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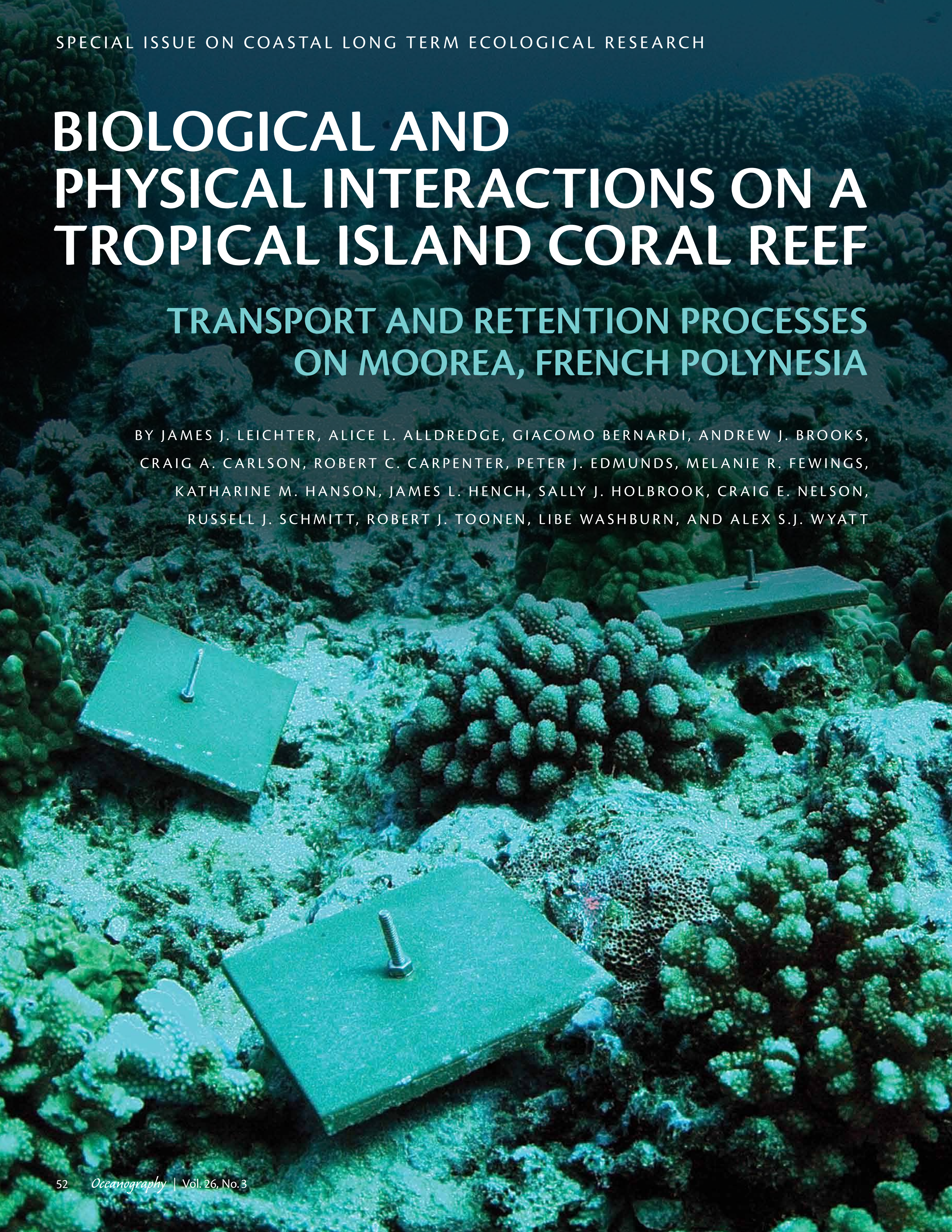
BIOLOGICAL AND PHYSICAL INTERACTIONS ON A TROPICAL ISLAND CORAL REEF

TRANSPORT AND RETENTION PROCESSES ON MOOREA, FRENCH POLYNESIA

BY JAMES J. LEICHTER, ALICE L. ALLDREDGE, GIACOMO BERNARDI, ANDREW J. BROOKS, CRAIG A. CARLSON, ROBERT C. CARPENTER, PETER J. EDMUNDS, MELANIE R. FEWINGS, KATHARINE M. HANSON, JAMES L. HENCH, SALLY J. HOLBROOK, CRAIG E. NELSON, RUSSELL J. SCHMITT, ROBERT J. TOONEN, LIBE WASHBURN, AND ALEX S.J. WYATT



ABSTRACT. The Moorea Coral Reef Long Term Ecological Research project funded by the US National Science Foundation includes multidisciplinary studies of physical processes driving ecological dynamics across the fringing reef, back reef, and fore reef habitats of Moorea, French Polynesia. A network of oceanographic moorings and a variety of other approaches have been used to investigate the biological and biogeochemical aspects of water transport and retention processes in this system. There is evidence to support the hypothesis that a low-frequency counterclockwise flow around the island is superimposed on the relatively strong alongshore currents on each side of the island. Despite the rapid flow and flushing of the back reef, waters over the reef display chemical and biological characteristics distinct from those offshore. The patterns include higher nutrient and lower dissolved organic carbon concentrations, distinct microbial community compositions among habitats, and reef assemblages of zooplankton that exhibit migration behavior, suggesting multigenerational residence on the reef. Zooplankton consumption by planktivorous fish on the reef reflects both retention of reef-associated taxa and capture by the reef community of resources originating offshore. Coral recruitment and population genetics of reef fishes point to retention of larvae within the system and high recruitment levels from local adult populations. The combined results suggest that a broad suite of physical and biological processes contribute to high retention of externally derived and locally produced organic materials within this island coral reef system.

INTRODUCTION

Transport and retention of water and water-borne materials and organisms fundamentally shape coral reefs and their interactions with the surrounding ocean. Transport governs the movement of new water, as well as nutrients and organic materials, into and through reef systems and the exchange and dispersal of individuals and propagules among spatially isolated habitats. Retention is critical for the accumulation of nutrients and organic matter within reefs and for the development of biogeochemical reef environments distinct from those of surrounding offshore waters. Coral reefs are generally surrounded by clear, nutrient-depleted waters, and high rates of water transport into, and material retention within, reef systems have long been thought necessary for the development and maintenance of the high biomass and productivity characteristic of these communities (Odum and Odum, 1955; Johannes et al., 1972).

Mass transport of water-borne materials over a reef can be described as the time-integrated product of flow velocity and material concentration per unit reef area. Changes in velocity are driven by physical factors such as wind, waves, tides, density structure of the water column, and coastal- and regional-scale currents. On reefs, water flow interacts with structures such as coral colonies, reef crests, lagoons, and passes, producing areas with relatively quiescent versus much more rapid flows. Variations in concentration within these flows are caused by physical processes of advection and mixing and biological processes that add or remove materials. For example, photosynthesis and respiration add and remove oxygen and carbon dioxide, nutrients and dissolved organic compounds are taken up and regenerated by organisms, and particles are captured and released by suspension-feeding invertebrates and fishes.

Retention can be broadly described as the holding (or increased residence times) of materials within a reef system. It is useful to distinguish between the retention of water itself and the retention of water-borne materials, including dissolved nutrients, gases, particles, and plankton. Both can be retained through local reduction in velocity and recirculation. Water-borne materials can also be retained when sessile organisms extract the materials from the flowing water, and fish and many zooplankton taxa can resist transport and increase their retention in a system by directed swimming against or across the flow. A complex suite of interacting physical and biological processes influences retention within reef systems. Biogenic reef structures such as atolls and reef lagoons develop in relation to flow dynamics, and these structures in turn modify wave exposure, tidal currents, and mean water levels (Wolanski and Hamner, 1988; Callaghan et al., 2006). The spatial arrangement and behaviors of reef organisms also strongly influence net transport and retention. For example, upstream production and recycling supply material to downstream consumers (Smith and Marsh, 1973; Miyajima et al., 2007; Wyatt et al., 2012), and the congregation of fishes on fore reefs leads to retention of nutrients captured from consumption of oceanic plankton (Pinnegar and Polunin, 2006; Hamner et al., 2007; Wyatt et al., 2013). Retention does not necessarily change simply with velocity. In some cases, slow flow speeds and long water residence times, for example, in a reef lagoon or semi-enclosed bay, can lead to extensive growth and accumulation of plankton populations (Hamner and Hauri, 1981). In other cases, slow flow speeds can limit particle capture and nutrient uptake across the boundary layers above reef organisms. Uptake of these materials often increases with increasing flow velocities to maximum levels (Patterson et al., 1991; Atkinson, 2011). Thus, perhaps counterintuitively, the rate at which dissolved and particulate materials are removed from moving water and retained in a reef ecosystem may be highest in areas with high flows and short water residence time.

STUDY SITE

Moorea (17°30'S, 149°50'W) can be seen as a case study representing the large number of islands and coral reefs in the central South Pacific. The Moorea Coral Reef Long Term Ecological Research (MCR LTER) project began in 2004 and includes six main study areas encompassing the fringing reef, back reef, and fore reef habitats on the north, southwest, and southeast sides of the island (Figure 1). A barrier reef ~ 0.5–1.5 km from the shore surrounds the island, and the protected inshore lagoons are connected to the open ocean by a series of passes (Figure 1). The lagoon on the north shore connects to bays ~ 5 × 1 km. The offshore reef and underlying island edge slope steeply to > 500 m depth within 1–2 km of the reef. Tidal amplitudes are ≤ 30 cm. The seasonal climate is dominated by a warm, wet season from November to April (austral summer) and a cooler and drier season from May to October (austral winter). The outer reef slopes around Moorea are low-relief coral spur-and-groove formations running approximately perpendicular to the reef crest from 2 to ≥ 60 m depth. The fringing and back reefs are dominated by coral aggregations one to several meters in diameter, separated by patches of sand, rubble, and reef pavement. Inshore water depths are 0.5–3 m in the back reef, up to 10 m in the lagoons, and 20–30 m in the two large bays on the north shore.

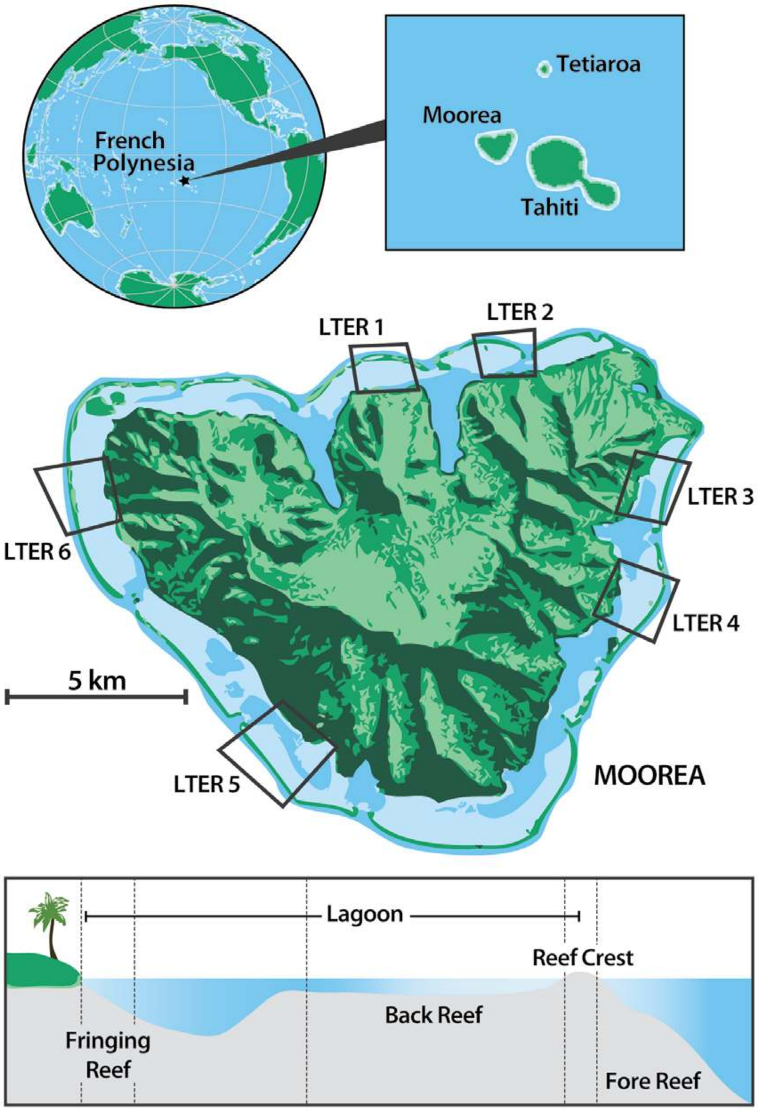


Figure 1. Map of Moorea showing the Moorea Coral Reef Long Term Ecological Research (MCR LTER) sampling locations and a cross section through a typical section of the reef. The typical cross section on Moorea represented in the lower panel is 1–2 km from the fringing reef to the fore reef.

PHYSICAL TRANSPORT PROCESSES

The westward South Equatorial Current (SEC) dominates regional-scale flow near Moorea, forming the northern portion of a large, counterclockwise subtropical gyre in the Central South Pacific (Rougerie and Rancher, 1994). The adjacent, larger island of Tahiti is predominantly upcurrent of Moorea, and the wake generated by the SEC flowing past Tahiti likely influences circulation around Moorea. The offshore pycnocline extends broadly across depths, with continuous stratification observed to at least 500 m. Maximum density stratification occurs at depths of 50–60 m in summer and deepens to 150–200 m in winter. We have measured currents nearly continuously at bottom depths of 15 and 40 m at fore reef sites on each side of the island since 2005. Water column velocities are relatively rapid and oriented in the alongshore direction on each of the three main shores. Peak velocities are 0.4–0.5 m s^{-1}, root mean squared speeds on order of 0.1 m s^{-1}, with reversals in direction at the semidiurnal tidal frequency (Leichter et al., 2012). Transport on the deeper portions of the fore reef slopes (at bottom depths > 20 m) is also influenced by transient elevations of the offshore thermocline and oscillating surges of upslope and downslope flow. Internal waves that are observed around the island, with peak activity in austral summer (Leichter et al., 2012), impact the reef slope by driving these surges and the accompanying rapid changes in bottom temperature. Internal waves likely play a large role in physical variability and trophic dynamics of deep reef environments (e.g., depths > 30 m).

Surface waves breaking on the reef crests are a significant driver of water motion in the back reef and lagoon. We have observed surface waves from bottom-mounted pressure sensors and directional-wave current meters on the southwest, southeast, and north fore reefs of Moorea since 2005. These observations were coupled to back reef velocity measurements during a series of focused studies. Typical significant wave heights are 1–2 m with periods of 5–12 s, but significant wave heights up to 5–8 m with peak periods exceeding 20 s have been measured often, associated with storms and large, remotely forced swells (Hench et al., 2008). Wave exposure is modulated seasonally and varies among sides of the island. The southwest and southeast shores, which are open to swell generated in the Southern Ocean, receive the largest wave heights and longest periods, with peak wave energy occurring from May to September. The north shore generally has smaller wave heights and shorter periods, with peaks from December to February, corresponding to swell generated in the Northern Hemisphere winter. Wave shoaling and breaking at reef crests forces water into and across the reef flats and lagoons (Monismith et al., 2013). These wave-driven flows are subject to significant drag by the complex bottom topography in the back reef (Rosman and Hench, 2011). Transport out of the reef passes balances water entering the back reef and lagoon. During large wave events, the momentum of jets exiting the reef passes may transport surface waters and materials from the lagoon to the fore reef and offshore. The prevailing southeasterly trade winds and the diurnal sea breeze also influence surface flows near Moorea and in the lagoons. Local storms, including strong, episodic northward winds locally termed *mara'amu*, can force surface waters out of the bays and lagoons, with compensatory inflow of subsurface water into the deep channels of the reef passes (Wolanski and Delesalle, 1995).

James J. Leichter *(jleichter@ucsd.edu) is Associate Professor, Scripps Institution of Oceanography, La Jolla, CA, USA.* **Alice L. Alldredge** *is Research Professor, Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA, USA.* **Giacomo Bernardi** *is Professor, Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA, USA.* **Andrew J. Brooks** *is Deputy Program Director, Moorea Coral Reef Long Term Ecological Research, Marine Science Institute, University of California, Santa Barbara, CA USA.* **Craig A. Carlson** *is Professor, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, USA.* **Robert C. Carpenter** *is Professor, Department of Biology, California State University, Northridge, CA, USA.* **Peter J. Edmunds** *is Professor, Department of Biology, California State University, Northridge, CA, USA.* **Melanie R. Fewings** *is Assistant Professor of Marine Sciences, University of Connecticut, Groton, CT, USA.* **Katharine M. Hanson** *is Postdoctoral Fellow, American Museum of Natural History Center for Biodiversity and Conservation, New York, NY, USA.* **James L. Hench** *is Assistant Professor, Nicholas School of the Environment, Duke University, Beaufort, NC, USA.* **Sally J. Holbrook** *is Professor, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, USA.* **Craig E. Nelson** *is Assistant Researcher, Department of Oceanography, University of Hawai'i at Mānoa, HI, USA.* **Russell J. Schmitt** *is Professor, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA USA.* **Robert J. Toonen** *is Associate Researcher, Hawai'i Institute of Marine Biology, University of Hawai'i, Kāne'ohe, HI, USA.* **Libe Washburn** *is Professor, Department of Geography, University of California, Santa Barbara, CA, USA.* **Alex S.J. Wyatt** *is Research Fellow, Department of Chemical Oceanography, Atmosphere and Ocean Research Institute, University of Tokyo, Tokyo, Japan.*

PHYSICAL AND BIOLOGICAL EVIDENCE FOR RETENTION

Net Alongshore Flow Around Moorea

Many processes cause reversals of alongshore currents on the fore reef on time scales from hours to a few days, including tides, wind, surface waves, and internal waves. These processes are revealed by narrow peaks in the spectra of alongshore current velocity at frequencies near one and two cycles per day and at the inertial frequency of 0.6 cycles per day. Current fluctuations on time scales of one hour and faster dominate the raw flow records (Figure 2A), but when these records are low-pass filtered with cut-off periods corresponding to 1.5 days, one week, two weeks, and three weeks, a pattern of net, residual flow becomes progressively more evident (Figure 2B,C,D, and E, respectively). We find a surprising result of a net, low-frequency alongshore flow to the west on the north shore (LTER Site 1), to the southeast on the southwest shore (LTER Site 5), and to the northeast on the southeast shore (LTER Site 4; Figure 3). The long-term mean velocity of the residual alongshore flow averaged on the three shores is ~ 0.03 m s^{-1}, suggesting there may be a counterclockwise (CCW) residual flow around the island. The residual alongshore flow is strongest near the surface and appears to decrease and to turn offshore with depth on the southwest and southeast sides of the island (gray to white vectors in Figure 3). These changes in direction near the bottom appear to be consistent with the interactions of the Coriolis effect on bottom friction within the benthic boundary layer, producing a bottom Ekman layer with flow vectors rotated to the right (in the Southern Hemisphere) with increasing proximity to the bottom (Ekman, 1905).

Additional analyses and modeling of the timing of flow reversals on each shore and further observations near the three "corners" of the island where currents would have to turn sharply to maintain continuity are required to determine whether there actually is a net continuous CCW flow around the island. Assuming the continuity and direction change at the island corners, it is possible that passive particles carried by the flow would take ~ 30 days to circle Moorea. However, passive particles would also transit over half the length of a side of the island (~ 20 km) in a six-hour half tidal cycle at the peak velocity of the tidally varying currents (0.5 m s^{-1}). At present, it is unresolved whether a residual CCW flow would, in fact, lead to particles effectively circling the island.

Several mechanisms might cause a CCW flow around Moorea. Surface waves impinging on the fore reef at oblique angles might drive alongshore, residual currents (Thornton and Guza, 1986); however, measured vectors of wave energy flux around the island are not consistently in the direction required to support a CCW flow. Tidal rectification, in which sloping topography interacts with tidal currents and the Coriolis effect, could produce alongshore flows as observed on continental features such as Georges Bank (Loder, 1980; Chen et al., 1995). However, tidal amplitudes at Moorea are relatively small, and it is not clear whether tidal currents alone

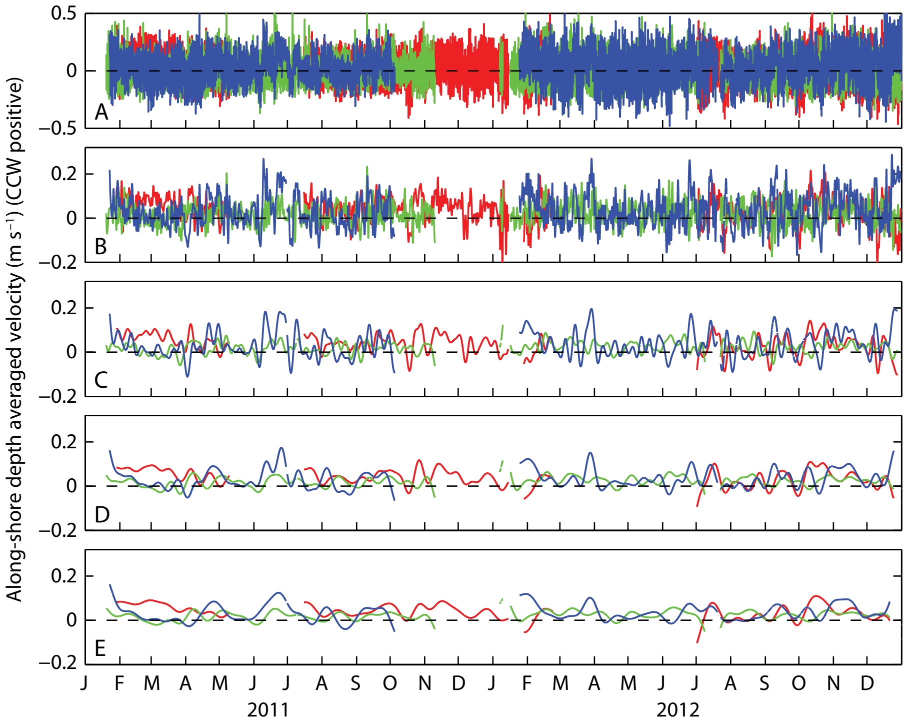


Figure 2. Time series of vertically averaged alongshore currents at three oceanographic moorings (LTER 1 = red, LTER 4 = green, LTER 5 = blue; locations shown in Figure 1). Positive alongshore velocities refer to counterclockwise current directions. Currents are low-pass filtered at (A) 1-hour, (B) 1.5 days, (C) 1 week, (D) 2 weeks, and (E) 3 weeks.

are sufficiently strong for tidal rectification to be important. The dominance of westward flow of the SEC, combined with eddies in the wake of Tahiti or Moorea itself, could also influence a CCW flow around the island. However, available data are insufficient to test this possibility. An offshore gradient in water buoyancy near the island could also drive a net geostrophic flow CCW around the island. Solar heating and freshwater runoff increase buoyancy of water in the lagoons. We hypothesize that as this buoyant water exits reef passes, the Coriolis effect turns it to the left, and, over a period of days, the flows out of multiple reef passes distributed around the island merge and come into geostrophic balance as a coastally trapped CCW flow. Hydrographic profiling to date has failed to show a consistent cross-shore gradient in surface buoyancy seaward of the reef. However, this may be because local wind events are sufficiently strong and intermittent to obscure measurement of any weaker mean cross-shelf density gradients that may support a net CCW flow. We suspect that the flow around Moorea may be an example of a generalized tendency for weak low-frequency flows to circulate anticyclonically around islands that act as sufficiently large sources of buoyant water formed from solar heating and freshwater runoff.

Distinct Chemical and Microbial Signatures Over the Reef

Average water column properties measured twice per year on the north shore of Moorea since 2005 suggest that inshore and fore reef habitats are persistently different from oceanic waters 5 km offshore. Oceanic waters tend to be clearer, with lower concentrations of nutrients, particulate organic carbon and nitrogen (POC and PON), chlorophyll *a*, and water column primary production as well as higher concentrations of dissolved organic carbon (DOC) relative to waters over the reef. For example, average summer and winter concentrations of nitrate (in μmol L^{-1}) range from 0.30–0.34 offshore, versus 0.36–0.38 on the fore reef and 0.41–0.58 in the lagoon. Average concentrations of POC (also in μmol L^{-1}) are 2.1–2.4 offshore, 2.9–3.5 on the fore reef, and 2.9–3.1 in the lagoon (Alldredge and Carlson, 2011). We find that the strongest horizontal gradients in nitrate and DOC concentrations occur within the first 100 m inshore of the reef crest (Figure 4). Rapid rates of biological activity and/or mechanisms increasing local water retention must be present near the reef crest to sustain these patterns. Drifters released on the north shore of Moorea typically take one to several hours to cross the back reef, and a simple fluid mass balance estimate suggests that the back reef flushes on the order of hours to tens of hours depending on wave conditions (Hench et al., 2008). Water samples taken alongside drifters on the back reef show marked decreases in DOC within the first 100 m after water crosses the reef crest (Figure 4). Net removal of DOC on time scales of tens of minutes to hours over the back reef is surprising, given that oceanic DOC in the surface waters of subtropical gyres is largely comprised

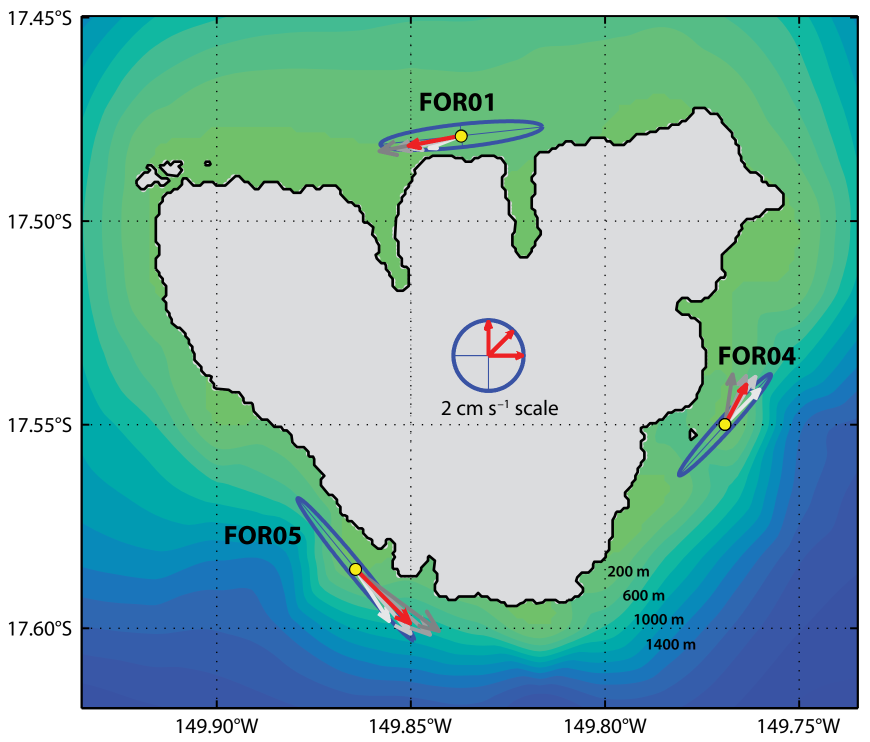
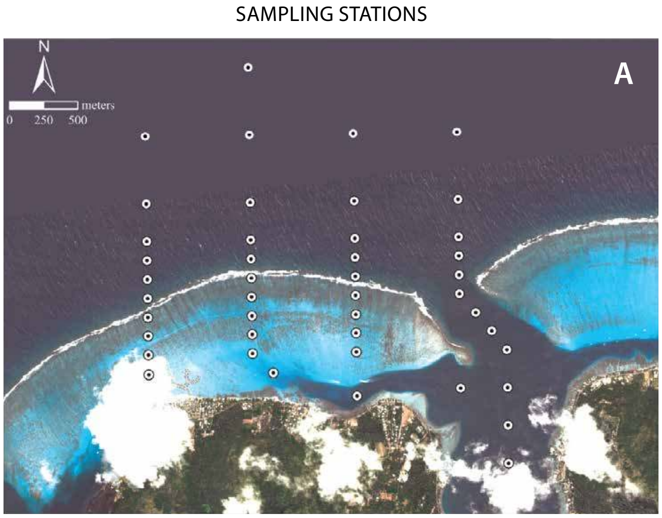


Figure 3. Long-term averages of currents from three oceanographic moorings placed at 15 m depth on three sides of Moorea. Ellipses represent the variance in the major (alongshore) and minor (cross-shore) velocity records with magnitude indicated by the scale at the center of the plot. Red arrows indicate water column integrated mean flow, and arrows grading from dark gray to white indicate depth-specific means at depths of 3, 6, 10, and 13 m, respectively.



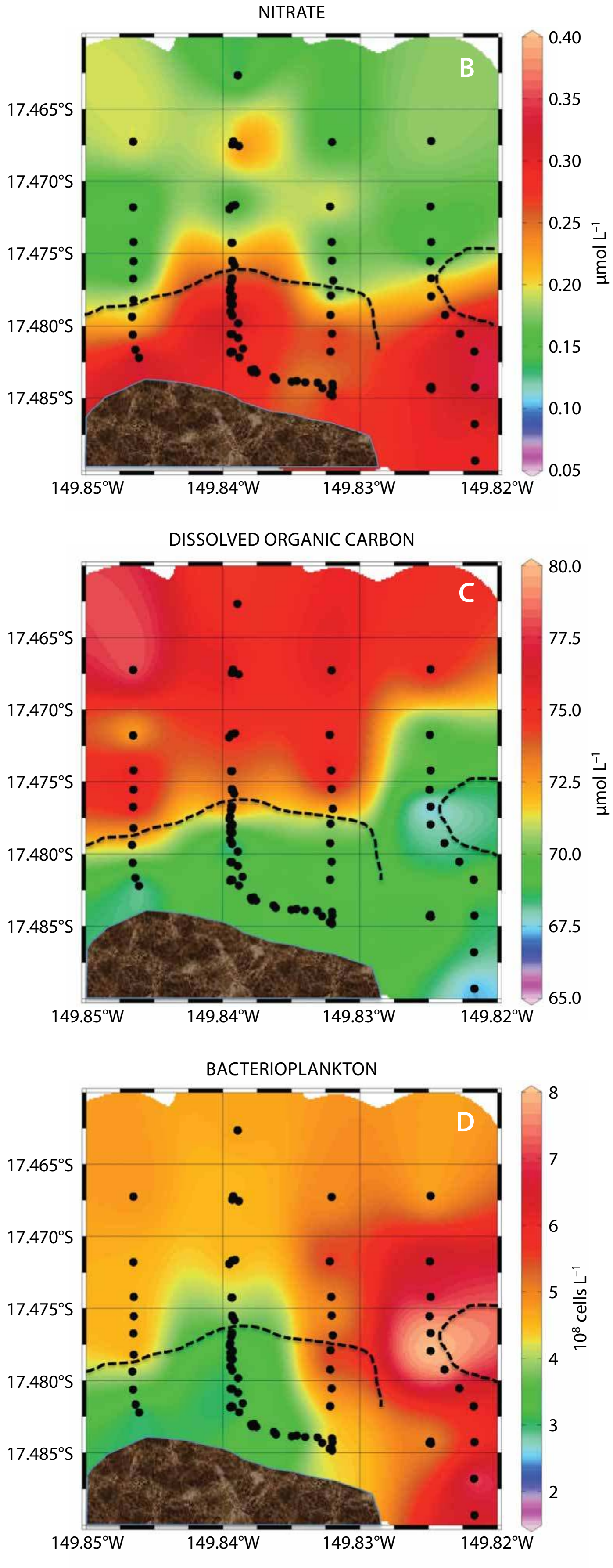


Figure 4. Sampling stations (white dots in A) and kriging interpolated false-color contour plots showing elevated concentrations of nitrate (B) and depleted concentrations of both dissolved organic carbon (C), and bacterioplankton cells (D) in the surface waters of the north shore back reef lagoon relative to offshore surface waters. Surveys were conducted in September 2010 and measurement methods are described in detail in Nelson et al. (2011). Contour plots were constructed in Ocean Data View (Schlitzer, 2004) using the weighted averaging algorithm VG gridding, with x and y length scale set at 150 per nautical mile. The black line in panels B–D denotes the approximate position of the reef crest as seen in panel A.

of semilabile material that is remineralized by bacterioplankton on time scales of days to months (Carlson, 2002). Simultaneous consumption and release of reef-derived, and perhaps more labile, DOC by reef microbes and inorganic nutrients released by reef organisms may produce a priming effect in which remineralization of labile organic substrates enhances the removal of more recalcitrant compounds (Carlson et al., 2004; Bianchi, 2011). Removal of DOC by benthic microbes and consumers such as sponges inside reef cavities (Yahel et al., 2003; de Goeij and van Duyl, 2007) may also be important and would be enhanced by the rapid fluxes and thin boundary layers characteristic of the back reef.

Reef topography also affects water retention. Coral colonies occupy a relatively large proportion of the water column on the reef flat, and water can become trapped and recirculated in their wakes (Hench and Rosman, 2013), leading to increased spatial and temporal variability of residence times. Investigations of possible dilution from low DOC groundwater and DOC precipitation on air bubbles generated by breaking waves yield no evidence that these mechanisms account for the depletion gradients in Moorea (Nelson et al., 2011). The composition of microbes in the various reef habitats provides further evidence of extensive water retention in this system. The bacterioplankton communities appear to be distinct between the offshore, bay, back reef, and fore reef habitats, with back reef habitats enriched in members of the broad clades Gamma-, Delta-, and Beta-Proteobacteria, Bacteriodetes, Actinobacteria, and Firmicutes (Figure 5; Nelson et al., 2011, 2013). These patterns suggest there may be release of reef-associated bacteria taxa into the water column over the reef, and imply that water residence times in the back reef and lagoon habitats are sufficient for distinct microbial communities to develop. Runoff might also enrich the bay and fringing reef habitats in distinct microbial taxa.

Zooplankton Composition, Distribution, and Consumption

The abundance, behavior, and vertical distribution of zooplankton in Moorea all suggest relatively long residence times within the back reef and lagoon. The zooplankton community is dominated by reef-associated mollusc and crustacean larvae, mysids, amphipods, ostracods, isopods, polychaetes, and many copepods only rarely found in open ocean waters (Alldredge and King, 2009). In the 2–3 m deep back reef, zooplankton are five to eight times more abundant in the uppermost 50 cm than nearer the bottom, and almost all zooplankton taxa swim up near the surface both during the day and on moonlit nights, probably to avoid being consumed by suspension-feeding corals and visually oriented fish predators sheltering near the bottom. By contrast, oceanic zooplankton avoid visual predators by migrating into darker, deep waters during the day and swimming up to feed in phytoplankton-rich surface waters at night (Enright and Honegger, 1977). Alldredge and King (2009) hypothesized that the distinct behavioral pattern observed among reef-associated zooplankton would likely develop and be maintained only if populations were largely resident near reefs for multiple generations.

Several mechanisms may explain retention of zooplankton on the back reef despite flow rates that are often tens of centimeters per second or greater. Larger taxa may be able to swim sufficiently rapidly to counter transport that might export them from the reef. Slower or more heterogeneous flow patterns near the bottom and behind coral heads may provide refuges from the peak water velocities. Higher zooplankton

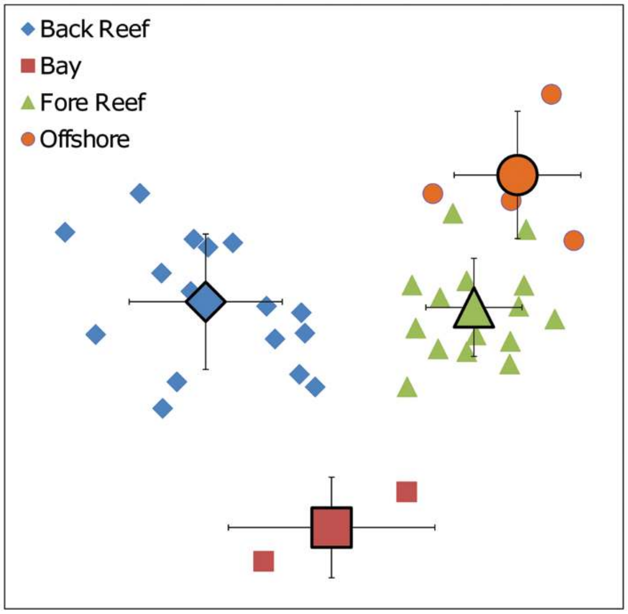


Figure 5. Bacterial communities sampled at Moorea are differentiated among different nearshore and offshore habitats. The differentiation of community signatures from adjacent habitats suggests sufficient residence time of water in the reef to allow shifts in abundances of bacterial taxa. Samples are ordinated according to similarity in proportional bacterial taxon abundances and color/shape-coded according to where in the reef they were collected. Larger symbols represent the mean ordinal position of samples from each environment with whiskers showing one standard deviation of the mean. The two axes are derived using nonmetric multidimensional scaling (stress = 0.09) from a higher order Bray-Curtis community similarity matrix of 40 DNA samples in 150-dimensional bacterial taxon relative abundance space (150 phylotypes measured by terminal restriction fragment length polymorphism analysis of the 16S ribosomal RNA gene). The nonmetric multidimensional scaling ordinations are unitless projections with no meaningful axis units explicit or implied.

abundances in the deeper channels of the lagoon, bays, and fringing reef suggest accumulation of zooplankton where flows slow down. Water from the bays and deep channels also exits the passes and is likely to be transported in the alongshore flows on the fore reef. Some of this surface water might be retained near the island in a net CCW flow and could eventually be forced back over the reef crests by incident waves (Monismith et al., 2013), potentially carrying zooplankton onto the back reefs again.

Consumption of zooplankton by corals and fish may be an important mechanism by which organic material is retained within the reef system. We have observed that oceanic zooplankton dominate the diet of damselfish in fore reef habitats, while reef-associated taxa comprise 60–90% of the diets of fish inhabiting the shallow back reef and lagoon habitats (Hanson, 2011). The behavior of both the planktivores and their prey influence the consumption of both oceanic and reef-associated zooplankton. For example, the planktivorous damselfish *Dascyllus flavicaudus* selects copepods that are brightly pigmented, have distinct swimming motions, or carry large, pigmented egg sacs (Hanson, 2011), and predator distributions and settling cues determine the vertical positioning of reef-associated zooplankton and larvae (Kingsford et al., 2002; Alldredge and King, 2009). Many planktivorous damselfishes shelter among branches of corals where they excrete nitrogenous wastes (primarily ammonium) that enhance the growth rate of their host corals (Holbrook et al., 2008, 2011), thus shunting to the reef nutrients derived from consumption of zooplankton.

> “MOOREA IS AN IDEAL SYSTEM TO FURTHER OUR UNDERSTANDING OF THE ROLES TRANSPORT AND RETENTION PLAY IN SHAPING CORAL REEF ECOSYSTEMS.”

Coral Recruitment

Patterns of recruitment of the benthic fauna on Moorea integrate the effects of water transport and retention across time and space. The weakly swimming coral larvae are likely transported by flow and settle in locations determined by the complex interactions among water motion, characteristics of benthic surfaces, and selection behavior of the larvae themselves. The duration of the swimming coral larval stage in the field is poorly known, but is likely to be on the scale of days to tens of days. It is difficult to detect these delicate larvae in plankton tows, but we have been assaying their availability in Moorea since 2005 by measuring coral settlement rates on 15 × 15 cm tiles secured to the reef. In approximately six-month deployments, mean recruitment in the back reef typically varies between zero and six corals per tile, but with as many as 22 recruits on a few tiles (Edmunds et al., 2010).

Despite high spatial and temporal variation in coral recruitment, our observations point to the influences of transport and retention on coral recruitment in the back reef. During a study conducted between 2005 and 2007, adult corals in the family Acroporidae were rare on the back reef but relatively abundant on the fore reef. Thus, recruitment of acroporids in the back reef was likely dependent on larvae produced by adult colonies on the fore reef. In the austral fall and winter when acroporids are reproducing, coral recruitment is elevated on the southwestern shore where wave exposure and transport into the back reef is greatest (Figure 6). In this period, wave exposure along the north shore is more limited, and reduced cross-reef transport there probably deprives the back reef of acroporid larvae. Acroporids have finished reproduction by the time wave exposure increases on the north shore. In contrast, corals in the family Poritidae recruit in relatively large numbers throughout the year, and during 2005–2007 adult *Porites* were common on both the outer reef and back reef habitats. We suspect poritid larvae settling in the back reef originate from adults in both the fore reef and back reef environments, and they are transported repeatedly into the back reef. Patterns of coral reproduction and recruitment, and the ways in which these processes are affected by transport and retention, will likely be particularly important in coming years as the outer reef of Moorea recovers from the recent major disturbances created by the outbreak of the Crown-of-Thorns starfish *Acanthaster plancii* beginning in about 2006 and Cyclone Oli in 2010 (Adam et al., 2011; Kayal et al., 2012).

Larval Fish Recruitment and Population Connectivity

Transport and retention also play critical roles in the recruitment and population connectivity of reef fishes. A fundamental obstacle to understanding reef fish population biology is the difficulty of tracking larvae and identifying dispersal pathways. For many decades, reef fish larvae were thought to be transported long distances by currents to settle on reefs far removed from parent adults. However, studies in the late 1990s examining the chemistry of fish otoliths (ear bones) demonstrated that larvae of coral reef fish were sometimes retained and recruited back to their natal reefs (Jones et al., 1999; Swearer et al., 1999). Subsequent studies, using anemonefish as model systems, assigned recruits to parents based on genetic paternity analyses, and uncovered unexpectedly high levels of larval retention within island populations (e.g., Planes et al., 2009; Berumen et al., 2012).

In French Polynesia, we have found high genetic diversity in populations of the three-spot damselfish, *Dascyllus trimaculatus* (Leray et al., 2010). Yet, despite this high diversity, at least 14% of juvenile damselfish recruiting to an experimental anemone array on the northwestern shore of Moorea were very close relatives, related on the order of half siblings or greater (Bernardi et al., 2012). Members of at least one pair that recruited on the same night were full siblings who likely completed their entire pelagic larval phase together. This study added to growing evidence that larval fishes and invertebrates are often not well mixed, and at least some species can remain together from birth to settlement despite relatively long planktonic durations (e.g., Selkoe et al., 2006; Buston et al., 2007). In another study, we sampled the genetic signatures of 378 adult and 101 juvenile anemonefish, *Amphiprion chrysopterus,* on Moorea, and identified 27% of the juveniles as offspring from the island's adults (Beldade et al., 2012), indicating significant larval retention. Knowing the date of capture and the age of the juveniles, we can back-calculate the hatching date for each juvenile and, potentially, test hypotheses of larval trajectories, self-recruitment, water movement, and retention in relation to currents around the island.

CONCLUSIONS

Moorea is an ideal system to further our understanding of the roles transport and retention play in shaping coral reef ecosystems. Many physical and biological patterns around Moorea reflect the dynamic balance between transport and retention processes. Alongshore and cross-reef transport affect nutrient fluxes, recruitment of coral larvae, diets of planktivorous fish, and fish population connectivity between habitats. Biological and chemical patterns, including the distinct chemical signatures of the water over the various reef habitats, patterns of microbial and zooplankton composition, and observations of reef-specific zooplankton and planktivore behaviors,

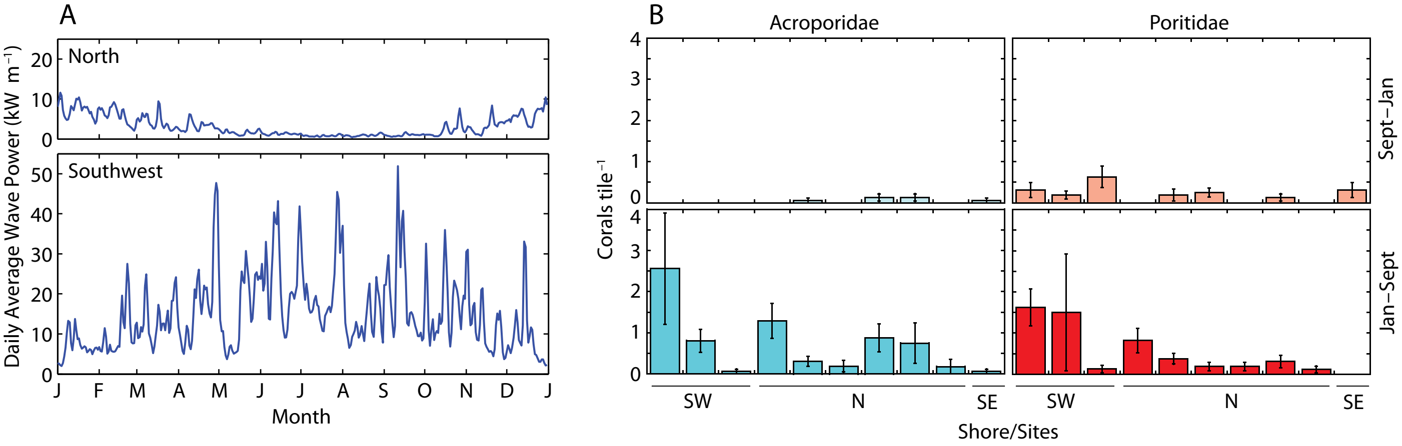


Figure 6. Multiyear patterns of wave exposure and coral recruitment at multiple sites around Moorea. (A) Wave power is averaged across years 2005–2008. Power, with units of kW m^{-1}, is calculated using deepwater approximations and is the product of wave period, significant wave height squared, and a constant (see Edmunds et al., 2010). (B) Panels show coral recruitment to settlement tiles placed in the back reef for two periods between 2005 and 2006. Tiles were fixed to the reef at ~ 2 m depth and were deployed for five to seven months for sampling September to January and January to September for 10 sites along the three shores of Moorea. This analysis was carried out for two years with only one year displayed here for simplicity. Bars show the mean and standard error for the two most common families of corals, Acroporidae (black) and Poritidae (white), settling on the tiles (n = 2 samplings).

suggest high degrees of physical retention of water and biological retention of water-borne materials within the reef system. The potential for a net, low-frequency circum-island current suggests a pathway by which larvae and other biological particles might stay in relatively close proximity to the island over periods of days to weeks. As described for islands in the Caribbean (Cowen and Castro, 1994; Cowen, 2002; Paris and Cowen, 2004), attenuation of alongshore current velocities with depth suggests that plankton with active swimming behavior, such as fish and coral larvae, may increase retention near the island by vertical migration to depth. The possibility that Tahiti's island wake affects Moorea suggests that the metapopulation dynamics of fish, corals, and other invertebrates on both islands, as well as on the nearby atoll Tetiaroa and the island of Maiao, may all be linked by pathways of dispersal and population connectivity.

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