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Effects of island mass: Water flow and plankton pattern around a reef in the Great Barrier Reef lagoon, Australia¹

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Abstract

Water currents and zooplankton distributions are described for Pandora Reef, a coralline platform reef topped by a small sand spit, subject to tidal currents within the Great Barrier Reef lagoon (Queensland, Australia). Oncoming tidal currents separated 500 m upstream of the 1-km oblong reef. Zooplankton accumulated around the reef variously according to taxonomic group. Copepods and chaetognaths were most abundant directly upstream in an entrained water mass near the reef face and on top of the reef at high tide. Larvaceans were less abundant near the reef and were at low densities downstream. Zooplankton distributions were correlated with flow patterns. Water currents flowed asymmetrically around the reef due to shape of the platform and direction of main tidal flow. Flow separation at one end of the reef created a shear zone and strong gyres that shed periodically downstream. The other end of the reef was without flow separation but generated eddies and a weaker, stationary gyre. Downstream effects of flood and ebb exhibited major differences in flow, due to subtleties of reef morphology, and tidal height. The "island mass effect" of upstream increased primary productivity is in reality a spectrum of biological and physical events upstream, adjacent to, and downstream of islands and reefs. Existing laboratory models and mathematical theory apparently correctly predict flow around islands. At Pandora Reef little upstream water passed directly over the reef top at high tide in calm weather, and prior estimates of coral reef nutrition based on the assumption that nutrient-poor oceanic water crosses the reef may be in error.

Doty and Oguri (1956) first drew attention to the increased productivity upstream of islands bathed by otherwise nutrient-poor oceanic water. They observed increased primary productivity up to 28 km windward of Oahu, Hawaii, and termed this phenomenon the "island mass effect." Patterns of biomass accumulation or increased production near islands have been frequently described (e.g. Hardy and Gunther 1935; Emery 1964; Ashmole and Ashmole 1967; Alldredge and Hamner 1980; Johannes 1981). Only a few of these investigations have been accompanied by details of water motion.

Uda and Ishino (1958) did the first laboratory experiments on water motion around small-scale models of islands.

They related their simulation models to actual distributions of food fishes around real islands and demonstrated coincidence of fish accumulation to features of the model and to known oceanographic phenomena such as shear zones, large-scale eddies, divergences, and convergences. Their exercise proved of sufficient predictive value that weather reports in some Japanese newspapers now publish daily oceanographic charts to indicate local patterns of water motion and current anomalies (Laevastu and Hela 1970). Chopra (1973) and Pingree and Maddock (1979) have since contributed important theoretical and numerical mathematical models of flow patterns around islands. Lafond and Lafond (1971) presented pictorial hypotheses regarding the effects of islands on water motion. Actual field measurements of water motion around islands or reefs seem to be rather limited (von Arx 1954; Patzert 1969; Hamner and Hauri 1977; Wolanski and Jones 1980; Atkinson et al. 1981), and no one has made comprehensive measurements of water motion

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around an entire island or reef. The biological effects of island mass clearly are sufficiently important to affect large-scale commercial fishing strategies, yet many unexplored steps remain between the original and surprisingly still unique simulation model of Uda and Ishino (1958) and the distribution of tuna schools up to 1,000 km downstream of large islands in von Kármán vortex streets (Barkley 1972; Murphy and Shomura 1972).

Various factors affect motion of water around islands and reefs: direction and speed of prevailing current and of wind, size of island or reef platform, topography of island or reef and shape of surrounding shelf, presence or absence of other obstructions upstream, and latitude. Because of directional flow, downstream physical events can also dominate island mass effects: eddies, gyres, separation zones, divergences, and convergences continue dynamically unless physically disrupted—the gyres decaying with distance and time—recognizable at distances downstream of 10–15 times the diameter of the island (Chopra 1973). Besides upstream increased productivity (Doty and Oguri 1956), local inshore effects have been observed also. Alldredge and Hamner (1980) demonstrated, as indicated by Uda and Ishino (1958), that zooplankton are aggregated inside shear zones of recurrent eddy systems formed by strong tidal flow around islands at densities up to 40 times greater than outside the shear zone 10 m away.

At sea, mechanical events associated with convergences (Beebe 1931, 1934), Langmuir circulation (Stavn 1971), internal waves (Kamykowski 1974, 1976), and oceanic gyres (Wiebe et al. 1976) affect local distribution patterns (*see* Haury et al. 1978). Active behavioral response of the organisms themselves also dramatically alters horizontal distributions at sea, even for zooplankton as neurologically simple as jellyfish and appendiculareans (Owen 1966; Hamner and Hauri 1981; Omori and Hamner in prep.). The effects of island mass on biological distributions add additional fine structure to the water column at sea. The original mix of zoo-

plankton in a topographically generated downstream gyre is not simply a subsample of the surrounding sea, as it is for dynamically generated systems such as the Gulf Stream rings (Wiebe et al. 1976) or the oceanic eddies of the Kuroshio (Uda and Ishino 1958). Depending on where individual species originally accumulate around the island or reef, downstream gyres are disproportionately either depleted or enriched with particular species. Since these distributions affect all later biological events around islands, initial patterns must be described as a first step in understanding subsequent more complex events such as occur when vorticity builds and gyres break free downstream.

The investigation described herein is the third report on water currents and plankton distribution around islands and reefs in the Great Barrier Reef lagoon (Hamner and Hauri 1977; Alldredge and Hamner 1980). We report here on both water currents and plankton distribution around the entire Pandora Reef (Fig. 1), a 1-km oblong reef near Townsville, Queensland, Australia.

Pandora Reef rises sharply from a flat lagoon floor free of obstructions (Fig. 2). It lies 16 km offshore and is 12 km from the nearest island, the wake of which does not appear to impinge on Pandora Reef. The platform reef is teardrop-shaped, lying oblique to the prevailing tidal currents. The reef has rounded edges, reducing topographic effects of embayments and points. Atop the reef is a raised coral rubble ridge at the eastern end and a tidally exposed spit that runs most of the length of the platform. We worked when winds were low, $<11 \text{ km} \cdot \text{h}^{-1}$, and when tidal currents were directional and predictable. Our investigation is concerned with tidal currents, reef morphology, and zooplankton distribution.

Materials and methods

To track water motion we used three types of drogues. Surface drift cards and Woodhead sea surface drifters (Woodhead 1970; Hamner and Hauri 1977) were used close to or atop Pandora Reef

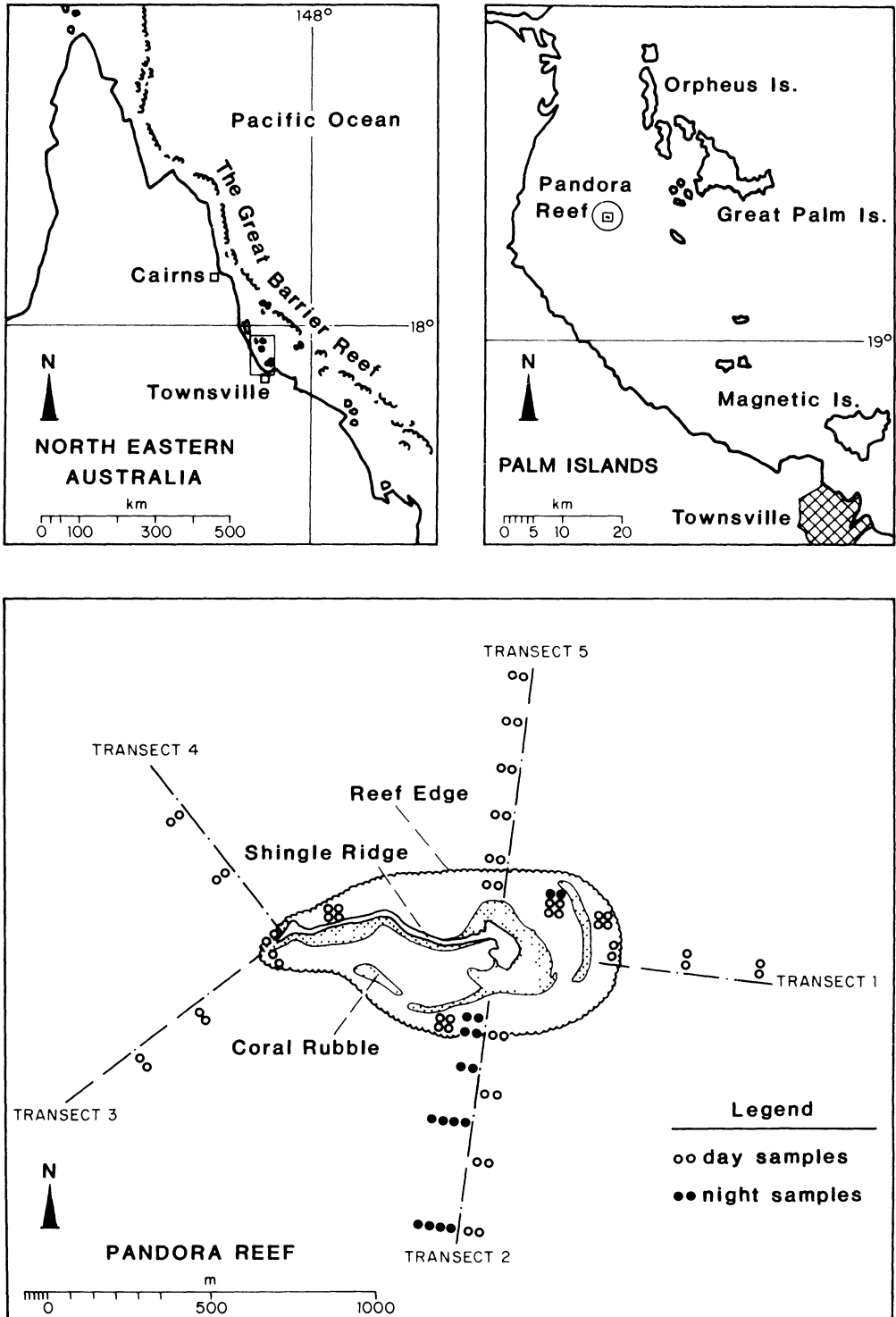


Fig. 1. Location of Pandora Reef, transect lines, and sampling locations.

and curtain drogues fitted with radar reflectors were used in deeper water. Curtain drogues were fitted with a 1.8×1.5 -m panel of heavy cotton fabric attached at the top to a 25-mm-diam plastic pipe and weighted at the bottom by a heavy 25-mm-diam aluminum pipe which kept the curtain vertical. After releasing drogues the boat was anchored, its position determined and drift rates of the drogues measured from the ship's radar. Performance of the curtain drogue was assessed visually by divers and by observing motion of the drogue relative to a large patch of fluorescein dye released during a $65 \text{ km} \cdot \text{h}^{-1}$ wind in an area where prevailing current ran counter to the wind. The drogues tracked into the wind and stayed with the dye patch for over 30 min.

We used a Tokyo Keiki MR-70 marine radar with a mechanical cursor and equipped with a 1.2-m antenna installed on a 12-m boat. On a 5-m pole the radar unit had an effective range of 6.5 km. Tide cycle charts for Lucinda Point, Queensland, were used to time the start of drogue runs. Predicted and actual tides corresponded closely and correction factors were not applied. We released drogues sequentially, spaced at a minimum of 125 m apart to eliminate merging of the reflected images on the radar screen. The location of the shipboard radar station was determined in relation to radar beacons fixed on the reef top. Positional readings for each drogue were taken about every 20 min. The data were transferred immediately to a chart to eliminate subsequent error. Between 5 and 10 sightings for each drogue were recorded. On two separate cruises, 27–31 July 1976 and 8–10 September 1977, we followed 74 individual radar drogues and 62 surface drifters during flood- and ebb-tides for about 1,000 sightings.

Aerial photographs taken from altitudes up to 7,000 m provided additional information on features such as tidal gyres (size, position, and rotational direction), fronts, and boundary layers, with silt patterns as a natural dye indicator (see Hamner and Hauri 1977).

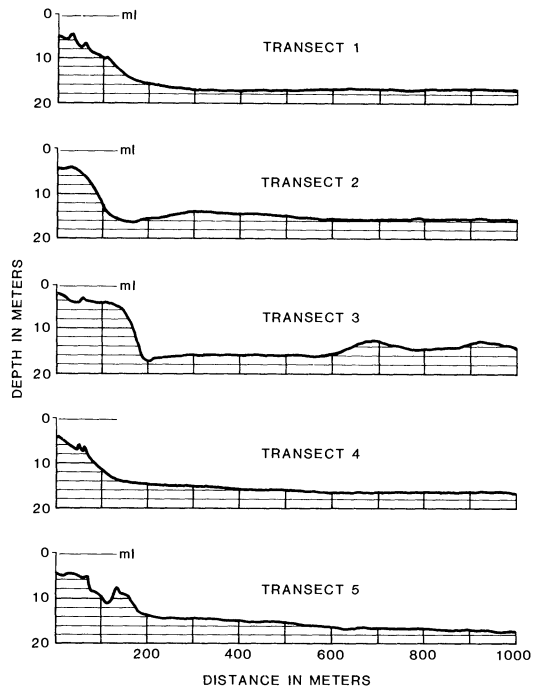


Fig. 2. Depth contours of five transects depicted in Fig. 1. Depths in meters below mean low (ml) water.

Plankton samples were taken along five transects (Figs. 1, 2) extending from atop the reef to about 2 km away from it. Two 0.5-m-diam plankton nets, one with $235\text{-}\mu\text{m}$ mesh and one with $550\text{-}\mu\text{m}$ mesh, both metered and without bridles, were fished simultaneously from either end of a boom attached across the bow of a rubber boat. Each net was fastened by the top of the ring to a line suspended from one end of the boom and was depressed by a 5-kg weight hung from the lowest arc of the ring, so that the nets fished at 1-m depth alongside the bow. In several instances plankton samples were also taken with 20-liter water bottles. Zooplankton were later subsampled and sorted into 20 different taxonomic groups and samples were adjusted to $\text{No.} \cdot \text{m}^{-3}$. For several groups the catch was uneven and in other cases too few individuals were collected to be of significance. Consequently we plot distributional data only for total biomass, chaetognaths, copepods, and larvaceans.

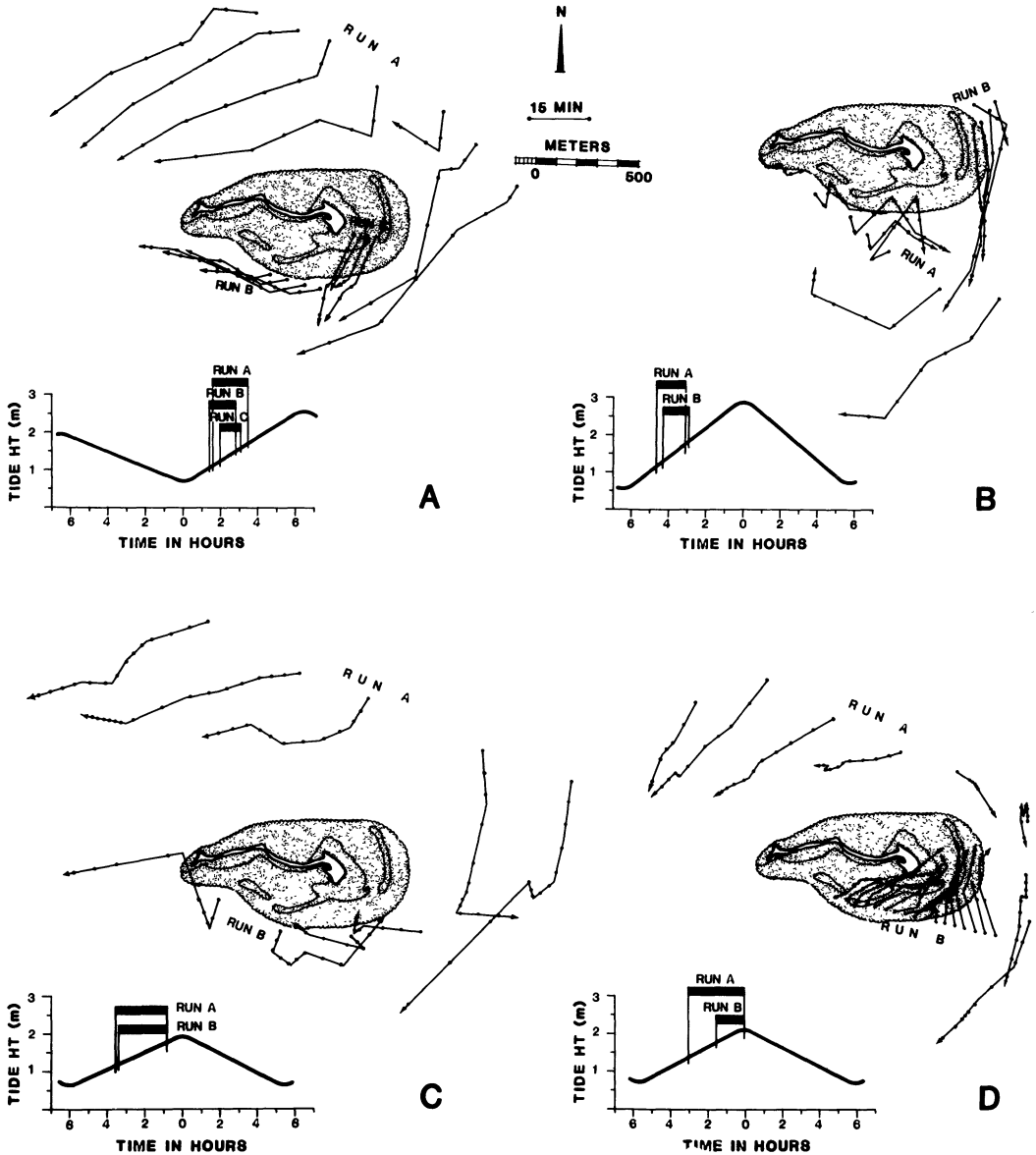


Fig. 3. Charts of drogue movement around Pandora Reef on floodtides (see text).

Results

Separate groups of drogues released on given days are plotted in Figs. 3 and 4 as separate "runs." Drogues released atop the reef were always drift cards; drogues released close to the reef were Woodhead sea surface drifters; drogues released at some distance from the reef were surface curtain drogues (with one

exception, Fig. 3C, run A, where the curtain drogues were deployed at 7-m depth). Drogues were released in linear sequence and can be identified by run or linear sequence reading from left to right. The location of drogues at each sighting is marked on the charts as a solid black dot superimposed on a directional arrow. Figures 3 and 4 are sequenced from low

to high to low tide. Each chart shows the actual tide height for the day that set of drogues was followed. Data from the two cruises are combined to cover the complete tidal cycle.

Floodtide—Figure 3A: Tidal current from NE, max. velocity $0.8 \text{ km} \cdot \text{h}^{-1}$. Main water mass deflected around reef 500 m upstream, with noticeable deflection of drogues (run A). Drogues directly upstream deflected or reversed. Drogues released in island lee (run B) did not drift SW but drew west. Drift cards atop reef (run C) moved SW. Later in rising tide these cards reversed and drew directly NE.

Figure 3B: Main flood still from NE at $0.8 \text{ km} \cdot \text{h}^{-1}$. Close to lee of reef, four drogues in run A reversed and drew east along reef edge. The fifth drogue turned full circle clockwise and the sixth rotated clockwise to run N. Run B drogues released to NE near the reef edge converged into a streamline that moved south along the eastern reef margin. Drogue reversals indicate presence of gyres.

Figure 3C: Deeper curtain drogues (run A, 7-m depth) still toward SW on flood, current somewhat slower (15-min dots closer together). Oncoming current deflected 500 m upstream. One drogue deflected east after initial 2 h south. Run B indicates complex eddies and gyres. First and third drogues drew south, then west. Second drogue ran south, then east. The fourth drogue ran west, then north onto reef top.

Figure 3D: Flood race diminished in strength (run A, decreased interdot distance with time). Drogues released NE of reef stalled or reversed, stalled, and reversed again. Deflection of drogues away from reef 500 m upstream continued. Two drogues released east of the reef converged, then moved steadily SW. Run B drogues released in lee near peak high all drew N-NE, directly opposite to main tidal flood 500 m upstream. These drogues moved variously thereafter (not plotted). Some stalled, others diverged either to east or to west.

Figure 5, aerial photograph: Large de-

tached gyres visible south of Pandora Reef, outlined by silt stirred from island along western shear zone. Larger gyre visible in original photo SE of reef, decaying 4–5 km south. Separation of main current around reef 500 m upstream.

Figure 6, floodtide interpretation: Water moving SW on floodtide was deflected around the reef 500 m upstream, 300 m before the platform shelves upward off the otherwise flat bottom of the Barrier Reef lagoon. An almost stationary, locally entrained water mass occurred at a distance upstream equal to half the length of the reef. Where the main current impinged on this entrained water mass, the current stalled. The reef lies 45° oblique to the NE flood, with the tail of the reef toward the west and the head to the east. Water flowing from the NE along the northerly reef edge therefore was deflected only slightly and proceeded apace with the main force of the flood current. At the western tip of the reef, flow separation occurred with formation of a visible shear zone that ran almost due south and which separated the nonturbulent southerly flow past the western end from the turbulent westerly flow south of the reef. Water flowing along the eastern side of the reef also was deflected away. At high tide a second, weaker gyre developed off the eastern end that threw water in a retrograde motion back across the reef top (Fig. 3D: run B), directly opposite to the main southwesterly tidal flow. Very subtle differences in height of water and growth of coral atop the reef modified the direction of this local flow. This eastern gyre rotated opposite to the main western gyre inside the southerly projecting shear zone. The eastern gyre was stable over the rising tide whereas the western gyre shed three or four times during rising tide and generated the downstream disturbances that could be seen in aerial photographs.

Ebbtide—Figure 4A: Tidal current from SW; max velocity $0.8 \text{ km} \cdot \text{h}^{-1}$. Note differences in scale and time. Reef 1 km long; readings 30 min apart. Drogues released 1–3 km away from reef, upstream and downstream, to assess movement of

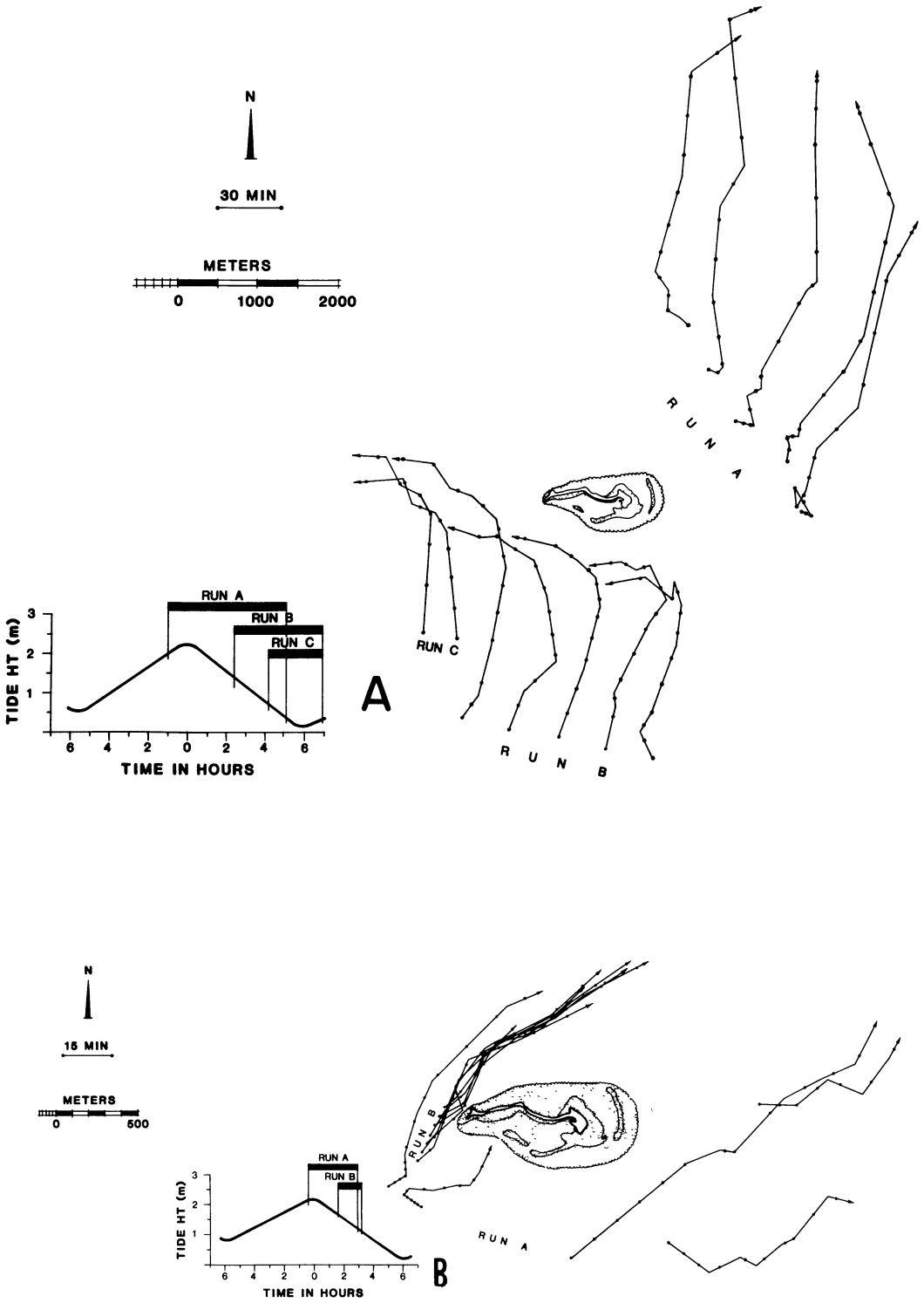


Fig. 4. Above and right, as Fig. 3, but for ebb tides.

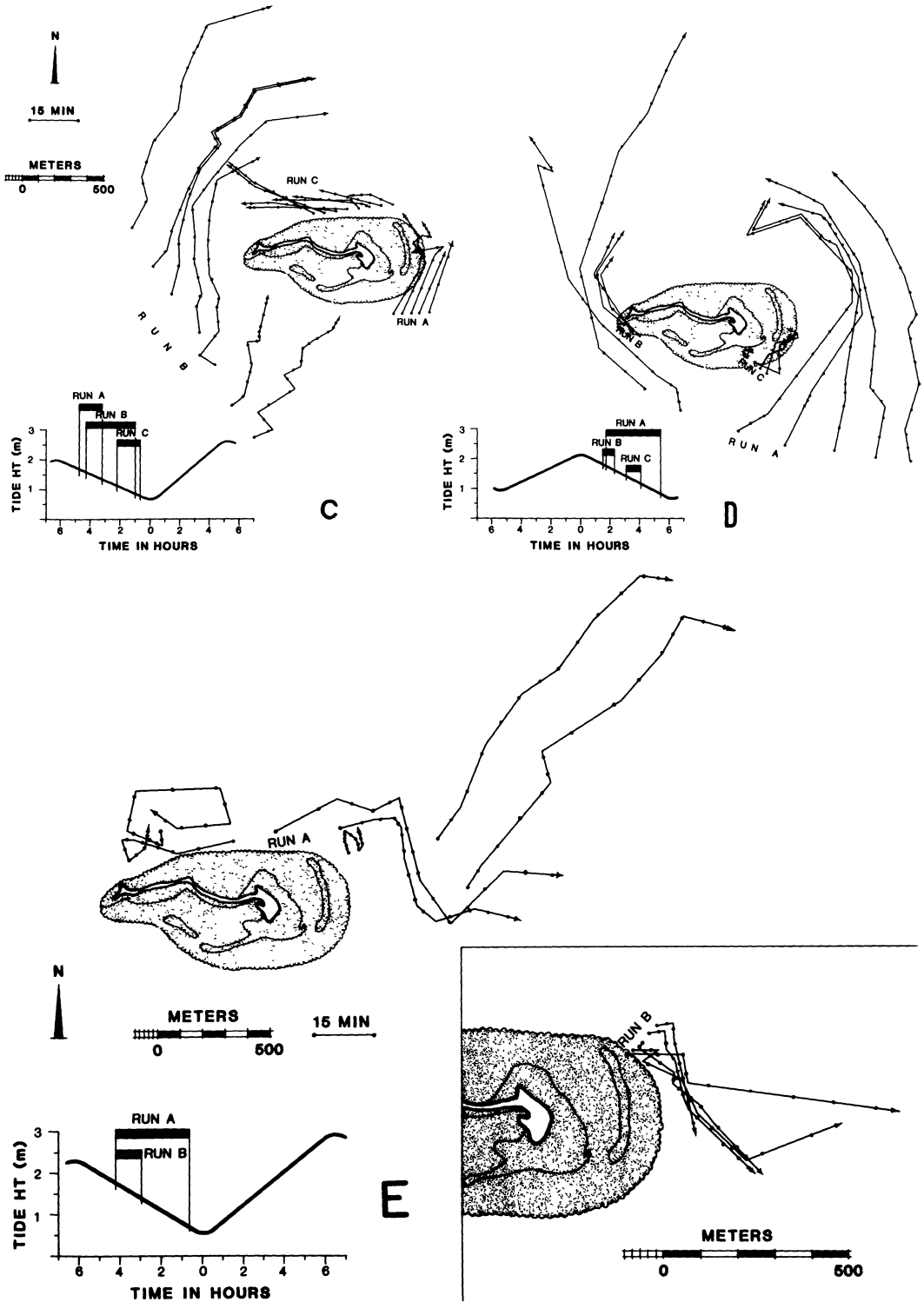


Fig. 4. Continued.



Fig. 5. Aerial photograph of gyre formation downstream on floodtide (*see text*).

main ebb current up to 4 km away from reef. Ebbtide toward NNE; slight but discernible interdrogue motion. Flow patterns generally parallel, with deflections to west as tide turned (runs B and C).

Figure 4B: Run A drogues dropped upstream south of reef. The most westerly drogue ran NE around reef, with deflection to north 500 m upstream. The drogue directly upstream of reef ran west, then east, then NE directly toward reef. Other drogues moved NE with modest but real

differences in direction. Run B drogues converged into a NE streamline.

Figure 4C: Drogues released off east end of reef (run A) moved NE, but the three closest to reef deflected to west near NE tip. In run B, the two most southerly drogues drew erratically NE toward reef, then stalled. Other drogues were deflected by entrained water mass of reef and drew north past west tip before joining normal NE flow. Run C drogues all drew west.

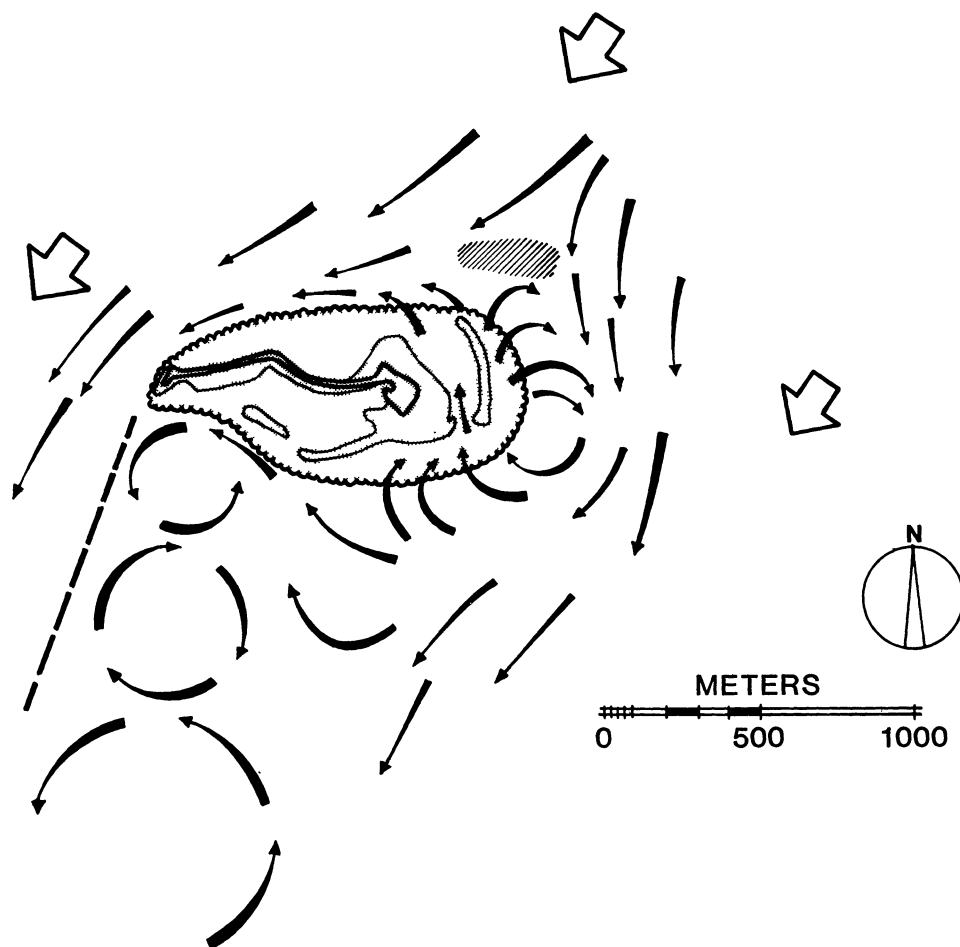


Fig. 6. Interpretation of floodtide flow pattern around Pandora Reef.

Figure 4D: Unlike similar drogues in Fig. 4B, run A drogues moved NNW after passing the eastern reef edge. The two closest to reef recurved back to NE. Run B drogues moved around reef in a NW course, then turned east to join main ebb current. Run C drogues stalled, twisted, and turned on the SE reef top.

Figure 4E: Run A drogues in complex eddies off north reef edge. The two most westerly drogues rotated in opposite directions. Two drogues meandered, one stalled. The two most distant from the reef ran to NE. Run B (Fig. 4E, insert) depicts SE motion with crossovers and angular changes of drogues off east edge.

Aerial photographs (not included be-

cause of poor reproduction): A 300-m band of discolored water adhered to south edge of reef during ebb, moving slowly east and merging with counterclockwise gyre from north side of reef. Clear water visible immediately adjacent to reef and between merging water masses. Farther west along north edge second gyre in process of formation. Sequential photographs demonstrated that this gyre later expanded after east gyre shed. Streamlines of water running NE seen in color originals.

Figure 7, ebbtide interpretation: The pattern of water motion during ebbtide generally resembled that described for flood except that the ebb current im-



Fig. 7. As Fig. 6, but for ebbtide.

pinged on the western tail of the reef first and moved more gently around to the northeast. Water stalled on the southern edge of the reef (as it did on the northern edge during flood), diverging up to 500 m upstream of the reef. Water then flowed sharply past the western tail of the reef in a series of parallel and visible streamlines, and moved thereafter around the northern side of the reef with less force and with no apparent turbulence. Although the western streamline was strong, and although a strong westerly current formed immediately adjacent to the northwestern reef edge, these currents merged without forming a visually apparent convergence. The NW gyre was stable and persisted throughout ebbtide; because of reef topography it was smaller than the southwesterly counterpart during floodtide. The tail of the reef hooks

toward the ebb current, permitting flow without separation. On the northeasterly reef edge a series of small gyres formed which grew and were steadily shed throughout the ebbtide sequence. Clear water visible in aerial photographs of the center of these smaller gyres may indicate local upwelling. Drogues in these locations either stalled or rotated erratically. These vortices did not drift directly NE downstream, but moved easterly, as seen in sequential aerial photographs made over the course of an hour.

Plankton distributions—Isopleths are plotted only for samples taken with the 235- μ m-mesh net (which captured significantly more copepods) and for ebbtide samples taken during daylight hours (for which we have the most complete sample sequence).

During ebbtide, plankton biomass

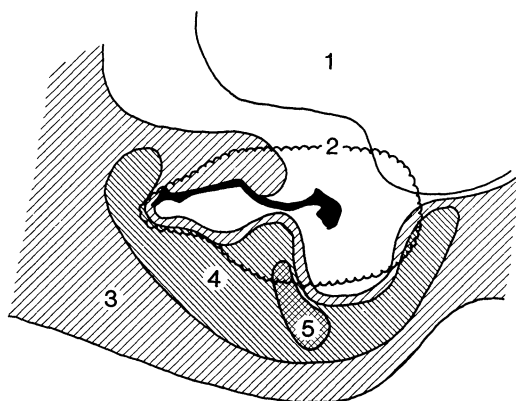


Fig. 8. Ebbtide biomass distribution (ash-free dry wt, $\text{mg} \cdot \text{m}^{-3}$)—zone 1, <5 ; zone 2, 5–9.5; zone 3, 10–15; zone 4, 15–20; zone 5, >20 .

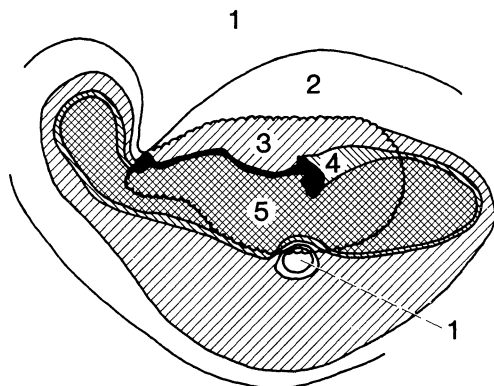


Fig. 9. Ebbtide copepod distribution ($\text{No.} \cdot \text{m}^{-3}$)—zone 1, <500 ; zone 2, 500–1,000; zone 3, 1,000–1,500; zone 4, 1,500–2,000; zone 5, $>2,000$.

(Fig. 8) was greatest in the waters on the southern side of the island facing into the oncoming current. Accumulations $>20 \text{ mg} \cdot \text{m}^{-3}$ occurred in the slack water where the tidal current divided upstream to pass around the platform. Generally low plankton biomass occurred on the reef top at high water at the beginning of ebbtide. Samples with $15\text{--}20 \text{ mg} \cdot \text{m}^{-3}$ ash-free dry weight were taken along the reef front, in a 200–400-m-wide band that extended seaward of the reef face and partly included the top of the reef. Farther upstream the main tidal current contained lower plankton biomass, with $5\text{--}15 \text{ mg} \cdot \text{m}^{-3}$. In the lee of the reef, biomass was $<5 \text{ mg} \cdot \text{m}^{-3}$.

The distributions of copepods (Fig. 9) and chaetognaths (Fig. 10) generally followed the basic biomass pattern but exhibited some significant differences. In particular, copepods were found in greatest numbers atop the reef and upstream in the entrained water mass. Copepods were collected in significant concentrations ($>2,000 \cdot \text{m}^{-3}$) up to 300 m from both the east and west ends of the reef, apparently reflecting movements there of the ebb current. Outside the influence of the reef, some 500 m away, concentrations of copepods dropped to $<500 \cdot \text{m}^{-3}$. Two replicated samples on the most southerly portion of the reef were anomalously low.

Chaetognaths were disproportionately

abundant atop the reef at high water during the early stages of ebbtide. This distribution closely matched that of copepods, upon which they feed. Chaetognaths numbered $>40 \cdot \text{m}^{-3}$ atop the reef, but $<2 \cdot \text{m}^{-3}$ in waters farther from the reef.

Larvacean distribution during ebbtide was quite different (Fig. 11), with highest concentrations ($7,500 \cdot \text{m}^{-3}$) in the Great Barrier Reef lagoon waters which, in general, did not approach the reef directly. Larvaceans were present on the reef top at high tide at lower densities ($300\text{--}500 \cdot \text{m}^{-3}$). Directly downstream larvacean concentrations were $<50 \cdot \text{m}^{-3}$.

Sixteen night samples were also collected, but visual triangulation for specific location against fixed beacons on the reef top became logistically difficult at night when the small boat was any distance from the reef. A rising swell made work far from the reef in small boats unsafe. The night catches were dominated by larger crustaceans, mysids, polychaetes, and pteropods. These were as abundant atop the reef as they were offshore.

Discussion

Physical aspects of water flow—The motion of seawater around islands and reefs is affected by a bewildering array of variables. A semblance of order emerges, however, if one considers first only the

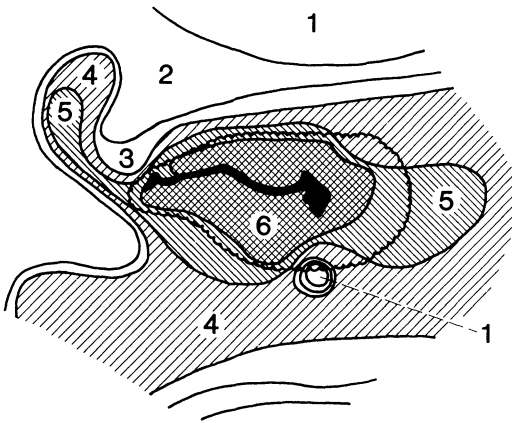


Fig. 10. Ebbtide chaetognath distribution ($\text{No.} \cdot \text{m}^{-3}$)—zone 1, <2 ; zone 2, 2–7; zone 3, 7–15; zone 4, 15–25; zone 5, 25–40; zone 6, >40 .

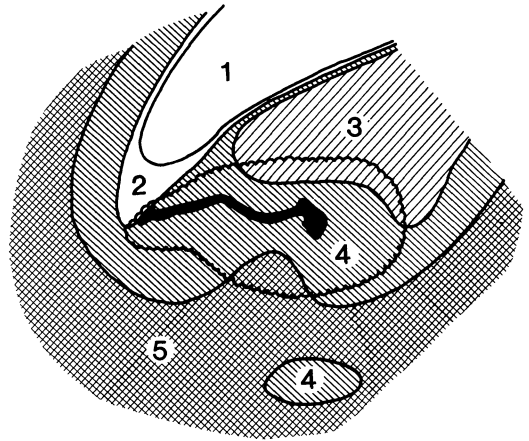


Fig. 11. Ebbtide larvacean distribution ($\text{No.} \cdot \text{m}^{-3}$)—zone 1, <50 ; zone 2, 50–100; zone 3, 100–300; zone 4, 300–500; zone 5, >500 .

effects of speed of the current and size of the island or reef. These two variables are mathematically related to one of the most important problems encountered in fluid mechanics, the change of state in a fluid when it shifts suddenly from laminar to turbulent flow.

Consider first the effect of change of speed in a fluid as it flows past a perfectly round object of constant size. During laminar flow (Fig. 12A) a slow current separates around an obstruction and its entrained boundary water, the thickness of this boundary layer decreasing with increasing current speed. At the sites of upstream divergence and downstream convergence, zones of relatively stationary water occur. The currents converge below the leeward stagnation zone without turbulence and laminar flow persists downstream.

When the current speed increases beyond some critical value, the flow suddenly shifts from a laminar to a turbulent state (Fig. 12B) and stationary downstream eddies and gyres develop and persist in the lee, as described for the area downstream of Tobi Island (western Pacific) by Johannes (1981). If current speed increases even more, rotational energy accumulates in these downstream gyres; and, with increased vorticity, downstream events become unstable,

producing two types of wakes—symmetric or asymmetric. Should the object or island be effectively symmetrical (Fig. 12C), vorticity becomes localized in one of the two major gyres, which then builds in size and rotational energy at the expense of the other. When this dominant gyre possesses enough vorticity to escape entrainment, it breaks free of island influence and sheds downstream in the wake of the island. The subordinate gyre meanwhile begins to grow on the contralateral side of the lee, rotating with equal vorticity but in the opposite direction, until it in turn sheds downstream. These gyres alternately grow and shed with mathematical predictability and the downstream wake of alternating and expanding gyres takes on a characteristic appearance called a von Kármán vortex street (as for Johnston Atoll: Barkley 1972).

The sequence of events described above for increasingly swift currents around a perfectly round object also occurs when speed is held constant and the size of the object increased. The relationship of these two variables is expressed as a nondimensional Reynolds number:

$$Re = U_o \frac{d}{k}$$

where U_o is speed of incident flow, d is

effective diameter of the island, and K is the eddy viscosity of seawater (taken to be $2.2 \times 10^6 \text{ cm}^2 \cdot \text{s}^{-1}$; Barkley 1972). Using Barkley's eddy viscosity figure and assuming Pandora Reef to be effectively circular with a diameter of 1 km and with current speed of about $0.8 \text{ km} \cdot \text{h}^{-1}$, we calculate that Pandora Reef has a Reynolds number of 10—below the 20–70 range estimated by Barkley (1972) to be necessary for von Kármán wake formation downstream of Johnston Atoll. Pandora thus is too small and the current too slow to generate the alternately rotating gyres of a vortex street. In addition Pandora Reef is exposed to a semidiurnal reversing tidal current, which presents short term sinusoidal changes in current speed and direction, further adversely affecting the speed and time factors required for long term vortex street persistence.

The second type of wake occurs when the gyres are forced asymmetrically from one side by wind or waves, by downstream events generated by other obstructions, or by asymmetry of the island or reef itself. Under these conditions the gyre on the side opposite to the secondarily imposed lateral force strengthens at the expense of the weaker sibling gyre until it develops sufficient vorticity to escape entrainment and shed downstream. Due to the persistent lateral force or island shape, however, a sibling gyre does not then develop on the opposite side of the lee, but another similar gyre forms in the same location. Direction of rotation depends on a variety of conditions, but in any case the resultant wake is one-sided, without the paired symmetry seen in a von Kármán vortex street. An asymmetric circulation system due to imbalance imposed by the topography of the island is shown in Fig. 12D.

This rendition of an asymmetric wake, fully representative of the generalized case, also represents the actual ebbtide current regimen for Pandora Reef (cf. Fig. 7). This remarkable similarity of real events to a simple flow model should not be too surprising. We selected Pandora Reef because of its structural simplicity,

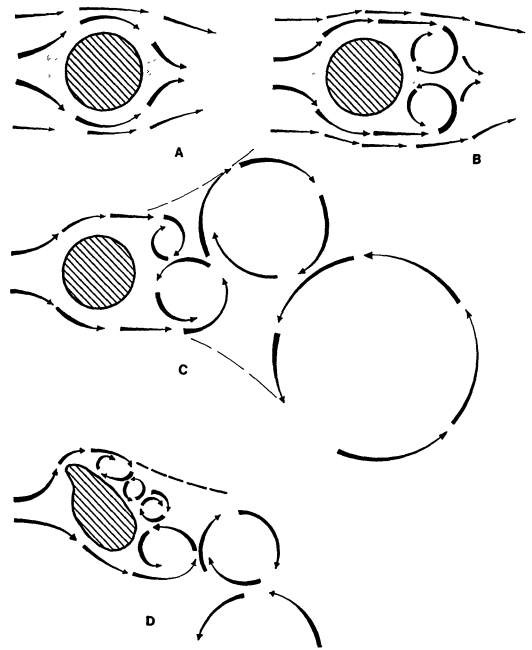


Fig. 12. Effects of current speed and island shape on flow dynamics. Stippling upstream and downstream of islands indicates locations of limited water movements (see text).

isolation from other wakes, and smooth subsurface topography. We intentionally worked when winds were low and waves were absent, thus eliminating many potential complexities from our investigation. Nonetheless, it is comforting that such simple elements of flow theory apply so well to the actual motion of seawater around a real platform reef. There was, of course, no reason to think that this theory would not apply, but in the absence of direct confirmation in the field one is never sure, and the water currents for Pandora Reef provide the first clear confirmation of flow theory for currents around an island.

Pandora Reef is not round, but oblong. The laws of fluid dynamics quickly become complicated when the effect of topography on flow is considered, and fluid mathematicians we approached recommended an empirical approach with laboratory modeling of scaled islands. With this approach, the downstream eddies of Pandora Reef resemble the water cur-

rents near Goto Island west of Kyusyu, Japan, modeled by Uda and Ishino (1958: fig. 12) as an asymmetric flow downstream of an island having a bay. Empirical laboratory scale-modeling probably will be the only practical means to deal with subtleties of topographically generated current anomalies around any given island. Consider Pandora Reef during floodtide (Fig. 6). The tide floods from the northeast and flows past the eastern end of the island reasonably smoothly, generating a small eddy to the southeast. Flow at the western end of the reef is more turbulent, with flow separation and generation of a gyre which sheds downstream. Even the slight variations of the angle at which the tide impinges on Pandora, of course, would generate major changes in the downstream flow field, and it is probable that this does occur with only modest shift in current, as when southeasterly winds modify tidal currents.

Although the prerequisites of size and current speed are well understood for generation of symmetric wakes of the von Kármán vortex street variety, there is no information in the oceanographic literature on asymmetric wakes. These apparently can be generated by considerably smaller islands and much slower currents, as we see for Pandora Reef. Although less energy apparently is required for their formation, asymmetric wakes may have a lifespan approaching that of symmetric wakes. If this is so, then a significant portion of the central and southern Pacific Ocean may be affected by downstream topographically generated turbulence.

Biological consequences of water flow—Various biological effects attend the interaction of water currents and obstructions of varying morphology. Even the simplest case (Fig. 12A), where water flow is laminar, has significant biological consequences. Due to steady lateral divergence of the oncoming current, water immediately upstream is constantly stripped away at the surface and replaced from below by upwelled water (Miller 1974). This zone may become locally en-

riched by animals usually living deeper or by animals that prefer cooler water. Upwelled water upstream of small islands probably does not remain in residence long enough to stimulate increased productivity, but for large islands like Oahu, upstream upwelling and local enrichment are quite significant. The original "island mass effect" of upstream primary productivity (Doty and Oguri 1956; Gilmartin and Revelante 1974) certainly results from combined upwelling and increased turbulence of the water column due to island shelving. Zooplankton also accumulate upcurrent (this paper; Miller 1974). Additional information is needed.

Movement of water along the sides of an island or reef platform also significantly affects biotic events. Turbulence generated at the boundary of the entrained water layer moves surface water both upward and downward, as described for lateral motion of longshore currents along surge channels of windward reef faces (Roberts et al. 1975). Zooplankton aggregate in recurrent eddies formed inside shear zones (Uda and Ishino 1958), and birds and fishes feed on these aggregations (Alldredge and Hamner 1980). Fishermen in Queensland commonly troll for mackerel along the sides of coral reefs where the prevailing currents separate around the reef.

In the lee of the reef or island there is often a zone of quiet water beyond which the separated water current once again converges. One of us (W.M.H.) has seen this clearly demonstrated at Turtle Rocks, south of Bimini, Bahamas, on the western edge of the Grand Bahamian Banks. There the receding tide drains a large area of shallow water atop the banks, moving plankton and sargassum seaward around the rocks. In the relatively stagnant lee, buoyant organisms accumulate in enormous densities and escape from this entrained stationary water mass only at the point of merger of the right and left currents, bleeding off into the Gulf Stream in a thin, continuous band of sargassum and zooplankton (mostly copepods and ctenophores)—a band up to 10

m wide and several meters deep that moves seaward as long as the tide continues to draw. These "zoocurrents" (Haeckel 1893) often enter the Gulf Stream at right angles and override the cooler waters of the current, extend up to 15 km from shore, and bend north into sinuous bands easily visible from the surface (frontispiece: Stommel 1958). The bands of plankton are accompanied by fishes below and birds above that feed on the organisms mechanically accumulated in the lee of an island now many miles distant (Johannes 1981). Water in the island lee may be either warmer or colder than the surrounding sea (Lafond and Lafond 1971). Should the lee be large and upwelling strong, the water may be cooler and enriched by nutrients from below. If winds are low and solar irradiation intense, and if warm surface waters are not moved laterally by gentle winds, the waters in the lee may be warmer with different subsequent effects downstream.

The biological consequences of island mass effects are even more significant when downstream turbulence develops. The initial distribution of plants and animals in the gyres drifting downstream is determined by the internal structure of the gyres. If the flow pattern creates a series of gyres that alternate in rotational direction, as in Fig. 12C, then all the gyres shed from one side will have cold cores and those shed from the other side will have warm cores. Plants and animals that prefer one system over the other therefore will be disproportionately abundant either on the left or on the right of the von Kármán vortex street. Gyres drifting downstream expand and decay with distance and time. Distances involved typically are 10–15 times the diameter of the island or reef which produced the gyres; for Hawaii some 1,000–1,500 km downstream (Chopra 1973), and for Johnston Atoll some 600 km (Barkley 1972). Temporal successional events downstream depend on the size of the island and the speed of the downstream current within which the gyres rotate. Each downstream gyre below Johnston Atoll has a lifespan of about 15 days, suf-

ficient time for a host of localized successional biological events such as depletion of nutrients, increased productivity, depletion of phytoplankton due to increased grazing, elimination of small grazers by larger predators, etc. Events at the surface may be matched by corresponding activities of organisms in deeper midwater communities which migrate to the surface at night. Yellowfin tuna and sea birds exploit these locally enriched plumes of waters far downstream of the island (e.g. *see* Ashmole and Ashmole 1968). Finally, events at the surface probably are mirrored in the sediments of the sea floor, but there does not seem to be any information in the literature on the relationship of sediment pattern to downstream vortex streets.

Reef morphology—Pandora Reef influences the passage of water around the reef and then downstream in an expected fashion although shape and the angle presented to the currents generate obvious departures from theory. Effects of Pandora Reef on water motion are a variant of Fig. 12C and are presented schematically for ebbtide in Fig. 12D. Here, due to the oblique angle of the reef to the prevailing current and the oblong shape of the reef itself, the downstream gyre is one-sided, with the near side gyre and eddy system stable (as in Fig. 12B) and the far side (as in Fig. 12C) shedding sequentially downstream. Any lateral forcing agent, be it wind, subsurface topography, downstream effects of other obstructions, or asymmetries in shape, may change the rotational direction of downstream gyres.

The gyres and eddy currents at Pandora Reef are of great importance to the local distribution of plankton and fishes. For example, on the flood near peak high tide, the eastern gyre and eddy system are so strong that they throw a retrograde current back across the reef top directly into the oncoming flood. The planktivorous fishes on the northern reef face at this time face the reef to feed on materials brought across the reef top from the island lee. This retrograde current across the reef top is affected by differences in

reef height as small as 60 cm. Subtle topographic changes in reef shape and in water depth markedly alter the current regimen and subsequent biological events around a reef.

Our sampling of zooplankton around Pandora Reef was less extensive than our measurements of water motion. Nonetheless we demonstrated interesting patterns of plankton distribution related to reef shape and local water motion. Copepods, which comprised the bulk of the catch and which were most abundant atop the reef, were species we had observed in swarms (*see* Hamner and Carleton 1979) and probably are resident reef species. These copepods also occurred outside the reef system, but at lower densities and not in swarms. The upcurrent, entrained reef water is less subject to removal, and the densities of copepods were higher upstream and atop the reef than downstream. Such was the case also for chaetognaths, which tracked their copepod prey onto the reef top at high tide. The reef environment is a less satisfactory environment for larvaceans, since larvacean houses are delicate, and larvaceans were scarce on the reef. The distinctive distributions of copepods and larvaceans, both herbivores but specialists on phytoplankton of different type and size, suggest that behavioral habitat selection is extremely important in the local distribution of particular zooplankton in the vicinity of reefs and islands.

Bearing on coral reef nutrition estimates—Oceanic currents do not closely approach most reef systems; they diverge far upstream (500 m for Pandora). Inasmuch as all prior discussions of reef nutrition (Odum and Odum 1955; Johannes et al. 1970; Tranter and George 1972; Glynn 1973; LIMER 1976) assume that nutrient-poor oceanic water flows directly over the reef top, this observation for Pandora Reef is especially important. We have shown for Pandora Reef that upstream currents (in this case, Barrier Reef lagoon water) do not flow over the "up current" reef. Instead the oncoming water divides around the reef with its entrained water mass. Although the up-

stream current drives all of the subsidiary current systems in the island lee, when winds are low these larger water currents do not appear to directly affect the reef front or the edges of the reef itself. The reef edges, the reef fishes, benthic invertebrates, plants, and resident zooplankton are all affected mostly by local movements of entrained water and small-scale local currents. This also has been demonstrated clearly for Lizard Island (LIMER 1976) and Davies Reef (Gentien pers. comm.). Obviously the great ocean currents must part upstream in order to flow around a reef, and water that comes directly over the reef top, as in the Marshalls (von Arx 1954; Atkinson et al. 1981), is probably water that has been upwelled (Roberts et al. 1975) and already enriched (Doty and Oguri 1956). Great currents must diverge and mix upstream of the reef. The coral reef ecosystem, therefore, is not really an oasis of biological productivity surrounded by a nutrient-poor sea, but is a rich ecosystem that persists at high levels of productivity partly because of upstream divergence, island mass effect, and resulting complex currents. Elaborate topographically generated gyres upwell nutrients, renew resources, and retain species, including populations of plankton generally considered primarily pelagic but now known to be residents of the reef environment (Johnson 1949, 1954; Tranter and George 1972; Alldredge and King 1977; and Pandora Reef). More extensive studies of fine-scale interactions among physical, chemical, and biological events around islands and reefs are badly needed.

References

- ALLDREDGE, A. L., AND W. M. HAMNER. 1980. Recurring aggregation of zooplankton by a tidal current. *Estuarine Coastal Mar. Sci.* **10**: 31-37.
- , AND J. M. KING. 1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island lagoon, Great Barrier Reef. *Mar. Biol.* **41**: 317-333.
- ASHMOLE, M. J., AND N. P. ASHMOLE. 1968. The use of food samples from sea birds in the study of seasonal variation in the surface fauna of tropical ocean areas. *Pac. Sci.* **22**: 1-10.
- ASHMOLE, N. P., AND M. J. ASHMOLE. 1967. Comparative feeding biology of sea birds of a trop-

- ical oceanic island. Peabody Mus. Nat. Hist. Bull. 24: 131 p.
- ATKINSON, M., M. V. SMITH, AND E. D. STROUP. 1981. Circulation in Enewetak Atoll lagoon. *Limnol. Oceanogr.* **26**: 1074-1083.
- BARKLEY, R. A. 1972. Johnston Atoll's wake. *J. Mar. Res.* **30**: 201-216.
- BEEBE, W. 1931. A round trip to Davy Jones' locker. *Natl. Geogr. Mag.* **59**: 653-678.
- . 1934. A half mile down. *Natl. Geogr. Mag.* **66**: 661-704.
- CHOPRA, K. P. 1973. Atmospheric and oceanic flow problems introduced by islands. *Adv. Geophys.* **16**: 297-421.
- DOTY, M. S., AND M. OGURI. 1956. The island mass effect. *J. Cons. Cons. Int. Explor. Mer* **22**: 33-37.
- EMERY, A. R. 1964. The ecological effects of current patterns around islands with special reference to Barbados. Ph.D. thesis, McGill Univ. 145 p.
- GILMARTIN, M., AND N. REVELANTE. 1974. The 'island mass' effect on the phytoplankton and primary production of the Hawaiian Islands. *J. Exp. Mar. Biol. Ecol.* **16**: 181-204.
- GLYNN, P. W. 1973. Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope: Part 1. Meteorology and hydrography. *Mar. Biol.* **20**: 297-318.
- HAECKEL, E. 1893. Planktonic studies: A comparative investigation of the importance and constitution of the pelagic fauna and flora [transl.]. Append. 6 Rep. Comm. 1889-1891. U.S. Comm. Fish Fish., p. 565-641.
- HAMNER, W. M., AND J. H. CARLETON. 1979. Copepod swarms: Attributes and role in coral reef ecosystems. *Limnol. Oceanogr.* **24**: 1-14.
- , AND I. R. HAURI. 1977. Fine-scale surface currents in the Whitsunday Islands, Queensland, Australia: Effect of tide and topography. *Aust. J. Mar. Freshwater Res.* **28**: 333-359.
- , AND ———. 1981. Long-distance horizontal migrations of zooplankton (Scyphomedusae: *Mastigias*). *Limnol. Oceanogr.* **26**: 414-423.
- HARDY, A. C., AND E. R. GUNTHER. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926-1927. *Discovery Rep.* **11**: 1-456.
- HAURY, L. R., J. A. MCGOWAN, AND P. H. WIEBE. 1978. Patterns and processes in the time-space scales of plankton distributions, p. 277-328. *In* J. H. Steele [ed.], *Spatial pattern in plankton communities*. Plenum.
- JOHANNES, R. E. 1981. Words of the lagoon: Fishing and marine lore in the Palau District of Micronesia. Univ. Calif.
- , S. L. COLES, AND N. T. KUENZEL. 1970. The role of zooplankton in the nutrition of some scleractinian corals. *Limnol. Oceanogr.* **15**: 579-586.
- JOHNSON, M. W. 1949. Zooplankton as an index of water exchange between Bikini lagoon and the open sea. *Trans. Am. Geophys. Union* **30**: 238-244.
- . 1954. Plankton of northern Marshall Islands: Bikini and nearby atolls, Marshall Islands. U.S. Geol. Surv. Prof. Pap. 260-F, p. 300-314.
- KAMYKOWSKI, D. 1974. Possible interactions between phytoplankton and semidiurnal internal tides. *J. Mar. Res.* **32**: 67-89.
- . 1976. Possible interactions between plankton and semidiurnal internal tides. 2. Deep thermoclines and trophic effects. *J. Mar. Res.* **34**: 499-508.
- LAEVASTU, T., AND I. HELA. 1970. Fisheries oceanography. Fish. News (Books) Ltd.
- LAFOND, E. C., AND K. G. LAFOND. 1971. Oceanography and its relation to marine organic production, p. 241-265. *In* J. D. Costlow [ed.], *Fertility of the sea*, v. 1. Gordon and Breach.
- LIMMER 1975 EXPEDITION TEAM. 1976. Metabolic processes of coral reef communities at Lizard Island, Queensland. *Search* **7**: 463-468.
- MILLER, J. M. 1974. Nearshore distribution of Hawaiian marine fish larvae: Effects of water quality, turbidity and currents, p. 217-231. *In* J. H. Baxter [ed.], *The early life history of fish*. Springer.
- MURPHY, G. I., AND R. S. SHOMURA. 1972. Pre-exploitation abundance of tunas in the equatorial central Pacific. *Fish. Bull.* **70**: 875-913.
- ODUM, H. T., AND E. P. ODUM. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.* **25**: 291-320.
- OWEN, R. W., JR. 1966. Small-scale, horizontal vortices in the surface layer of the sea. *Deep-Sea Res.* **24**: 56-65.
- PATZERT, W. C. 1969. Eddies in Hawaiian waters. *Hawaii Inst. Geophys. Rep.* 69-8. 51 p.
- PINGREE, R. D., AND L. MADDOCK. 1979. Tidal flow around an island with a regularly sloping bottom topography. *J. Mar. Biol. Assoc. U.K.* **59**: 699-710.
- ROBERTS, H. H., S. P. MURRAY, AND J. N. SUHAYDA. 1975. Physical processes in a fringing reef system. *J. Mar. Res.* **33**: 233-260.
- STAVN, R. H. 1971. The horizontal-vertical distribution hypothesis: Langmuir circulation and *Daphnia* distribution. *Limnol. Oceanogr.* **16**: 453-466.
- STOMMEL, H. 1958. The Gulf Stream: A physical and dynamic description. Univ. Calif.
- TRANter, D. J., AND J. GEORGE. 1972. Zooplankton abundance at Kavaratti and Kalpeni Atolls in the Laccadives, p. 239-256. *In* *Corals and coral reefs*. Proc. Symp., 1969, Mar. Biol. Assoc. India.
- UDA, M., AND M. ISHINO. 1958. Enrichment pattern resulting from eddy systems in relation to fishing grounds. *J. Tokyo Univ. Fish.* **44**: 105-129.
- VON ARX, W. S. 1954. Circulation systems of Bikini and Rongelap lagoons. U.S. Geol. Surv. Prof. Pap. 260-B, p. 265-273.
- WIEBE, P. H., AND OTHERS. 1976. Gulf Stream cold core rings: Large-scale interaction sites for

- open ocean plankton communities. *Deep-Sea Res.* **23**: 695-710.
- WOLANSKI, E., AND M. JONES. 1980. Water circulation around Britomart Reef, Great Barrier Reef, during July 1979. *Aust. J. Mar. Freshwater Res.* **31**: 415-430.
- WOODHEAD, P. M. 1970. Sea-surface circulation in the southern region of the Great Barrier Reef, spring 1966. *Aust. J. Mar. Freshwater Res.* **21**: 89-102.

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