ocean: near islands, primary productivity [the "island mass effect" in DOTY and OGURI (1956)] and chlorophyll content (HEYWOOD *et al.*, 1990) may be greater. Zooplankton species composition and abundance (JONES, 1962; HERNANDEZ-LEON, 1988), larval fish assemblages (LEIS and MILLER, 1976; SMITH *et al.*, 1987; FEDORYAKO, 1989; present study) and acoustic scattering as an indicator of biomass (HARGREAVES, 1975) are all characterized by unique features near islands. Most other studies of ichthyoplankton near islands, however, have considered large islands where surveys could not surround the island (LEIS, 1982b), or island groups where the origin of the neritic larvae could not be determined with certainty (WILLIAMS *et al.*, 1984). In our study, certain components of the ichthyoplankton originating from Johnston Island are retained in near-island waters, typically concentrated in the area downstream of the island (Figs 7 and 8; Tables 2 and 3). A variety of mechanisms may be responsible for the observed distributions, but understanding them may require information on both vertical distribution and physical processes (BAKUN, 1988).

Vertical distribution

The general pattern of vertical distribution, with the peak abundance of both island and oceanic larvae in the 50–100 m stratum (Fig. 5; Table 1), was rather surprising. This is typically deeper than suggested in most studies of tropical ichthyoplankton, especially since all samples were taken at night, when many larvae migrate vertically to shallower water (AHLSTROM, 1959; GORBUNOVA, 1977). We undersampled the neuston, however, and larvae of some taxa probably were more abundant in surface waters than our results indicated.

Patterns of vertical distribution of oceanic fishes in our study were similar to those observed in other studies in tropical and subtropical waters (GORBUNOVA, 1977; LOEB, 1979; CASTONGUAY and MCCLEAVE, 1987). Although the centers of vertical distribution for many of the midwater species are deeper than the sampling in our study (JOHN, 1984), high densities were observed in the strata sampled (Fig. 5; Table 1). Many of the oceanic species we captured were also sampled by LOEB (1979), but her sampling location was farther north, at 28°N. Comparisons of species occurring abundantly in both studies (myctophids *Hygophum proximum* and *Ceratoscopelus warmingi* and the photichthyid *Vinciguerria nimbaria*) demonstrate that the centers of vertical distributions in our study are consistently deeper by 25–75 m. This may be due to temperature; her study site was characterized by a shallow thermocline near 40 m, as opposed to 60–105 m in our study (Fig. 2). Peak larval densities from LOEB (1979) were in the depth stratum containing the thermocline, as was also true in our samples (Table 1). Similarly, night-time distributions of microplankton, mesozooplankton and copepod densities at two stations in the tropics were highest at "upper thermocline" depths (SAMEOTO, 1986). Thus, temperature in general and the thermocline in particular conceivably play important roles in modifying the vertical distribution of these species. The closer correspondence of our results with thermal profiles and distributions (myctophids *Symbolophorus evermanni*, *Hygophum proximum* and *H. reinhardti*; photichthyid *Vinciguerria nimbaria*) from equatorial Pacific samples (GORBUNOVA, 1977) supports this interpretation.

Patterns of vertical distribution in tropical island fish larvae have not been described in detail. Most studies describing vertical distribution have been in relatively shallow waters of embayments (WATSON, 1974) or to depths of 6 m in the lagoon of the Great Barrier Reef (LEIS, 1986). MILLER (1979) classified larval vertical distribution patterns as only "surface" or "subsurface". None of these studies is therefore directly comparable with our results, particularly given that the peak abundance of island larvae occurred in the 50–100 m stratum (Fig. 5). Exceptions to this generality include the holocentrids, chaetodontids and *Aulostomus chinensis* in the 0–50 m stratum and the chlopsids, callionymids and *Apogonichthys perdix* in the 100–200 m stratum (Table 1). Some relatively abundant taxa were equally abundant in all strata; the best example is the creediid *Limnichthys donaldsoni*.

Patterns of ontogenetic change in vertical distribution have been noted in several studies (LOEB, 1979; CASTONGUAY and MCCLEAVE, 1987); the most common pattern is younger stage larvae at greater abundance in shallower water, moving deeper with increasing length. The opposite was true for certain mid-water taxa, notably *Serrivomer* sp. and *Symbolophorus evermanni* (Fig. 6A). SCHOTH and TESCH (1984) noted that smaller larvae of *Serrivomer beani* in the Sargasso Sea were typically restricted to shallower water. Larvae in our study were not measured and were instead classified as described earlier, so our youngest may be recently hatched larvae. GJOSAETER and TILSETH (1988) suggest that buoyant eggs of *Benthosema pterotum* are spawned deep and that larvae hatch there, moving to shallower habitat with growth; a similar pattern has been noted for *Maurolicus muelleri* (JOHN and KLOPPMANN, 1989). The earliest larvae (<5 mm) of *Anguilla* sp. are relatively deep-living, apparently characteristic of the adult spawning habitat, but later larvae show a pattern of increasing length with depth during the day but not at night (CASTONGUAY and MCCLEAVE, 1987). Thus, most of the smallest larvae of *Serrivomer* and *Symbolophorus evermanni* may be present at 100–200 m because of spawning, but the scarcity of yolk-sac larvae precludes confirmation of this pattern. The pattern evident in island fish larvae (that is, younger stage larvae in shallower water; Fig. 6B) also may be related to the shallower spawning habitat.

Horizontal distribution

Several studies of tropical island ichthyoplankton have documented onshore–offshore gradients in abundance (LEIS and MILLER, 1976; LEIS, 1982b). A variety of mechanisms may maintain these gradients. LEIS (1982b) has suggested that larvae distributed offshore are passively advected, whereas those remaining near-shore are characterized by active swimming and the use of favorable currents. Various larval behaviors have been proposed to interact with patterns of upwelling, localized eddies or onshore water movements at various depths to retain the larvae nearshore. Epibenthic schooling (LEIS *et al.*, 1989) or other behavioral mechanisms may allow retention of larvae in shallow water, often directly adjacent to reefs, where they are undersampled in larger scale surveys such as ours (KOBAYASHI, 1989).

On a larger horizontal scale, however, the role of mesoscale oceanographic features in larval distributions must be considered. LOBEL and ROBINSON (1986) proposed that eddies downstream of the Island of Hawaii could both entrain island larvae and later return them to near-shore regions to promote recruitment, but their biological sampling and taxonomic resolution of larvae were inadequate to support this contention. Other studies have documented offshore displacement of spawning and larval habitats for fishes by eddies (FIEDLER, 1986). Topographically controlled fronts around small islands have been shown to accumulate buoyant coral eggs (SAMMARCO and ANDREWS, 1989; WOLANSKI *et al.*, 1989), and creediid eggs have been used as passive tracers of water masses by LEIS (1982a). At Johnston Island, fish eggs were significantly more abundant in the putative downstream retention area in the 50–100 m stratum (Fig. 8), and the larvae of the creediid *Limnichthys donaldsoni* were significantly more abundant in both the 0–50 and 50–100 m strata (Table 2). There may thus be a passive component to the aggregation of fish eggs in the downstream retention area that is maintained by larval behavior after hatching.

HAMNER and HAURI (1981) and WOLANSKI and HAMNER (1988) have described mechanisms by which topographically-induced fronts can result in aggregation of planktonic organisms. The wakes of islands can develop contra-rotating eddies, and BARKLEY (1972) has observed von Kármán vortex streets extending downstream in the wake of Johnston Island. Our objective analysis modeling (Fig. 3) suggests the presence of the margins of two eddies (or meanders) within the domain examined, leading to an area of stagnant waters or possibly return flow that coincided with areas abundant in fish eggs and island larvae. It should be pointed out, however, that the distance of these nominal eddies from Johnston Atoll suggests that they are not produced by currents interacting with the island. Nonetheless, we propose that the situation of return flow leads to the retention of locally spawned eggs and larvae in the vicinity of Johnston Atoll. That the concentrating mechanism does not affect most oceanic species suggests that either larval behavior or localized spawning is required. Both processes may occur for the oceanic scombrid *Thunnus* spp., which may preferentially spawn in waters near islands (MILLER, 1979; LEIS *et al.*, 1991). This is consistent with the trend toward higher abundance of larvae of this genus in the shallow stratum of the downstream retention area (Table 2). For reef fish larvae, however, LEIS (1982b) rejected the hypothesis that higher densities near-shore were the result of a fixed site for spawning followed by dilution and passive drift, again supporting the role of larval behavior.

Without concurrent studies of the spatial and temporal pattern of settlement on the reefs, the importance of our observations to recruitment at Johnston Atoll is uncertain. High densities in the retention area occur at distances far from shore, beyond the swimming capacity of most larvae (Fig. 8), so some form of modulated transport may be necessary to bring larvae competent to settle to nearshore areas. If this is indeed the case, one would expect to see regional variation in the densities of new recruits in reef habitats at the downstream side of the island. Coral recruitment, for example, is highest where flushing rate is low and residence time is high (SAMMARCO and ANDREWS, 1989). Similarly, regional variation in recruitment may be caused by persistent oceanographic features associated with coastal headlands (EBERT and RUSSELL, 1988).

The temporal stability of our putative retention area is also unknown; our sampling occurred over a period of less than 2 weeks. BARKLEY (1972), who described seasonal differences in the incident ocean current patterns at Johnston Island, observed relatively fast (60 cm s^{-1}) incident flow during winter that resulted in a von Kármán vortex street, but in autumn he observed 15–20 cm s^{-1} incident flow with no evident wake. The currents observed during the latter period [fig. 2 in BARKLEY (1972)] are remarkably similar to those inferred from dynamic heights in our study during November (Fig. 3). BARKLEY (1972) interpreted the eddies around Johnston Island as part of a line of vortices associated with the frontal zone. However, the slow incident flow evident in summer and autumn may promote the kind of eddies or meanders observed in our study and, concomitantly, the retention of fish larvae in downstream waters. If this feature is seasonally consistent, it would be interesting to determine the spawning seasonality and recruitment patterns of island fish to evaluate the hypothesis that spawning in tropical islands occurs in seasons optimal for retention in island water (JOHANNES, 1978). Existing evidence for this hypothesis is not compelling; ROBERTSON (1990) failed to find a linkage between the seasons of peak spawning and peak recruitment in several species of tropical reef fishes. For Johnston Atoll, the fish fauna is relatively depauperate but is most closely associated with that from Hawaii (RANDALL *et al.*, 1985), where late autumn is the low point in the annual cycle of fish recruitment (WALSH, 1987). Despite our sampling in this season, many species of island larvae were present in moderate to high densities. If the retention area is important for recruitment but temporally infrequent, this would indicate that longer term patterns of recruitment may be driven by more anomalous events (COWEN, 1985; CHOAT *et al.*, 1988; COLIN and CLAVIJO, 1988).

Evaluation of these ideas will require further research. Biological studies must determine the ontogenetic changes in vertical and horizontal distributions of larvae, the relative mortality rates of larvae inside retention areas and the resulting patterns of recruitment to the island. A better understanding of the physical oceanography will be required to assess the persistence of larval retention, with direct measurement of currents and tidal flux relative to larval advection.

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