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Transport Between Palau and the Eastern Coral Triangle: Larval Connectivity or Near Misses

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Key Points:
- Drifters released off Palau were transported around the Philippine Sea by the Mindanao Eddy, the Mindanao Coastal Current, and by the NECC
- None of the drifters made it into nearshore waters as would be required for connectivity of reef-sourced larvae
- Estimates of connectivity made using large-scale models are upper bounds because they do not represent weak cross-shore transport

Supporting Information:
- Supporting Information S1
- Movie S1

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Abstract Physical connectivity by transport of larvae between different habitats plays a fundamental role in marine population dynamics and is often assessed using circulation models assuming that computed large-scale connectivity describes the actual connectivity. This paper presents observations of drifters released into the Philippine Sea offshore of the western lagoon of Palau that were tracked as were first carried by the Mindanao Eddy toward Mindanao and other parts of the Celebes and Sulu Seas, where they were removed from the water. While following expected transport pathways for this region, our drifters remained at least several kilometers offshore of the various islands they passed by, suggesting that larvae moving similarly would have been too far offshore to recruit to nearshore reefs. Thus, estimates of connectivity made using large-scale models must be taken as upper bounds to connectivity across ocean basins.

Plain Language Summary A major consideration in marine conservation is the connectivity between different habitats or regions of the ocean, that is, the degree to which populations in those places are linked to each through the movement of eggs, larvae, eggs, or adults between them. One area of particular interest is the Western Pacific and its connections with the Coral Triangle. In this study, we deployed a set of satellite-tracked surface drifters offshore of the west side of Palau that moved in the local ocean circulation toward and then past Mindanao, in some cases completing multiple circuits around the Philippine Sea. These drifter tracks demonstrate an important aspect of connectivity in the ocean: In the absence of strong and directed swimming, local flow processes on ocean shelves that can act to transport materials toward shore may control the real extent of connectivity across ocean basins. Thus, the degree of connectivity inferred from large-scale flows (either modeled or observed remotely) is an upper bound on the actual degree of connectivity. Importantly, these results demonstrate that marine conservation efforts for coral reefs based on ocean-basin scale connectivity need to include consideration of flow behavior at ocean boundaries where reefs are located.

1. Introduction

A popular saying states that "Close only counts for horseshoes and hand grenades." This issue is significant when considering the physical connectivity of larval reef organisms, for example, coral planulae or the larvae of reef fishes (Cowen et al., 2006; Gawarkiewicz et al., 2007; Kool et al., 2011). Depending on the forcing (tides and or surface waves), larvae from a given reef may be retained on that reef. For example, on the north shore of Moorea a substantial fraction of water (and presumably the biota contained therein) that exits the reef via the pass is entrained by the wave-driven shoreward flow over the reef crest (Herdman et al., 2017). Alternatively, planktonic organisms may be carried away from the reef, for by the jet typically found at reef passes, and thus enter the circulation offshore where they can be transported to a reef some distance away and presumably settle (Herdman et al., 2017). Given possible periods of larval competence of ~100 days (cf. Richmond, 1987), long-distance connections between reefs, at least in energetic current systems like the North Equatorial Counter Current is possible, for example, 100 days in a current of 0.2 m/s would give a distance of 1,700 km.

There is a problem however in that if a larva comes close to the reef in the sense of the regional circulation, that is, tens of kilometers, it might never reach the new reef since most mesoscale flows tend to be parallel to the shore (Pineda et al., 2007). There are physical mechanisms for carrying larvae from offshore to the nearshore, notably Stokes drift due to surface waves (Monismith & Fong, 2004), internal bores (Pineda, 1991), upwelling relaxation (Roughgarden et al., 1988), and buoyancy-driven cross-shore flows (Molina et al., 2014). Given that many of these finer-scale processes may not be resolved in large-scale circulation models

Table 1
Summary of Drifter Tracks

Drifter	Start time[a]	Closest approach to Mindanao (km)	Notes
78	12-02 16:20	9	Removed from water near Brunei[b]
79	12-02 18:30	14	Removed from water off Mindanao
80	12-02 21:01	29	Removed from water off Mindanao
81	12-09 00:30	na	Stopped[c] in middle of Philippine Sea
82	11-29 21:00	29	Removed from water off Mindanao
83	11-29 21:00	32	Removed from water off Mindanao
84	12-06 22:40	>100	Removed from water off Mindanao
85	11-27 01:03	87	Passed by Mindanao twice. Removed from water off Sulawesi
86	12-06 07:00	>100	Stayed near Palau
87	12-02 17:00	27	Removed from water off Mindanao
88	12-02 09:00	>100	Stayed near Palau
89	12-12 13:20	97/2.3	First pass: traveled back to Palau. Second pass: removed from water off Negros Island
91	12-01 14:01	35	Removed from water off Mindanao
92	12-02 18:40	>100	Stopped in water northeast of Mindanao
93	11-28 20:01	21	Removed from water off Mindanao
94	12-09 21:40	>100	Stopped in middle of Philippine Sea
95	11-28 14:00	42	Removed from water off Mindanao
96	11-28 18:00	1.7	Removed from water in Celebes Sea
97	11-28 13:01	21	Removed from water off Mindanao

[a]First fix outside Palau lagoon. [b]Removed from the water = still transmitting but drifter is not in water. [c]Stopped = stopped transmitting.

like HYbrid Coordinate Ocean Model (HYCOM; Chassignet et al., 2007) used to assess connectivity (e.g., Kool et al., 2011), these models may exclude important determinants to connectivity. That is, if there is no cross-shore transport when a larva passes by a section of coast, it cannot recruit and thus may remain in deeper offshore waters until it is no longer able to settle. Equivalently, places where cross-shore transport is active may end up being key locations of long-range connectivity.

We note that the role of physical connectivity may be very different for larval fish than for coral planulae, in that the former can swim at substantial speeds for substantial times, for example, tens of kilometers over tens of hours (Leis & McCormick, 2002), whereas the latter have very limited swimming abilities, ones better suited to substrate exploration on the reef than to active swimming in the open ocean (Hata et al., 2017). Thus, when considering large-scale connectivity, coral planulae may reasonably be approximated as passive particles. Observations of spawning events on the Great Barrier Reef suggest that coral planulae may remain near the water surface (Willis & Oliver, 2012), although open ocean measurements of coral planulae distributions are nonexistent and so they might equally well be distributed over the upper mixed layer of the ocean.

In this paper we discuss a set of tracks of surface drifters released on the western coast of Palau that illustrate this problem. Carried by the Mindanao Eddy (Lukas et al., 1996) over several months, surface drifters released on the west side of Palau were carried to Mindanao and parts of Indonesia and in two cases returned to Palau. Of these only one actually made back to a reef along its path (on Palau), the rest either passing by various islands along their path or were picked up by fisherman. Thus, while at the large-scale Palau and Mindanao appear to be connected, that connection may in reality be quite weak. Finally, because we used near-surface drifters that were completely passive, the results we present below should be considered most applicable to coral planulae, and so, that will be the focus of the rest of this paper.

2. Methods

As part of research on sediment transport from the watershed to reefs in Ngermeduu Bay, Palau, and its adjacent lagoon, we deployed 19 Pacific Gyre Microstar satellite-tracked Global Positioning System drifters (https://www.pacificgyre.com/microstar-gps-drifter.aspx) in November 2015. The drag element on these drifters is a 1.4-m^2 blind drogue centered at 1-m depth. They report their position via a satellite uplink at user-selected intervals. In our case, we varied the interrogation time to increase temporal and thus spatial resolution near coasts. Data on position and submergence were acquired at intervals ranging

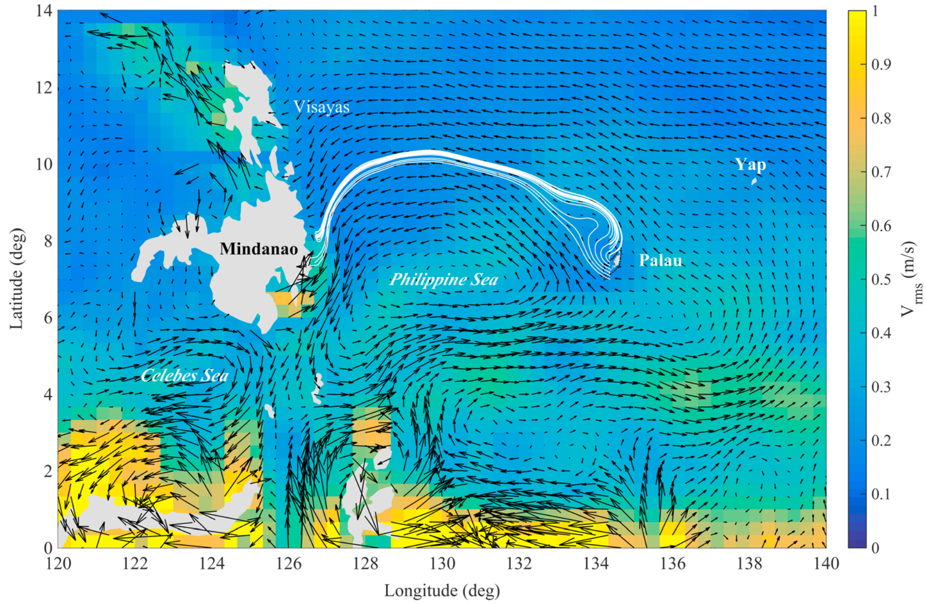

Figure 1. Ocean Surface Current Analysis Real-time flow fields 16 November 2015 to 11 August 2016. The arrows mark local average current vectors and the colors show root-mean-square (rms) speeds. The white tracks show a set of particle tracks (streamlines) starting 10 km west side of the Palau reef edge and distributed along a 100-km-long north-south line.

from 10 min to 12 hr. Position accuracy is estimated to be <10 m. Ohlmann et al. (2005) describe the performance of these drifters, showing that their velocities differ by less than 2 cm/s from Lagrangian water particle velocities, with the largest differences being attributed to the fact that the drifters do not follow large surface waves with total fidelity. Nonetheless, they are in common use in the coastal ocean community (see, e.g., Ohlmann et al., 2017). Velocities were computed in MATLAB™ by fitting cubic smoothing splines to the position data and then analytically differentiating the fitted splines. Drifter tracks were assumed to end when the drifters appeared to come out of the water, presumably the result of the drifter being "caught" by fisherman.

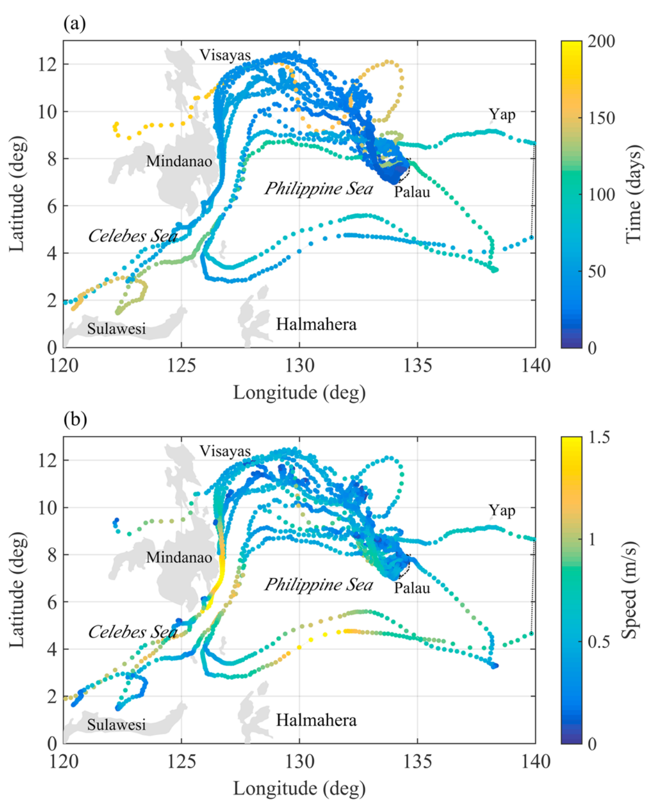

Figure 2. All drifter tracks 19 November 2015 to 14 August 2016: (a) Each drifter fix is color coded by time in days since 27 November 2015, and (b) each drifter fix is color coded by speed.

Given that the primary purpose of the drifter work was to evaluate transport patterns inside the barrier reef of western Palau, the drifters were initially deployed (19 and 20 November) within the shallow (<10 m deep) Ngermeduu Bay and then in most cases recovered and redeployed in the West Channel, the primary channel between the main western Palau lagoon, or nearby offshore of the reef crest (see Table 1).

In addition to our drifter data, we downloaded the Ocean Surface Current Analysis Real-time (OSCAR) surface current data from (https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg—accession dates: 11 to 12 October 2017). These represent global estimates of surface velocity fields at a spatial resolution of (1/3)° (Bonjean & Lagerloef, 2002). The primary purpose of using the OSCAR fields was for qualitative evaluation of the spatial structure of the velocity field in the western Pacific near the Philippines and Palau. We also downloaded daily (1/12)° resolution surface velocity fields computed by the circulation model HYCOM (GOFS ver. 3.0 https://hycom.org/dataserver/—accession date 29 January 2018) and Wavewatch 3 wave data (http://coastwatch.pfeg.noaa.gov/

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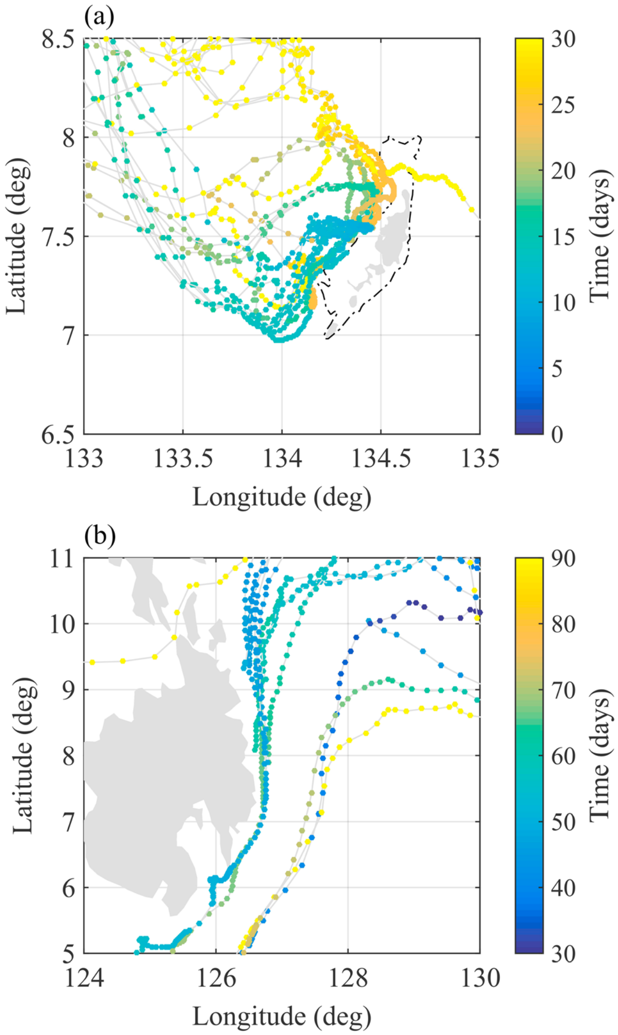

Figure 3. Details of tracks: (a) Near Palau and (b) near Mindanao. In both panels, fixes are color coded with time as in Figure 2.

erddap/griddap/NWW3_Global_Best.html—accession date 26 January 2018). Finally, drifter tracks for this region contained in the Global Drifter data set (http://www.aoml.noaa.gov/phod/dac/dacdata.php—accession date 1 October 2017), all made by surface drifters with 15-m "holey-sock" drogues, were also downloaded for comparison to those of our drifters.

3. Results

The region through which our drifters traveled has a number of significant circulation features, notably the Mindanao Current, the strong coastal current off Mindanao, the Mindanao Eddy that sits between Mindanao and Palau, and the North Equatorial Counter Current (NECC), which passes to the south of Palau (Wijffels et al., 1995). All three of these features are visible in the OSCAR-derived average surface current field for the period (dates) that the drifters were deployed (Figure 1). As seen in Figure 1, there are also regions of strong current variability, particularly near the equator; in contrast, the region to the immediate northwest of Palau involves relatively weak currents and hence weak variability. Particle trajectories, $\vec{x}(t)$ were computed from this average velocity field, $\vec{u}(\vec{x})$, for an array of points starting on the west side of Palau using the forward Euler method with a time step, Δt of 1 day, that is,

$$\vec{x}(t+\Delta t) = \vec{x}(t) + \vec{u}(\vec{x}(t))\Delta t \tag{1}$$

Since flow is assumed steady, particle trajectories are streamlines. Given that all these streamlines end in Mindanao coastal waters, and that streamlines cannot end on a sold boundary, presumably near Mindanao there is a either a shore-parallel flow not resolved by OSCAR or there is a more complex 3-D circulation involving subduction of surface waters.

The observed drifter tracks show drifter movement around the Mindanao Eddy from Palau toward Mindanao (Figure 2a; see also supporting information), generally taking ~40 days to travel from the west side of Palau to within approximately 20 km of the coast of Mindanao. The key feature of these tracks however is that nearly all of them remain more than 10 km offshore (median distance 24 km—see Table 1), although two drifters did make it to within ~2 km of the coast. However, neither of the drifters that passed close to the coast, actually made it to the coast.

The four drifters that were not removed from the water or stopped transmitting quickly transited the coast of Mindanao in the Mindanao Current at speeds of up to 1.5 m/s (Figure 2b) and passed into the Celebes Sea. Of these, two (78 and 96) were picked up and two (85 and 89) continued into the southern branch of the Mindanao Eddy and returned to the ocean near Palau ~100 days after leaving Palau. One of these (85) passed by (100 km) Yap, ultimately ending up back in the Celebes Sea, ~150 days after leaving Palau. Although both passes past the south tip of Mindanao are nearly identical, on the first pass, this drifter turned eastward into the NECC whereas on the second pass it veered westward instead. The second drifter (89) entered the northern Palau lagoon and ending up being picked up near Negros Island north of Mindanao nearly 200 days after its initial release. Thus, of the original 19 drifters, only one made it back to a reef environment.

It appears that an important aspect of what determines the timing of the arrival near Mindanao of larvae offshore of Palau are the relatively variable and complex flows near Palau itself (Figure 3a). The various drifters deployed near the West Channel exit went either north or south depending on when they were actually outside the western barrier reef edge, with the first set heading south and the second set, which exited the lagoon approximately 2 weeks after the first set heading north. Both sets headed west into the Mindanao Eddy after moving outside the wake-like region that extends roughly northwest from Palau, with the first

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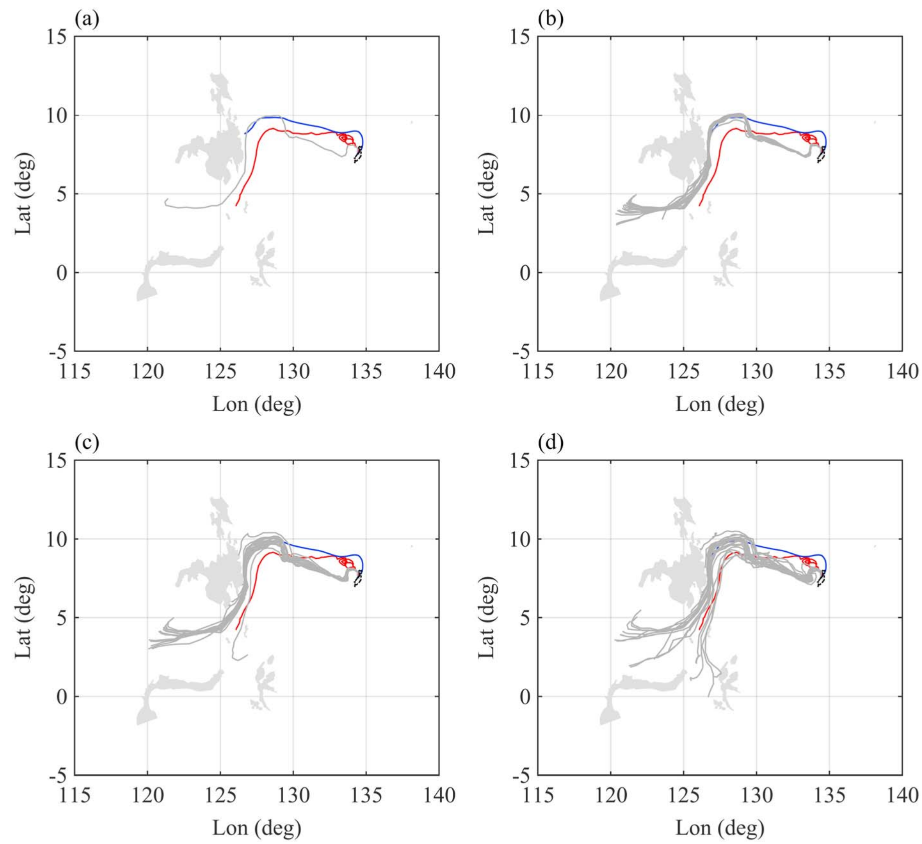

Figure 4. Effects of subgrid-scale diffusion computed using a random walk (equation (2)) and (a) $K = 0$ m^2/s^2, (b) $K = 10$ m^2/s^2, (c) $K= 30$ m^2/s^2, and (d) $K = 100$ m^2/s^2. In all cases the integrations were done for 50 days starting on 12 December 2015. In each panel gray lines represent 20 realizations, the blue line represents the trajectory computed using the Ocean Surface Current Analysis Real-time velocity fields, and the red line is the measured trajectory of drifter 89 for the same period.

set arriving at Mindanao approximately 2 weeks before the second set. The three tracks that pass farther offshore of Mindanao were created by two drifters (85 and 89), both of which did so twice, although with very different end destinations: One (85) finishes in the Celebes Sea, whereas the other (89) ends its journey in the Sulu Sea 6 months after it was released.

4. Discussion and Conclusions

The tracks of the 19 drifters deployed just outside the western lagoon of Palau suggest connectivity between the reefs of Palau and those of the southern Philippines. The time required to transit the Philippine Sea riding the currents of the Mindanao Eddy ranged from 20 to 50 days, well within the potential competency period of coral planulae (larvae), which might be as large as 100 days (Richmond, 1987). Likewise, the two that drifters returned to Palau or nearby did so ~50 days after leaving Indonesian or Philippine waters, suggesting also that coral planulae from the heart of the Coral Triangle could also viably make it to Palauan reefs. Our drifter tracks are quite similar to those shown in Lukas et al. (1991), data that are included in the Global Drifter data set. Indeed examination of all drifter tracks that pass between Palau and Mindanao contained therein show behavior remarkably like that which we see in our more limited data set (supporting information Figures S2–S4).

However, the key aspect of the present set of drifter tracks is that on their passage from Palau to Mindanao, none of the drifters came very close to Mindanao's reefs (Figure 3b). No doubt this reflects the dynamical and kinematic constraints on large-scale flows like the Mindanao Eddy and coastal current that in general they must be parallel to topography (Pedlosky, 1996) and thus, in general parallel to coastlines. Thus, what is essential for physical connectivity of organisms that have limited swimming ability, for example, coral planulae, is smaller-scale, ageostrophic flows like the buoyancy-driven flows documented in Molina et al. (2014), wave- and wind-driven flows like those described by Rosman et al. (2007) and Lentz et al. (2008), or internal waves (Pineda, 1991). As seen in the famous rubber ducky "experiment" (Ebbesmeyer & Scigliano, 2009), objects floating on the surface do make it to shore, in this case, presumably by Stokes drift transport. Thus, we conclude that to properly model and understand larval connectivity at ocean basin scale (Cowen et al., 2006; Kool et al., 2011), account must also be made of smaller-scale flows operating on inner shelves.

The cross-shelf velocities required to take particles from offshore to the nearshore are not large. For example, drifter 78 takes 5 days to transit Mindanao while remaining ~20 km offshore. A persistent difference in the shoreward velocity of ~5 cm/s between near-surface particles and the drifters would suffice to move these particles off the drifter track and onto nearshore reefs. Using the standard expression for Stokes drift for deep water waves (see, e.g., Dean & Dalrymple, 1991), 5 cm/s would require a 4-m-high 10-s-period wave, that is, rather energetic waves. The Wavewatch 3 model results for the period 1 January 2016 to 3 January 2016 show a median significant height of 2 m. Other possible mechanisms for cross-shore transport might be instabilities of the Mindanao Current, although presumably the drifters would follow any such motions. Buoyancy-driven flows associated with surface heat fluxes over variable topography can drive flows of ~3 cm/s (Monismith et al., 2006) but generally reverse directions twice daily as the driving surface heat flux changes sign and so may not be effective at transport over scales of tens of kilometers that might take several days to accomplish.

Our drifter data set also shows that in the Philippine Sea, Lagrangian trajectories computed from OSCAR and HYCOM may have limited accuracy. For OSCAR and HYCOM fields these trajectories were computed by integration using interpolation of the velocity field with daily time step. An example of these tracks, computed for drifter 89, is given in Figure 4a. The integrations start 12 December 2016 and extend 50 days for the OSCAR data (at which time the drifter is off the OSCAR grid) and 50 days for the HYCOM data. As seen in Figure 4a, transport by the Mindanao Eddy is reflected in both computed tracks as well as the actual drifter track. However, whereas the actual drifter moved east in the NECC and then returned near Palau (ultimately), the HYCOM track extends into the Celebes Sea. However, like the drifter, the HYCOM track also goes parallel to the coast, meaning that from a perspective of assessing connectivity of reef organisms, some form of nearshore model like ROMS (see, e.g., Rogers et al., 2017) would be required to represent possible cross-shore flows.

In some models (e.g., Cowen et al., 2006; Marinone et al., 2008), the effects of eddies and (presumably) other physical (and biological) transport mechanisms operating at scales smaller than the grid are represented by Fickian diffusion modeled using a random walk (e.g., Colucci et al., 1998; Dimou & Adams, 1993) to supplement the deterministic velocity field. That is, one computes the trajectory as (again using forward Euler)

$$x_i(t+\Delta t) = x_i(t) + u_i\left(\overrightarrow{x}(t), t\right)\Delta t + \sqrt{2K\Delta t}Z \quad (2)$$

where x_i and u_i are ith components of the position and velocity vectors, K is the assumed to be isotropic diffusion coefficient, Δt is the time increment, and Z is a random variable with unit variance and zero mean. In the present case, the HYCOM data are supplied on an approximately 10 km × 10 km grid ([1/12]°). Poje et al. (2014) present data showing that at this scale, 10 m^2/s $< K <$ 30 m^2/s, depending on how one translates between spatial scale of spread of the group of drifters, 3σ, and the HYCOM grid scale, Δ; that is, if $3\sigma \equiv \Delta$, then $K \approx$ 10 m^2/s, whereas if $\sigma \equiv \Delta$, $K \approx$ 30 m^2/s. In Figures 4b–4d, we have plotted 20 realizations of integrations of equation (2) using K = 10, 30, and 100 m^2/s for an integration period of 50 days. For K = 10 m^2/s, the trajectories with and without diffusion are quite similar and do not show any drifters making it to the coast. In contrast, with K = 100 m^2/s, 20% of the drifters reach the shore. Given that Nencioli et al. (2013) found a median value of $K \approx$ 2 m^2/s in their study of submesoscale dispersion, it appears that $K \approx$ 10 m^2/s is likely to be a more appropriate value of K to use with the HYCOM velocity fields than is $K \approx$ 100 m^2/s. Indeed, per Poje et al., $K \approx$ 100 m^2/s is appropriate for motions of scale ~100 km, that is, in the present case likely to be associated with some of the larger-scale features of the Mindanao current. Thus, computing trajectories from HYCOM with physically relevant diffusion is not likely to produce substantially more physical connectivity than one would find in the absence of diffusion, at least for times on the order of a month or two. Moreover, as discussed by (e.g.) Figueiredo et al. (2014), mortality can play a major role in overall connectivity.

Nonetheless, there is some genetic evidence of connectivity between the Coral Triangle and Palau (Davies et al., 2015), presumably via the NECC, something that is also suggested by the fact that one drifter (85) made it from the Celebes Sea into the northern reef lagoon of Palau. Reflecting this eastward transport, the graph-based representation of ocean currents in the western Pacific used by Treml et al. (2015) suggested that only 12% of larvae from Palau would make it to the region they labeled the Indo-Pacific, as opposed to 89% of larvae from the Indo-Pacific being transported to Palau. Again, at the large scale, our data suggest that a much larger fraction of larvae, approximately two thirds, from Palau would make it to the Philippine and the Indonesian waters. However, given that *none* of our drifters actually made it close enough to shore to reach places where reefs might be found, the true connectivity from Palauan to the Philippine reefs appears to be nearly zero.

Westward connectivity is also possible: Golbuu et al. (2012), estimated that 9% of the time, Yap (400 km to the northeast) could seed Palauan reefs (also seen in the data of Davies et al., 2015). In the present case, the only drifter that went anywhere near Yap, missed both Yap (100 km) and Palau (48 km). This is not surprising given that both HYCOM and OSCAR velocity fields for the region between Palau and Yap tend to show mostly zonal flow for the period the drifters were out. Examination of 170 days of HYCOM (1 November 2015 to 18 April 2016) velocity fields showed only six separate days where flows could have conceivably connected Yap to Palau and none where the transport could have occurred from Palau to Yap. Thus, connectivity between Yap and Palau must be quite intermittent.

In summary, the behavior exhibited by this set of drifters has they passed across the Philippine Sea make clear that connectivity between reefs may be controlled ultimately by nearshore and submesoscale processes that drive or support cross-shore transport. Thus, estimates of connectivity made using large-scale models like HYCOM or with velocity fields synthesized at similar scales using satellite observations as are the OSCAR fields must be taken as upper bounds to connectivity across ocean basins.

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