There is evidence that both DNA strands of the herpes simplex virus ICP-0 gene (*10*), the murine c-*myc* gene (*11*), the rat insulin II (*12*), a pupal cuticle gene of *Drosophila* (*13*), and the human gonadotropin-releasing hormone gene (*14*) are transcribed. In addition, the complementary DNA strand mRNAs of the last two genes are known to be translated into protein. Thus, there are precedents for bidirectional transcription and concomitant protein synthesis of eukaryotic genes. Therefore, the ORF on the DNA plus strand of HIV may represent a genuine gene sequence that ultimately encodes a protein with novel features.

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9. A plus strand DNA ORF of approximately 200 amino acids is also present in the X gene region (the 3′ end of the linear genome) of 18 out of 18 isolates of hepatitis B virus (HBV) and HBV-like viruses of animals. Other, shorter ORFs are found in the DNA plus strand complementary to: (i) the gene sequence encoding the transactivating protein of human T cell leukemia virus types 1 and 2, bovine leukemia virus, and simian T cell leukemia virus; and (ii) the *env* region of HIV type 2, visna virus of sheep, equine infectious anemia virus, and the simian immunodeficiency virus. The plus strand DNA ORFs of these viruses are heterogeneous in size and many do not possess initiation codons within the 5′ region of the ORF. Computer analysis suggests that the plus strand ORF of the ancestral virus of HIV-1, and the other viruses, was once much longer, but is gradually shrinking in size because of the accumulation of termination codons. It is possible that the plus DNA strand of many of these viruses has lost the ability to encode protein during the course of evolution.
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18 September 1987; accepted 2 February 1988

Localized Dispersal and Recruitment in Great Barrier Reef Corals: The Helix Experiment

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To examine the problem of how far coral larvae disperse from their natal reef, coral recruitment densities were experimentally determined at distances up to 5 kilometers from a small, relatively isolated platform reef, Helix Reef, on the central Great Barrier Reef for 7 months. High concentrations of recruits, accounting for up to 40 percent of all recruitment, were found downstream of the reef in areas of high water residence time, suggesting that near-field (proximal) circulation has a profound influence on dispersal and recruitment of coral larvae. Coral recruitment declined logarithmically with distance from the reef, decreasing by an order of magnitude at radial distances of only 600 to 1200 meters. On an ecological time scale, advective dispersal of semipassive marine larvae with relatively short planktonic lives (minimally days) may be extensive, but success of recruitment is highly limited. Through evolutionary time, sufficient dispersal occurs to ensure gene flow to reef tracts hundreds or possibly thousands of kilometers apart. In the short term, however, coral reefs appear to be primarily self-seeded with respect to coral larvae.

MANY MARINE ORGANISMS POSsessing larvae with potentially high longevity are assumed to be long-range dispersers (*1*). Short-range dispersal in reproductive propagules with high dispersal capabilities has long been known to occur in the terrestrial environment (*2*), but evidence for such in the marine environment has only recently emerged (*3, 4*), prompting us to surmise that localized dispersal and recruitment may be important in reef corals. Thus we examined coral recruitment around a relatively isolated reef.

Two major modes of coral reproduction are release of fully developed larvae (*5*) and external fertilization (*6, 7*). Estimates of larval longevity vary widely. The minimum post-release period for settlement in brooded planulae is 4 hours (*8*); externally fertilized eggs have an obligate planktonic development period of 24 to 72 hours (*7, 9*). Upper time limits for dispersal and settlement of coral planulae approach 3 months (*10*). Until now, the patterns of effective larval dispersal in corals and the resultant distribution of their settlement have not been known.

Twenty-four oceanographic moorings were deployed around Helix Reef (central Great Barrier Reef: 147°18′E, 18°38′S), which is 800 m in diameter, 10 km from its nearest neighbor, and rises from a continental shelf floor of 55 m depth. Moorings were placed at 0, 0.3, 0.6, 1.2, 2.5, and 5.0 km

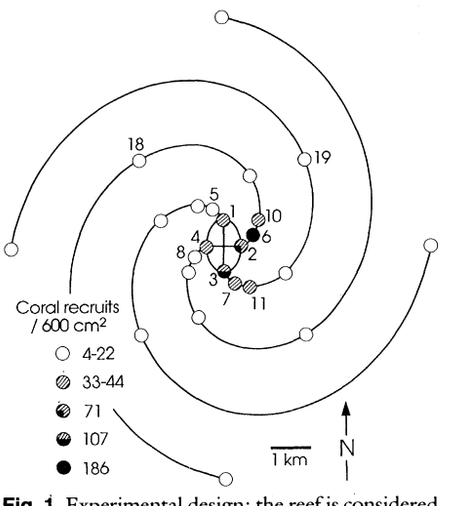

Fig. 1. Experimental design: the reef is considered to be an ellipse; circles represent recruitment sample points where arms of 270° spiral intersect concentric ellipses at 0, 0.3, 0.6, 1.2, 2.5, and 5.0 km from perimeter. Selected station numbers shown. Coral recruitment density is designated by shaded circles; each group differs significantly from next [$P < 0.001$, one-way analysis of variance; $P < 0.01$, sum-of-squares simultaneous test procedure; $(Y + 0.5)^{1/2}$ transformation used for analysis].

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from the perimeter along counterclockwise spiraling arms, covering approximately 100 km^2 (Fig. 1). Settling substratum was composed of 600 cm^2 disks of coral skeleton. Five plates were mounted on racks (*11, 12*) oriented into the current by vanes and stationed at 18 m depth. Moorings were deployed for 7 months from October 1983, encompassing the Australian summer coral spawning period. Meters recorded far-field (distant) currents 2.5 km from the reef (stations 18 and 19 in Fig. 1) at depths of 18 and 50 m each half-hour throughout the experiment. Tides were recorded on the reef.

Ambient currents had three components. (i) A persistent seasonal flow (*13*) from the northwest at 8 to 10 cm sec^{-1} followed the isobaths along the shelf. (ii) Low frequency winds (weather band, Fig. 2a) (*13*) imposed a 10 to 20 cm sec^{-1} fluctuation on the seasonal flow (Fig. 2b), accelerating the flow during northerly (point A) and calm (B) periods and retarding or reversing flow (C) during southeasterly winds. (iii) In contrast, largely semidiurnal tidal currents (Fig. 2c; amplitudes, ~20 cm sec^{-1}) ebbed and flooded across the isobaths (*14*).

Corals in the central Great Barrier Reef region spawn during the third lunar quarter in October, November, or December or in any contiguous combination of these 3 months (*7, 9*). In 1983, spawning occurred from 24 to 27 November (*15*) when winds were moderate from the south and weak low-frequency currents flowed to the south-southeast (Fig. 1). The influence of tides on circulation patterns was important since the neap reduction in tidal amplitude was moderate. Rather, the form of the tides shifted from semidiurnal before spawning to diurnal during spawning (peak velocities, ~10 cm sec^{-1}; Fig. 2).

Using wind, tide, and surface sea level gradient data, we simulated near-field currents using a nonlinear numerical hydrodynamic model incorporating Coriolis and bathymetric effects (*16*) (Fig. 3). Although current pattern varied greatly with the tide, some consistent dynamical features emerged. In one "snapshot" 5 hours before high tide (Fig. 3B), the current bifurcated at the nose (point A), accelerated along the flanks (B), flowed around an eddy in the lee (C), and turned eastward along the southern perimeter (D) until it converged with the eastern branch (E). This overall pattern generally revolved around the reef as the tidal current rotated, with certain features becoming dominant, depending upon reef shape and strength and direction of far-field currents. Time-averaged currents revealed the net influence (Fig. 3A). Residence time was very high in the southern lee and in the lee of the northeastern arm. It was also relatively high on the reef flat and the northern face. High flushing rates occurred to the northwest, west, and southeast.

The model results are consistent with earlier studies of interactions between ambient currents and reefs of the Great Barrier Reef (*16, 17*), but here the grid resolution (50 m) reveals for the first time the intricate dependence of flow pattern and flushing rate on small-scale reef structure. Small-scale hydrodynamic features (for example, eddies) such as those generated here are known to contain dense aggregates of plankton (*18*).

The two stations having the lowest flushing rates possessed the highest levels of recruitment (*19*). The highest concentration was located at the east-northeast site (station 6: $\bar{X}$ = 186.4 per 600 cm^2, SD = 28.2, n = 5) (Figs. 1 and 4), accounting for 26% of all recruits. One plate there yielded 287.2 recruits per 600 cm^2, the highest density of

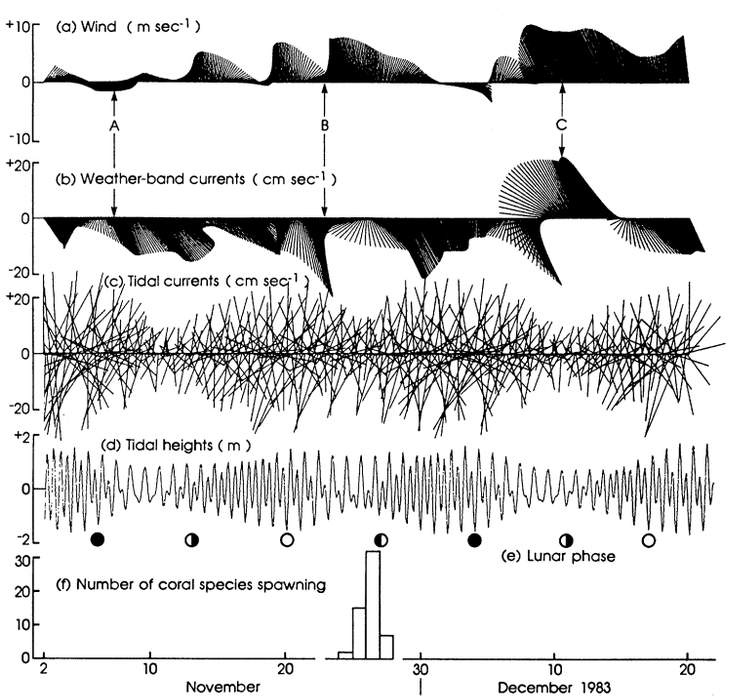

Fig. 2. Times series of (**a**) winds, (**b**) and (**c**) currents, (**d**) sea levels in the far-field of Helix Reef, (**e**) lunar phase, and (**f**) number of coral species spawning per day [data derived from (*15*)]. Currents separated into (c) rotary tidal and (b) low-frequency currents dominated by (a) regional winds. Tidal cycle during spawning peak (f) diurnal in character; tidal and weather-band currents equal at 7 to 10 cm sec^{-1} in presence of 7 m sec^{-1} southerly wind. North is upward (↑).

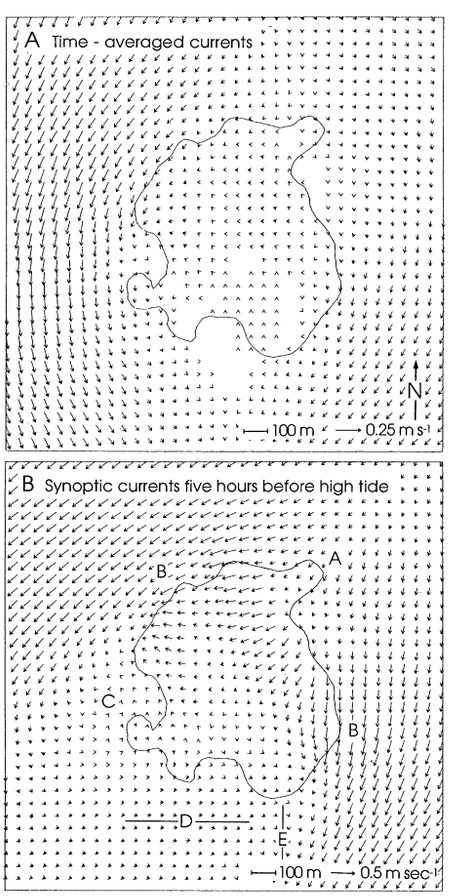

Fig. 3. Currents around Helix Reef during spawning period (see Fig. 2f). Numerical model forced by winds (7 m sec^{-1} from south), tidal surface slopes (axial current ellipse amplitudes 8 and 3 cm sec^{-1}), diurnal frequency (orientation 75°), and far-field low-frequency surface slope (yielding 10 cm sec^{-1} current to south). (**A**) Currents averaged over tidal cycle, showing residuals generated by nonlinear interactions and low-frequency forcing. (**B**) Time-varying currents 5 hours before high tide showing "typical" pattern. Transient eddies, recirculation zones, nose and lee stagnation points, acceleration on flanks, and convergence in lee evident. Features move with time; flushing rates shown here are less meaningful than averages in (A).

coral recruitment reported to date. The second highest concentration (107.6 per 600 cm^2) occurred 200 to 300 m south of the perimeter (station 3), accounting for a further 15%.

The third highest recruitment area was the poorly flushed eastern perimeter (station 2). The fourth highest densities were found in the remaining on-reef stations (1 and 4), in a "downstream plume" extending 900 m south (stations 7 and 11), and on the northeastern arm (station 10) (Fig. 1 and 4). Lowest densities occurred in the far-field beyond 1200 to 1500 m and also in the rapidly flushed northwest sector (stations 5 and 8) only 300 m from the reef. Such differences in coral recruitment imply that certain reef areas, such as the lee, possess higher growth rates than others, such as upcurrent.

It is not known whether any relationship exists between local coral cover and recruitment density. Most on- and near-reef stations were surrounded by thriving adult coral communities.

Coral recruitment declined significantly with distance from the reef (Fig. 5), approximating a Poisson distribution (*20*) highly skewed to the right with a mode at 300 m. More than 70% of all recruits settled within 300 m of the reef. Recruitment declined asymptotically from an average of 52.5 corals per 600 cm^2 (SD = 26.93, n = 15) at the perimeter to 6.6 to 7.4 per 600 cm^2 (SD = 4.89 to 5.00, n_i = 20) at a distance of 2.5 to 5.0 km. Recruitment densities in the far-field were uniform, exhibiting small variances. This low, predictable recruitment is indicative of constant background levels of larval dispersal. This signal is important because it indicates gene flow between reefs separated by tens to hundreds (*21*) or thousands (*10*) of kilometers.

Relative abundance of the dominant acroporid (predominantly externally fertilized) recruits was higher off the reef, implying higher dispersal capabilities than brooders. Reduced representation of other groups, however, was insufficient to account for decline in overall recruitment with distance.

These results are consistent with an earlier large-scale transplant experiment (*12*) showing some geographic isolation with respect to coral recruitment across the continental shelf.

Coral recruitment in the central Great Barrier Reef is highly localized, and reefs like Helix appear to be largely self-seeded, particularly on an ecological time scale (*3*). As in many marine organisms (*1*), the upper limits of coral larval dispersal are quite high (*10*), promoting gene flow and permitting low levels of long-distance colonization, particularly when integrated over evolutionary time (*22*). Although potential for long-distance advection exists in the sea (*1, 22, 23*), even small distances can represent an effective barrier to success of larval recruitment. The effective distance scales for larval dispersal and successful recruitment apparently differ.

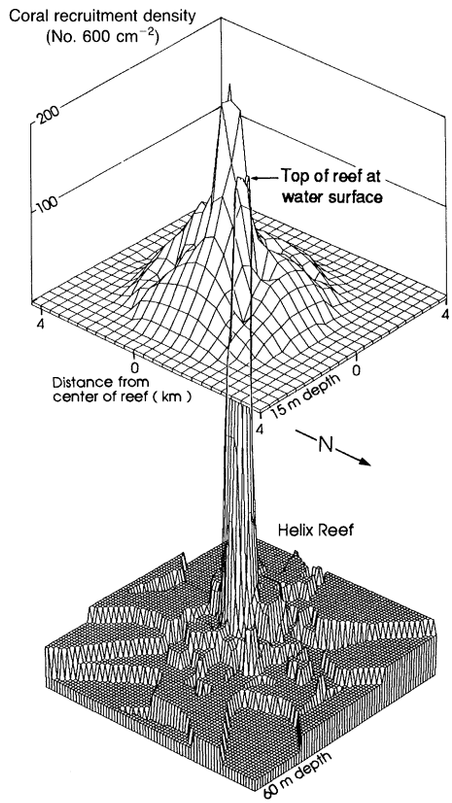

Fig. 4. Coral recruitment at 15 to 18 m depth as a function of position relative to Helix Reef. Bathymetry is digitized. Mean current from north-northwest (right to left). Recruitment is downstream with peaks immediately south and northeast of reef and depressions on the northern face.

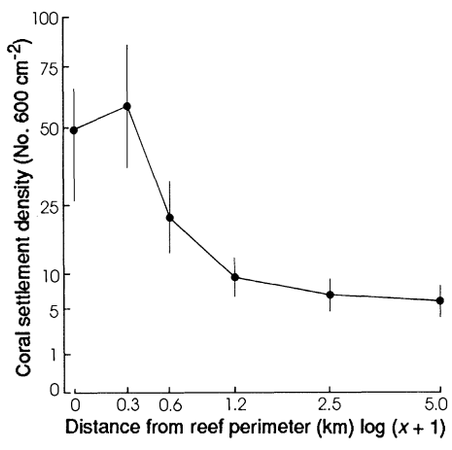

Fig. 5. Coral recruitment in number per 600 cm^2 with 95% confidence limits as a function of distance from the reef perimeter. Data transformed by square root; distance by $\log_{10}(X + 1)$. Statistically significant decrease ($P < 0.01$, linear regression analysis).

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24. A. Mackley and J. H. Carleton assisted with fieldwork, laboratory processing, and data analyses. S. Gay adapted the flow model, loaned by K. Black, and processed field data. R. McAllister and L. Harris also assisted in the field. The Royal Australian Navy supplied hydrographic data. The study required shipping restrictions for 7 months; we thank the Australian Department of Transport–Marine Operations Center, Australian Coast Guard, Professional Trawlermen's Association (Townsville), Australian Broadcasting Commission, local bait and tackle shops, and local charter boat operators and fisherman for their cooperation. We thank D. Burrage and J. Pandolfi for helpful comments on the manuscript. Australian Institute of Marine Science Contribution No. 401.

13 October 1987; accepted 20 January 1988