Topographically Controlled Fronts in the Ocean and Their Biological Influence

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Headlands, islands, and reefs generate complex three-dimensional secondary flows that result in physical and biological fronts. Mixing and diffusion processes near these reefs and headlands are quite different from these processes in the open sea, and classical advection-diffusion models that were developed for the open sea are not valid near shore. Topographically generated fronts affect the distribution of sediments, and they aggregate water-borne eggs, larvae, and plankton. This aggregation influences the distribution and density of benthic assemblages and of pelagic secondary and tertiary predators.

FRONTS ARE THE BOUNDARIES BETWEEN TWO DIFFERENT water masses in the ocean. Frontal systems have a major influence on the biology of pelagic organisms because the secondary currents associated with fronts result in zones of convergence and eddies where debris and organisms accumulate (*1*). Such phenomena have been well documented for open ocean environments but generally at large scales (several to hundreds of kilometers). Such large-scale eddy systems are quasi–two dimensional. Fronts at small scales (less than several kilometers) have not been studied as well as at large scales, and most of the work has been on the dynamics of Langmuir circulation and internal waves (*2*). Langmuir cells are wind-driven, screw-like motions of water near the surface; these cells commonly produce rows of slicks that are generally parallel to the wind. Large-amplitude internal waves in density-stratified water can also form surface slicks. Such slicks can aggregate buoyant organisms such as seaweeds, crab larvae, and jellyfish (*2*).

A variety of physical phenomena are important at small scales where currents interact with local topography to produce complex flows that are strongly three-dimensional. These flows can significantly influence the local distribution of benthic and pelagic organisms (*3–8*). The effects of fine-scale physical phenomena on the biology of pelagic organisms have been of concern to plankton biologists for more than a century. The most detailed description of these phenomena during the 19th century was by Ernst Haeckel (*3*). He distinguished four types of marine currents: (i) the halicurrents (the great oceanic currents); (ii) the bathycurrents (the manifold deep currents or undercurrents); (iii) the nerocurrents (the littoral currents or local coastal currents); and (iv) the zoocurrents (the local planktonic streams or crowded "animal roads").

In this article we describe the processes that generate zoocurrents where nerocurrents are important. Although we primarily discuss processes that occur on or near coral reefs, zoocurrents occur throughout the ocean in response to any topographic features of a scale or shape similar to those exhibited by coral reefs.

Little is known about nerocurrents in topographically complex environments, such as near islands, reefs, and headlands. However, it is in this type of environment that zoocurrents are the most obvious and spectacular. Nerocurrents can accumulate plankton in long and narrow bands. These bands are zoocurrents. As Haeckel (*3*, p. 565) noted: "Their breadth is usually between 5 and 10 meters, but sometimes 20 meters or more; their length is sometimes only a few hundred meters, and at others several kilometers. Highly remarkable is the sharp boundary of the smooth, thickly populated 'animal roads,' especially if the less inhabited and plankton-poor water on both sides is rippled by the wind. A new study of the zoocurrents is one of the most urgent problems of planktology."

The Effects of Island Wakes

In shallow coastal waters, the interaction of topography with a prevailing current results in complex downstream currents. Eddies are formed downstream of headlands, islands, and reefs (*5–11*). These eddies can take various forms, from stable, island-size eddies with strong, recirculating currents, to unstable eddies that generate meanders far downstream in the prevailing current. Where these

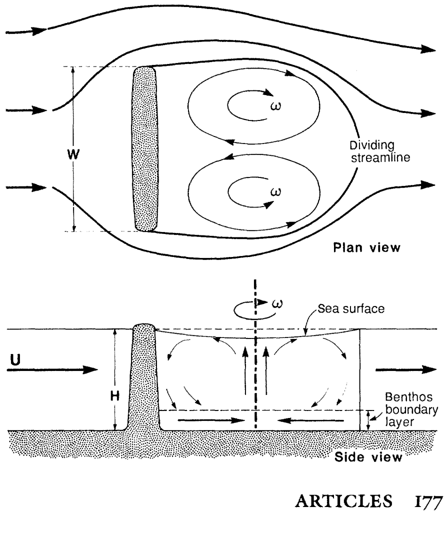

Fig. 1. Sketch of the internal circulation in an island wake in shallow coastal waters. The vertical scale is exaggerated, as typically depths are less than 40 m, whereas horizontal scales are of the order of 1 km. The governing parameters determining the characteristics of an island wake are the prevailing water velocity (U), the water depth (H), and the island width (W).

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meanders become too large and degrade in turbulent eddies, slab-shaped wakes are formed with no organized internal flows (*12*).

Stable island wakes are common in shallow coastal waters that are vertically well mixed in terms of salinity and temperature. In shallow water, bottom friction generates a secondary circulation (*10*) such that sea level slopes upward from the eddy center. The slope of the surface generates a pressure gradient that is in equilibrium with the centrifugal acceleration. This balance cannot hold near the bottom because friction decreases the azimuthal velocity, whereas the radial pressure gradient is maintained everywhere throughout the eddy, including at the bottom. As a result, water that is near the bottom flows radially toward the eddy center, and upwelling occurs near the center and downwelling occurs near the outer edges (Fig. 1).

In shallow coastal waters, this secondary circulation significantly affects sediment transport and distribution. Fine, clay-sized sediment is carried to the surface near the eddy center. From there, the sediment-enriched water that has been upwelled forms spirals out from the eddy center because the surface waters have a radial velocity (Fig. 2A). At depth, both fine (clay-sized) and coarse (sand-sized) sediment are advected toward the eddy center by the secondary currents. However, only the fine sediment can be carried upward to the surface and then outward away from the eddy center. As a result, sediment on the bottom is sorted (*12*) such that the concentration of fine sediment is less near the eddy center than elsewhere (Fig. 3). This secondary circulation also affects the distributions of benthic organisms inasmuch as their distribution is associated with sediment size.

Secondary circulation in island wakes is also important for sorting organisms in the water column. Because coral eggs float, they are an excellent tracer to study the dispersion of water-borne particulates near coral reefs. For instance, on the Great Barrier Reef large numbers of coral species spawn synchronously (*13*). The eggs are initially distributed on the surface over the whole area of the reef, which is approximately several square kilometers for a typical reef. In a few hours they typically aggregate in slicks (*14*) instead of diffusing over an ever widening area as would result from normal oceanic diffusion processes. The number of eggs released is large, and the slicks that form are readily visible from the air (*14*). It is not uncommon to see slicks that are trapped along the curved outer edges of an island wake where turbid water (due to upwelling in the

Fig. 2. (**A**) Oblique aerial photograph of Rattray Island, North Queensland, Australia, showing the island wake and the spirals of upwelled muddy water near the surface. (**B**) Oblique aerial photograph of an eddy shed from a single separation point (a headland) in the Whitsunday Island area, North Queensland. Depth is about 10 m. The waters in the eddy are turbid because of internal upwelling, and a coral egg slick is visible at the front that separates eddy water from offshore water. (**C**) Oblique aerial photograph of a passage through the Ribbon Reefs, Great Barrier Reef, at flood tide, that shows the separation streamlines behind two separation points. (**D**) Low-altitude aerial photograph of a coral reef in the central Great Barrier Reef, showing a turbulent boundary layer and a coral egg slick (white line) at the front between the boundary layer and the offshore waters. The scale of the picture is not known precisely; however, the airplane was only about 33 m above the sea surface and therefore the boundary layer is a few meters thick. The thickness of the coral slick (white) is about 1 m. (**E**) Oblique aerial photograph showing the front between turbid reef lagoon waters and clear offshore waters at Bowden Reef, Great Barrier Reef. A coral outcrop, about 30 m in diameter, is visible on the right hand side. A coral egg slick (white line) is visible along the front. (**F**) Oblique aerial photograph of a coral reef in the central Great Barrier Reef. It shows the front that is generated by lagoon waters flowing over the reef flat and displacing clear offshore waters. A coral egg slick (white line) is visible at the front, which is located about 50 to 100 m offshore from the edge of the reef.

eddy) is separated by a sharp front from the clearer coastal waters (Fig. 4). A strong downwelling has been observed in the wake near such fronts (*10*). Hence, in shallow coastal waters, the internal circulation in a topographically generated eddy (Fig. 1) sweeps together floating coral eggs that were initially distributed over a vast area and concentrates them in slicks near the fronts where, because of their positive buoyancy, the eggs cannot be carried downward by downwelling. Topographically controlled currents, therefore, commonly aggregate buoyant particulates and prevent the dispersion of these particulates, as would likely happen in the open sea.

Two separation points, such as produced by an island, are not needed to generate an eddy downstream; one separation point (for example, a headland) is sufficient, as has been demonstrated analytically (*10*) and is apparent also from direct field observations (Fig. 2B). Zooplankton are commonly aggregated by the secondary circulation downstream from a single separation point (*7*). As a result, fishes and seabirds also congregate near these topographically controlled fronts (*7, 8*). Some eddies are occasionally carried away from the headland by prevailing currents, but these eddies may not mix rapidly with the surrounding water when drifting downstream but retain their integrity for several hours (*5*). Plankton concentrations are typically much higher near the front than in the surrounding waters, even where the fronts are unstable and unsteady (*6*).

The Tidal Jet

Strong currents in a reef passage typically cause upwelling of water from in front of the reef by Bernoulli suction (*15*). This upwelled water is then carried away from the reef passage by the tidal jet generated by the strong currents in the passage. Because the upwelled water is colder, it is negatively buoyant and remains near the bottom with little mixing with the surface waters once it has entered the shallow reef passage. The tidal jet carries the water toward a pair of jet-generated vortices. These vortices increase the time that the nutrient-enriched water stays near the bottom in that area, and this process helps form benthic meadows of the calcareous alga *Halimeda* in many areas of the Great Barrier Reef lagoon (*11*).

The surface waters that enter the reef passage are drawn radially from a semi-circle of the ocean that is centered at the entrance of the passage. Flow separation occurs at two points on the upstream side of the passage (Fig. 2C). As a result, two vortices are generated in the passage, one downstream of each separation point; two separation streamlines (fronts) are present (Figs. 2C and 5), and these merge in a single front farther downstream. Water in these passages in the Great Barrier Reef is shallow (typically 30 to 40 m) so that bottom friction causes a secondary circulation that converges at the surface in the center of the passage. Surface flow in this secondary circulation is from the sides toward the front (Fig. 5). Buoyant plankton and debris accumulate and concentrate in a slick at the center of the passage (Fig. 2C). Even if the flow does not separate, the curvature of the current near the inlet generates, because of bottom friction, an internal circulation that results in a convergence at the surface along the axis of the channel (Fig. 5). This secondary circulation has been recently verified by measuring the trajectory of near-surface sail drogues that were released at flood tide at the entrance between Ribbon Reefs 3 and 4, Great Barrier Reef (*16*). The near-surface drogues moved away from the walls of the passage and toward its axis.

Whales and whale sharks have been observed swimming in the center of these passages in the Ribbon Reefs (*17*). The whales, often several, swam in a straight line one behind the other along the axis of the passage, swimming against the current but remaining stationary and apparently feeding on the plankton slick.

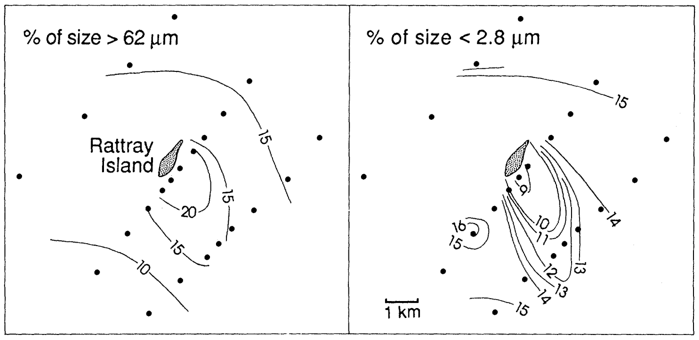

Fig. 3. Distribution (in percent dry weight) of the fine and coarse sediment on the sea floor around Rattray Island, North Queensland, Australia. [Reproduced from (*12*) by permission of Springer-Verlag]

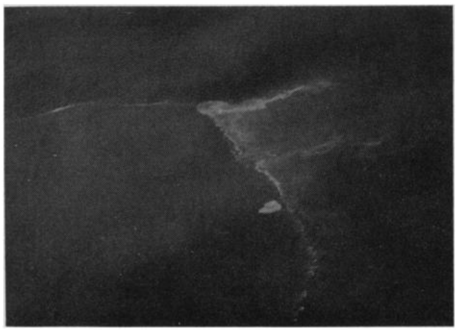

Fig. 4. Oblique aerial photograph of the island wake downstream of Fantome Island, Palm Island Group, North Queensland, with a coral egg slick (white line) at the front. The fingers extruding from the slick are due to disturbances by the boat. The waters in the island wake are turbid because of the internal upwelling. Water depth is about 20 m. [Courtesy of Oliver and Willis; reproduced from (*14*) by permission of Springer-Verlag]

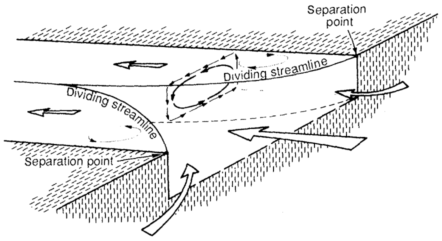

Fig. 5. Sketch of the internal circulation in a reef passage on the upstream side.

Boundary Mixing

Boundary mixing is the process of increased mixing due to increased shear at solid boundaries. Mixing is particularly strong if the surface is rugged or if there is shoaling and breaking of internal gravity waves on a sloping solid boundary (*18*). Biological oceanographers have only recently recognized that boundary mixing has important effects on the distribution of organisms. For instance, mixing on the floor of the continental slope can generate turbid nepheloid layers at a certain depth; prevailing currents can advect these layers farther offshore. Boundary mixing along island slopes at the thermocline locally enriches surface waters that are near the island in nutrients from below the thermocline (*19*).

Boundary mixing can generate fronts. In a density-stratified fluid, boundary mixing can generate a secondary circulation (Fig. 6) with flow toward the solid boundary both near the surface and near the bottom and with flow away from the boundary in between (*18*). The flow away from the boundary is largest at the depth of the maximum vertical buoyancy gradient. Boundary mixing may explain the observation that plankton that are trapped at the top of the pycnocline are concentrated away from the sloping bottom of the Chesapeake Bay (*18*). A similar situation prevails in calm weather in

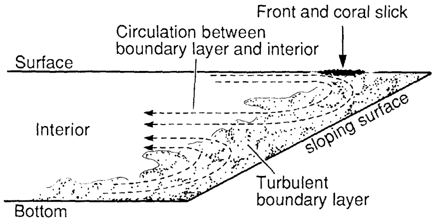

Fig. 6. Sketch of the internal circulation that is generated by boundary mixing (side view).

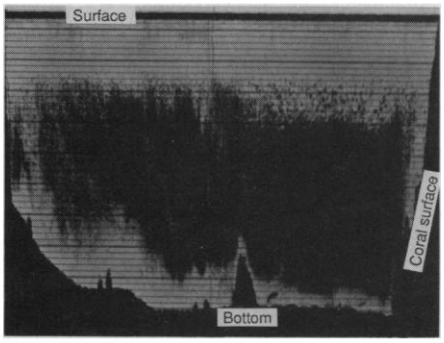

Fig. 7. High-frequency (210 kHz) echo-sounding transect over a sloping coral surface in the lagoon of Davies Reef, Great Barrier Reef. Maximum depth is approximately 15 m and the panel spans about 50 m horizontally. The thickness of the boundary layer where isotherms are close together is a few meters.

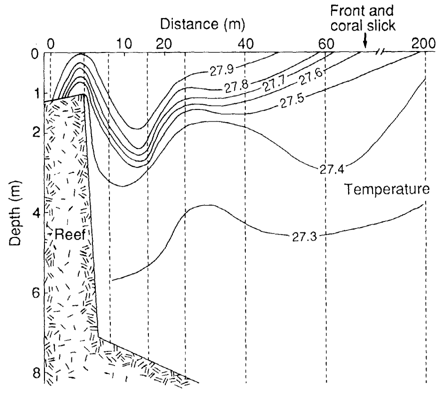

Fig. 8. The temperature distribution (degrees Centigrade) across the reef edge and upper reef slope of Bowden Reef, Great Barrier Reef, in summer at the time of coral spawning, when a front, such as the one in Fig. 2F, was visible.

coral reef lagoons where high-frequency echo-sounders have shown that clouds of scatterers (presumably plankton) are located at the depth of the maximum vertical temperature gradient (*20*); these clouds generally were offshore from the sloping surface of the coral reef (Fig. 7). Temperature profiles that have been collected around coral reefs also suggest that mixing is strong near reef surfaces; the extended roughness of coral-reef surfaces presumably enhances mixing (*20, 21*).

The secondary circulation that is generated by boundary mixing (Fig. 6) may cause floating coral eggs to accumulate in a lagoon on a line parallel to the trend of the coral reef when wind is light or calm. This process is occasionally visible in reef lagoons because of the slick of coral eggs at the front between the turbulent boundary layer and the less turbulent waters farther away from the reef (Fig. 2D).

Buoyancy Effects

Many reefs in the Great Barrier Reef have a lagoon, typically 10 to 20 m deep, with a shallow opening that links the lagoon with the shelf waters. The remainder of the reef perimeter is typically a reef flat that is slightly below the level of the low spring tide. The bulk of the tidal exchange of water between the lagoon and shelf waters takes place through the opening to the lagoon. In summer, the waters in a reef lagoon are generally warmer (salinity differences are negligible) and thus more buoyant than the shelf waters. When water is moved from the lagoon by wind or falling tides, its buoyancy inhibits mixing with shelf waters. Instead, the warm lagoon water forms a buoyancy front as it displaces the water on the shelf (Fig. 2E). In the secondary circulation associated with such fronts, surface water typically converges at the front from both the warm and cold sides and downwelling occurs at the front to conserve mass (*1, 22*). All the floating material from the lagoon can accumulate along this front (Fig. 2E).

Fronts are also formed when, at certain tide stages and wind conditions, warm water leaves the lagoon and moves offshore by flowing over the reef flat, often toward the windward side of the reef. A front that is oriented parallel to the reef is then created offshore (Fig. 2F). Isotherms are compressed and shallow near the front; temperature is an indicator of the origin of the waters as previously discussed (Fig. 8). The warm water emanating from the lagoon forms a buoyant plume that can concentrate floating coral eggs in a slick along the front (Figs. 2F and 9). Hamner *et al.* (*23*) sampled zooplankton in the warm-water plumes during flow from the lagoon across the windward reef face, and they showed that the zooplankton concentration increases at the front to more than ten times the concentration in the adjacent lagoon or shelf waters.

Wind blowing gently but obliquely onto the shore of an island on a warm day similarly moves warm surface water toward and along the shore in a shallow longshore current. Buoyant particles and plankton are entrapped and aggregated in the resulting slick where seabirds, giant manta rays, and whales may congregate (*24*).

Fronts and the Distribution of Organisms

Secondary flow patterns, some of which are described in this article, play a dominant role in concentrating buoyant particulates in topographically complex environments. In the open ocean, it is generally believed that particles will disperse, although a number of three-dimensional secondary flow patterns can aggregate buoyant particles. Particles may aggregate near oceanic fronts, in near-surface wind-driven Langmuir cells, and in surface slicks driven by internal tides (*1, 2*). Rip currents on a beach can also aggregate surf diatoms (*25*). These processes require either water masses of different buoyancy or a sustained wind. We have shown that near coral reefs, islands, and headlands strong three-dimensional flows can concentrate buoyant particles along fronts even in vertically well-mixed waters or in the absence of wind. We expect these hydrographic phenomena to affect larval recruitment.

In the Great Barrier Reef these topographically controlled secondary flows have a dominant influence on the fate of buoyant coral eggs. Almost all the coral eggs and sperm are concentrated along such fronts (*14*). The eggs and sperm, once aggregated by topographically controlled processes, can be advected away from the reef by the prevailing currents as a thin (a few meters wide) but long (hundreds to thousands of meters long) cloud with a high concentration of eggs.

Coral eggs are larger and more buoyant than most other eggs from animals that have a planktonic stage and will tend to float even in areas of downwelling. Other eggs and larvae could be distributed through the water column by island wake effects, depending on their buoyancy. The eggs of the crown-of-thorn starfish, of concern because of its current infestation of the central region of the Great Barrier Reef, are also buoyant. Underwater photographs of spawning crown-of-thorn starfish show the eggs rising to the surface (*26*). These eggs may also aggregate because of topographically controlled secondary currents. Coral egg slicks typically form in a few hours after a spawning event; therefore, crown-of-thorn starfish eggs do not need to remain buoyant for long to become aggregated along

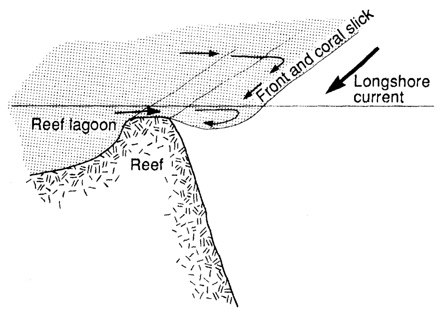

Fig. 9. Sketch of the water circulation for Figs. 2F and 8. The warm water emanating from the lagoon forms a buoyant plume which is deflected parallel to the reef by the prevailing current on the shelf. The secondary circulation in this plume forms a coral slick along the front.

topographically controlled fronts. These surface aggregative processes have been neglected in earlier models of the distribution of crown-of-thorn starfish.

Many reef fish migrate great distances to spawn at particular sites. Most workers have generally assumed that fish seek out areas of strong currents near reefs to maximize the chance of the eggs being carried away from the reefs. Instead, they may spawn in areas where the eggs will likely be retained near reefs or, alternatively, in areas that initially aggregate these eggs (*27*). Surveys of fish spawning behavior in this context would be useful.

Another area of interest is the distribution patterns of large schooling and plankton-feeding species. Secondary and tertiary predators, such as fishes, whales, and seabirds, make use of the food aggregations along topographically controlled fronts. The potential importance of such food aggregations suggests that ideas concerning plankton distribution, fish reproductive behavior, schooling fish distribution, and biological connectivity between coral reefs need to be reexamined. Many large species can be mapped visually under appropriate wind conditions. A knowledge of fronts would be useful in planning aerial survey sampling.

The accumulation of water-borne particulates in topographically controlled fronts and slicks implies that classical (depth-averaged) two-dimensional diffusion concepts and models are not valid and should not be used to model the fate of positively buoyant particulates in topographically complex environments such as near headlands, islands, and coral reefs. Nor should these models be applied to study the distribution of dense particles near the bottom. These models may be useful, however, when the particulates lose their buoyancy, for example, when the coral larvae emerge. The initial conditions for these models would then be provided by the distribution of the slicks after the larvae become distributed uniformly with depth. This may well occur far downstream from the natal reefs; furthermore, it may take several days for surface aggregations to become vertically homogenized.

Classical diffusion principles imply that particulates should disperse widely over a vast area, somewhat like a cloud of ever-increasing dimension. This is not the case for buoyant particles, such as coral eggs near reefs and headlands. Complex topographically controlled currents muster the eggs into aggregation in a few hours. The buoyant eggs are thereafter traveling in zoocurrents, and the fate of these zoocurrents will determine both the degree of self-seeding of reefs and the degree of biological connectivity among reefs. Zoocurrents may well play a key role in the ecology of topographically complex marine environments and need to be studied further.

REFERENCES AND NOTES

1. J. LeFevre, *Adv. Mar. Biol.* **23**, 163 (1986).
2. S. F. Brastow, *Mar. Environ. Res.* **9**, 211 (1983); W. M. Hamner and D. Schneider, *Limnol. Oceanogr.* **31**, 171 (1986); M. Kingsford and J. H. Choat, *Mar. Biol.* **91**, 161 (1986); I. Langmuir, *Science* **87**, 119 (1938); A. L. Shanks, *Mar. Ecol. Prog. Ser.* **24**, 289 (1985); R. A. Weller *et al.*, *Science* **227**, 1552 (1985).
3. E. Haeckel, *Planktonic Studies: A Comparative Investigation of the Importance and Constitution of the Pelagic Fauna and Flora* (Research Communication for 1889 to 1891, U.S. Commission Fish Fisheries, Appendix 6, 1893), pp. 565–641.
4. N. P. Ashmole and M. J. Ashmole, *Peabody Mus. Nat. Hist. Yale Univ. Bull.* **24**, 1 (1967); M. Omori and W. M. Hamner, *Mar. Biol.* **72**, 193 (1982); R. W. Owen, in *The California Islands*, D. Power, Ed. (Museum of Natural History, Santa Barbara, CA, 1980), pp. 237–267; R. W. Owen, in *Analysis of Marine Ecosystems*, A. R. Longhurst, Ed. (Academic Press, London, 1981), pp. 197–233; M. Uda, *Geophys. Mag.* **41**, 307 (1938).
5. W. M. Hamner and I. R. Hauri, *Aust. J. Mar. Freshwater Res.* **23**, 333 (1977).
6. ——, *Limnol. Oceanogr.* **26**, 1084 (1981).
7. A. L. Alldredge and W. M. Hamner, *Estuarine Coastal Mar. Sci.* **10**, 31 (1980).
8. M. Uda and M. Ishino, *J. Tokyo Univ. Fish.* **44**, 105 (1958).
9. R. G. Ingram and V. H. Chu, *J. Geophys. Res.* **92**, 14521 (1987); C. Pattiaratchi, A. James, M. Collins, *ibid.*, p. 783; R. D. Pingree and L. Maddock, *Mar. Geol.* **32**, 269 (1979).
10. E. Wolanski, J. Imberger, M. L. Heron, *J. Geophys. Res.* **89**, 10553 (1984).
11. E. Wolanski, E. Drew, K. Abel, J. O'Brien, *Estuarine Coastal Shelf Sci.* **26**, 169 (1988).
12. E. Wolanski, in *Physics of Shallow Estuaries and Bays*, J. van de Kreeke, Ed. (Springer-Verlag, Berlin, 1986), pp. 154–167.
13. B. L. Willis, R. C. Babcock, J. K. Oliver, C. C. Wallace, in *Proc. Fifth Int. Symp. Coral Reefs* (1985), pp. 343–348.
14. J. K. Oliver and B. L. Willis, *Mar. Biol.* **94**, 521 (1987).
15. R. O. R. Y. Thompson and T. J. Golding, *J. Geophys. Res.* **86**, 6517 (1981); R. E. Thomson and E. Wolanski, *J. Mar. Res.* **42**, 787 (1984).
16. E. Wolanski, personal observation.
17. W. M. Hamner, personal observation.
18. O. M. Phillips, J. H. Shyu, H. Salmun, *J. Fluid Mech.* **173**, 473 (1986).
19. R. R. Dickson and I. N. McCave, *Deep-Sea Res.* **33**, 791 (1986); J. H. Simpson *et al.*, *Cont. Shelf Res.* **1**, 15 (1982).
20. E. Wolanski, *Limnol. Oceanogr.* **32**, 735 (1987).
21. H. H. Roberts, S. P. Murray, J. N. Suhayda, in *Proc. Third Int. Symp. Coral Reefs* (1977), pp. 508–515.
22. J. Imberger, *Mech. Eng. Trans. Inst. Eng. (Australia)* **8**, 171 (1983).
23. W. M. Hamner, M. S. Jones, J. H. Carleton, I. R. Hauri, D. McB. Williams, *Bull. Mar. Sci.*, in press.
24. W. M. Hamner, personal observations in Baja California and Palau.
25. M. M. B. Talbot and G. C. Bate, *Estuarine Coastal Shelf Sci.* **25**, 707 (1987).
26. B. Hartwick, personal observation at Wheeler Reef, Great Barrier Reef.
27. R. E. Johannes, *Environ. Biol. Fish.* **3**, 65 (1978).

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