

LOCAL RETENTION OF PLANKTONIC EARLY LIFE STAGES IN TROPICAL REEF BANK DEMERSAL SYSTEMS: THE ROLE OF VERTICALLY-STRUCTURED HYDRODYNAMIC PROCESSES

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ABSTRACT: The question of the extent to which local tropical reef bank demersal fish populations may constitute open or closed systems with respect to recruitment is crucial to resource management as well as to scientific investigation of the causes of recruitment variability. Connotations of the almost universal commitment to extended periods of pelagic larval drift among coral reef fishes, as well as certain evidence of largely locally-based recruitment in these systems, are discussed. A variety of vertically-structured hydrodynamic processes, pertinent to the problem, are introduced. An observational focus on vertical structure in both biological and physical aspects is advocated as offering a means to circumvent extreme difficulties involved in applying conventional recruitment research methodologies to tropical systems. Interregional comparative studies may offer a particularly efficient avenue of inquiry. Important inputs from a broad range of marine scientific specialities are envisaged.

## 1. INTRODUCTION

The early life stages of fish species inhabiting oceanic reefs and banks are characterized by extended periods of planktonic drift, during which the mean ocean surface currents would tend to carry freely drifting offspring great distances from the local spawning habitats of their parents. This has led quite naturally to a perception of the effect of local spawning as being mainly a contribution to some larger regional-scale (or even ocean basin-scale) 'pool' of dispersing larvae from which recruitment to the various local populations occurs by random diffusion, or by direct advection by prevailing currents from upstream populations. This perception lends support to a view that fishery management on a local scale may be futile, or at least nonessential and locally unprofitable. However, various fragments of evidence that this may not always be the case are discussed below. It is arguable that this question of the spatial scale from which recruitment is ordinarily generated is in fact the most crucial aspect of the recruitment problem with respect to immediate utility of scientific results in improving management of human impacts on tropical oceanic demersal resources.

Recent studies in which coherent observational programs have been maintained over interyear time scales (e.g., Williams, 1980 & this vol.; Victor, 1983; Doherty, 1983) have suggested that even unexploited coral reef fish populations may not generally be in resource-limited or predation-controlled equilibrium, but rather that their population dynamics may be controlled principally, as in other types of studied fish stocks, by recruitment variability. In addition, synthesis of information obtained from artisanal fishermen as well as from scientific studies (Johannes, 1978, 1981), and computer simulations incorporating vertical migratory behavior (Doherty *et al.*, 1985), have provided new hypotheses as to the role of larval drift in reproductive strategies of fishes associated with coral reef systems. The capacity of vertical migratory behavior to interact with vertical structure in the flow field to produce larval trajectories differing greatly from ambient flow patterns has been strikingly demonstrated with respect to prawn stocks of the Gulf of Carpenteria (Rothlisberg, 1982; Rothlisberg *et al.*, 1983).

## 2. WHY PELAGIC STAGES ?

The fact that marine organisms associated with oceanic islands and banks face a problem of conserving, rather than dispersing, their pelagic stages has been recognized for many years. Boden (1952) suggested that planktonic forms were maintained in the vicinity of Bermuda by convergences associated with an observed anticyclonic circulation pattern over the subsurface bank underlying the island group. Ehrlich (1975) cited evidence that species inhabiting the isolated oceanic island, Johnston Atoll, were not recruited from the Hawaiian Islands, the nearest upstream source, but had characteristics indicating endemic reproduction; this led him to remark on the "enormous losses" of reproductive products which must be borne by the local marine fauna. Johannes (1978) enumerates various adult reproductive behaviors apparently explicitly adapted to cause the reproductive products to be transported offshore where they would be most subject to such losses. Sale (1980) commented on the ubiquity of the pelagic reproductive mode, and noted that in only a single case has absence of a pelagic phase in the early life history of a coral reef fish been demonstrated. A typical length for the pelagic phase appears to be of the order of three to ten weeks (Brothers *et al.*, 1983; Victor, 1986).

It is possible that very large lagoons such as that of Enewetok Atoll, which appears to have a mean water residence time of the order of a month (Atkinson, Smith & Stroup, 1981), could be important to local larval retention. However, reef lagoons of more common sizes appear to have such short flushing times (Leis, 1982; Wolanski & Picard, 1983) that retention of significant numbers of larvae through their entire pelagic phase is unlikely (Williams *et al.*, 1984). Thus it seems improbable that retention of reproductive products in enclosed lagoons can be a primary basis for widespread reproductive adaptations.

This leads to an obvious question: Why does the pelagic mode of reproduction so dominate among fishes of these systems? This can be re-phrased: How have the fishes utilizing the pelagic mode of reproduction been able to compensate for the apparent overwhelming reproductive energy losses, so as to avoid having been replaced by fishes having more conservative evolutionary adaptations such as livebearing, continuous brooding of offspring, etc.? If we believe in evolution by natural selection, we must conclude that the prevalence of the pelagic mode is due to the fact that it has turned out to be more successful, on the long term at least, than any of the alternatives that could be developed.

Doherty, et al. (1985) cite Barlow's (1981) suggestion that dispersal is necessary to prevent extinctions in a situation where an uncertain environment cannot ensure maintenance of viable local populations of spawning adults. Few are likely to argue with that line of reasoning (although, if this were the sole function of the pelagic reproductive strategy, one might wonder if the particular need might not be more efficiently met by other adaptations such as intermittent migrations of 'pioneer' groups of adults). Doherty et al. (1985), while accepting Barlow's general statement, remain unconvinced that it accounts for the extreme degree of dispersal that actually occurs. They specifically "do not address the question of why these animals 'broadcast' rather than 'brood'" but suggest that species committed to pelagic offspring will be under selection to disperse siblings to spread the risk of failure among members of a cohort. They support this hypothesis with a computer simulation wherein larvae which were dispersed in an environment containing a horizontally patchy food distribution, and possessed vertical migrating behavior by which their position relative to the surface flow pattern could be altered when the relation to food distribution was unfavorable, experienced better average survival than larvae which did not disperse. Johannes (1978) notes the disadvantages of live-bearing, including low fecundity, increased stress, and increased vulnerability of adults carrying young; his major point is that given the egg-laying reproductive mode, the pelagic strategy functions to remove eggs and hatched larvae from the intense predation of the reef areas inhabited by the adults.

#### 2.1 An 'aside': Is there a potential long-term advantage of erratic recruitment?

In this section we turn briefly to a speculative discussion of another factor possibly favoring the prevalence of the pelagic reproductive mode among the fishes successfully inhabiting these systems. (Note that the degree of 'real-world correctness' of the particular line of reasoning presented in this section is not deemed to be in any way crucial to the main line of argument developed in subsequent sections of the paper; it is inserted here because the ideas are related to the other topics being developed and also might constitute some useful hypothetical framework for interpreting results of potential interregional comparative studies which are advocated later in the paper.)

Intermittency, characterized by peaks of high abundance separated by very much wider intervals of very low abundance, is quite a pervasive characteristic of marine populations. Intermittency in time and space may serve, among other possibilities, to defeat predator populations by denying them a continuously accessible food source. Since a predator can have only a limited energy storage capacity, presenting it with much more food than can be utilized at each encounter, while stringently minimizing the frequency of encounters, favors maintenance of the prey population's biomass. Perhaps more importantly, such a tactic prevents growth and maintenance of large resident predator populations which could decimate, or even cause extinction of, the prey population. Schooling behavior is one way spatial

intermittency is achieved. In the case of reef/bank demersal systems, space may be too valuable a resource to expend in this manner. Therefore, temporal intermittency may offer the only means by which the growth of destructive levels of predation pressure might be interrupted.

A temporal analogue of schooling behavior consists of intermittent pulses in abundance. Shorter term intermittency allows a predator population to be temporarily overwhelmed by numbers of prey such that adequate survivors may pass through a particularly vulnerable stage (e.g., transition to demersal life style, etc.) to recruit to the adult stock. Longer term intermittency may serve to preclude the establishment of a dependent predator population. In fact, some non-regular mixture of frequencies (i.e., unpredictable and therefore impossible for a predator to counter by any selective adaptations) may be an optimal situation for a population which is seriously vulnerable to predation. A "red noise" spectrum of variability (i.e., increased variance at lower frequencies, in contrast to "white noise" which has equal variance across the spectrum (Figure 1)), where groups of episodes of extremely low prey availability are embedded within longer periods of relative scarcity, could be particularly advantageous in causing collapse of specialized predator populations.

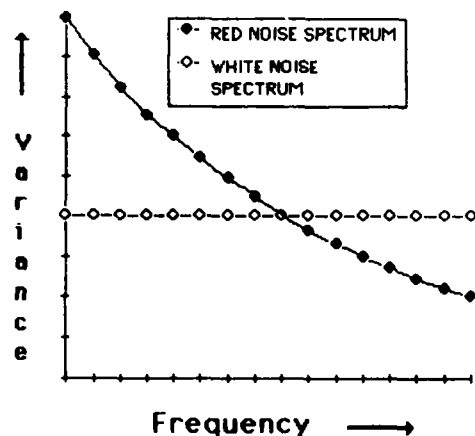


Figure 1. Example 'red noise' and 'white noise' spectra.

Development of biological adaptations to achieve such intermittency in abundance may not be feasible. For example, a survival advantage to more adapted individuals over less adapted individuals in the population, which could thereby direct the selection process, would not exist in this case. Also, synchronization of irregular variability (as opposed to regular periodicities) among individuals, so that it could be effective in this sense, may be difficult via purely biological mechanisms. However, variability in nearly all aspects of the earth's coupled ocean/atmosphere hydrodynamic system is known to be characterized by red-noise spectra. Organisms whose abundance at particularly vulnerable stages (e.g., at recruitment) is subject to this variability may be favored over those with more uniform reproductive output. One mechanism by which demersal organisms might not only incorporate the ocean's available red-noise variability via pelagic early life stages, but also experience reduced losses of those stages from the local habitat and thereby achieve large episodic recruitment pulses, is described in the following section. (Note that this argument does not necessarily depend on existence of any need to defeat directed predation on recruits on the shorter-term year-to-year time scale; the fact that no directed predator on these stages may be present in substantial abundance could be a result of the fact that intermittency has precluded its establishment. To the question of "why would the adults not need similar intermittency in abundance?", a partial answer may lie in the array of individual reef structures themselves, as constituting a spatial intermittency constraint with respect to organisms of large enough size to be major predators on adult reef fishes.)

### 3. THE STRATIFIED TAYLOR COLUMN

A classical laboratory demonstration (Taylor, 1923) of the special properties of fluid flow in a rotating coordinate system (note that for large scale flows such as ocean currents, the earth functions as a rotating system) proceeds as follows. A large flat-bottomed tank of water is set on a rotating turntable. Some solid object is placed on the tank-bottom so as to represent a 'bump' protruding from the tank floor. A dye marker is placed in the water above the bump. If the object is then moved slowly along the tank floor, the dye in the water above is observed to follow along with it, showing that the water column above the bump is effectively trapped relative to the bump.

The same phenomenon occurs if the bump is stationary and the water is moving relative to it (analogous to a submerged bank in the path of an ocean current). The water above the bump remains trapped in position, and the moving water is deflected around, rather than over, the bump. The trapped water column above the bump is referred to as a "Taylor column" or less commonly, as a "Proudman pillar", after

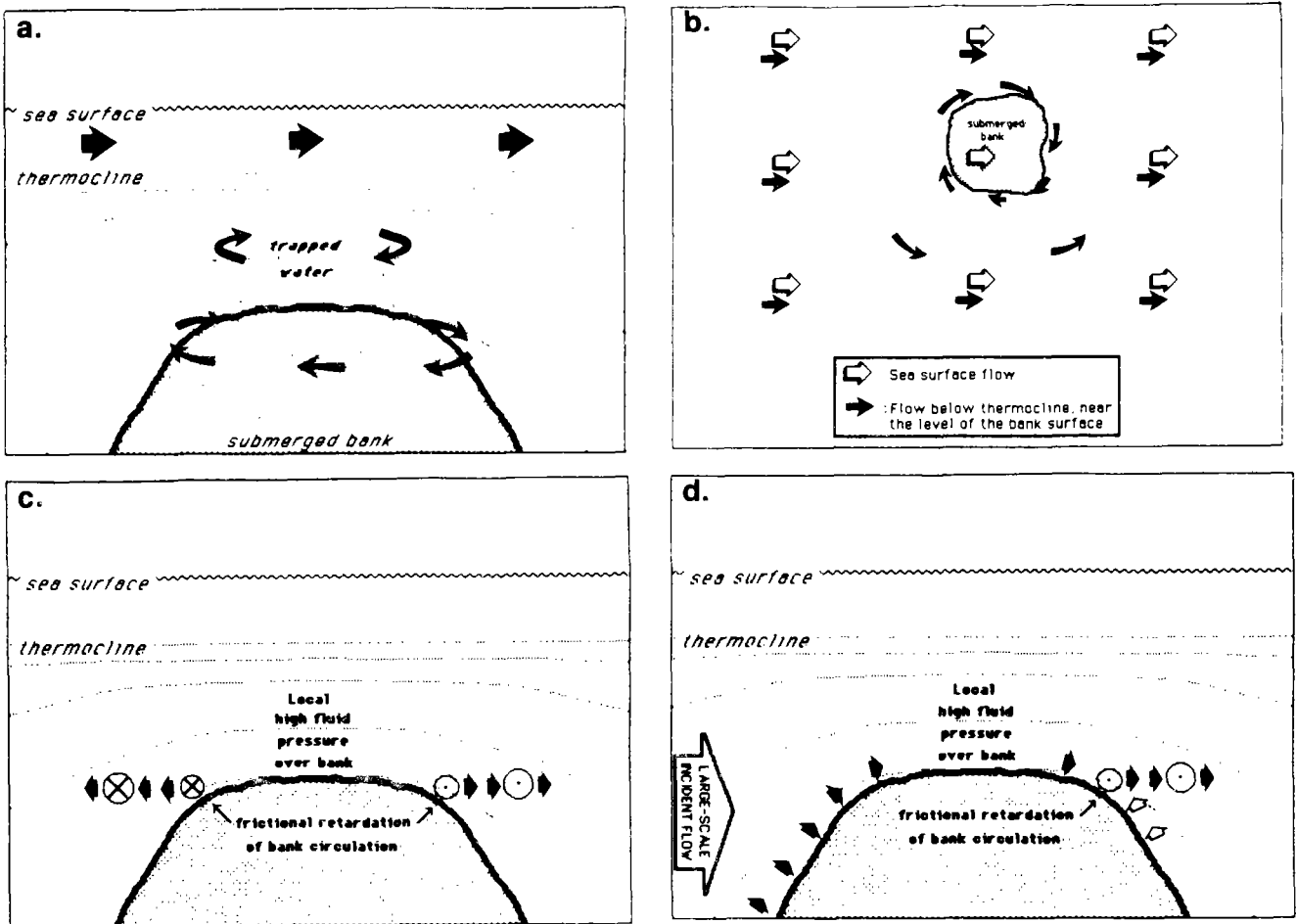


Figure 2. Schematic representation of a stratified Taylor column over a submerged bank: (a) horizontal view; (b) plan view; (c) profile view indicating frictional retardation of flow adjacent to bank surface resulting in sub-geostrophic flow and associated unbalanced pressure gradient, leading to a secondary radially-directed outflow (short black arrows) from the bank area (circles containing 'x' indicate flow of the primary around-bank circulation into the plane of the figure; circles containing dots indicate flow out of the figure); (d) representation of upwelling circulation which may balance radial outflow (see text). Note that these two-dimensional representations are heuristic rather than exact; in the real situation, interaction with the pressure gradient which is in balance with the large-scale incident flow causes the situation to be inherently three-dimensional. Examples depicting more complex actual numerical model results are presented by Huppert & Bryan (1976).

the scientists who originally deduced the effect theoretically (Proudman, 1916; Taylor, 1917). Interestingly, the Great Red Spot of Jupiter has been attributed to the existence of an enormous Taylor column in the Jovian atmosphere (Hide, 1961). Shomura & Barkley (1980) suggested Taylor columns as an explanation for the ability of populations of organisms having pelagic egg and larval stages to maintain themselves as components of ecosystems associated with banks and seamounts.

Hogg (1980) provides a useful review of recent application of Taylor column theory to the circulation of a stratified ocean. In the stratified case the Taylor column effect is bottom-intensified and may be largely isolated, by inhibition of turbulent transfer through density clines, from any frictional coupling to the upper layer flow field. For example, in the rotating tank demonstration, if the water were stratified, dye placed very close to the top of the moving object would follow the movement, while dye placed near the water surface would remain in place. Huppert and Bryan (1976) used a numerical model to investigate the evolution of a stratified Taylor column over a small bump in the sea floor. At the initial impingement of a current flow on the bump, relatively heavy water is raised upward by the flow over the bump. This results in higher fluid pressure at the top of the bump, which at some point exerts a pressure force sufficient to oppose any further flow onto the bank. Meanwhile, the pressure force directed radially outward from the bank comes into balance with Coriolis forces via an anticyclonic (*i.e.*, clockwise in the northern hemisphere, anticlockwise in the southern hemisphere)

circulation around the high pressure center and thus around the bank, such that no flow crosses the bank in the lower layer (Figures 2a & 2b).

Dooley (1984) analyzed records from current meters moored on the flanks of Rockall Bank, and demonstrated the anticyclonic flow 'signature' characteristic of a Taylor column. Rockall is an isolated bank off northwestern Scotland, some 370 km from the Outer Hebrides. The area shallower than 250 m is about 300 km by 100 km in size, but the bank lies mostly deeper than 100 m except in a small area near Rockall Island. The bank is the site of important demersal fisheries, and the stocks, particularly haddock, exhibit great variability in year class strength. The local haddock stock appears to be distinct from nearby North Sea stocks, despite a pelagic larval stage of up to four months. Dooley suggests that confinement of the water mass over the bank by the Taylor column effect is an important factor in maintaining the population. Large amplitude variability observed in the strength of the circulation around the bank, and corresponding changes in water properties, suggest intermittent breakdown of the Taylor column flow structure, accompanied by episodic replacement of the waters over the bank. Dooley advances the hypothesis that interyear variability in these phenomena may govern recruitment variation in haddock and other demersal fishes.

An interesting aspect, which (to this writer's knowledge) has not yet been specifically addressed, is the likelihood of continued local enrichment of the trapped water volume by frictionally-driven upwelling. Note that the part of the flow around the bank that is directly adjacent to the bank surface will be retarded, relative to the main anticyclonic circulation, by friction. Thus the Coriolis force is lessened with the result that the pressure gradient force directed radially outward from the bank is no longer balanced locally. The result should be lower order flow directed horizontally outward from the bank (Figure 2c). Under certain circumstances (e.g., more stable stratification above the level in question, etc.), it is possible that some upwelling along the flanks of the bank might be induced (Fig. 4, white arrows), from which dissolved nutrients could be diffused into the trapped region over the bank. The other possibility is that the frictional outflow would be supplied from the layer above the bank surface; in that case the effect could be similar because the resultant draining away of the pressure head could allow the incident large scale flow to lift more relatively dense, nutrient-enriched deeper water onto the bank to reestablish the Taylor column balance (Fig.4, black arrows). The specifics of these processes merit theoretical investigation, as they regulate the character of flow through the trapped volume, i.e., the balance between local enrichment of larval habitat and loss of entrained larvae. They also may have connotations for such ecological problems as "Darwin's question" (Andrews & Gentien, 1982), "the island mass effect" (Doty & Oguri, 1956), etc. For example, they might be important in providing nutrient enriched water to the vicinity of a reef edge where it might be available for uplift and supply to the reef surface by more local mechanisms such as discussed by Wolanski & Picard (1983) and Thompson & Wolanski (1984). In a somewhat deeper oceanic situation, Genin & Boehlert (1985) found higher chlorophyll concentrations where domed isotherms over Minami-kasuga Seamount (260 m minimum depth), resembling Taylor column effects, penetrated into the lower euphotic zone.

A very attractive aspect for experimental efforts is the well defined and apparently readily monitored anticyclonic flow 'signature' associated with these structures. Dooley (1984) has shown that it is possible to extract reasonable interpretations from near-bottom current records from as few as two locations on opposite flanks of the bank. Bottom-moored continuously recording meters seem ideal, but the recent development of various types of acoustic, expendable, or inexpensive and easily deployed retrievable current profiling instruments might provide some alternative methodologies. The characteristic temperature doming can be easily measured by standard bathythermograph sections, etc., but unfortunately existence of such doming is a necessary, but not a sufficient, condition for a 'trapped' Taylor column type of structure. In a case where its existence is demonstrated, the well defined and understood, organized nature of such a structure would simplify investigation of the associated biological effects, e.g., a restricted sampling of vertical distributions might substitute for full three-dimensional coverage.

How likely are such effects in tropical demersal habitats? At present we have no definite answer to the question. Certainly, in equatorial regions the Coriolis constraint becomes weak, and such vorticity-dependent hydrodynamic structures would seem less likely. This might be constricted to some extent in those tropical areas where storm-forced flow variability, capable of disrupting the structures, may be less frequent and intense. There are certainly major tropical reef areas which are

not in the immediate vicinity of the equator. The geostrophic flow relationship, which likewise depends on the Coriolis constraint, is considered to hold to a reasonable degree to within several degrees latitude of the equator (e.g., Montgomery & Stroup, 1962). This problem is one where investigation via the comparative scientific method might be particularly effective, e.g., one might look for patterns in species composition, and (where information can be generated) apparent recruitment variability and rate, etc., as functions of distance from the equator, stratification, dispersal-related adaptations, etc.

Many tropical demersal habitats are characterized by particularly shallow, irregular topography related to coral structures; thus frictional effects might seem to disrupt the simple dynamic balances associated with an ideal Taylor column. However, one expects such quasi-geostrophic hydrodynamic features to be of rather large scale in any case. We would therefore expect the essential circulation to be located over the deeper flanks of the banks; in this case the shallow areas would constitute the trapped regions of no net large scale flow, and local frictional effects would be irrelevant. In fact the basic mechanism could apparently act around single large islands, groups of islands sharing a common subsurface topographic feature, etc., whenever a local horizontal fluid pressure 'high' becomes established at the feature and the scale is large enough that rotational effects dominate the frictional effects. Note that Rockall Bank, the site of Dooley's suggestive findings, does itself break the surface in one location.

#### 4. HYPOTHESIS: RECRUITMENT REGULATION BY TOPOGRAPHICALLY-TRAPPED HYDRODYNAMIC STRUCTURES

The hypothesis that recruitment variability may be governed by variations in ocean flow conditions affecting local retention of larvae is of course neither novel nor new (e.g., Hjort, 1926; Walford, 1938; Johannes, 1978). However, it has sometimes been viewed in terms of variations in the transport of the bulk of the larvae. Of course, because of the enormous reduction in numbers from the time of hatching to the time of recruitment, what happens to the average larvae, or to 90 percent of the larvae, or even to 99.9 percent of the larvae, may be irrelevant. The considerations presented above suggest the possibility that even a relatively small fraction of the larvae, contained locally in some type of trapped hydrodynamic structure, etc., could be the major source of local recruitment. This in turn implies that the bulk of the larvae, drifting in the upper layers or elsewhere, may have little or no prospect at all of experiencing eventual recruitment although they would serve the important function of maintaining the possibility of chance re-establishment of the species in distant, and presumably rare, situations where local extinction may have occurred. And it is perhaps discomfoting to realize that in such a case, painstaking efforts to define variability in distributions, concentrations, probable trajectories, etc., of this 'bulk of the larvae', could be useless in attempting to account for observed recruitment variability.

Thus, we might adapt Dooley's (1984) hypothesis to tropical reef/bank systems by (1) including the possibility of a particularly beneficial effect of local enrichment of the trapped water parcel and (2) to explicitly recognize the fact that the trapped volume may be small in comparison to the volume occupied by recently spawned eggs and larvae. Whether or not the trapped structure particularly resembles an ideal stratified Taylor column over isolated topography, as depicted in Figure 2, should not be crucial; in areas of complex topography the structures might be correspondingly complex, and different spatial scales might interact in a non-simple manner. The hypothesis may therefore be stated as follows: Recruitment is largely generated from larvae which have been retained in some (perhaps locally-enriched) hydrodynamic structure which may be isolated by stratification from the surface flow field; recruitment variability is introduced by the transitory nature of the structure in reaction to "red noise" forcing by the larger ocean / atmosphere scales. The corollary is that the larvae not so contained will not enjoy substantial survival due to (1) loss, by dispersion, of the advantage of numbers in withstanding predation, (2) possible lack of local enrichment or other conditions leading to appropriate food concentrations, (3) nonlikelihood of randomly encountering suitable habitat for recruitment in a suitable time frame.

The hypothesis has appeal in that it is in accord with some particularly puzzling aspects of recruitment in these systems. For example, there are three types of adult reef fish species assemblages in the central Great Barrier Reef inhabiting nearshore, mid-shelf, and outer shelf areas respectively (Williams, 1982). Newly settled recruits are found to follow the same pattern as the adults

(Williams, 1983a), and in fact Williams (1985) finds indications that the spatial distributions of pelagic larvae, still in the water column but approaching the recruitment stage, may also correspond to this distributional pattern. Flow conditions in this region are such that freely drifting larvae should have been spread spatially, in a well-mixed distribution, over the entire shelf during the pelagic phase (Williams, *et al.*, 1984). One possible explanation is that larvae may be specifically adapted to special conditions in the water column which may involve important cross-shelf gradients. In such a case, differential survival could account for the observed distributions of survivors. This explanation faces the difficulty that there is large interyear variability observed in the magnitude of recruitment (Williams, 1983b). If a poor recruitment were due to changes in the survival conditions in the water column, one would expect the hypothetical cross-shelf gradients to be shifted such that species of larvae which ordinarily survived to recruit on the mid-shelf, for example, would be observed to recruit either in the nearshore or outer shelf areas. Such spatial shifts are not observed. An alternative hypothesis explaining these observations is the one developed here: that the larvae which are surviving in substantial numbers to the recruitment stage are those which are locally retained in the immediate vicinity of the spawning grounds.

The hypothesis is in accord with the observed 'spikey' nature of recruitment variability in reef fishes (e.g., Williams, 1981, 1983b; Victor, 1983) which, incidentally, resembles that for haddock (e.g., Hennemuth *et al.*, 1980). Occasional spikes of good recruitment may be attributable to situations where integrity of the trapped structure may have been maintained over an entire larval pelagic period; more frequent mediocre recruitment years might result when "red noise" disruptions of the flow or stratification fields may cause breakdown of the structures and dispersion of the trapped water parcels. An explanation of the generally observed non-relationship of recruitment rate to adult population size is afforded by the assumption that the occasional strong recruitments occur when some variable small fraction of the total amount of reproductive product is locally retained, with the variation in this effect obscuring the dependence on spawning stock size; note however that in this case the conclusion is not that recruitment is independent of spawning stock size, but rather that the resultant recruitment, although variably modified by these hydrodynamic effects, is in any particular situation directly proportional to the amount of spawning that occurred. Boden (1952) reports most reproductive activity in the fishes and marine invertebrates of Bermuda to be concentrated in the summer, when the overlying air is hot and humid (both effects promoting stratification), and when winds are calm (promoting both stratification and absence of wind-driven transients in the flow field). Williams *et al.* (1984) state that the time of release of larvae, of both scleractinian corals and fishes in the Australian Great Barrier Reef is concentrated in spring - summer (*i.e.*, outside the trade wind season). Navaluna & Pauly (this vol.) show annual spawning of a variety of Phillipine fishes to be bimodal, with modes corresponding to periods of relaxed trade winds. Johannes (1978) presents similar examples from other locations throughout the tropics where shallow marine fishes tend to spawn at times of year when prevailing winds or currents are weakest.

The hypothesis would seem to be in accord with the high degree of endemism exhibited by tropical reef fishes; e.g., evidence (1) that certain fishes inhabiting the small isolated Johnston Atoll are differentiated from those of the Hawaiian Islands, the logical source of external supply of larvae (Erlich, 1975), (2) that even within the Hawaiian Islands, some species with pelagic oceanic larvae have genetically distinct populations around different islands (Johannes, 1978), etc. It also would seem to explain decadal-scale delays in recovery of geographically isolated demersal stocks destroyed by overfishing, in spite of apparent adaptation of the affected organisms to particularly extended pelagic phases (e.g., Lutjeharms and Heydorn, 1981a, 1981b). The mechanism would seem also in accord with the very high degree of speciation which characterizes the fish communities of these systems. In addition to the obvious effect of promoting endemism which might lead to speciation, small scale spatial pattern in larval habitat, featuring limited highly favorable habitat space surrounded by much larger regions of unfavorable space, might favor local adaptations in adult reproductive behavior (e.g., location of spawning aggregations, etc.) to maximize possibilities of inserting adequate numbers of larvae in a particular parcel of favorable space; the benefit derived might be sufficient to promote development of mechanisms of reproductive isolation among segments of a somewhat contiguous adult population in order to protect these local adaptations.



## 5. STRATIFIED OR NON-STRATIFIED ?

Trapped hydrodynamic structures which are not isolated from the surface flow by stratification, e.g., 'non-stratified' Taylor column structures and various types of stationary eddies and swirls (e.g., Johannes, 1978, 1981) also may constitute plausible larval retention mechanisms. Brainard & Wittmann (1985) show doming in the density structure (in the sense required for existence of a Taylor column) over Southeast Hancock Seamount, northwest of the Hawaiian Islands, to be trapped below the seasonal thermocline in summer but to extend into the surface layer in winter. Flow patterns suggested for Bermuda by Boden (1952) and for Johnston Atoll by Barkley (1972) show the anticyclonic curvature at the sea surface which might characterize non-stratified Taylor column effects. (Note that the jargon terms 'stratified Taylor column' and 'non-stratified Taylor column' specifically refer to stratification in the flow field rather than in the density field, although these fields are certainly interdependent. Accordingly, a 'non-stratified Taylor column' is one in which the characteristic circulation is similar in form throughout the water column even though the fluid may be stratified in the sense of having some degree of density stratification. A 'stratified Taylor column' is one in which the circulation pattern existing near the bottom is largely absent, or in the opposite sense, near the sea surface. Density stratification is, however, a necessary condition for a stratified Taylor column to exist.) Stationary eddies in tidal flows found in the Great Barrier Reef (e.g., Hamner & Hauri, 1981; Wolanski et al., 1984) appear to be too transitory to retain larvae over the time scales required for significant recruitment effects (Williams et al., 1984).

The physics involved suggest that stratified Taylor column structures would tend to be more 'sticky' with respect to topography than their non-stratified analogues, i.e., to be more resistant to being shed from their topographically-trapped positions by transients in the larger scale incident flow and pressure fields. Whereas the atmosphere is heated from below, the ocean is heated from above and so the stratification in the ocean tends to be particularly stable and resistant to vertical turbulent transfers of momentum and mechanical energy. Thus, where the flow field is isolated from the surface layers by substantial density gradients, it is much less subject to alteration by storm-induced transients. In addition, because of the large density difference between air and water, the local fluid pressure 'high' controlling the trapping mechanism may, in the barotropic (non-stratified) case, represent a local rise in sea surface level of a centimeter or less; thus a very small total volume of fluid need be dissipated (by mechanisms of the sort represented in Figure 2c) for the structure to become dislodged. In the baroclinic (stratified) case, because of the much smaller density contrast between surface water and sub-thermocline water, a local pressure 'high' of similar magnitude might represent vertical isotherm displacements of tens of meters, with the result that much greater volumes of water would have to be shifted for comparable alteration of the local horizontal pressure field to occur.

Areas of the ocean in which tidal mixing on the continental shelf is expected to be low enough for density stratification to prevail have been delineated by Hunter & Sharp (1983); their map is reproduced in slightly modified form in Figure 3. Thus the shallow shelf areas where bottom-trapped hydrodynamic structures, isolated by stratification from upper layer flows and disturbances, would be most likely to exist include the Caribbean and Gulf of Mexico regions, the areas off the northern, western, and southern coasts of Australia, the area around New Guinea, the Java Sea, the South China Sea, the Gulf of Thailand, the Philippines, the western portion of the Bay of Bengal, virtually the entire east and west coasts of Africa, the Iberian Peninsula and Bay of Biscay, most of the east coast of Brazil, the Peru - Humboldt Current region, and the California Current region. These are also the regions where vertical current shears associated with stratified conditions might allow vertical migratory behavior to exert substantial control on advection trajectories. Note that areas near oceanic islands and banks which are not on continental shelves, and so are not treated in Figure 3, will generally be minimally subject to tidal mixing and so can be considered as falling within the 'stratified' classification.

## 6. OTHER VERTICALLY-STRUCTURED FLOW AND RETENTION MECHANISMS

In addition to topographically-trapped rotating flow phenomena, of which stratified Taylor columns are an example, a variety of other mechanisms can introduce organized vertical structure into the transport fields experienced by pelagic larvae. Some of those having possibilities for interaction with vertical larval distributions in ways that might significantly affect larval retention and export in oceanic reef and bank systems are discussed briefly below.

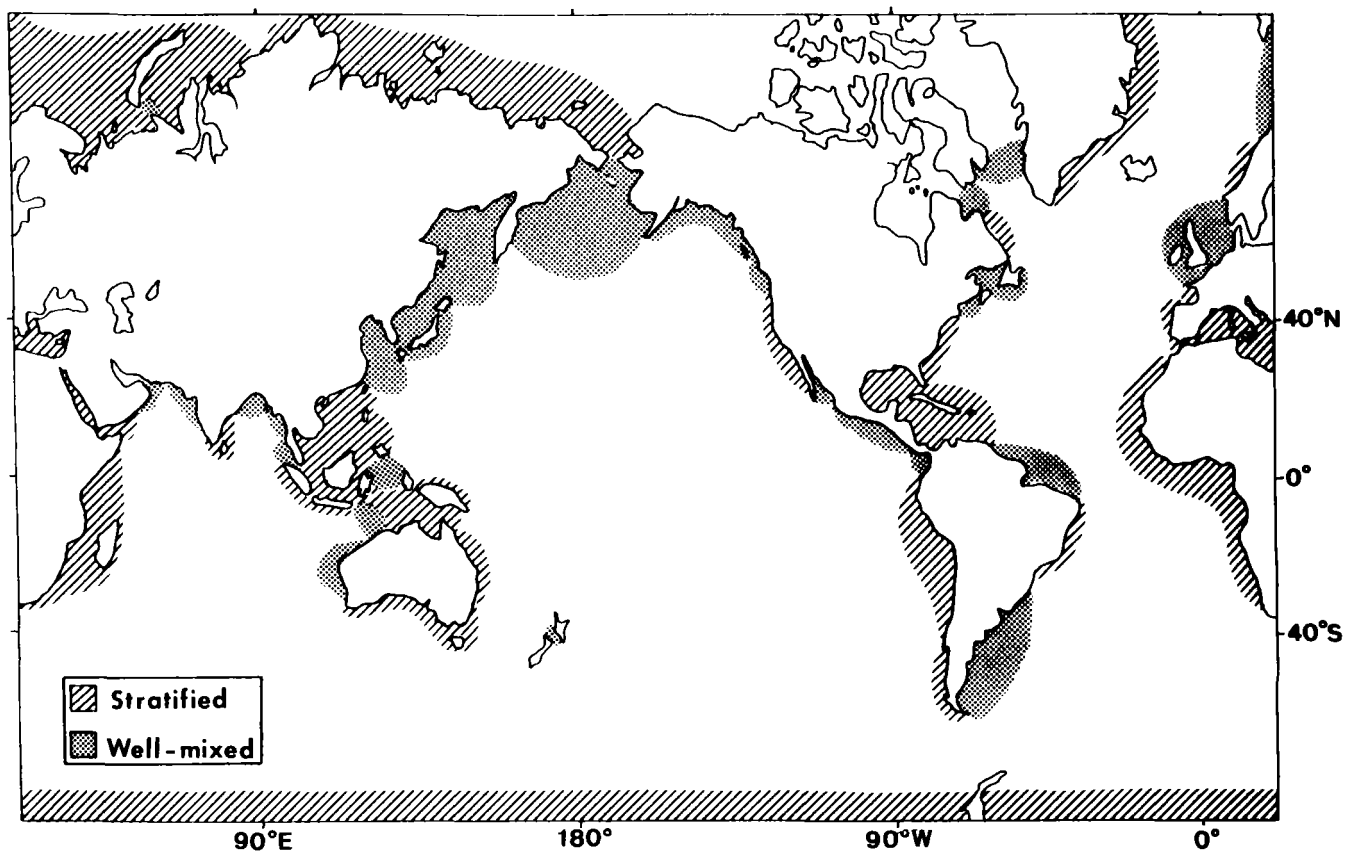


Figure 3. Map of tidal dissipation in shelf areas (after Hunter & Sharp, 1983). Regions of weak tidal mixing, where the water over the continental shelf is likely to be substantially stratified, are indicated by diagonally-lined shading. Regions of more intense tidal mixing, where the water over the shelves would tend to be well-mixed, are indicated by dotted shading.

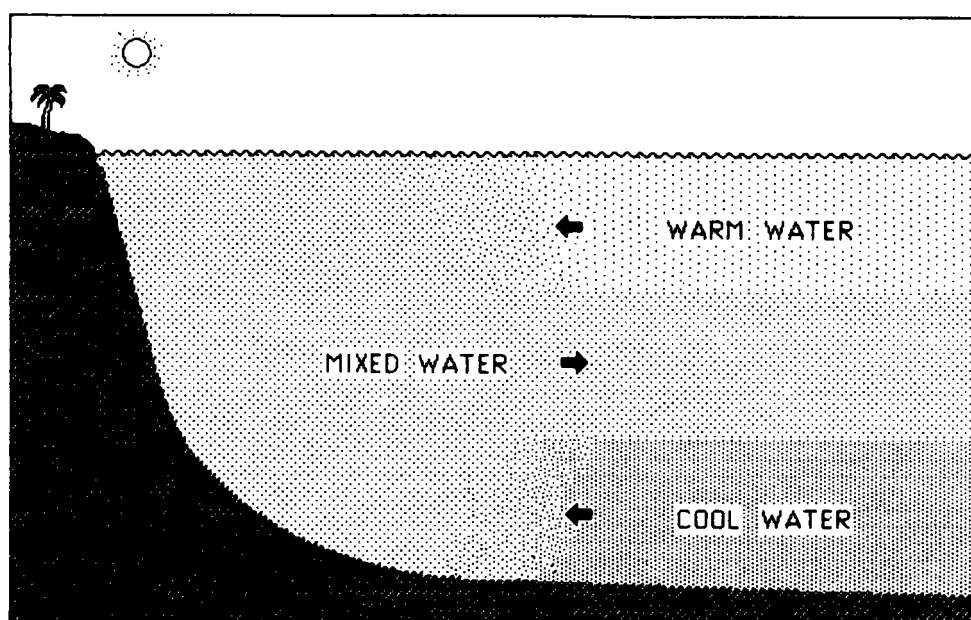


Figure 4. Schematic representation of the manner in which tidal mixing over shallows may induce density-driven onshore flow in the surface and bottom layers of the adjacent stratified waters, as discussed by Hunter & Sharp (1983).

### 6.1 Shelf sea fronts

When tidal flows over shallow shelf areas are sufficiently strong, stratification may be destroyed by turbulent mixing. When this occurs the density of the water becomes nearly constant from bottom to surface. This results in surface water of greater density, and bottom water of lesser density, over the shelf compared to water at the same depths offshore. The natural consequence is that at the offshore edge of the well-mixed region the 'lighter' offshore surface water tends to override the 'heavier' mixed water which in turn tends to flow under the lighter water resulting in a convergent surface front; similarly at the level of the shelf bottom, the heavier offshore water will tend to flow under the mixed shelf water resulting in a convergence zone near the bottom (Figure 4). Thus larvae that maintain themselves either near the surface or near the bottom in such regions would tend to be retained in these convergent fronts. Hunter & Sharp (1981) present a rather complete review of the mechanisms and associated theory; they present a map outlining the general regions where such tidally mixed regimes, required for this type of retention mechanism, would tend to occur (shown here in Figure 3, stippled areas). Among these are the whole northeast coast of South America from Guyana to Cabo de Sao Roque, the eastern edge of the Pacific from Columbia to the Gulf of California, the region from the southern end of the Phillipines to New Guinea, Western Australia to Java, the Andaman Sea and northern Bay of Bengal, and the northern Arabian Sea.

### 6.2 Vertical geostrophic shears

Where the ocean is stratified, there is a tendency for the sea surface slopes which determine geostrophic surface currents to be compensated by opposite sloping density surfaces at depth. The result is variation of horizontal pressure gradients with depth and corresponding vertical shear in the geostrophic flow field. These effects are strong enough that flow near the bottom, even in shelf regions, may be opposite in direction to the surface flow. Organisms undertaking vertical migrations, such that time is apportioned among oppositely-directed flows, would be aided in maintaining geographical position. In addition, vertical migration within a flow having vertical shear has the effect of altering a planktonic organism's position relative to conditions being advected horizontally at a particular level. For example, in a horizontally patchy environment, if pelagic larvae experiencing unfavorable food concentrations were to initiate vertical migration behavior, while those experiencing adequate concentrations did not, it would lead to a greater proportion of larvae finding and remaining within favorable food patches (Doherty et al., 1985).

### 6.3 Bottom boundary layers

Directly adjacent to the ocean bottom, flow is retarded by friction. Thus an organism that settles to the bottom, or even grasps the bottom in some manner, may largely avoid advection. Organisms that undertake vertical excursions off the bottom in synchrony with oscillating tidal flows may thus experience net horizontal displacements which are very different from average flow trajectories (e.g., Rothlisberg, et al., 1983). In large-scale, fairly long-period flows (i.e., longer than a half-pendulum day, which becomes infinitely long at the equator), the effect of the earth's rotation is important, and bottom boundary flow is deflected to the left (right) of the interior flow in the northern (southern) hemisphere. This is termed a 'bottom Ekman layer'.

### 6.4 Surface wind drift

Present understanding of large time- (again, longer than a half-pendulum day) and space-scale transport of water in the surface layer by the direct action of the wind is based on Ekman's (1905) theory which involves a balance between vertical friction and rotational deflection (Coriolis). The fine-scale vertical structure of the Ekman velocity field depends on vertical eddy viscosity characteristics which are not well known. However the total transport of water in the layer between the sea surface and the depth at which surface wind drift becomes negligible does not depend on these characteristics, but depends merely on the stress of the wind on the sea surface and the latitude. The stress varies as the square of the surface wind velocity. The latitude dependence of the associated Ekman transport is as the reciprocal of the sine of the latitude. For example, a steady 10 m/sec wind at 10 degrees latitude induces a transport of about 6 cubic meters per second across each meter of width; at 30 degrees latitude this is reduced to about 2 cubic meters per second. This 'Ekman transport' is directed

ninety degrees to the right (left) of the wind in the northern (southern) hemisphere. The depth of this 'Ekman layer' is generally considered not to exceed 100 m, and most of the transport probably occurs typically within the upper 10 to 30 m. The uppermost part of the Ekman layer moves at a lesser angle to the wind; Ekman's steady-state theory has the actual sea surface moving 45 degrees to the right (left) of the wind. Drifting objects, drogued bouys (e.g., McNally et al., 1983), etc., often exhibit trajectories which are at lesser angles to the wind, indicating contributions of flow components other than Ekman drift (see sections on Langmuir circulations and on surface wave transport, below). Near the equator, the earth's rotational effect becomes minor and the dynamic balance tends to be between vertical friction and fluid acceleration. The consequence is a tendency for upper layer movement in response to wind events to be more toward the downwind direction.

### 6.5 Langmuir circulations

The streaks or slicks on the sea surface that are often observed to parallel the wind direction under moderate wind conditions have been shown by Langmuir (1938) to correspond to surface convergence zones associated with a series of counter-rotating vortices, with axes oriented parallel to the wind, in the surface layer of the ocean. Leibovich (1983) presented a recent review of the phenomenon. Downwelling velocities beneath the surface convergences have been observed to be of the order of 3 to 7 cm/sec. Downwind ocean surface velocity is greater within the convergent streaks than between (indicating a possible mechanism for downward transfer of momentum supplied by the wind through a downwind-moving surface slab to a frictional Ekman layer below). Thus, organisms able to maintain themselves very near the surface are concentrated in a region of most rapid downwind transport. The circulations tend to form within a few minutes of wind onset. The depth of penetration of the cells appears to be limited to the first significant density discontinuity; there is evidence that the shape of the vortices is somewhat circular and so the penetration depth will tend to be of the order of half the distance between the surface convergences marked by the slicks.

### 6.6 Surface wave transport

Linear (infinitesimal amplitude) wave theory predicts movement of water particles in closed orbits which are circular in shape in deep water and elliptical in shallow water; thus no net drift of water is indicated. However, the higher order theory that describes waves of finite amplitude, features orbits which are not closed and therefore a net transport in the direction of wave advance (e.g., Phillips, 1977). This is commonly referred to as Stokes transport. The magnitude of Stokes transport in an inviscid fluid varies with the square of the wave height and inversely with the product of wavelength and period. Since, in deep water, orbit diameters and associated particle velocities attenuate exponentially as a function of the ratio of depth over wavelength, Stokes transport attenuates with depth in the same manner, attenuation being therefore more rapid at shorter wavelengths. For example, a wave of 2 m height, 125 m length, and 9 sec period would have an associated net forward Stokes velocity at the surface of 0.035 m/sec. At a depth equal to 1/4 wavelength, the Stokes velocity falls to less than 5% of its surface value. Over the total depth of surface wave influence, our example 2 m, 9 sec wave would have an associated forward transport of 0.35 cubic meters per second across each meter width. A shorter wave (2 m height, 25 m wavelength, 4 sec period) would generate a Stokes transport more than twice as large (i.e., 0.79 m<sup>3</sup>/sec/m). Note that waves of this height would be locally generated by winds of the order of 10 m/sec (e.g., Anon. 1951); thus the Stokes transport in a locally produced wave field would be considerably less than the associated surface Ekman transport (see above section on surface wind drift).

The effect of fluid viscosity on Stokes transport has been investigated by Longuet-Higgins (1953). Where wave-induced velocities reach the sea floor, viscous retardation due to proximity to the solid boundary acts more strongly on the lower portions of each orbit. The result is augmented forward drift along the bottom, increased in magnitude by a factor of 2.5 over that which would occur at that depth according to the non-frictional profile which describes the Stokes drift field at depth levels not directly adjacent to the bottom (Phillips, 1977). A similar viscous effect causes augmentation of the Stokes drift directly adjacent to the sea surface.

Although Stokes drift may be generally smaller than Ekman drift in a locally produced wave field, it is possible that Stokes drift associated with long period swell propagating from other regions (particularly from higher latitudes, etc.) into low wind situations could constitute a significant retention mechanism. Such

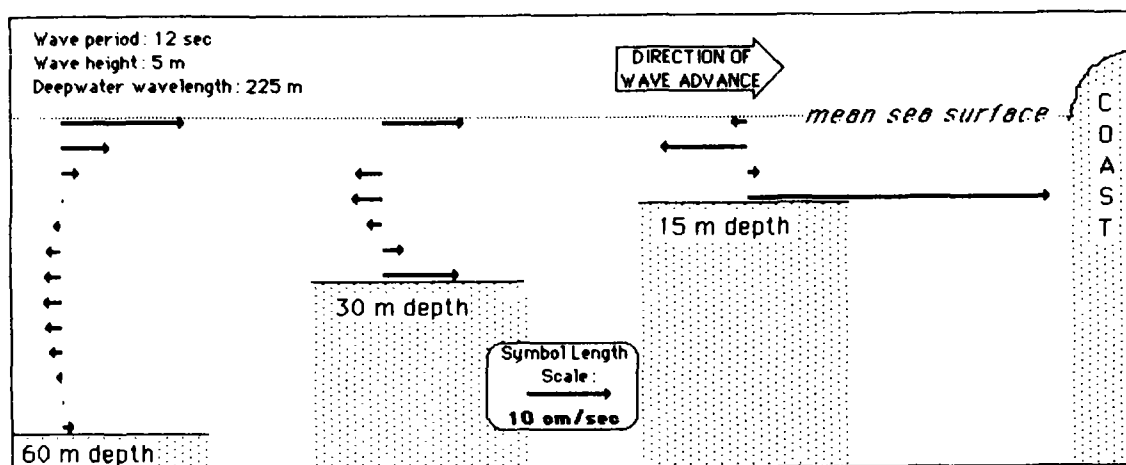


Figure 5. Vertical profiles of Stokes mass transport velocity computed according to the model of Longuet-Higgins (1953), which includes the effect of viscosity in enhancing forward transport at the sea surface and sea bottom and a return flow distributed through the water column. The example shows mass transport velocity vectors at 5-metre depth intervals under a 5 metre high, 12 second period, shoreward-directed swell in total water depths of 60, 30, and 15 metres, respectively.

long waves would begin to be refracted toward shallower water relatively early upon encountering subsurface shoaling. Wave transport in such a situation is directed invariably onshore at sufficiently shallow depths. Pressure driven rip currents, etc., which would have a more constant profile with depth, provide the offshore-directed return flow required to maintain a mass balance. Thus, organisms that maintain a position near the sea surface, or in the narrow layer of enhanced drift near the sea floor, would experience shoreward transport on average. Figure 5 provides an example of the alteration of the Stokes drift profile in shallow water, according to Longuet-Higgins' (1953) analysis of flow in a closed-ended channel where Stokes drift must be balanced by an equal return flow. Although the combination of Stokes drift toward an open coast with its balancing return flow would be highly three-dimensional (rather than two-dimensional as in a narrow channel), spatially-distributed drifting larvae would tend to average out the along-shore pattern in the flow field, so the net effect would be according to the two-dimensional representation in the figure.

In the surf zone, the situation changes radically. Breaking waves push large volumes of water shoreward in violently turbulent motions which would preclude any sort of maintenance of position or orientation by small organisms. The intense mechanical battering that characterizes the surf zone would seem to make it a very poor place for pelagic larvae to survive. In fact, the necessity for minimizing the incidence of larvae being pulverized in the surf zone would seem to constitute a possible alternate explanation to predation avoidance for the adaptive value of the spawning behaviors (i.e., favoring rapid offshore transport of larvae) and seasonalities (i.e., avoiding seasons of strong winds and associated surf conditions) enumerated by Johannes (1978).

#### 6.7 Surface slicks coupled to internal waves

Ewing (1950) described lines of surface slicks parallel to the shoreline of Southern California, which are apparently coupled to trains of long internal waves in a shallow thermocline. The orbital velocities in the upper layer, associated with the internal waves, result in lines of surface convergence parallel to the crests but lagging the crests by one-fourth wavelength. The convergence lines collect organic materials, causing damping of surface ripples and resulting visible slicks. The slicks move shoreward at about 25 cm/sec, which is near the phase speed of the waves observed. Rattray et al. (1969) describe a mechanism by which these internal wave trains are formed by tidal action at the continental shelf break. Shanks (1983) proposed this mechanism as a vehicle for return of larval crustaceans to the shallow coastal region. He showed shoreward transport of drifting objects within propagating slicks and reported concentrations of pelagic larvae of a variety of fishes and invertebrates 40 to 60 times greater at the sea surface within propagating slicks, than in the surface areas between the slicks. If Shanks' observations have widespread generality, this is apparently a mechanism by which pelagic larval stages, that have behaviors which keep them positioned within the neuston or associated with drifting objects, could be transported shoreward.

## 7. A FOCUS ON VERTICAL STRUCTURE

Determining complete representative vertical profiles of swimming planktonic organisms is a demanding, time-consuming process in itself (e.g., Longhurst, 1976). In addition, sampling of fish larvae in particular has usually been directed primarily toward determining total biomasses, i.e. for the purpose of estimating population size and productivity, or toward delineating seasonality and geography of spawning grounds. Thus vertical structure has often been viewed as merely an unfortunate additional complexity and a potential source of sampling error. As a result past emphasis has been on integrating vertical inhomogeneities via vertical or oblique tows. Consequentially we really have surprisingly little information as to the vertical distribution of larvae even in large well-studied fishery stocks (R.H.Parrish, pers. commun.). Efforts to develop this information seem overdue, particularly in view of recent scientific interest in the effects of vertical migration in vertically varying flow on larval trajectories (Rothlisberg, 1982) and on the ability of larvae to alter their position with respect to favorable food particle concentrations (Doherty et al., 1985).

### 7.1 Experimental advantages

By basing experimental and observational efforts on a framework provided by our level of understanding of vertical structure in the likely physical transport and retention mechanisms, some significant economies in required effort and resources may be afforded. We have noted a tendency for many of the potential mechanisms to be either bottom-intensified, surface-intensified, or both. Rather than assembling samples of complete vertical profiles, it may be reasonable to concentrate effort on demonstrating significant differences between larval concentrations at particular key depth levels with respect to given physical mechanisms (e.g., surface vs. mid-depth, bottom vs. mid-depth, etc.). Once a pattern of relationship or non-relationship is established, the theory of natural selection would provide a powerful deductive tool since reproductive success is the determining factor in the selection process. Thus, consistent patterns of apparent biological response to vertical aspects associated with one or another of these mechanisms would be strong evidence of natural selection and therefore of important causal linkage of the mechanism to reproductive success.

While weakly swimming pelagic fish larvae might generally have relatively little active control over their horizontal distribution, they might exert considerable control on their vertical distribution. Thus directed behavioral adaptations would be able in some degree to counter certain accidental or random displacements in the vertical, with the result that observations of vertical structure might be relatively free of unrelated random patchiness or 'noise' which might obscure the signal of the response. In such a case, assembly of a representative set of samples of vertical variability would be a much less demanding exercise than, for example, assembling a representative set of samples of variability in 'bulk' population abundance, where all the various scales of spatial patchiness would have to be somehow integrated in each estimate. Thus substantial economies of effort and resources might be realized by such a shift in point of view from quantitative three-dimensional closures of various "budgets" involved, to a single-dimensional focus on the characterization of vertical relationships among organisms, environmental properties, and dynamic processes. Observation of the manner in which these relationships might vary under varying external conditions, e.g., weather, seasonality, etc., could provide a rich source of material on which to base conclusions as to (1) the nature of the mechanisms which might have controlled the natural selection leading to the observed vertical associations, and (2) the effects of variations of the external conditions on local year-to-year recruitment variability.

Moreover, the formidable problem of taxonomic identification of early life stages of tropical demersal species could perhaps be less crucial in this type of approach; the greater emphasis would be on defining the vertical position in the water column of organisms of generalized type, under various environmental conditions, rather than on the biomasses and interactions of specific community components.

### 7.2 Interregional comparative studies

The opportunity for application of the comparative method among different local systems appears particularly promising. Certainly, checking for lack of covariation in recruitment variability is an obvious approach to defining the scales on which the stocks may function as closed populations. (Note however that

the converse is not necessarily true. Large-scale covariation might be due to some large-scale environmental variation acting similarly on a number of smaller scale closed population segments.) Characterizing the real spatial-average recruitment variability at multiple locations might be an enormous task. However, various functional dependencies intrinsic to the hypothesis that vertically-structured retention mechanisms may regulate recruitment variability (e.g., distance from the equator, isolation from external larval sources, degree of stratification, relation to large scale ocean current systems or atmospheric storm tracks, characteristic ocean wave spectra, etc.) facilitate the arraying of a variety of data, which might be available or obtainable, in a variety of different ways likely to yield informative patterns, even if actual time series of variability were unattainable. We can regard observed adaptations as being the integrated result of a great number of 'trial and error experiments' by the population, i.e. a clear 'signal' with the large amplitude, quasi-random 'noise' represented by environmental and community-structure transients having been largely filtered out. Thus if widespread consistency in biological pattern with respect to potential environmental causal mechanisms can be assumed to reflect processes of natural selection, comparative pattern recognition on local and interregional space scales, and on seasonal and selected interannual time scales, might yield much useful information that could be extremely difficult to derive via the experimental method (Bakun, 1985). Note that this approach also produces insights as to the degree of similarity in the crucial dynamics of geographically-separated ecosystems which, even if we do not understand these dynamics in detail, would aid in transferring experience among systems in order to foresee the effects of human actions or natural environmental perturbations on a given system by examining the record of similar actions or events in other systems. Finally, such a comparative effort based specifically on the question of larval retention and immigration, would provide a useful framework for addressing the basic ecological question of whether, and under what conditions, the population dynamics of tropical reef/bank fishes is controlled primarily by community interactions or by recruitment variability.

### 7.3 Multidisciplinary scientific effort

The class of problems treated in this paper may provide a framework for focusing efforts of a particularly broad range of marine scientific specialties on the problem of recruitment in tropical demersal systems. For example, previous interest of physical oceanographers in stratified Taylor column phenomena has been directed primarily toward the effect of these processes on the larger-scale ocean responses which are evident to humans in a more direct manner, rather than on the actual details of the processes themselves which may affect humans primarily through their effects on biological populations. Certain aspects needing theoretical investigation are mentioned above; opportunities certainly exist for important contributions from theoreticians and numerical modelers on various other aspects of the interactions of hydrodynamic and biological vertical structures. Large-scale descriptive oceanographic and meteorological input would be a crucial component of interregional comparative studies. Bottom-intensified transport processes would tend to leave identifying 'signatures' in sediment deposition patterns, affording an opportunity to enlist geological oceanographers in the effort. Of course, strong roles for biological oceanographers, ecologists, ecological modelers, sampling gear engineers, etc., are implied.

### 7.4 Socio-economic implications

In addition to addressing the causes for temporal variation in recruitment success, research activity on the class of hypotheses discussed here has the particular advantage of treating the extremely important question of the spatial scale on which recruitment may be generated; i.e., the scale on which a local situation may or may not function as an 'open' or 'closed' system (Roughgarden, Iwasa & Baxter, 1985). For example, in an open system, local over-exploitation may not have serious consequences on subsequent recruitment since recruitment is largely generated from larvae arriving from outside of the system. However, in a closed system, local recruitment is generated largely from local spawning, and there is a much stronger argument against local over-fishing. Therefore any incremental increase in understanding of the nature and effect of larval retention mechanisms could have value in terms of the basic way in which stock / recruitment issues in tropical demersal systems are viewed, even if detailed quantitative predictive capability were not a direct outcome. This in turn could have important effects on fundamental attitudes toward industrial investment, management and conservation, by illuminating the international, national, and local 'common property resource' aspects (Glantz, 1983) of tropical demersal biological communities. Addressing such basic oceanographic and ecological scientific issues under a framework having direct social-economic implications is in accord with the dual

"importance of OSLR for the development of marine science, integrating various biological and physical disciplines and various laboratory programmes around the world, in such a way as to serve the national interests of coastal states" (Anon. 1985).

#### 8. REFERENCES

- Andrews, J. C. & P. Gentien (1982) Upwelling as a source of nutrients for the Great Barrier Reef Ecosystem: a solution to Darwin's question? Mar. Ecol. Prog. Ser., 8: 257-269.
- Anonymous (1951) Techniques for Forecasting Wind Waves and Swell. H. O. Pub. 604, U. S. Navy Hydrographic Office, Washington, D.C. 37p.
- Anonymous (1985) IOC-FAO Guiding Group of Experts on the Programme of Ocean Science in Relation to Living Resources, First Session, Paris, 16-20 July 1984. Reports of Meetings of Experts and Equivalent Bodies (SC-85/WS/18), Intergovernmental Oceanographic Commission, Unesco, Paris, 36p.
- Atkinson, M., S. V. Smith & E. D. Stroup (1981) Circulation in Enewetak Atoll Lagoon. Limnol. Oceanogr., 26: 1074-1083.
- Bakun, A. (1985) Comparative studies and the recruitment problem: searching for generalizations. CalCOFI Rep., 26: 30-40.
- Barkley, R. A. (1972) Johnston Atoll's wake. J. Mar. Res., 30: 201-216.
- Barlow, G. W. (1981) Patterns of parental investment, dispersal, and size among coral-reef fishes. Env. Biol. Fish., 6: 91-115.
- Boden, B. P. (1952) Natural conservation of insular plankton. Nature, 169: 697-699.
- Brainard, R. & P. Wittmann (1985) Aspects of the thermohaline structure over Southeast Hancock Seamount. (Abstract 51F-05) EOS - Trans. Amer. Geophys. Un., 66: 1336.
- Brothers, E. B., D. McB. Williams & P. F. Sale (1983) Length of larval life in twelve families of fishes at "One Tree Lagoon", Great Barrier Reef, Australia. Mar. Biol., 76: 319-324.
- Doherty, P. J. (1983) Tropical territorial damselfishes: is density limited by aggression or recruitment? Ecology, 64: 176-190.
- Doherty, P. J., D. McB. Williams & P. Sale (1985) The adaptive significance of larval dispersal in coral reef fishes. Env. Biol. Fish., 12: 81-90.
- Dooley, H. D. (1984) Aspects of Oceanographic Variability on Scottish Fishing Grounds. Ph.D. Thesis, University of Aberdeen. 154p.
- Doty, M. S., & M. Oguri. (1956) The island mass effect. J. Cons. int. Explor. Mer. 22: 33-37.
- Ehrlich, P. R. (1975) The population biology of coral reef fishes. Ann. Rev. Ecol. Syst., 6: 211-247.
- Ekman, V. W. (1905) On the influence of the earth's rotation on ocean currents. Ark. Mat. Astron. Fys., 2(11): 1-55.
- Ewing, G. (1950) Slicks, surface films, and internal waves. J. Mar. Res., 4:161-187.
- Genin, A. & G. W. Boehlert (1985) Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment. J. Mar. Res., 43: 907-924.
- Glantz, M. H. (1983) Man, state, and fisheries: an inquiry into some societal constraints that affect fisheries management. In: Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, editors G.D.Sharp & J. Csirke, FAO Fish. Rep., 291(3): 99-115.
- Hamner, W. M. & I. R. Haury (1981) Effects of island mass: water flow and plankton pattern around a reef in the Great Barrier Reef lagoon. Limnol. Oceanogr., 26: 1084-1102.



- Hennemuth, R. C., J. E. Palmer & B. E. Brown (1980) A statistical description of recruitment in eighteen selected fish stocks. J. Northw. Atl. Fish. Sci., 1: 101-111.
- Hide, R. (1961) Origin of Jupiter's great red spot. Nature, 190: 895-896.
- Hjort, J. (1926) Fluctuations in the year classes of important food fishes. J. Cons. int. Explor. Mer., 1: 5-38.
- Hogg, N. G. (1980) Effects of bottom topography on ocean currents. In: Orographic Effects in Planetary Flows, editors R. Hide & P.W. White, GARP Pub. Ser., 23, World Meteorological Organization, Geneva: 169-207.
- Hunter, J. R. & G. D. Sharp (1983) Physics and fish populations: shelf sea fronts and fisheries. In: Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, editors G.D. Sharp & J. Csirke, FAO Fish. Rep. 291(3): 659-682.
- Huppert, E. H. & K. Bryan (1976) Topographically generated eddies. Deep-Sea Res., 23: 655-680.
- Johannes, R. E. (1978) Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish., 3: 65-84.
- Johannes, R. E. (1981) Words of the Lagoon. University of California Press, Berkeley. 245p.
- Langmuir, I. (1938) Surface motion of water induced by the wind. Science 87: 119-123.
- Leibovich, S. (1983) The form and dynamics of Langmuir circulations. Ann. Rev. Fluid Mech., 15: 391-427.
- Leis, J. M. (1982) Distribution of fish larvae around Lizard Island, Great Barrier Reef: Coral reef lagoon as refuge? Proc. 4th Int. Coral Reef Symp., 2: 471-477.
- Longuet-Higgins, M. S. (1953) Mass transport in water waves. Phil. Trans. A, 245: 535-581.
- Longhurst, A. R. (1976) Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. Deep-Sea Res., 23: 729-754.
- Lutjeharms, J. R. E. & A. E. F. Heydorn (1981a) The rock-lobster Jasus tristani on Vema Seamount: Drifting buoys suggest a possible recruiting mechanism. Deep-Sea Res., 26: 631-636.
- Lutjeharms, J. R. E. & E. F. Heydorn (1981b) Recruitment of rock lobster on Vema Seamount from the islands of Tristan da Cunha. Deep-Sea Res., 28A: 1237.
- McNally, G. J., W. C. Patzert, A. D. Kirwan Jr. & A. C. Vastano (1983) The near-surface circulation of the North Pacific using satellite tracked drifting bouys. J. Geophys. Res., 88(C12): 7507-7518.
- Montgomery, R. B. & E. D. Stroup (1962) Equatorial Waters and Currents at 150 W in July - August 1952. The Johns Hopkins Press, Baltimore. 66p.
- Phillips, O. M. (1977) The Dynamics of the Upper Ocean (2nd edition). Cambridge University Press, London and New York. 336p.
- Proudman, J. (1916) On the motion of solids in a liquid possessing vorticity. Proc. Roy. Soc., A 92: 400-424.
- Rothlisberg, P. C. (1982) Vertical migration and its effect on dispersal of penaeid shrimp larvae in the Gulf of Carpentaria, Australia. Fish. Bull., U.S. 80: 541-554.
- Rothlisberg, P. C., J. A. Church & A. M. G. Forbes (1983) Modelling the advection of vertically migrating shrimp larvae. J. Mar. Res., 41: 511-538.
- Roughgarden, J., Y. Iwasa & C. Baxter (1985) Demographic theory for an open marine population with space-limited recruitment. Ecology, 66: 54-67.

- Sale, P. F. (1980) The ecology of fishes on coral reefs. Oceanogr. Mar. Bio. Ann. Rev., 18: 367-421.
- Shanks, A. L. (1983) Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser., 13: 311-315.
- Shomura R. S. & R. A. Barkley (1980) Ecosystem dynamics of seamounts -- a working hypothesis. Proc. of 4th CSK Symposium: 789.
- Taylor, G. I. (1917) Motion of solids in fluids when the flow is not irrotational. Proc. Roy. Soc. A, 93: 99-113.
- Taylor, G. I. (1923) Experiments on the motion of solid bodies in rotating fluids. Proc. Roy. Soc. A, 104: 213-218.
- Thomson, R. E. & E. J. Wolanski (1984) Tidal period upwelling within Raine Island Entrance Great Barrier Reef. J. Mar. Res., 42: 787-808.
- Victor, B. C. (1983) Recruitment and population dynamics of a coral reef fish. Science, 219: 419-420.
- Victor, B. C. (1986) Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Mar. Biol., 90: 317-326.
- Walford, L. A. (1938) Effects of currents on distribution and survival of the eggs and larvae of haddock Melanogrammus aeglefinus on Georges Bank. U.S. Bull. Bur. Fish., 49: 1-73.
- Williams, D. McB. (1980) Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). Bull. Mar. Sci., 30: 159-170.
- Williams, D. McB. (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs, 1: 35-43.
- Williams, D. McB. (1983a) Longitudinal and latitudinal variation in the structure of reef fish communities. In: Proceedings: Inaugural Great Barrier Reef Conference, Townsville, Aug. 28-Sept. 2, 1983, editors J.T. Baker, R.M. Carter, P.W. Samarco & K.P. Stark. James Cook University Press: 265-270.
- Williams, D. McB. (1983b) Daily, monthly and yearly variability in recruitment of a guild of coral reef fishes. Mar. Ecol. Prog. Ser., 10: 231-237.
- Williams, D. McB. (1985) Structure and dynamics of Great Barrier Reef fish communities. Unpublished notes for U.S. Seminar June/July 1985. 36p.
- Williams, D. McB., E. Wolanski & J. C. Andrews (1984) Transport mechanisms and the potential movement of planktonic larvae in the central region of the Great Barrier Reef. Coral Reefs, 3: 229-236.
- Wolanski, E., J. Imberger & M. L. Heron (1984) Island wakes in shallow coastal waters. J. Geophys. Res., 89(C6): 10553-10569.
- Wolanski, E. & G. L. Picard (1983) Upwelling by internal tides and Kelvin waves at the continental shelf break on the Great Barrier Reef. Austral. J. Mar. Freshwater Res., 34: 65-80.

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**IOC/FAO Workshop on  
Recruitment in Tropical Coastal  
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Ciudad del Carmen, Campeche, Mexico, 21-25 April 1986

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A page bearing the following text and immediately preceding the Introduction was omitted in error:

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