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ORIGINAL ARTICLE

Potential larval sources, destinations, and self-seeding in the Mariana Archipelago documented using ocean drifters

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Abstract Identifying transport pathways and sources of reef larvae is an essential component of ecosystem science. Ocean drifters tracked by satellite around the Mariana Archipelago were used to evaluate the possible pathways of transport among islands for passive larvae of reef organisms present in the surface layer. Reef taxa vary in their minimum and maximum larval duration from several days to a few months. Drifters leaving the Marianas required more than 16 days of transport prior to arriving near any adjacent island groups. Drifters arriving at the Marianas required more than 35 days of transport before being tracked back to any adjacent island groups. All arrived from the east or southeast via the North Equatorial Current. Roughly 27 % of the drifters that began in the Marianas returned. The majority of returning drifters (65 %) ended to the north of their starting point. Over 70 % of the drifters that returned to the Marianas after starting there did so in less than 40 days. Overall, this suggests that self-seeding may be of great importance to sustaining Mariana reef populations and that position within the archipelago affects connectivity among islands.

Keywords Coral reef · Larvae · Connectivity · Larval transport · Pelagic larval duration

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1 Introduction

Oceanic transport is almost entirely passive for the pelagic larvae of many corals and reef invertebrates because of their small size and limited swimming capabilities (Harrison and Wallace 1990; Richmond and Hunter 1990; Pechenik 1999). Even fish larvae must first become fertilized eggs and at least partially develop before they become the competent swimmers some are known to be (Thresher 1984; Fisher 2005). During this developmental period before settling into residence at juvenile habitats on reef ecosystems, pelagic larvae are subject to transport via surface currents (defined here as 0 to ca. 15 m depth) as primarily passive, neutrally buoyant particles. This life stage varies among reef taxa from a few days to several weeks and is termed pelagic larval duration (PLD) (e.g., Brothers et al. 1983; Olson 1987; Ramofafia et al. 2003; Wilson and Harrison 1998).

Larval connections among Pacific islands are difficult to evaluate because of the small size of the organisms and vast size of the environment involved. Computer transport simulations are often used to explore the range of potential larval connections among islands (Treml et al. 2008; Kool et al. 2011; Kendall et al. 2013; Wood et al. 2013) but their findings need to be validated through empirical approaches. Genetics and otolith chemistry studies offer a great source of relatively direct evidence but require field samples from many locations to establish patterns (Campana 1999; Kawakami et al. 2010). Drifter data offer another independent form of physical evidence for evaluating possible pathways and timing of larval transport among islands (Hansen and Poulain 1996; Lugo-Fernandez et al. 2001; Fossette et al. 2012; Kendall and Poti 2011).

The NOAA Global Drifter Program and its partners maintain an array of thousands of drifters throughout the

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world's oceans, dozens of which have passed directly through the Mariana Archipelago (Hansen and Poulain 1996; NOAA Global Drifter Program 2012). These drifters are embedded in ocean currents by drogues at 15 m depth and have been specifically engineered to track the velocity and direction of currents in the surface layer (for technical specifications, see Lumpkin and Pazos 2006). Data transmitted to satellites by a surface float are used to estimate drifter position, speed, and heading every 6 h. Drifter paths are expected to mimic those of passive larvae embedded in surface waters to a depth of 15 m and can therefore be used to represent the potential sources, destinations, and self-seeding pathways of such larvae in a region of interest.

The gametes of many reef organisms are initially positively buoyant and, in the case of mass coral spawning, are visible floating on the surface for a few days. Developing larvae of many reef invertebrates then shift below the air–sea interface by several meters to avoid the damaging effects of solar radiation but are still concentrated in the upper ca. 20 m of the surface layer (e.g., corals reviewed in Harrison and Wallace 1990). Pelagic larvae of many reef fish may vertically migrate depending on time of day, proximity to land, larval age, and other factors, but are still often concentrated in the upper 0–20 m of the surface layer (reviewed in Leis 2006).

As with reef systems worldwide over the last 30 years, there have been frequent calls for a better understanding of larval connectivity in the Mariana Archipelago. These recommendations have come in response to a wide variety of studies from reef fish (Triani 2011; Priest et al. 2012; Taylor et al. 2012), to invertebrates (Vermeij et al. 1983; Richmond et al. 1996; Yasuda et al. 2009), and whole reef ecosystems (Goreau et al. 1972; Quinn and Kojis 2003; Houk and Starmer 2010). Some have theorized that owing to the Marianas perpendicular orientation to prevailing ocean currents or geographic isolation, larval retention may be the chief means of sustaining local populations (Johannes 1978; Quinn and Kojis 2003; Priest et al. 2012). Indeed, taxonomic composition and relative abundance of planktonic larvae differ in open waters east and west of the archipelago (Suntsov and Domokos 2012). These researchers all have explicitly noted the need for a greater understanding of oceanic transport processes and larval connectivity to improve management of local fisheries and ecosystems.

Larval connectivity is among the most important concepts for fisheries, conservation, and natural resource agencies to incorporate into their long-term management strategies (Botsford et al. 2001; McCook et al. 2009). Sufficient sources of larvae upstream or in connected loops in ocean currents must be identified and preserved such that reef populations can maintain themselves and repopulate each other in response to sustainable fisheries extraction or between disturbance events (Allison et al. 2003; Steneck et al. 2009).

In this study, the potential patterns of larval transport in the Mariana Archipelago are examined using NOAA Global Drifter Program records. Primary ocean currents in the region are the westward flowing North Equatorial Current (NEC) which has typical velocities of 20–30 cm s^{-1} and the eastward flowing North Equatorial Counter Current (NECC) (20–40 cm s^{-1}) (Fig. 1) (Reverdin et al. 1994). The objective was to infer possible larval transport patterns in the Marianas by determining each of the following: (1) potential sources of drifters arriving at the Mariana Archipelago, (2) potential destinations of drifters leaving the archipelago, and (3) transport pathways and durations for drifters that left the archipelago and eventually returned.

2 Analysis of drifter data

Paths of surface drifters in the region (165–120°E longitude and 2°S–37°N latitude) were downloaded from the NOAA Global Drifter Program, Data Assembly Center for the years 1990–2011. Only those 145 drifters that passed directly through the Marianas were used for these analyses (i.e., crossed the axis of the archipelago between ca. 13° N including Santa Rosa Reef located ca. 40 km south of Guam, and ca. 21° N including Farallon de Pajaros). Some drifters actually beached on one of these closely spaced islands, others passed between them. Dates when drifters crossed the axis of the archipelago were evenly distributed throughout the year and are not biased toward any particular season. Forty-eight drifters passed through in December–February, 42 in March–May, 43 in June–August, and 45 in September–November with some individual drifters passing through the archipelago multiple times. Preliminary evaluation indicated a broadly consistent pattern of drift among seasons and therefore all the drifter data were combined into a single analysis.

Paths of individual drifters were then further split into multiple segments for analysis. A single path could often be divided into two or more segments including arriving, self-seeding, and departing components. There were 144 path segments that arrived in the Mariana Archipelago (representing potential larval sources), 130 that left the Marianas and never returned (representing potential larval destinations), and 51 that left and subsequently returned (representing potential self-seeding).

For those drifters arriving at the Marianas, paths were plotted on a map of the region and coded according to the number of days until arrival. Source regions and distances to the Marianas were summarized for a range of drift durations representing potential PLDs. Similarly, for those

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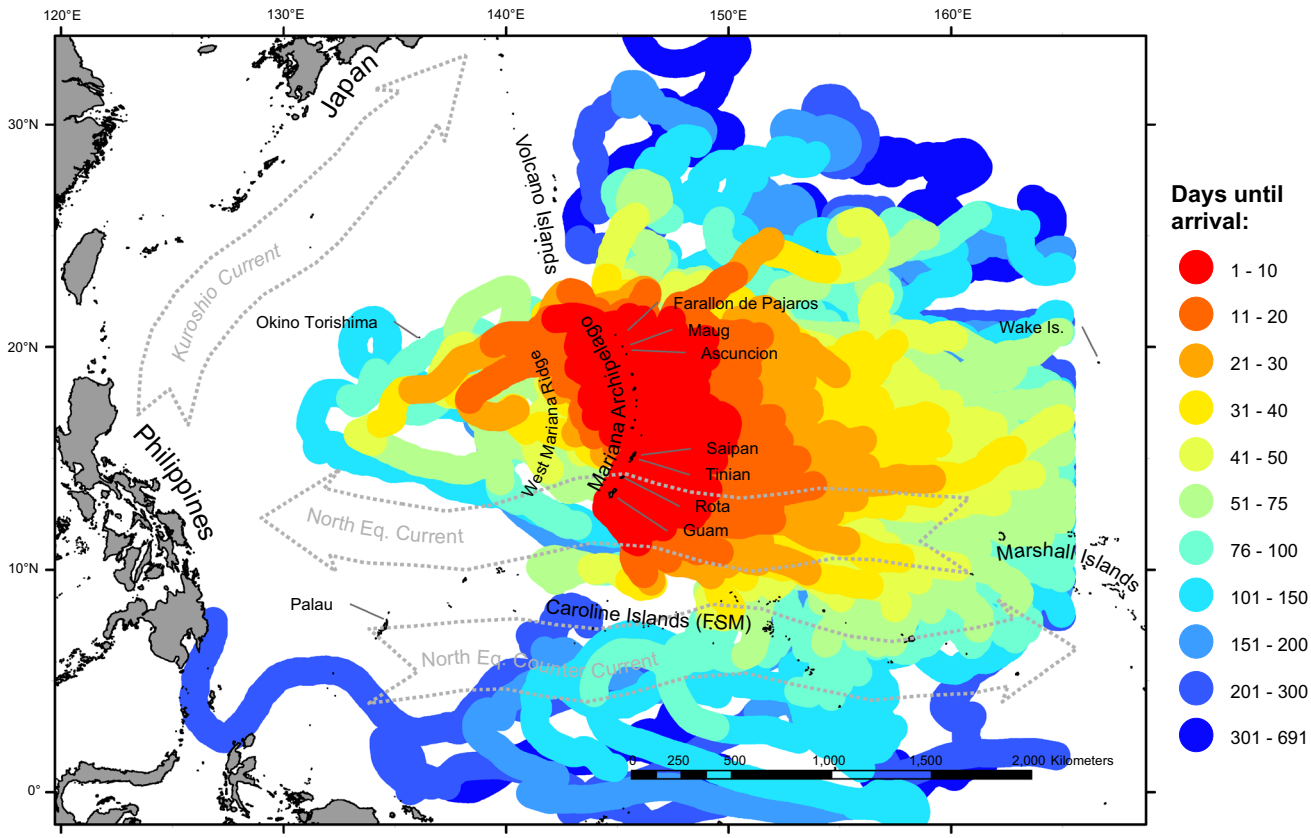

Fig. 1 Pathways of drifters arriving at the Marianas ($n = 144$). *Colors* denote the number of days prior to arrival and are stacked from shortest (*top*) to longest (*bottom*). Therefore, maximum possible distance travelled for incoming larvae is shown. General directions of major ocean currents are shown as *light gray arrows* (adapted from Reverdin et al. 1994 and Qui and Lukas 1996)

drifters leaving the Marianas, paths were plotted on a map of the region and coded according to the number of days since departure. Destination regions and distances from the Marianas were summarized for a range of drift durations representing potential PLDs.

Those drifters that left and subsequently returned to the Marianas were classified on the basis of their drift duration, which was calculated as the number of days between departure and return. A histogram was used to summarize the transit durations of all returning drifters to enable comparison with known larval durations of reef taxa. In addition, each returning drifter was categorized according to its returning position in the archipelago and the path it took to return. Drifters were coded as either returning north or south of their departure location, transiting east or west of the archipelago, and also according to the major island or island group within the Marianas where it began and ended. Geopolitical island groups considered in this analysis were (1) US Territory of Guam, the southernmost island in the Mariana Archipelago, (2) Saipan, Tinian, and Rota, the three southern islands and population centers of the Commonwealth of the Northern Mariana Islands, and (3) all of the small volcanic Northern Mariana Islands north of 15.75°N (Fig. 1). This enabled an understanding of patterns in directional transport within the Marianas and which island groups may rely on others as sources of larvae. To determine if the proportion of larvae ending northward or southward was significantly different than random (50:50), a *G* test with Williams' correction was used. This test provides a better approximation of the Chi square distribution than the unadjusted *G* statistic and a more conservative test at low sample sizes (Sokal and Rohlf 1981). Contingency table analysis and Fisher's exact test were used to determine if the proportion of larvae moving north or south was independent of transit path (east or west of the archipelago).

2.1 Arriving drifters: sources and timing

Drifters arriving at the Marianas represent possible pathways of incoming larvae (Fig. 1). None of the 144 incoming drifters were tracked back to any significant larval source in an adjacent island group until being transported for a minimum of 36 days. There are three seamounts east of the Marianas that could be connected in ca. 20 days but these are small, moderately deep, widely

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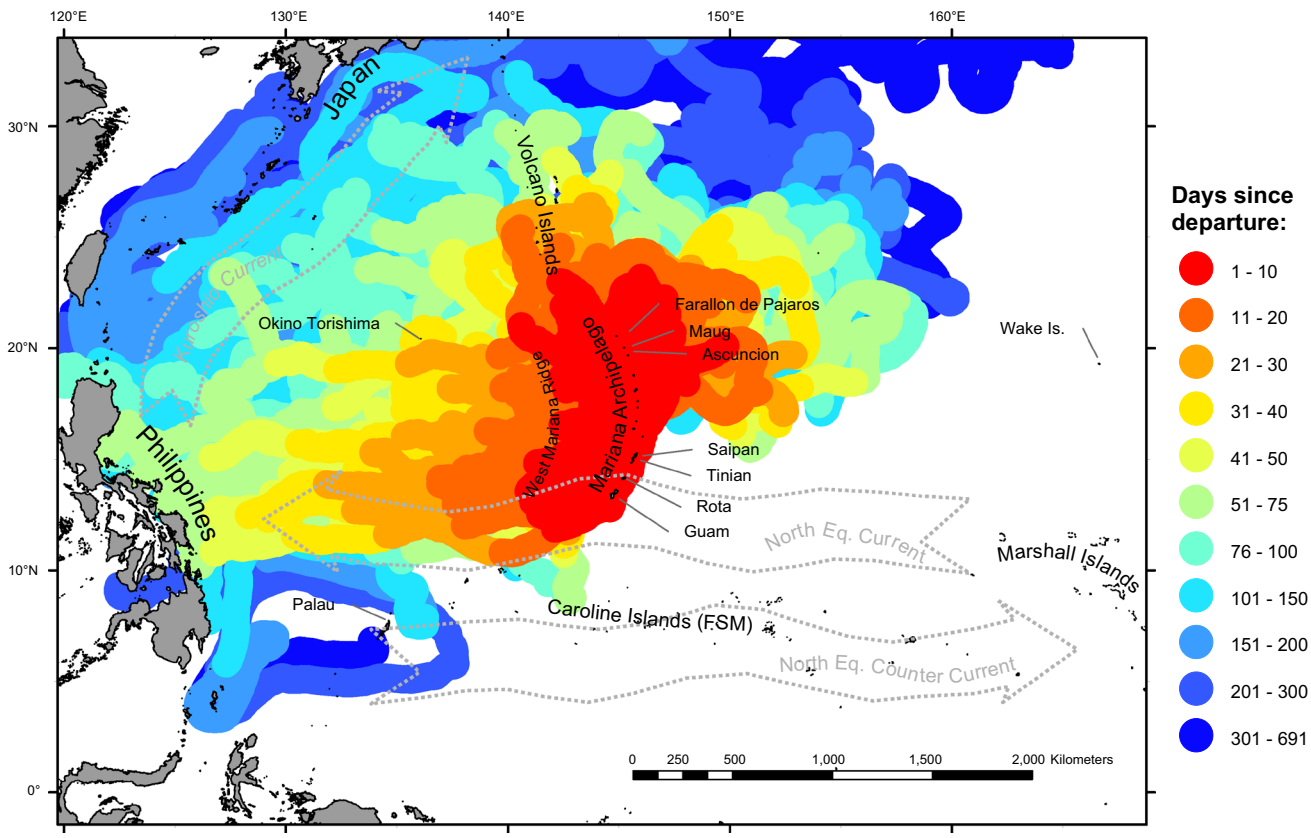

Fig. 2 Pathways of drifters departing the Marianas ($n = 130$). *Colors* denote the number of days after departure and are stacked from shortest (*top*) to longest (*bottom*). Therefore, maximum possible distance travelled for outgoing larvae is shown. General directions of major ocean currents are shown as *light gray arrows* (adapted from Reverdin et al. 1994 and Qui and Lukas 1996)

spaced, and unlikely to be large sources of reef larvae. The earliest incoming drifters arrived from the Caroline Islands after 40–50 days, but more typically required 75–100 days of drift. Earliest drifters from the Marshalls arrived after 65 days, but also more typically required 75–100 days of drift. Earliest drifters from Wake Island arrived after ca. 75 days. Overall, incoming drifters came primarily from regions to the east of the Marianas. This effect was more pronounced for Mariana Islands in the southern part of the chain including Guam and Saipan. All incoming drifters to these islands were from the east or southeast and were ultimately embedded in the NEC as the last vector of arrival.

2.2 Departing drifters: destinations and timing

Drifters departing the Marianas were used here to represent possible pathways of outgoing larvae (Fig. 2). The shallow banks of the West Mariana Ridge, ca. 250 km west of the Mariana Islands, could be reached in under 10 days. However, none of the 130 outgoing drifters were near any of the adjacent island groups until being transported for a minimum of 17 days. The first destination reached outside of the Marianas exclusive economic zones (EEZs; Guam or Commonwealth of the Northern Marianas) was in Japan's Volcano Islands group. Next was Okino Torishima, a small island ca. 1,000 km west of the Marianas, which was reached after 39 days. The Philippines were reached after 50–75 days. There were two major trajectories of departing drifters. Those leaving from the southern part of the archipelago between Saipan and Guam were primarily embedded in the very straight, westward flowing NEC. Those in the northern part of the archipelago were primarily subjected to the variable field of eddies between the NEC and Kuroshio Current (Ebuchi and Hanawa 2001).

2.3 Returning drifters: pathways and timing

Of the 179 drifters that began in the Marianas, 49 (27 %) returned. Two drifters looped through the islands twice. The general direction of transport was northward. Thirty-two drifters (65 %) ended up north of where they began in the archipelago whereas only 17 went southward (35 %) (Table 1). This was significantly different than the expected ratio if the direction of transport was random [null hypothesis 50:50, $G_{adj} = 4.6188 > \chi^2_{(0.05,\ 1)}$]. The ending

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Table 1 Contingency table analysis of pathways for self-seeding drifters within the Marianas

Count Total % Column % Row %	Northward or southward		
	N to S	S to N	Summary
Transit path			
Via east	13	7	20
	26.5	14.3	40.8
	76.5	21.9	
	65	35	
Via west	4	25	29
	8.2	51	59.2
	23.5	78.1	
	13.8	86.2	
Summary	17	32	49
	34.7	65.3	

Table 2 Summary of sources and destinations among the three Mariana regions considered

	Sources			
	Guam	Saipan, Rota, Tinian	Northern Is.	Summary
Destinations				
Guam	2	1	0	3
Saipan, Rota, Tinian	1	1	3	5
Northern Is.	0	9	31	40
Summary	3	11	34	Diag. sum: 34

position of drifters (N or S of starting point) was not independent of the direction travelled (east or west) [Pearson $\chi^2_{(0.05,\ 1)} = 13.7,\ p < 0.0002$]. Specifically, for those drifters ending northward, there was a significant probability of transiting west of the Marianas rather than east (Fisher's exact test, right tail, $p < 0.0003$).

Most returning drifters remained within the three geopolitical regions of origin (34 out of 49 or 70 %, Table 2) although the specific patterns of retention varied by region. The majority of returning drifters were in the northern islands which comprised the largest region. Over 90 % of the drifters (31 out of 34) that began in the northern islands remained there and only three ended southward in the Saipan/Tinian/Rota region. None went from the northern islands to Guam. Only one of the 11 drifters that began in the Saipan/Tinian/Rota region remained there. Over 80 % of the drifters that began in this region (nine out of 11) ended up in the northern islands. Only three drifters ended in the Guam region, two began there, one was from the Saipan/Tinian/Rota region.

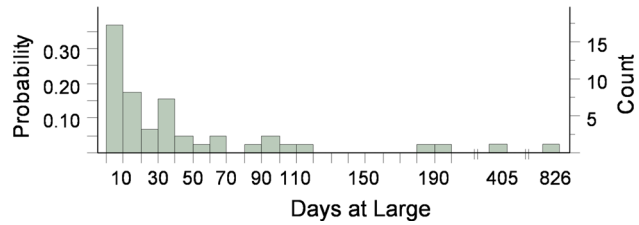

Fig. 3 Histogram of the number of drifters returning to the Marianas by days at large

The histogram of number of drifters returning within the Marianas after various durations revealed two key points (Fig. 3). First, a majority of drifters (25 out of 49) that returned to the Marianas after starting there did so in less than 20 days. Over 70 % returned in under 40 days (35 out of 49). Second, although the bulk of drifters returned after these short durations, a few drifters returned across a very wide range of longer drift times. Two drifters returned to the Marianas after an incredible 405 and 826 days at large although these were not included in the contingency table or directional analyses because of the very circuitous and long paths outside of the duration for pelagic larvae.

3 Discussion and summary

Because at least some of the larval period for so many taxa is thought to be influenced primarily by ocean currents, much can be inferred simply by looking at patterns of ingress and egress of drifters tracked by satellite through a region of interest. On the basis of analysis of drifter pathways and durations it is not likely that the Mariana Islands receive many larvae from their island neighbors for those taxa with larval durations below ca. 40 days. Passive transport via ocean currents is unlikely to enable such connections. This duration encompasses a large number and variety of coral reef taxa including many families of reef fish (many Pomacentridae, Apogonidae, and Pomacanthidae species; Brothers et al. 1983; Victor 1986; Thresher et al. 1989; Wellington and Victor 1989; Junker et al. 2006), commercially harvested sea cucumbers (Richmond et al. 1996; Ramofafia et al. 2003), diverse corals (Harrison et al. 1984; Harrison and Wallace 1990; Wilson and Harrison 1998; Miller and Mundy 2003; Heyward and Negri 2010), and locally important species such as rabbitfish (ca. 30 day PLD, Chirichetti 1996), humphead wrasse (ca. 30 day PLD, Slamet and Hutapea 2005), and even the crown-of-thorns starfish which may be close to their maximum larval duration at 40 days (Olson 1987). These drifter-based results do not indicate that larvae could never make the incoming connection in shorter time periods, but instead show that it may be uncommon given that none of the 144 drifters arriving in the Marianas

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over the last two decades made it faster than 36 days, and most took much longer. This suggests that spawning populations on other island groups are unlikely to contribute to populations of taxa with short PLDs in the Marianas.

The Marianas are also unlikely to serve as a large source of larvae to most of their island neighbors. Only the Volcano Islands south of Japan were reached in less than 20 days, and those drifters originated from the comparatively small islands in the northern extent of the Mariana chain. These include the three northernmost islands in the chain, Farallon de Pajaros, Maug, and Asuncion, which comprise the Remote Islands Unit of the Mariana Trench Marine National Monument where commercial fishing is prohibited (Presidential Proclamation 8335, 2009). Even this connection, while potentially short, was highly irregular and unpredictable because of the swirling eddies and sinuous currents that dominate this region (Ebuchi and Hanawa 2001). Overall, on the basis of evidence from drifters it appears that the Marianas are rather isolated from their island neighbors as either a destination or source of larvae.

Self-seeding of locally produced larvae may be of great importance to sustaining Marianas reef populations for those taxa with short PLDs. This is based on the lack of incoming drifters from elsewhere that were less than 40 days adrift and the relative abundance of drifters less than 40 days at large among all those starting and returning to the Marianas. At least a few drifters started and returned to the Marianas over quite a wide range of longer durations as well. This demonstrates the capability for many taxa with longer PLDs to passively return to the Marianas at least in some numbers. This may include some reef fish species in the Acanthuridae, Labridae, and Mullidae families (Brothers et al. 1983; Victor 1986; Wellington and Victor 1989) as well as some corals (Harrison et al. 1984; Harrison and Wallace 1990; Miller and Mundy 2003; Heyward and Negri 2010).

The direction of returning drifters was not random along the axis of the archipelago. The majority (65 %) of returning drifters ended to the north of their starting point. This tendency for northward transport should be considered during the coordination and design of management strategies for the archipelago. For example, enhancing spawning populations via marine protected areas (MPAs) and catch limits on southern islands may provide the greatest benefits to their island neighbors to the north. All else being equal, an MPA on Tinian, for example, may provide greater contributions of larvae to northern islands than MPAs at northern extremities of the chain. This does not take into account reef health and size of spawning populations which may counter this effect. Although islands and reef size are smaller towards the north they can have greater population density of some taxa owing to their remote location away from human population centers (Richards et al. 2012) and possibly because of their position as a larval destination as documented here.

For those drifters ending northward of their starting position, most transited to the west of the archipelago. This may bring them close to the few reefs and banks along the West Mariana Ridge, further enhancing the local retention opportunities for some taxa relative to abyssal depths to the east in the Mariana Trench. A smaller but potentially important amount of productivity (35 %) may be transported southward within the archipelago representing a key feedback loop for resilience of reef populations.

Patterns of returning drifters also varied depending on starting position in the archipelago. A large majority of returning drifters beginning in the northern islands remained there. Only a few drifters ended southward in the Saipan/Tinian/Rota region. MPAs in the northern regions, for example, may provide the greatest benefit to sustaining their northern island neighbors rather than exporting production to the south. In contrast to the retention of drifters beginning in the northern region, a large majority of drifters that began in the more heavily populated Saipan/Tinian/Rota region ended up in the northern islands rather than staying local or moving southward to Guam. Only three drifters ended in the Guam region, two of which began there. No drifters went from the northern islands to Guam. This may be due to the relative position of Guam which is continuously swept by the highly directional NEC. The current does, however, result in eddies in the lee of the island that likely promote self-seeding from local spawners (Wolanski et al. 2003; Storlazzi et al. 2009). For those Guam-based larvae that miss entrainment in the leeward eddies, the drifter data suggest that the next opportunity for settlement would be 50–75 days later on the coast of the Philippines.

One drifter departed the Marianas near Santa Rosa Reef south of Guam and was at large for over 2 years (826 days). It made several passes along the Philippine coast, nearly beached on Palau, meandered among and around various islands of the Federated States of Micronesia (FSM) in the Caroline chain, and looped near the Marshall Islands before finally returning to the Marianas north of Guam. This observation is useful to highlight another source of potential connectivity that was not focused on in this study, the transport process known as "rafting". In rafting, reef organisms including fish, corals, and a diversity of epifauna are attracted to and even settle and grow to maturity upon floating material such as volcanic pumice, logs, coconuts, net floats, and other buoyant objects such as NOAA drifters (Jokiel 1989; McCormick and Milicich 1993; Bryan et al. 2012). This process greatly expands the distance of possible connections far beyond the unassisted larval duration of reef organisms although its

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relative contribution to connectivity compared to simple larval transport is difficult to quantify.

Some drifters in this analysis actually ran aground directly on one of the Marianas but most simply passed between the islands. Our objective was not to quantify these direct hits in the Marianas, merely to broadly characterize where larvae could potentially come from or go to. However, these drifter pass-throughs may actually have a realistic chance at settlement were they larvae of some reef fish. There is growing evidence that many reef fish larvae do not have to hit a reef directly for successful settlement. Such larvae must merely come within some sensory range to smell (Gerlach et al. 2007; Paris et al. 2013), hear (Wright et al. 2011), or otherwise orient (Mouritsen et al. 2013) toward a reef habitat. They can then actively swim their way from the open ocean to settlement habitats even several kilometers away (Leis 2002; Fisher 2005). Although the islands and their surrounding reefs generally decrease in size with increasing latitude, they are fairly regularly spaced and may function as a screen offering settlement opportunities for larvae passing nearly anywhere between them. Consider that the archipelago extends roughly 900 km along its north/south axis. Approximately 20 % of this length is comprised of reef-fringed islands where larvae could settle directly and 80 % consists of spaces where currents can flow between islands. Average island size is 10.9 km along the north/south axis and average space between them is 51.8 km. These calculations exclude fringing reefs extending from island shores as well as several independent shallow reefs and banks between some islands that would further increase settlement opportunities. In addition, pass-throughs are often at least temporarily entrained in the eddies documented to form along the leeward edge of some of the Marianas (e.g., Wolanski et al. 2003). Collectively, the island size, spacing values, leeward eddies, as well as the sensory and swimming capabilities of some reef fish larvae suggest that certain taxa may have ample capability to reach juvenile habitats no matter where they pass through the archipelago.

Results here compare favorably with accepted marine biogeographic breakpoints. For example, Spalding et al.'s (2007) hierarchical classification scheme separates the Marianas as a distinct ecoregion, then nest it with the neighboring Caroline and Ogasawara islands in the Tropical Northwestern Pacific Province, and then more broadly group it with more distant locations such as Palau and the Philippines. Such a biogeographic hierarchy corresponds to the general pattern of breakpoints in connectivity documented here on the basis of drifters. Patterns from drifter data also validate recent computer simulations that predict the Mariana Islands to be interconnected when larvae have a 15 day PLD but isolated from neighboring archipelagos until PLDs reach ca. 30–60 days (Treml et al. 2008). Only at that duration were simulated connections possible for larvae from the Carolines, a finding supported by the empirical evidence from the drifters. Genetic analyses also corroborate the relative isolation of the Marianas as documented by drifters. For example, population structure of two very different taxa, crown-of-thorns seastar (*Acanthaster planci*) and scribbled rabbitfish (*Siganus spinus*) were evaluated through genetic analysis of samples collected at one or more Mariana islands and among nearby archipelagos (Priest et al. 2012; Timmers et al. 2012). Priest et al. (2012) used DNA microsatellite markers to demonstrate that *S. spinus*, a fish with a ca. 30 day PLD, from sites within the Marianas were from a genetically homogeneous population but were significantly isolated from those collected in the Caroline archipelago and elsewhere in the Pacific. Timmers et al. (2012) analyzed mitochondrial DNA to demonstrate that *A. planci*, an echinoderm with a ca. 15–40 day PLD, from locations in the Marianas had significant genetic partitioning with samples from the Carolines and elsewhere. Both taxa have a maximum PLD of ca. 30–40 days, and each study found evidence of genetic partitioning between Mariana and adjacent archipelagic populations as expected on the basis of drifter data.

It is important to note that the results of this study only apply to those taxa whose larvae spend a majority of their time embedded in the surface layer. Larvae that reside in deeper layers or close to the seafloor will be subjected to very different hydrodynamic forces than those investigated here.

A large number of drifters were used in this study to identify general transport patterns. The even distribution of drifter data among seasons reduced the potential for seasonal bias in the results. Unfortunately, at present there are not enough drifter tracks in the region to further subset and compare among years, months, or oceanographic cycles with sufficient rigor. This will likely change in coming years because the NOAA Global Drifter Program maintains an array of hundreds of drifters at large in the region annually that continuously add to this informative database. Because reef organisms often have seasonal cycles and interannual variations in reproduction, analysis of the accumulating drifter data will be an important means of understanding temporal variation in reef connectivity.

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