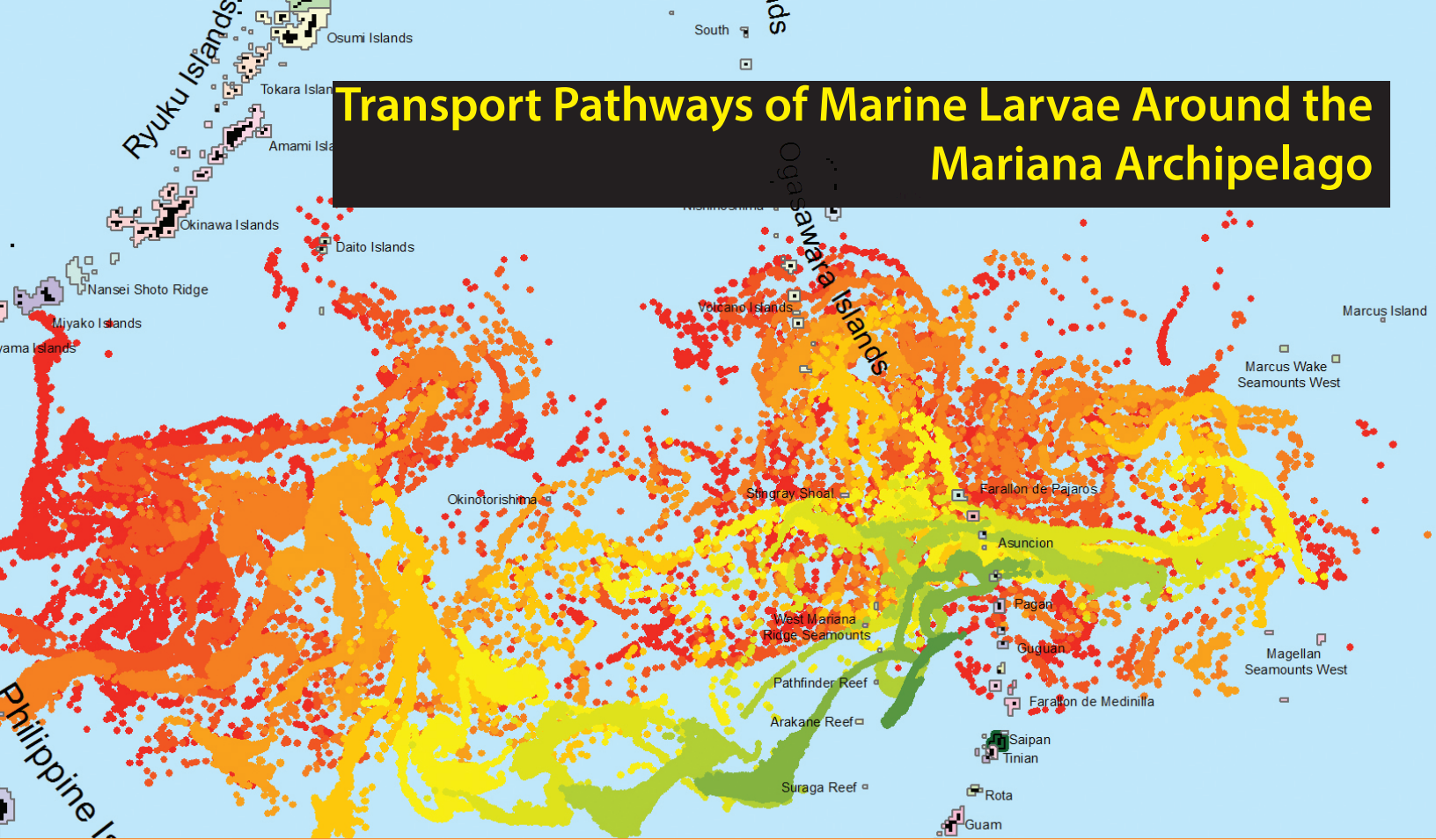
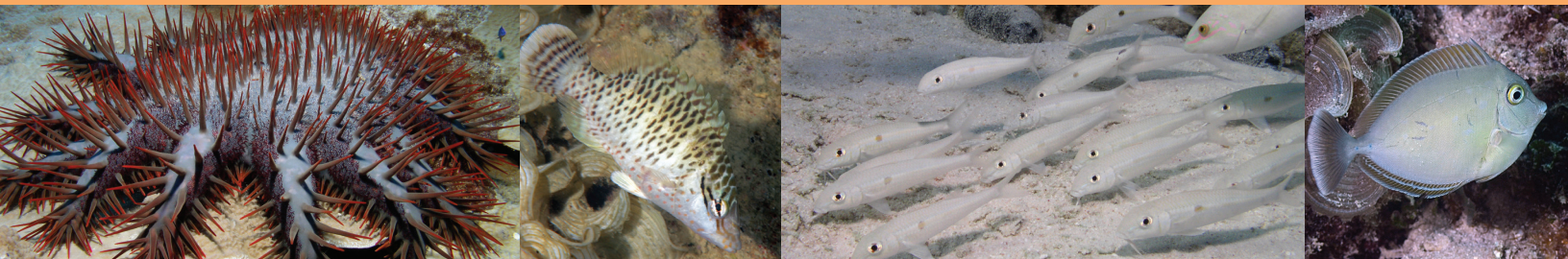


# Transport Pathways of Marine Larvae Around the Mariana Archipelago



NOAA National Centers for Coastal Ocean Science  
Center for Coastal Monitoring and Assessment

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## ABOUT THIS DOCUMENT

This assessment represents the continuation of an ongoing partnerships between NOAA's National Centers for Coastal Ocean Science (NCCOS), Center for Coastal Monitoring and Assessment (CCMA), Biogeography Branch, NOAA's Coral Reef Conservation Program (CRCP), and local partners in US States and Territories. The Biogeography Branch has applied a biogeographical approach to inform the management of coral reefs around the Pacific Islands since 2000 on a diversity of topics including larval transport. To date, most of the coral reef ecosystems in US States and Territories have had some level of biogeographic characterization or mapping completed through these partnerships.

For more information on this project and those in other reef ecosystems please visit the NCCOS webpage at <http://coastalscience.noaa.gov/> or direct questions and comments to:

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## EXECUTIVE SUMMARY

Many coral reef organisms have a larval development phase in pelagic environments. These larvae may be returned to their natal islands or dispersed downstream in ocean currents. Understanding the strength and geographic patterns of this larval connectivity is an important part of managing marine ecosystems through ecosystem based-fisheries management plans, marine protected area (MPA) network design, recovery strategies for endangered species, and promoting reefs that are resilient to disturbance. Sufficient sources of larvae must be maintained to sustain future generations.



*Bird Island Sanctuary, Saipan.*

*Photo credit: M. Poti, Biogeography Branch, NOAA.*

In recent years, there have been calls from scientists and managers in the Mariana Archipelago for a better understanding of larval connectivity. The Mariana Archipelago includes the Commonwealth of the Northern Mariana

Islands and Guam, and spans ~800 km of islands and submerged banks from ~12° to 21° N latitude along the ~146° E meridian. The Marianas experience a range of ocean currents, from the westward flowing North Equatorial Current (NEC) through the southern islands, to the eddies spun off the NEC through the northern islands.

The overall goal of the assessment was to evaluate ocean currents as a mechanism of transport and to compare connectivity among larvae with different life-history characteristics using computer simulations. Cumulative connectivity over a recent 9 year span was investigated for the entire region. Island roles as larval sources and destinations, as well as self-seeding versus larval import, were evaluated for each of the Marianas. For Guam and Saipan, the two most populous islands, the seasonal and inter-annual variation in larval supply was examined. The main objectives, approach, and key findings from each chapter are below.

### Chapter 1: Seasonal and inter-annual surface currents mapped with ocean drifters

- Currents are the principle mechanism of transport for passive larvae. Objectives of this chapter were to characterize the speed and heading of surface currents in the Marianas, including their acute (due to typhoons), seasonal, and interannual variability.
- Analysis was based on NOAA Global Drifter Program data, which uses satellites to track drogues deployed at 15 m depth. Over 1500 drifters passed through the region between 1990 and 2011.
- Results demonstrate different transport mechanisms depending on which current fields larvae are in, and potentially the season or year during which they are spawned.
- The North Equatorial Current (NEC) lies between ~9-16° N and flows consistently westward (280° median heading) across the southern Marianas, including Guam and often Saipan. Slowest flow is during Summer, the peak spawning season for corals.
- The North Equatorial Counter Current (NECC) lies between ~2-9° N and flows consistently eastward (~60° median heading) across the Federated States of Micronesia. Fastest and least variable flow occurs in the Fall.
- The NECC and NEC are alongside each other but flow in opposite directions resulting in eddy formation and looping flow between them. Particularly evident are eastward moving drifters from the NECC looping northward into the westward flowing NEC.
- The currents north of the NEC, including those around most of the northern Mariana Islands, are highly variable with almost random distribution of headings.

- NEC and areas north of it were ~50% faster in 2004-2007 relative to preceding or following years.
- Currents passing by the large islands, including Guam and Saipan, experience increased variation in heading due to eddy formation on leeward coasts.
- Larval transport may be affected in the few days following passage of typhoons through increased current speed, reduced water temperatures, and more variable headings. These mechanisms may affect larval physiology and physical transport.

## **Chapter 2: Patterns of larval connectivity and the influence of larval life-history investigated through transport simulations**

- Objectives were to: 1) describe larval connectivity within the Marianas and among surrounding archipelagos using computer simulations, 2) compare the relative influences of larval duration, spawning season, and larval swimming capabilities on connectivity, 3) evaluate the role of self-seeding, import, and export of larvae at each island in the Marianas, and 4) investigate a detailed time-series of simulated recruitment at Saipan and Guam.
- Computer simulations were used to track cohorts of virtual larvae transported according to an ocean circulation model. Daily current vectors for the 0-10 m depth layer were from the Hybrid Coordinate Ocean Model's (HYCOM) Global Hindcast. Virtual larvae were spawned seasonally from 2004-2012 at each of 116 starting locations. Larval production was scaled to each island's area of potential reef ecosystem. Maximum Pelagic Larval Durations (PLD) of 10, 20, 50, and 100 days were simulated where larvae were competent to settle once 60% of their maximum PLD elapsed. In one set of simulations, representing larvae with minimal swimming capabilities, larvae could only settle at a destination with potential reef habitat. In another set of simulations, representing larvae with strong sensory and swimming capabilities, larvae could settle anywhere within 18 km of potential reef habitat. A constant mortality rate was applied following competency, which resulted in 100 % mortality by the end of each maximum PLD.
- Simulations document interconnected webs of larval exchange within and among archipelagos that varied in size with PLD. Larvae with a 10 day PLD rarely settled beyond neighboring islands. Those with 20 day PLD showed moderate connectivity within each archipelago, but generally not to other archipelagos. The 50 day PLD enabled broad connectivity among many islands within each archipelago, but maintained separation of archipelagos, with a few exceptions. Once PLDs reached 100 days, a majority of islands within each archipelago were exchanging larvae and many archipelagos became interconnected.
- Enlarging the size of the settlement zone by 18 km had little effect on which islands were connected, but had a doubling effect on the connection strength. Spawning season did not have a large effect on either the number of successful larvae or number of interisland connections.
- Position of the NEC through the southern Marianas and the eddy field along the Marianas to the north were primarily responsible for connectivity patterns for taxa with a maximum PLD up to 50 days. Geographic break points in connectivity fell along the interface of these currents (positioned between Guam and Saipan among model years). There was also a northward bias to transport within the Marianas associated with eddies spinning off the NEC. Connections from FSM to the southern Marianas were enabled for larvae with PLDs of 50-100 days by the eastward NECC picking up larvae as it flows through the Federated States of Micronesia (FSM), the northward current loops that transport larvae in the NECC to the NEC, and the westward flow of the NEC that may deposit those larvae to the southern Marianas. For the longest PLD, the straight flowing NEC transported larvae from the Marshall Islands to the southern Marianas, and from the southern Marianas to the Philippines.
- Self-seeding supplied the majority of larvae with short PLDs for islands in the Marianas, including Guam, Saipan, Farallon de Medinilla, and islands north of Alamagan. Imports predominated at all Mariana locations for larvae with PLDs of 50-100 days.
- A time series of recruitment at Saipan and Guam based on each spawning event revealed that individual seasons and years of high recruitment can be followed by periods of low recruitment, and that even closely spaced islands can have quite different temporal patterns of settlement.

### Chapter 3: Patterns of larval connectivity for priority species

- Mariana scientists and managers identified 6 taxa of special significance due to their role in the ecosystem, importance in fisheries and culture, extreme rarity, or abundance. These were: mass spawning corals, post-larval yellowfin goatfish (*Mulloidichthys flavolineatus*), post-larval scribbled rabbitfish (*Siganus spinus*), humphead wrasse (*Cheilinus undulates*), bluespine unicornfish (*Naso unicornis*), and crown-of-thorns seastar (*Acanthaster planci*).
- Literature, local experts, and fisheries data were used to identify spawning and larval parameters for computer transport simulations specific to each taxon.
- Results suggest that PLD of corals will dramatically affect connectivity patterns. Those with 10-20 day PLDs will be almost entirely restricted to transport within their native archipelagos. For corals with 50-100 day PLDs, all islands were strongly dependent upon imported larvae.
- Both *M. flavolineatus* and *N. unicornis* larvae have long PLDs, and consequently, a large proportion of larvae arriving at each island in the Marianas was imported from elsewhere, with significant contributions from outside the archipelago. Fall spawning may enhance long distance transport for *N. unicornis* because the NEC has peak speed and highly directional flow in Winter, and the NECC has more northward headings that promote connections from FSM to the Marianas.
- Variations in currents can dramatically increase recruitment events for *S. spinus* and COTS at Saipan and Guam. Arriving larvae may differ in origin, and peaks are not synchronized among nearby islands.
- Although in need of protection wherever they exist until populations rebound, simulations identify potentially important sources of *C. undulates* larvae, such as Saipan.

### Management Applications

- Connectivity patterns vary widely among taxa, and therefore, there is no single best advice to provide managers for conserving larval sources to promote sustainability of reef communities.
- Each archipelago was relatively isolated from its neighbors for relatively short-lived larvae with 10-20 day PLDs. Larvae sustaining those populations may primarily come from self-seeding or neighboring islands, and the benefits of local management actions may be locally realized.
- Self-seeding was reduced and there was widespread larval exchange among more distant islands and archipelagos for long-lived larvae with 50-100 day PLDs. This offers a greater safety net for recovery following localized disturbance, however, management must involve coordinated decision-making among island nations. Benefits of local conservation may be realized elsewhere.
- Due to the northward bias in transport within the Marianas, activities that preserve spawning potential in the northern portions of the archipelago may have less benefit to the Marianas than those undertaken in the southern portions of the archipelago.
- The circular connection of larvae from the Marianas to Yap, Yap to Chuuk, and Chuuk back to the Marianas could be a focus of international coordination between these jurisdictions and may be critical for maintaining the overall resilience of reef ecosystems among these islands.
- If an island is heavily dependent upon larval imports to sustain local populations it does not mean that its local reefs can be harvested or allowed to decline without consequence. It may be an important source of larvae to downstream destinations.
- Model results can help determine which existing or potential MPA sites may provide the greatest return to reef communities and should be used in the process to plan interconnected MPA networks, including the Micronesia Challenge.
- Fisheries managers can locate key spawning stocks that sustain local fisheries. Results can be used to enhance the effects of traditional fisheries management tools at those sites, such as prohibitions on harmful fishing methods, temporary moratoria, and size or bag limits.





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## Introduction

Matthew S. Kendall<sup>1</sup>

Larval connectivity is among the most important concepts for fisheries, conservation, and natural resource agencies to incorporate into their long-term management strategies (McCook et al. 2009, Kool et al. 2011). Species ranges, density patterns, source and sink dynamics, biogeographic breakpoints, and biodiversity hotspots are all shaped, in part, by ocean currents and patterns of larval connectivity among islands. Conservation planning including design of marine protected area (MPA) networks and promoting reefs that are resilient to disturbance depends in part upon knowledge of larval connectivity (Amesbury 1996, Botsford et al. 2001, Wolanski et al. 2003, Almany et al. 2009). Sufficient sources of larvae upstream or in connected loops in ocean currents must be identified and preserved such that they can maintain themselves and repopulate each other between disturbance events (Allison et al. 2003, Hastings and Botsford 2006, Steneck et al. 2009). Fisheries managers must also seek to identify and preserve adequate sources of recruiting larvae to replace harvested individuals in order to maintain sustainable fisheries.



*Reef community at Managaha Marine Conservation Area, Saipan.  
Photo credit: M. Kendall, Biogeography Branch, NOAA.*

Many coral reef organisms possess a pelagic phase during which spawned gametes and developing larvae are transported by ocean currents for a period of days to many weeks. It is estimated that ~75-90% of scleractinian coral species are broadcast spawners (Harrison and Wallace 1990, Richmond and Hunter 1990). Even as fully developed planulae, swimming speeds of coral larvae (1-10 mm/s) are orders of magnitude slower than the current velocities encountered in the pelagic environment (Reverdin et al. 1994, Qui and Lukas 1996). Eggs and larvae from a wide variety of other benthic invertebrates, including gastropod, bivalve, polychaete, crustacean, and echinoderm larvae are also found in surface waters far from reef habitats of adults (Scheltema 1986). All are very small and passively drifting with the ocean currents in which they are embedded during their egg and larval stages. Even larvae for many taxa of reef fish are at least partly subject to dispersal in ocean currents. Approximately 70% of reef fish families have pelagic eggs and larvae (Thresher 1984). While older larvae of many fish species have recently been shown to have excellent sensory and swimming capabilities (Leis 2002), they too must begin life as eggs, sperm, embryos, and simpler forms lacking fins that are passively adrift in ocean currents (Thresher 1984). This less mobile, developmental period varies among fish taxa but has been estimated as encompassing roughly the first half of their larval duration (Fisher 2005).

Adults of many of these corals, reef fish, and other invertebrates also have spawning behaviors or characteristics that initially promote a pelagic existence for their larvae. Gamete bundles and early larvae of many corals are often positively buoyant and can be seen as surface slicks during mass-spawning events. Even sea cucumbers raise their anteriorly positioned gonopores to spawn up into the water column where fertilization and development of larvae can occur (Richmond et al. 1996). Reef fish may undertake many behaviors to

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enhance at least initial offshore transport. Of the reef fish that leave their normal habitat to spawn, most move toward deeper water using locations such as channels leading through the reef, promontories swept by currents, and outer reef slopes (Johannes 1978, Thresher 1984, Colin 2010). Many fish conduct a “spawning rush” towards the surface at the moment gametes are released and also time the release to coincide with falling tides that entrain larvae in outbound surface currents (e.g. Johannes 1978, Donaldson 1995, Colin 2010). Collectively, these processes and behaviors demonstrate that for at least the first part of their larval life-history, many coral reef organisms are subject to dispersal and transport primarily by ocean currents.



*Reef community at Lighthouse Reef, Saipan.  
Photo credit: M. Kendall, Biogeography Branch, NOAA.*

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 region. These recommendations have come in response to a wide variety of studies from single taxa to whole reef ecosystems. For example, researchers investigating stock structure of key fishery species in the Marianas, including various emperor fish (Triani 2011, Taylor et al. 2012), rabbitfish (Priest et al. 2012), and the many species of harvested sea cucumbers (Amesbury 1996, Richmond et al. 1996), all have explicitly noted the need for a greater understanding of oceanic transport processes and larval connectivity to improve management of local fisheries. Scientists examining controls on community structure of Mariana corals (Houk and Starmer 2010), molluscs (Vermeij et al. 1983), and other important reef invertebrates, such as crown-of-thorns seastars (COTS) (Yasuda et al. 2009), have speculated on the role that larval supply may play in the relative abundance of brooding versus broadcast spawning corals (Kojis and Quinn 2001), community succession, and recovery following disturbances, such as volcanic eruptions (Houk and Starmer 2010) and COTS infestations (Goreau et al. 1972, Quinn and Kojis 2003). Many have theorized that due to the Marianas’ orientation in prevailing ocean currents and/or geographic isolation, larval retention may be the chief means of sustaining local populations (Johannes 1978, Kojis and Quinn 2001, Quinn and Kojis 2003, Priest et al. 2012). These researchers all have noted the urgent need for additional studies of larval connectivity to explain biogeographic phenomena. In addition, coral reef managers in the Marianas recently identified their top priority research topics (Commonwealth of the Northern Mariana Islands and NOAA Coral Reef Conservation Program 2010), including identification of best locations for marine protected areas as part of the Micronesia Challenge ([www.micronesiachallenge.org](http://www.micronesiachallenge.org)), and understanding important sources of larvae to promote regional reef resiliency and sustainable fisheries.

Larval connections are difficult to evaluate and predict due to the small size of the organisms and vast size of the environment involved. Fortunately, there is a growing diversity of independent approaches for investigating larval transport. Each technique offers different but complementary information to broaden our understanding. Drifter-based studies have been used to track the actual speed, direction, and timing of ocean currents and offer real-world examples of potential transport patterns of pelagic larvae (Hansen and Poulon 1996, Lugo-Fernandez et al. 2001, Fossette et al. 2012). Otolith studies can be used to determine the pelagic lifespan of larval fish and even identify stock structure, migration pathways and the oceanic or coastal water masses that larvae have passed through (Wellington and Victor 1989, Campana 1999, Swearer et al. 1999, Soliman et al. 2010). DNA analyses can be used to identify species, calculate the relatedness of populations or even individuals, and also determine the direction and frequency of gene flow among islands (Mukai et al. 2009, Planes et al. 2009, Kawakami et al. 2010, Fitzpatrick et al. 2011, Priest et al. 2012). Computer simulations using an ocean circulation model can be used to transport millions of virtual larvae across vast seascapes with many larval sources and destinations, explore the influence of various larval traits on

connectivity, and predict impacts from climate change or oceanographic scenarios (Treml et al. 2008, Kool et al. 2011, Kendall et al. 2013, Wood et al. 2013). When interpreted together, multiple lines of evidence from these diverse fields can provide a more complete and robust understanding of transport processes.

The present study seeks to further our understanding of ocean currents in and around the Mariana archipelago and their potential influence on larval transport. We combined observational data on ocean currents from satellite –tracked surface drifters with computer simulations of larval dispersal driven by an ocean circulation model to achieve the following objectives:

1. Characterize the speed, direction, and variability (seasonal, inter-annual, Southern Oscillation state) of the ocean currents by which larvae are transported using satellite-tracked drifters.
2. Model the transport pathways of virtual larvae using computer simulations to determine key sources and destinations among islands. Quantify the influence of various life history traits on larval connectivity, including spawning season, larval duration and sensory/swimming capabilities.
3. Evaluate simulated connectivity for 6 locally important species identified by reef managers and scientists.





# Chapter 1: Seasonal and Inter-annual Surface Currents Mapped with Ocean Drifters

Matthew S. Kendall<sup>1</sup>, Matthew Poti<sup>1,2</sup>

## INTRODUCTION

Larval reef fish, corals and other organisms are transported among the Marianas and neighboring islands in a setting of interacting ocean currents. A first step in understanding potential larval transport is characterizing the position, direction, and speed of regional ocean currents and the connections between them. Reef organisms spawn at different times of year, have larval durations of days, weeks, or even months, and highly variable recruitment success among years. Therefore, the seasonal (e.g. wet versus dry), acute (e.g. typhoons), and interannual (e.g. El Niño Southern Oscillation hereafter ENSO) patterns of variability in ocean currents and their potential effects on larval transport must also be understood.

Ocean currents in the western Pacific have been coarsely characterized, but not at the scale of the Marianas region and not specifically in the context of larval transport. Broad regional studies reveal the main current in the Marianas to be the North Equatorial Current (NEC) (Reverdin et al. 1994) (Figure 1.1). This latitudinal current is flanked to the south by the North Equatorial Counter Current (NECC), and to the north by an area dominated by eddies and more sinuous flow that includes the northern Marianas. The Kuroshio Current bounds these regions to the north. Generally, broad-scale studies show that at the longitude of the Mariana Islands (145-146°E), the NEC runs westward all year between 9 and 16°N, with peak speed in January and lowest speed in July (Reverdin et al. 1994, Qui and Lukas 1996). At this longitude, the NECC runs eastward

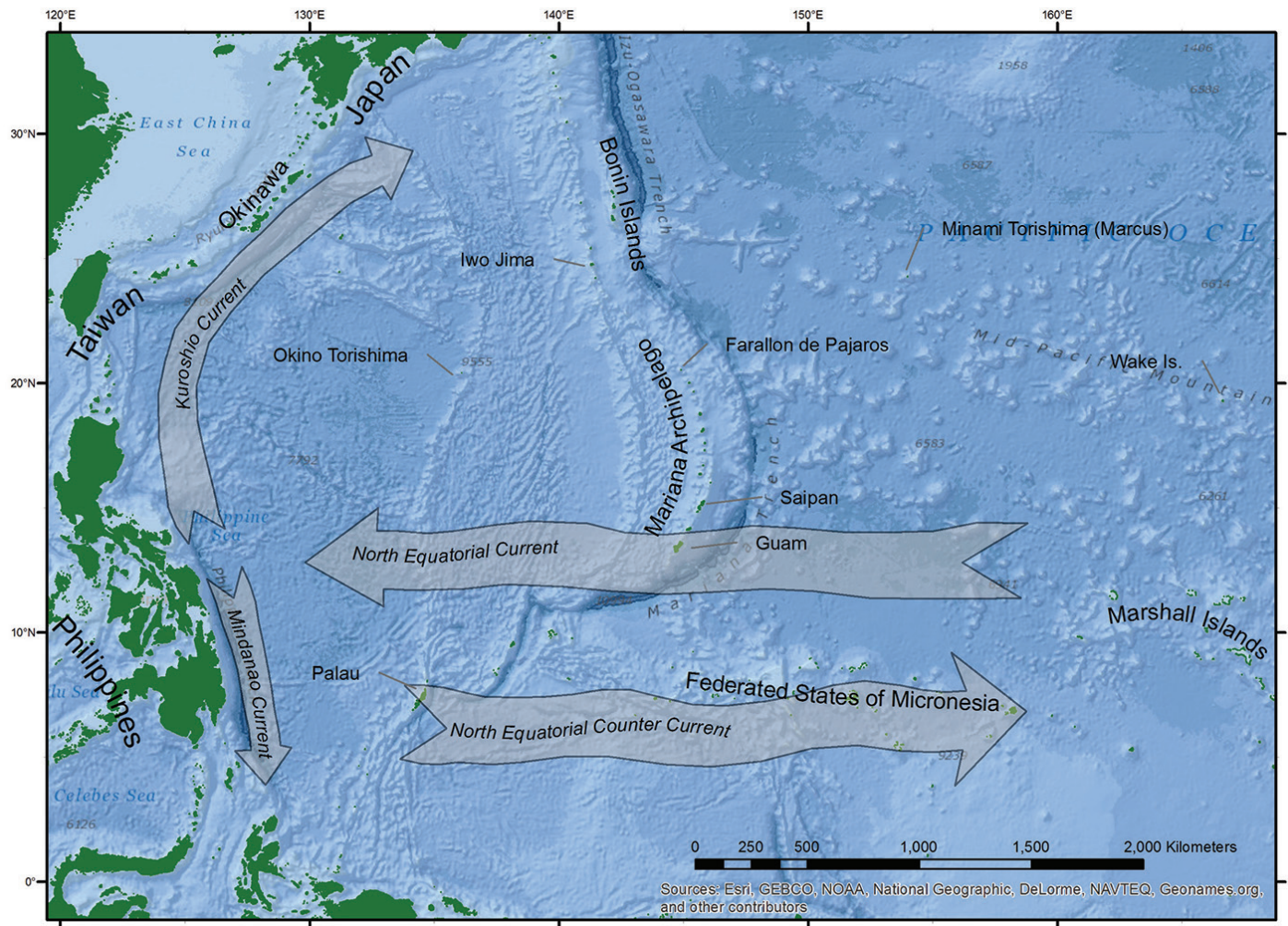


Figure 1.1. Major current patterns in the Northwest Pacific.

<sup>1</sup> NOAA/NOS/NCCOS/CCMA Biogeography Branch

<sup>2</sup> NOAA/NOS/NCCOS/CCMA/Biogeography Branch & Consolidated Safety Services, Inc., Fairfax, VA, under NOAA Contract No. DG133C07NC0616

all year between 2 and 9°N, with peak speed in July through October, and lowest speed in April and May. Farther west, the NEC bifurcates between 14° N and 16.5° N at the Philippine coast into the northward flowing Kuroshio Current and the southward flowing Mindanao Current (Qui and Lukas 1996).

Of particular importance is understanding the incoming and outgoing trajectories of currents passing through the archipelago. Mesopelagic plankton communities, including larval reef organisms, differ in waters east versus west of the Marianas (Suntsov and Domokos, 2012). Some questions that may be posed, are: “What are the origins of currents arriving at the archipelago?” “What islands do they pass by, and how long does it take the currents to reach the Marianas?” “Similarly, where do currents that pass through the archipelago end up?” These currents will carry larvae from the Marianas to other islands downstream, or possibly loop back to other islands within the archipelago.

Typhoons are also of potential importance for understanding the transport of marine larvae. The Marianas lie directly in the path of cyclonic storms that commonly develop in the northwestern Pacific. Typhoon passage may locally alter properties of surface waters, including current speed and direction and even salinity and temperature (Cheung et al. 2013, Fiedler et al. 2013). These physical changes may alter larval transport directly by changing flows, or indirectly by changing larval metabolism and longevity. An understanding of the timing, intensity, and frequency of storms and their impacts on surface flow is needed to determine their potential influence on larval transport.

Apart from the very broad and general characterizations (Reverdin et al. 1994, Qui and Lukas 1996), and a few very localized studies of coastal currents around parts of individual islands (Wolanski et al. 2003, Storlazzi et al. 2009), ocean currents have not been mapped at scales necessary for understanding larval transport and connectivity in the Mariana Archipelago. The goals in this chapter of the assessment were to: 1) characterize the speed, direction, and variability of the main surface currents along the north-south axis of the archipelago, 2) quantify the acute (due to typhoons), seasonal, and interannual variability in currents, 3) evaluate more detailed current patterns east (windward) and west (leeward) of the Mariana islands as currents flow through the archipelago, and 4) discuss the implications of these circulation patterns in the context of larval transport.

## METHODS

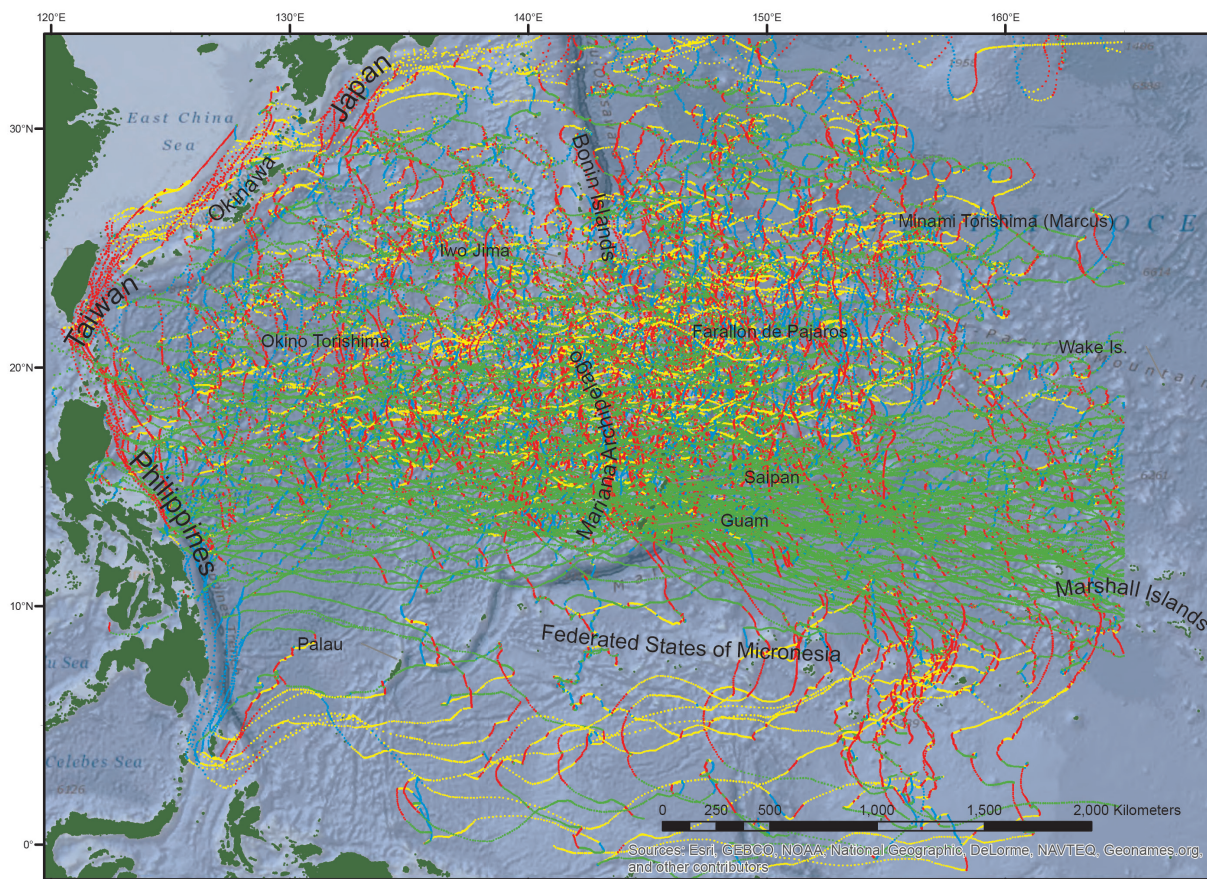
The NOAA Global Drifter Program uses satellites to track an extensive array of passively drifting drogues deployed at 15 m depth (NOAA Global Drifter Program, 2012). Drifter position, speed, and heading are recorded and then interpolated to six-hour intervals (Hansen and Poulain 1996). These smoothed data provide a detailed record of actual flow and were the primary dataset used in these analyses. Trajectories of many drifters analyzed in concert provide an excellent characterization of actual surface currents and their variability (Fossette et al. 2012).

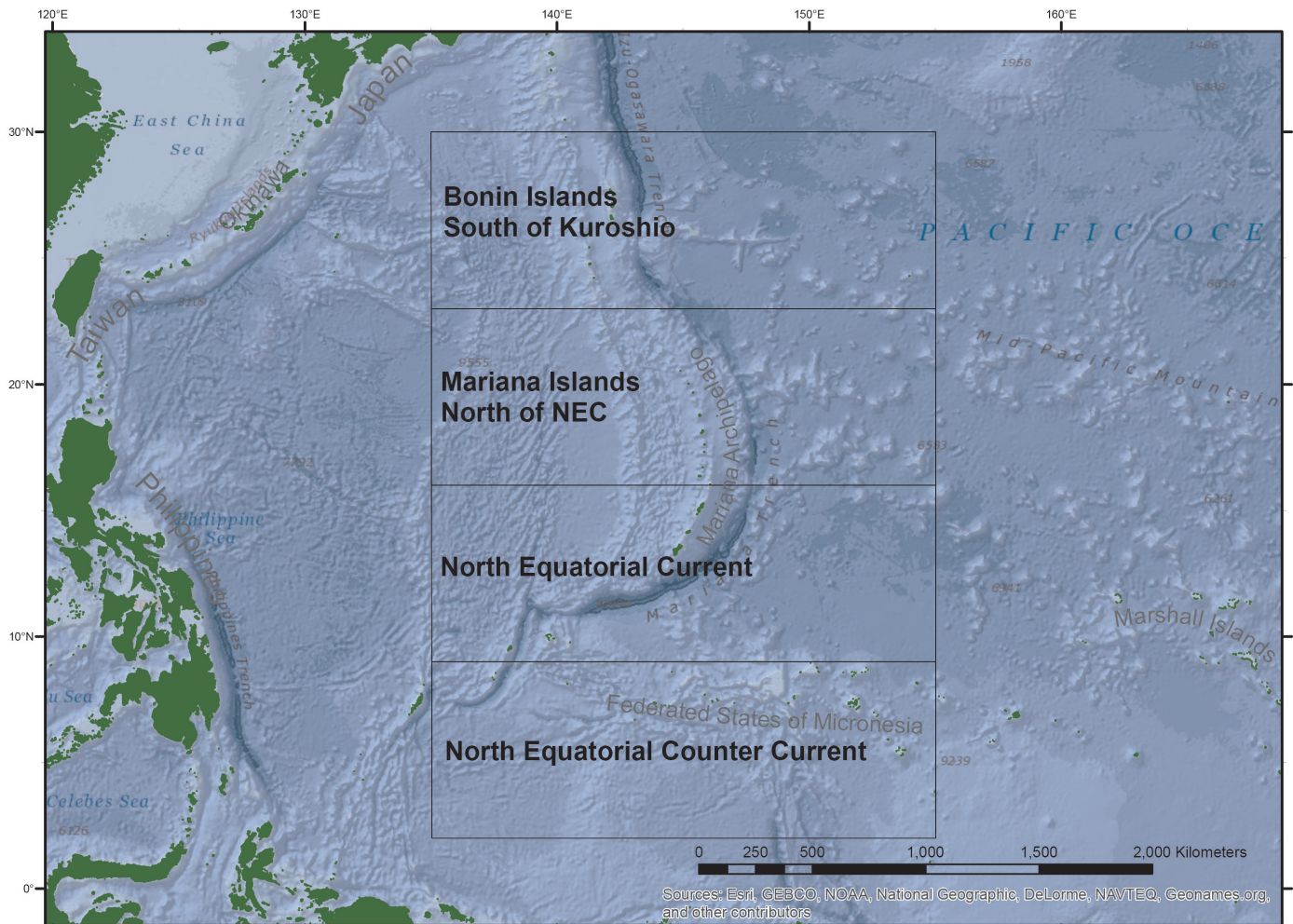
Data from all drifters passing through the Mariana region between 1990 and 2011 were downloaded from the Data Assembly Center on November 5, 2012 (<http://www.aoml.noaa.gov/phod/dac/meds.html>) (165° to 120° E longitude and 2° S to 37° N latitude). In addition to the quality control and processing procedures done by the NOAA Atlantic Oceanographic and Meteorological Laboratory (Hansen and Poulain 1996), records were deleted if they had missing velocity values, lost their subsurface drogue, or had only fragmented tracks at the fringes of the study area. This left a total of 1533 drifters for analysis (Table 1.1) (Figure 1.2). During this period there were ~700 to 900 drifters at large for every month and ~150-800 for every year. Longevity of individual drifters varied widely, from a few days to a few years, although most drifters were at large for at least several months before losing the subsurface drogue, washing ashore, or simply ceasing to transmit.

Analyses were focused on drifter speed and heading. Two sets of analyses were conducted to characterize currents. First, at the broadest scale surrounding the Marianas, segments of drifter paths lying within each current field were extracted. From south to north, the 4 current fields considered here were the NECC (2 to 9° N), NEC (9 to 16° N), the Marianas north of the NEC (16 to 23° N), and south of the Kuroshio Current around the Bonin Islands (23 to 30° N) (Figure 1.3). These equal-sized current regions were defined using previous studies and multiyear plots of drifter paths (Reverdin et al. 1994, Qui and Lukas 1996).

**Table 1.1.** The number of Global Drifter Program drifters at large in the study region by month and year following quality control procedures.

YEAR	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Totals
1990	14	21	21	26	22	34	27	22	16	14	12	9	238
1991	4	17	26	25	22	16	11	21	32	30	26	29	259
1992	34	49	54	48	42	34	35	43	54	51	54	56	554
1993	55	71	90	83	69	73	57	45	48	56	55	54	756
1994	52	47	39	35	37	33	44	39	36	37	41	37	477
1995	26	27	36	31	31	31	31	29	28	30	31	34	365
1996	32	30	37	31	36	31	31	36	32	27	25	19	367
1997	18	19	22	18	17	17	18	18	17	15	15	15	209
1998	15	14	16	16	12	11	12	10	10	13	12	14	155
1999	13	14	13	11	9	6	8	11	15	15	15	13	143
2000	19	18	18	18	19	19	21	22	19	17	20	22	232
2001	21	20	26	32	31	36	36	31	35	35	33	28	364
2002	25	25	22	19	18	27	26	27	36	39	35	25	324
2003	20	22	21	22	32	30	25	25	23	52	67	65	404
2004	59	50	50	42	40	49	44	43	57	54	54	53	595
2005	52	49	45	50	52	51	51	54	52	58	101	106	721
2006	96	89	70	59	68	69	74	64	52	55	47	45	788
2007	39	33	32	25	29	28	27	24	25	41	39	31	373
2008	24	26	26	24	30	33	33	34	49	50	51	47	427
2009	42	40	35	31	29	34	42	102	108	94	85	78	720
2010	70	63	53	50	53	56	42	46	64	76	74	72	719
2011	56	50	53	39	40	32	26	32	29	15	9	5	386
Totals	786	794	805	735	738	750	721	778	837	874	901	857	9,576

**Figure 1.2.** Tracks of the Global Drifter Program drifters at large in the study area ( $n=1,533$  drifters) from 1990 to 2011. Position is calculated every six hour and color coded by heading where red = northward, blue = southward, yellow = eastward, and green = westward.

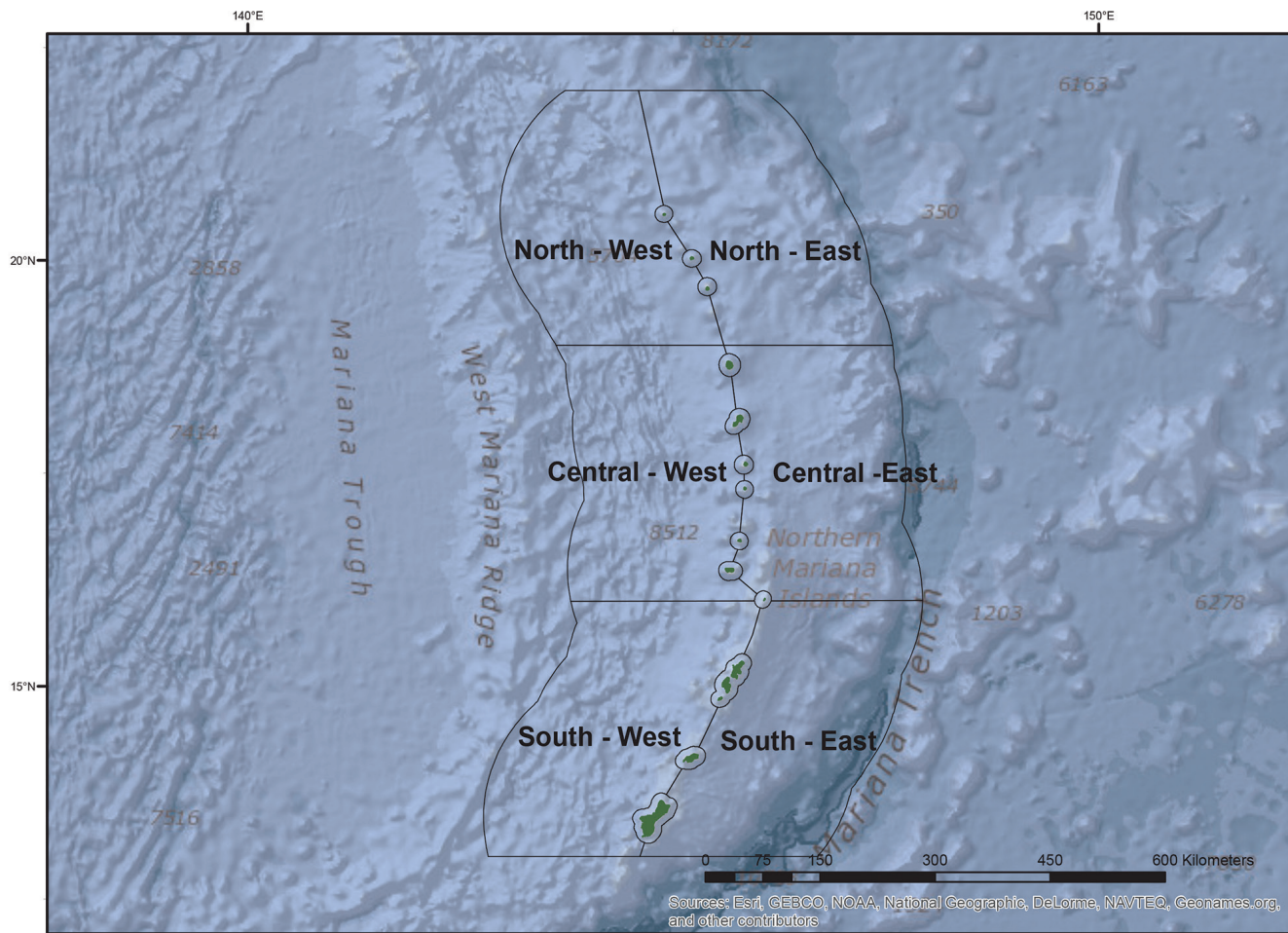


**Figure 1.3.** Regions defined for the broad-scale analysis of ocean currents.

Second, a finer-scaled analysis of current patterns just within the Mariana archipelago was conducted. For this, drifter segments were assigned to one of 6 zones according to their position along and across the archipelago (Figure 1.4). This was done to evaluate the finer-scale current patterns and likely transport environment for larvae along the major geographic divisions within the archipelago, as well as for windward versus leeward regions. Drifter paths were clipped to the region extending from 10 to 200 km around each island, separated along the axis of the archipelago into east and western areas, and then further split into three latitudinal zones. From south to north these approximately equal-sized areas consisted of a southern zone, including Guam to Saipan (13 to 16° N), a central zone from Farallon de Medinilla to Agrihan (16 to 19° N), and a northern zone from Agrihan to north of Farallon de Pajaros (19 to 22° N).

Mean drifter speed and heading were calculated for each drifter segment by current field and archipelagic zone and then displayed using box plots and compass plots. This enabled evaluation of median current conditions as well as variability. The bold line in the middle of the box plot denotes the median observation, the top and bottom of the box denote the interquartile range, whiskers extend to the point nearest 1.5 times the interquartile range, and more extreme values are plotted individually. The bold line in compass plots denotes the median heading and the thinner lines denote the interquartile range of headings. Box and compass plots for current fields and zones were used to evaluate speed and heading overall, and also separately among seasons, years, and by ENSO state to characterize their potential influence on drifter movement. ENSO states (El Niño, La Niña, or neutral) were obtained from the NOAA National Weather Service's Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/>).

Differences in speed among regions were evaluated by first using the Kruskal-Wallis ANOVA by ranks to determine if there was a difference in speed among groups. If a significant difference was found in the overall



**Figure 1.4.** Zones defined for the archipelagic-scale analysis of ocean currents around the Marianas.

test, a non-parametric multiple comparison test was conducted to determine which groups differed within plots. The Watson-Williams Test was used to determine if there was a significant difference among headings. In addition, the number, timing, and intensity (Saffir-Simpson Hurricane Wind Scale) of typhoons passing through the Marianas were summarized using archived hurricane track data from NOAA/National Weather Service (<http://weather.unisys.com/hurricane/>). All Category 1-5 typhoons passing through the 200 km archipelagic zones (Figure 1.5) around the Marianas from 1990 to 2010 were included in the analysis. Typhoons were summarized by year and category to understand the inter-annual variability of storms and frequency of potential effects on larval transport. Summaries based on month and storm category were used to understand which months, and therefore spawning seasons, were most likely to be affected by storms.

Typhoon influence on local currents was evaluated by first identifying dates when the paths of both a typhoon and a drifter crossed within 50 km of each other. Drifters stay in the area for many days, whereas typhoons quickly pass through in comparison. To determine if the passage of the typhoon had any effect on drifter variables, the drifter path was segmented into 2 components, the 3 days before the passage of the storm and the 3 days following its arrival. Preliminary evaluation indicated no perceptible effect on drifter behavior for typhoons farther than 50 km away and more than 3 days from a drifter path. Values for drifter speed, heading, and ocean temperature are provided as 6 hour intervals and were extracted for each segment (i.e. 4 per day for 3 days yields 12 values). First, it was determined whether the speed, water temperature, and heading values of each segment were significantly different “before” versus “after” the typhoon arrived. For differences in speed and temperature, one-tailed Mann-Whitney tests were used, and for heading, a Watson-Williams test for compass directions was used (Zar 1999).

In addition, due to low sample size where drifters and typhoons were coincident, a permutation analysis was performed. This was done to determine the probability that the observed differences in speed and tem-

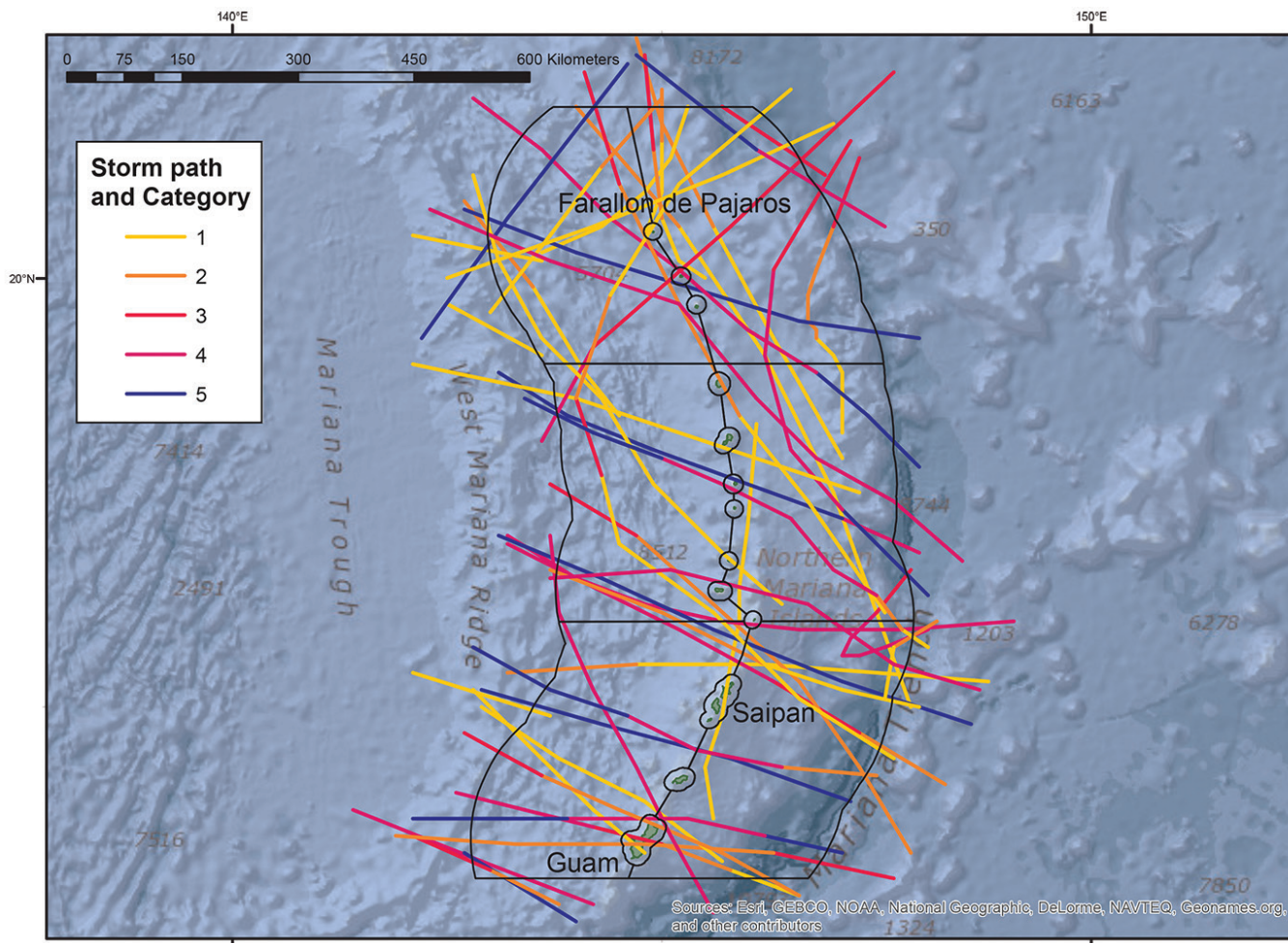


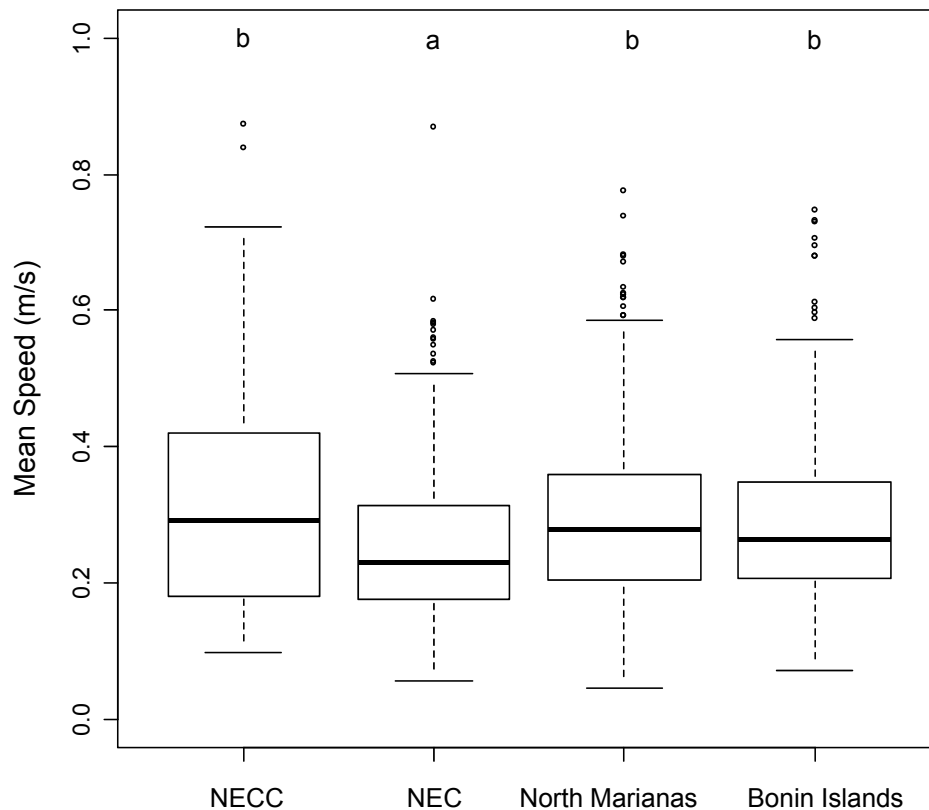
Figure 1.5. Path and severity of all Category 1-5 typhoons passing through the Marianas from 1990-2010.

perature resulting from typhoon passage could have arisen by chance in the drifter data. For this analysis, 100 segments of drifter data were randomly selected from the Mariana area whether or not a typhoon was present. Each segment consisted of 6 consecutive days and was split into 2 three-day segments, as in the previous analysis for “before” versus “after” a typhoon arrived. The difference in mean drifter speed and ocean temperature was calculated between the first 3 days and the second three days of each segment. This established a population of 100 typical differences that may occur in any 6 days of drift, which could be compared to the actual differences that occurred in drift when typhoons passed through. Next was calculated the percentage of times that a random drifter segment had a difference greater than or equal to the observed difference due to a typhoon. This served as a p-value, expressing the probability that an observed difference could have arisen by chance alone. Heading changes were more erratic and not amenable to this type of analysis.

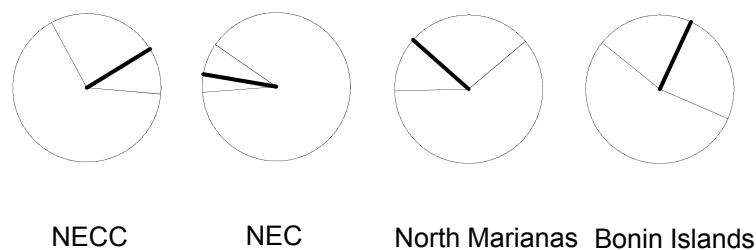
## RESULTS

### Drifter Speed, Heading, and Variability among Current Fields

Drifter speeds were broadly consistent among the four current fields that were considered. Median values for the NECC, NEC, north Marianas, and Bonin Islands ranged from  $\sim 23 \text{ cm s}^{-1}$  to  $29 \text{ cm s}^{-1}$ , with the NEC slowest and NECC fastest (Figure 1.6). Interquartile range, a measure of variability in current velocity, was also broadly consistent among the four current fields. In contrast, drifter headings were quite different among the current fields (Figure 1.7). Median heading was  $\sim 60^\circ$  (ENE) for the NECC,  $280^\circ$  ( $\sim$ W) for the NEC,  $310^\circ$  (WNW) for the north Marianas, and  $25^\circ$  (NNE) for the Bonin Islands. The range of drifter headings was also quite different among current fields. The NEC had a much narrower interquartile range, and therefore much less variation in drifter heading than other current fields. Current headings in the north Marianas and Bonin Islands were nearly randomly distributed around the compass.



**Figure 1.6** Box plots of mean drifter speed by current fields. Kruskal-Wallis chi-squared = 37.7973,  $df = 3$ ,  $p < 0.0000$ . Letters denote groups not significantly different from each other in multiple comparison test.

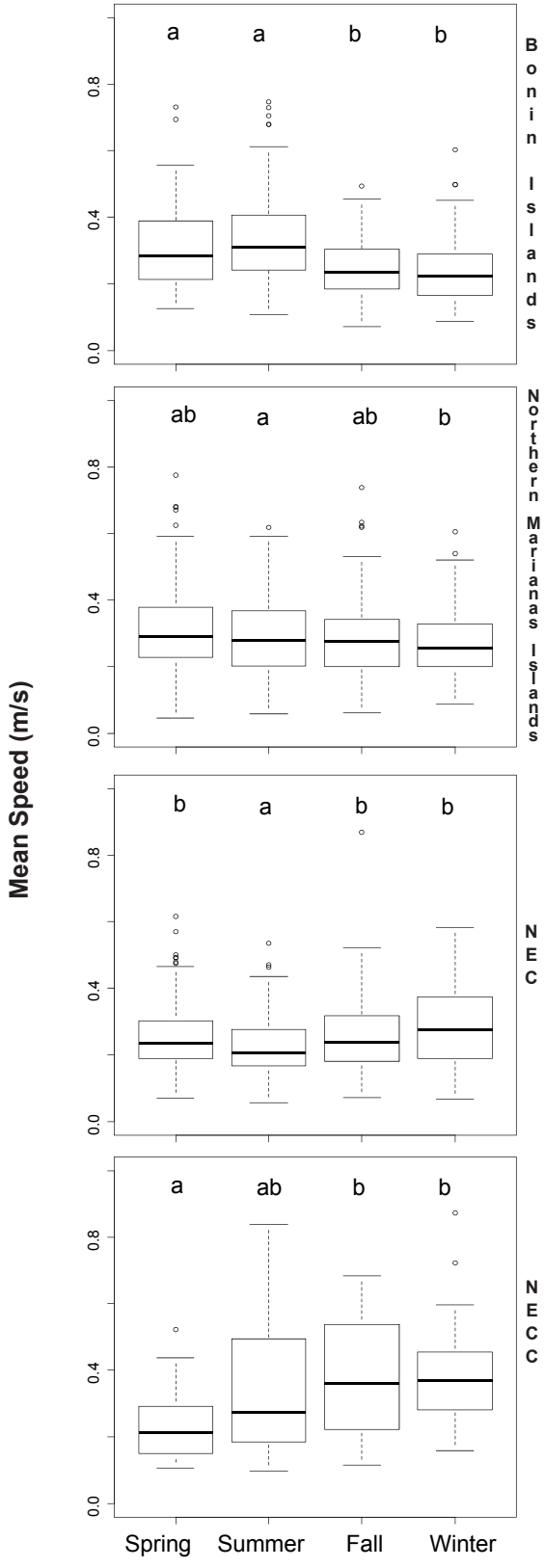


**Figure 1.7.** Compass plots of mean drifter heading among current regions. Bold line denotes median heading and thin lines denote interquartile-range. Watson-Williams Test  $F = 54.2$ ,  $df_1 = 3$ ,  $df_2 = 1845$ ,  $p < 0.0000$ .

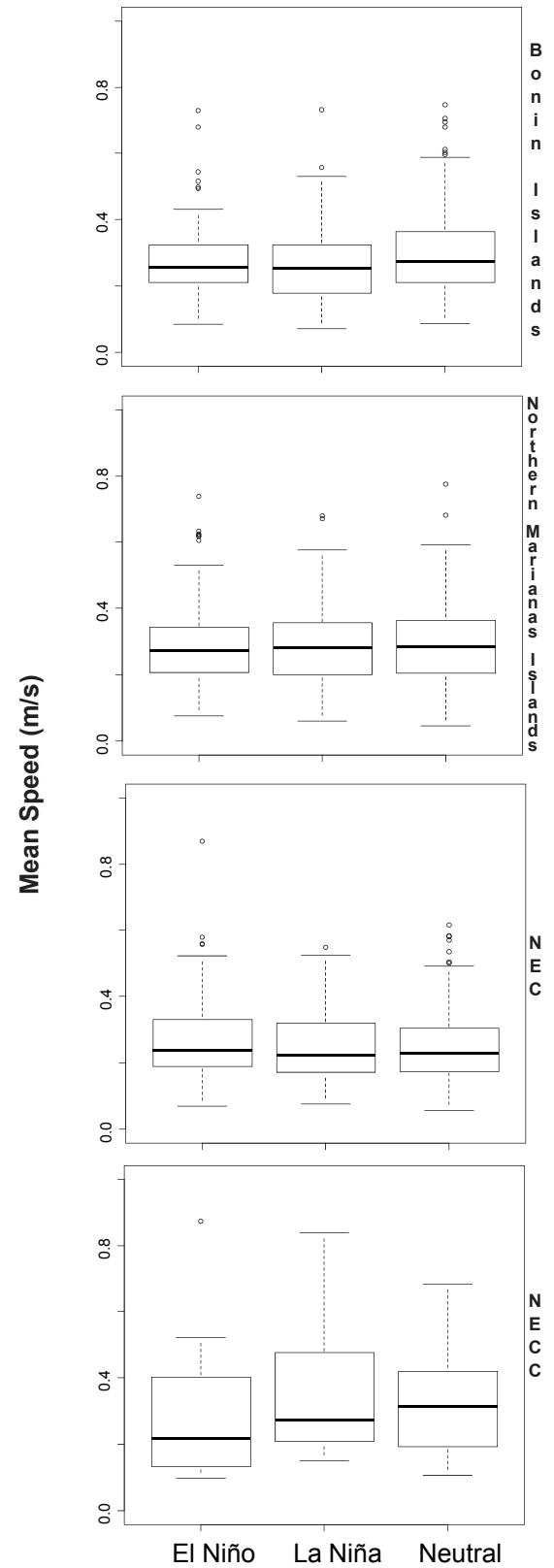
### Drifter Speed, Heading, and Variability among Seasons, ENSO States, and Years by Current Field

Drifter speeds were broadly similar among seasons in the four current fields (Figure 1.8). Minor exceptions were that drifters in the NECC had lower speed and narrower range of values in Spring than in Fall and Winter. The NEC was significantly slower in the Summer, whereas currents in the Bonin Islands were slower in the Fall and Winter compared to other seasons. ENSO state had no significant effect on drifter speed in any region (Figure 1.9). Drifter speeds varied among years, with the period from 2004-2007 showing somewhat higher velocities in the NEC and north Marianas regions compared to other years (Figure 1.10). There were too few drifters present in the NECC in many years to evaluate interannual patterns.

Drifter headings showed some seasonal differences within current fields. The NECC showed the most variation in drifter heading among seasons (Figure 1.11). In contrast, the NEC was most consistent, and flowed westward with little variability among seasons. Drifter headings in the Bonin Islands were nearly random

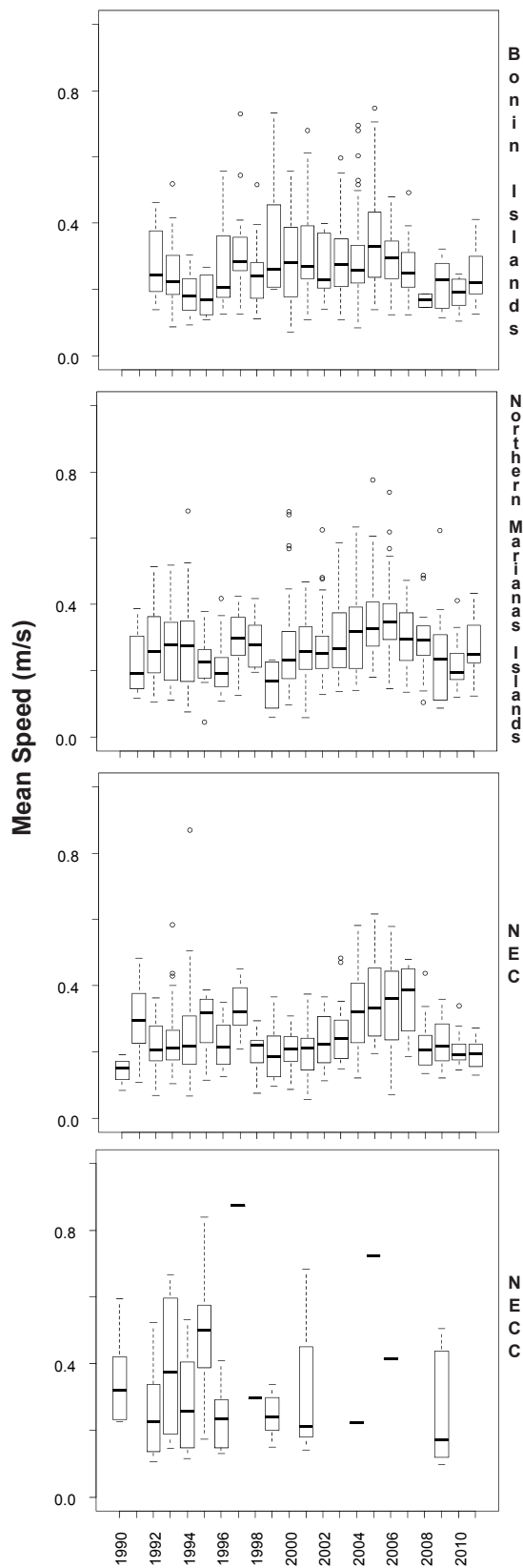


**Figure 1.8.** Box plots of mean drifter speed by season for each current field. Letters denote significant differences within groups in each plot in multiple comparison tests.

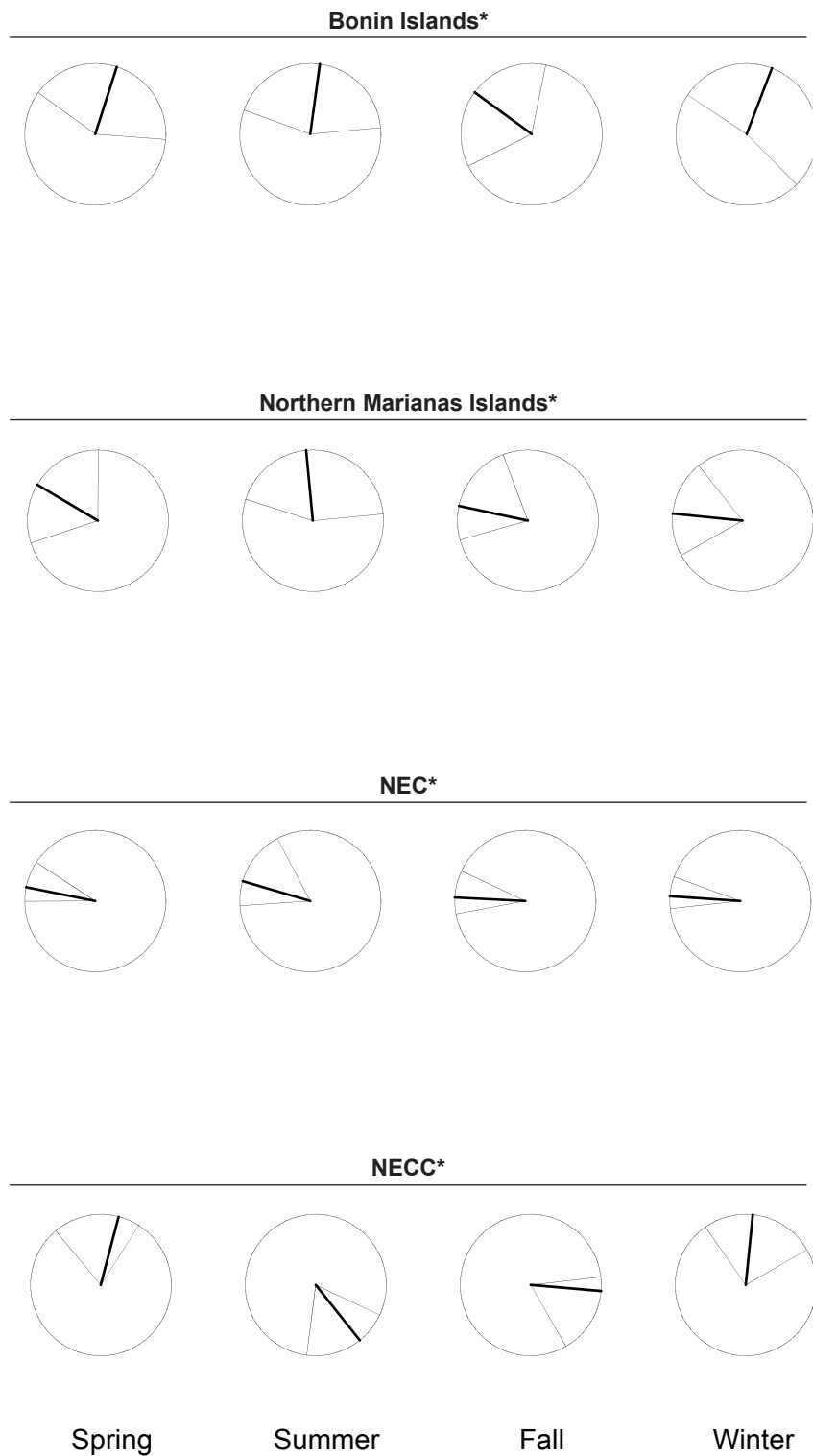


**Figure 1.9.** Box plots of mean drifter speed by ENSO state for each current field. No Kruskal-Wallis Tests revealed significant differences therefore no multiple group comparisons were warranted.



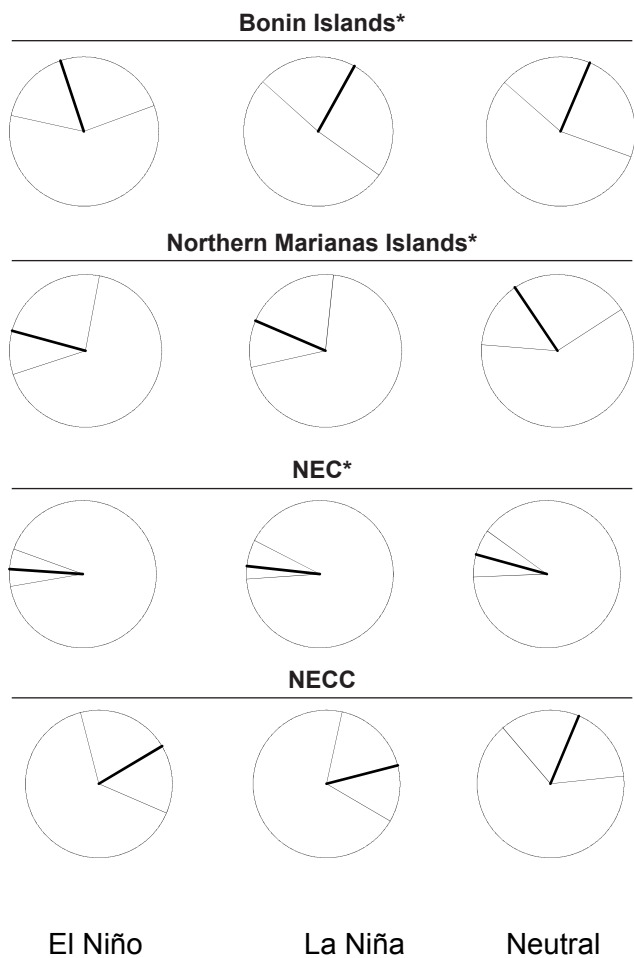


**Figure 1.10.** Box plots of mean drifter speed by year for each current field.

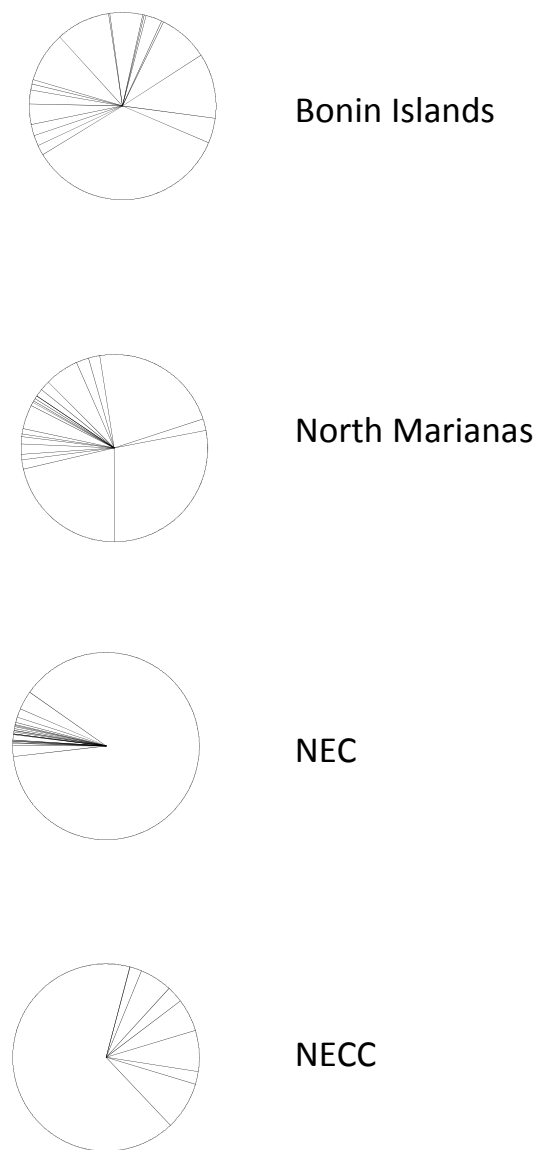


**Figure 1.11.** Compass plots of drifter heading by season for each current field. Bold lines denote median heading and thin lines denote interquartile-range. \* denotes significant result of Watson-Williams Test for differences among median headings  $p < 0.05$

among all seasons. Drifter headings were broadly consistent among ENSO states within all 3 current fields (Figure 1.12). Median drifter headings were consistently westward in the NEC among years, generally eastward in the NECC among years, northeastward in the northern Marianas in most years, and had the greatest variability among years around the Bonin Islands (Figure 1.13).



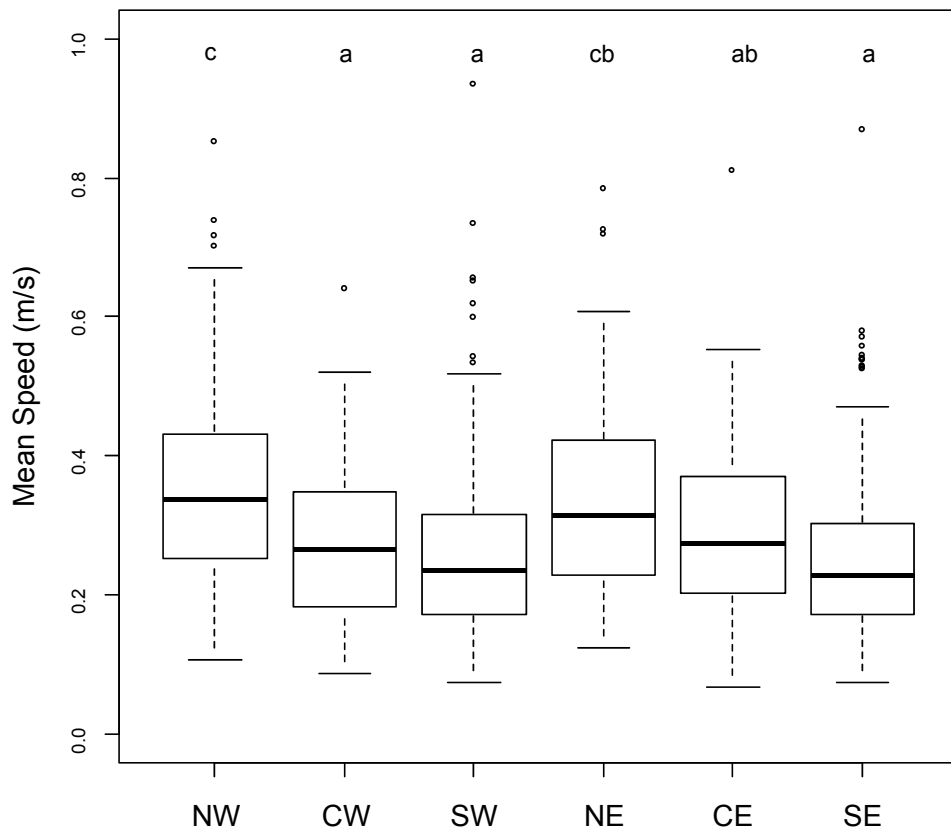
**Figure 1.12.** Compass plot of drifter heading by ENSO state for each current field. Bold lines denote median heading and thin lines denote interquartile-range. \* denotes significant result of Watson-Williams Test for differences among median headings  $p < 0.05$ .



**Figure 1.13.** Compass plot of drifter heading by year for each current field. Lines denote median heading for years with  $> 5$  drifters. \* denotes significant result of Watson-Williams Test for differences among median headings  $p < 0.05$ .

### Drifter Speed, Heading, and Variability among Archipelagic Zones

At the finer scale within the Mariana archipelago, drifter speeds showed a latitudinal pattern. The two northern zones had highest median speeds of  $\sim 32 \text{ cm s}^{-1}$  and the two southern regions had slowest median speeds of  $\sim 23 \text{ cm s}^{-1}$  (Figure 1.14). Interquartile range of speed was broadly consistent among the 6 zones. Drifter headings were generally westward or northwestward in the central and southern regions, between  $275$  and  $325^\circ$  (Figure 1.15). In contrast, the two northern zones had much wider interquartile ranges, distributed randomly around the compass, and therefore more variation in drifter heading than other zones. The two southern zones had relatively narrow interquartile ranges, and therefore the most consistent flow heading. Also, in the southern zones, the incoming current from the east had more consistent headings than the outgoing drifters to the west.

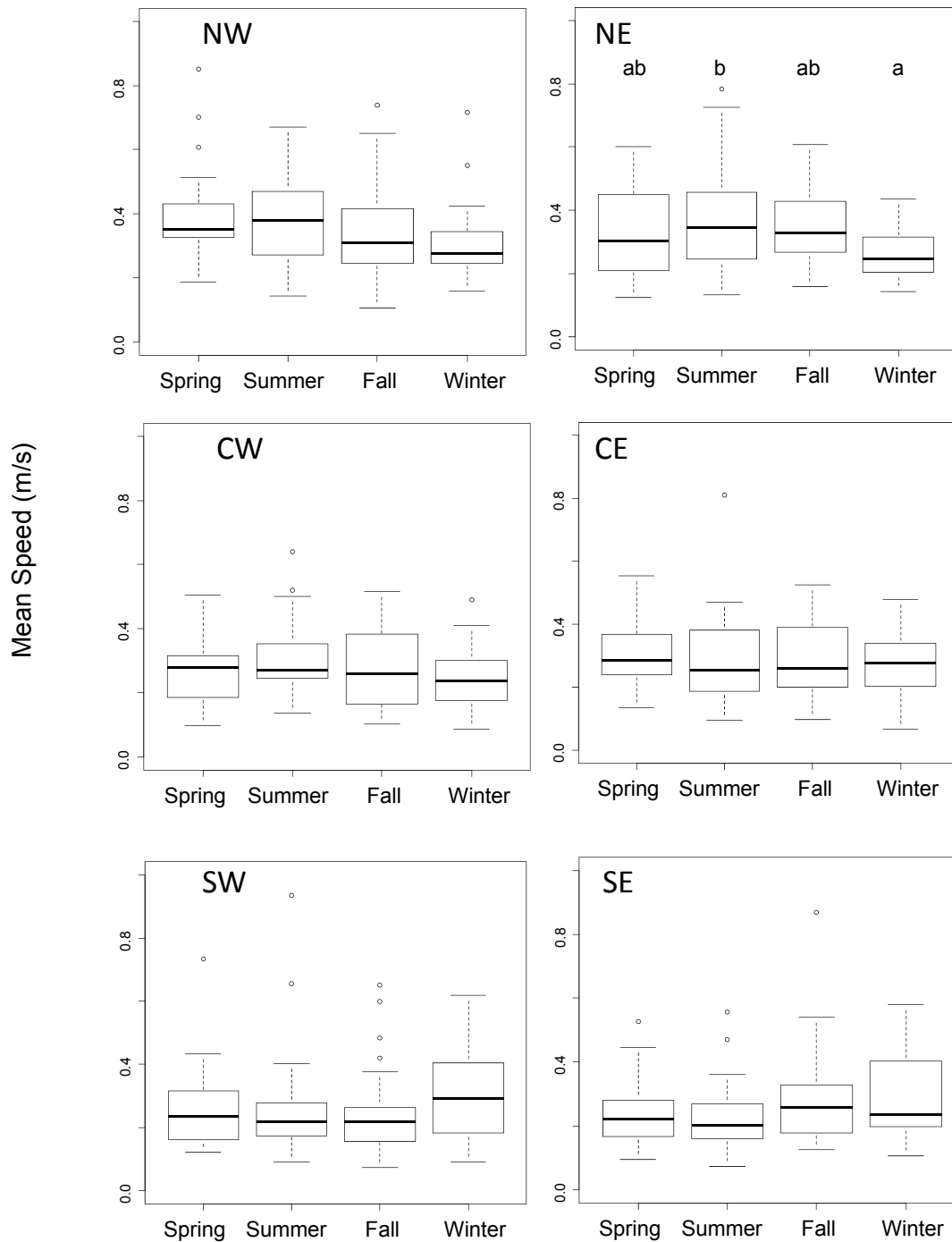


**Figure 1.14.** Box plots of drifter speed among archipelagic zones. Kruskal-Wallis chi-squared = 63.3,  $df = 5$ ,  $p < 0.0000$ . Letters denote groups not significantly different from each other in multiple comparison test.

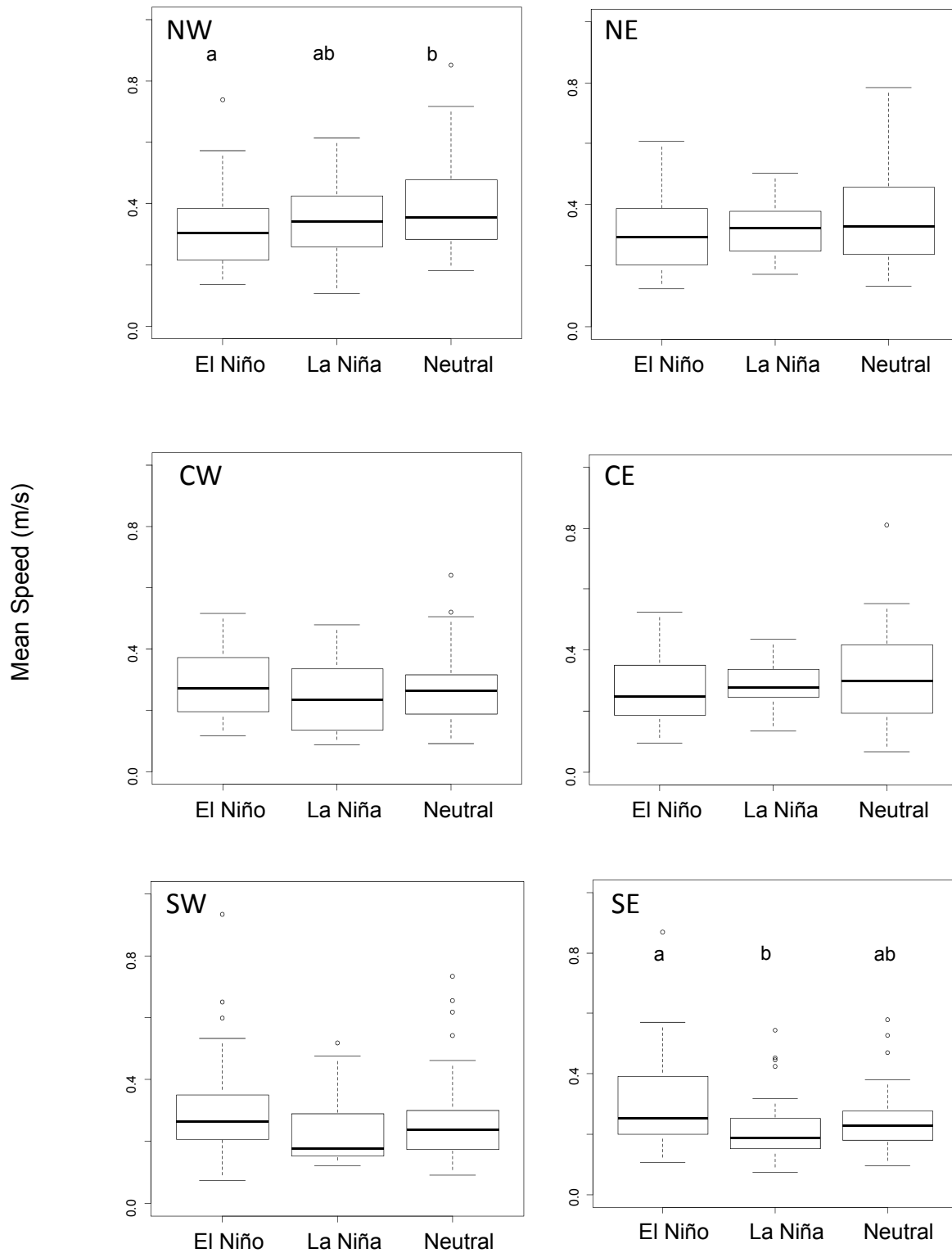
**Figure 1.15.** Compass plots of drifter heading among archipelagic zones. Bold lines denote median heading and thin lines denote interquartile-range. Watson-Williams Test  $F = 5.7$ ,  $df_1 = 5$ ,  $df_2 = 722$ ,  $p < 0.0000$ .

**Drifter Speed, Heading, and Variability by Season, ENSO State, and Year among Archipelagic Zones**

Drifter speeds were broadly similar among seasons in all zones with no consistent patterns (Figure 1.16). Only the NE zone had significant differences among seasons with lower speed and variability in Winter than in Summer. ENSO state also had no significant effect on drifter speed in most zones (Figure 1.17). Excep-



**Figure 1.16.** Box plots of drifter speed by season for each archipelagic zone. Only the NE zone had a significant Kruskal-Wallis test, chi-squared = 7.8, df = 3,  $p < 0.049$ . Letters denote groups not significantly different from each other in the multiple comparison test.



**Figure 1.17.** Box plots of drifter speed by ENSO state for each archipelagic zone. The SE and NW zones had significant Kruskal-Wallis tests. Letters denote groups not significantly different from each other in the multiple comparison test.

tions were the lower median drifter speeds in the SE and NW zones during La Niña and El Niño conditions, respectively. Drifter speeds varied considerably among years, with 2004-2007 showing higher speed in most zones. However, there were too few drifters present in each zone for many years to evaluate the statistical significance of interannual patterns (Figure 1.18).

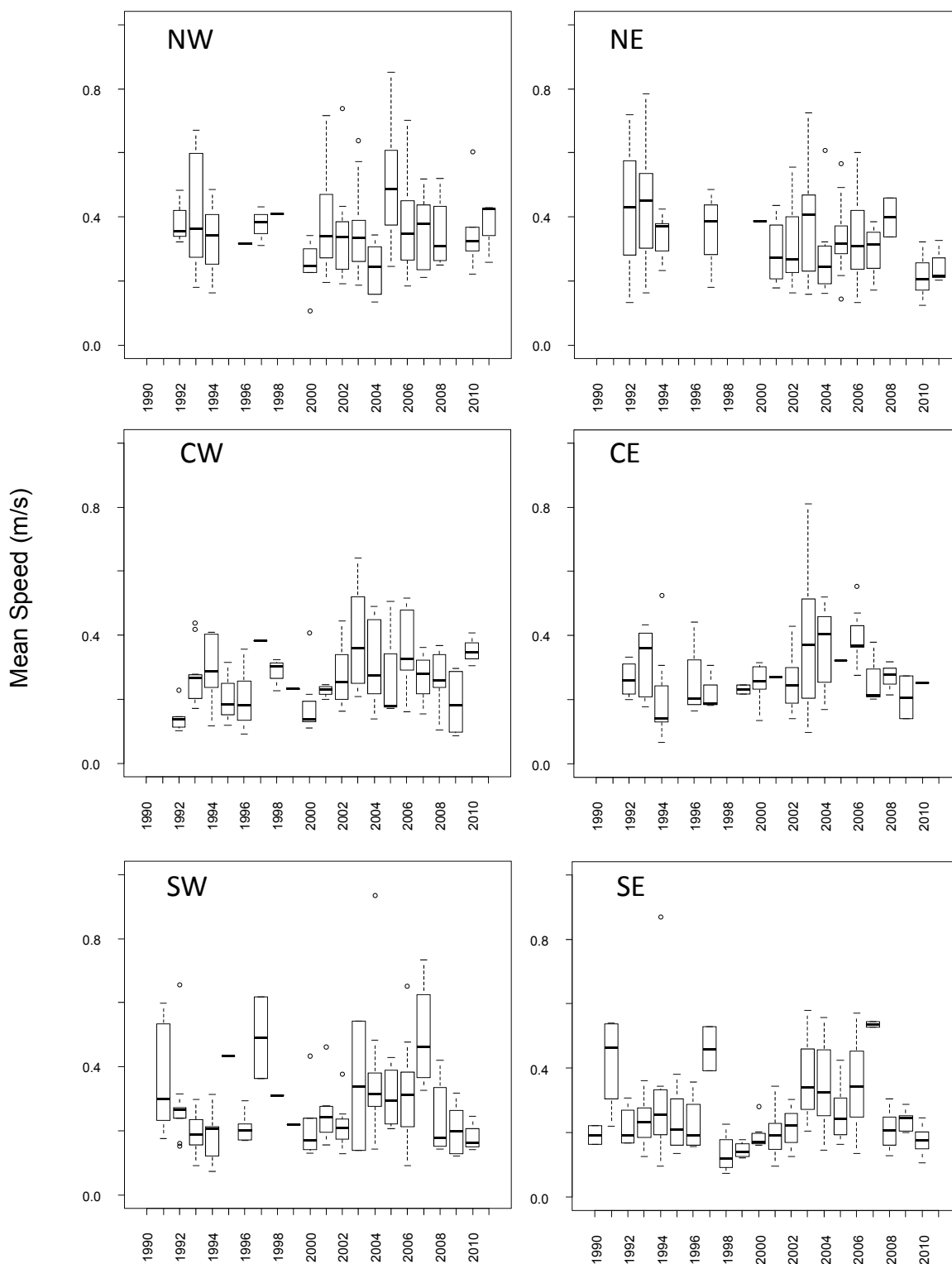
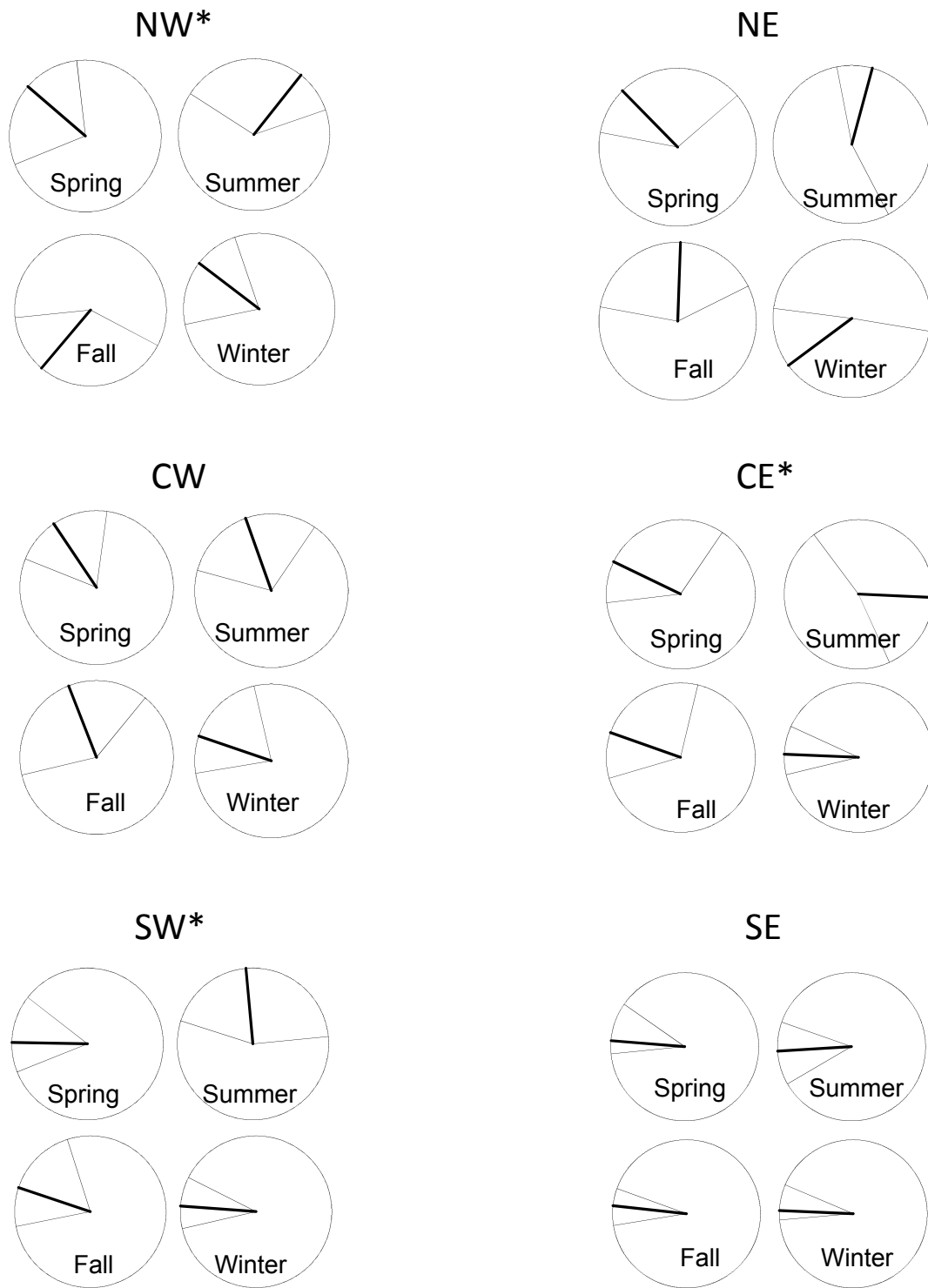


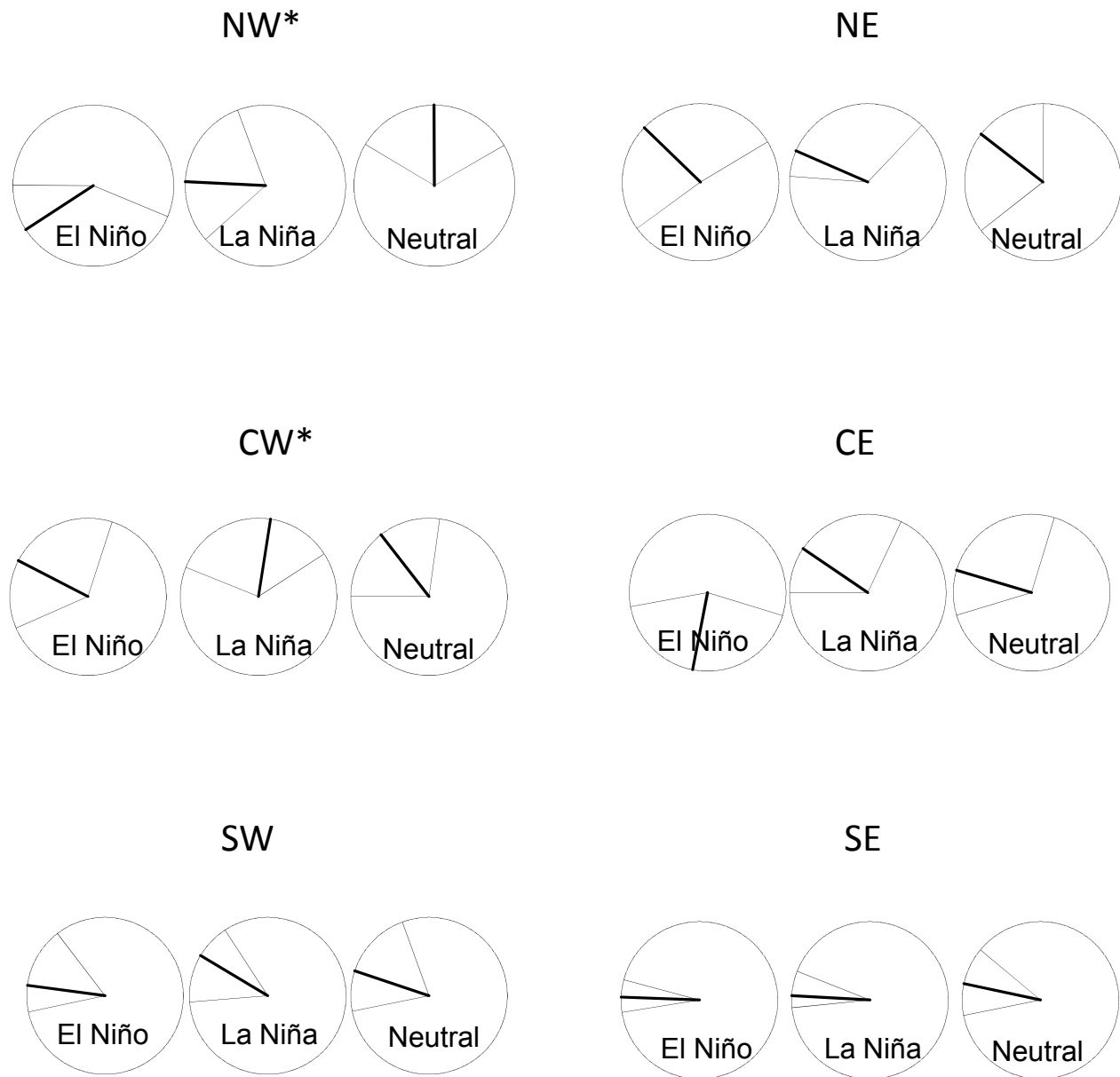
Figure 1.18. Box plots of drifter speed by year for each archipelagic zone.

Drifter headings were consistent among seasons in the SE and Central West (CW) zones (Figure 1.19). Drifter headings in summer were especially variable in the SW and Central East (CE) zones. The northern zones had much greater variation in heading and interquartile range among seasons. Drifter headings



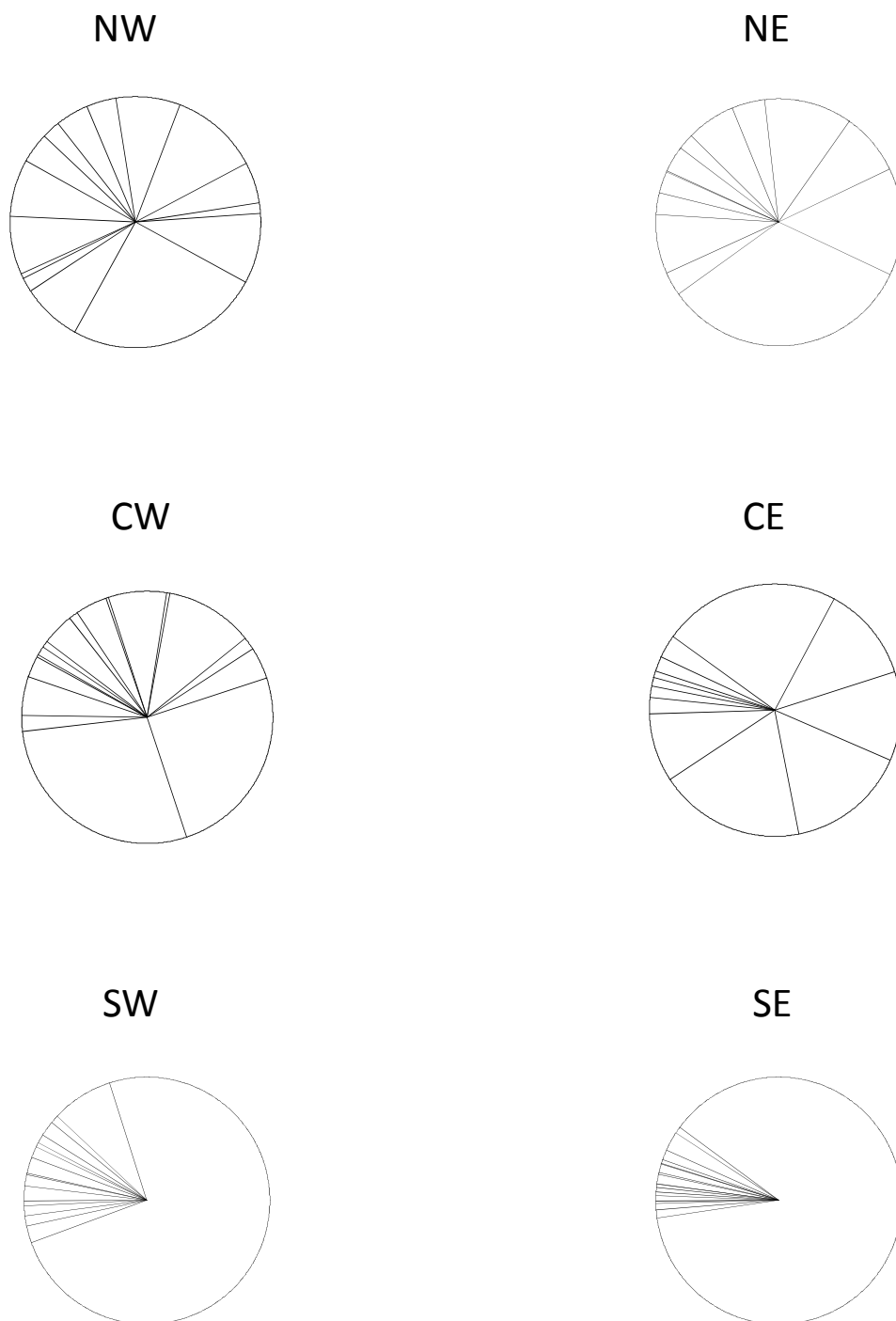
**Figure 1.19.** Compass plots of drifter heading by season for each archipelagic zone. \* denotes significant result of Watson-Williams Test for differences among median headings  $p < 0.05$

among ENSO states were broadly consistent within most zones, with the NW and CE zones showing the most variation (Figure 1.20). Drifter headings showed consistently westward flow in the SE among years, and still westward but slightly more variable in the SW zone (Figure 1.21). There was greater variability in headings in the central and northern zones.



**Figure 1.20.** Compass plots of drifter heading by ENSO state for each archipelagic zone. \* denotes significant result of Watson-Williams Test for differences among median headings  $p < 0.05$



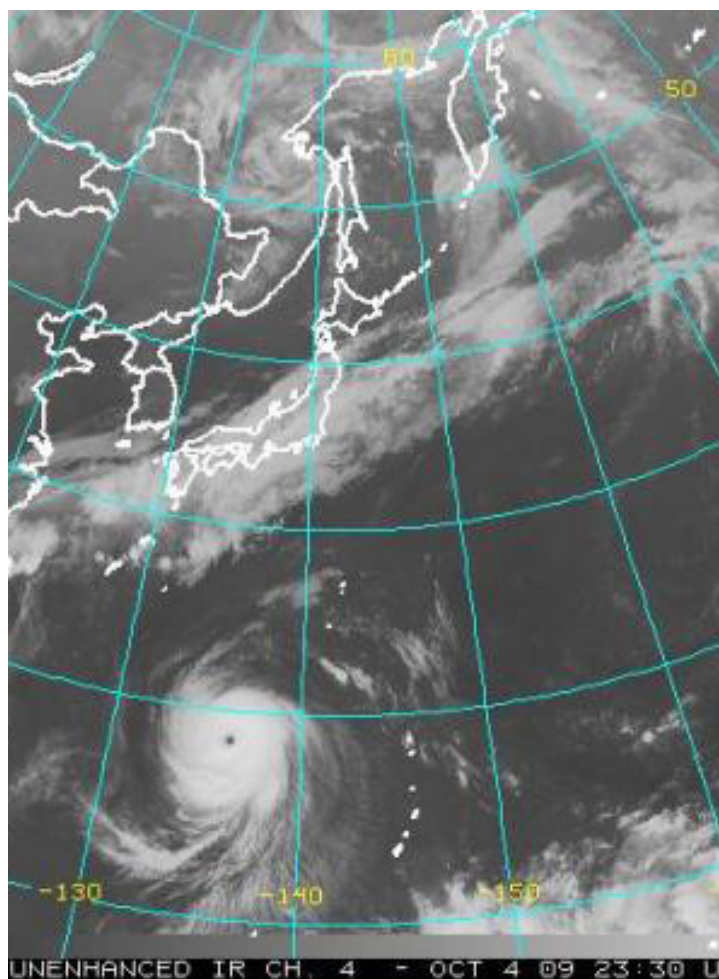


**Figure 1.21.** Compass plots of drifter heading by year for each archipelagic zone. Lines denote median heading for years with > 5 drifters. Missing values prevented use of the Watson-Williams Test for differences among median headings.

## Typhoon Influence

There were 47 typhoons spread throughout the study area between 1990 and 2010, with roughly equal numbers in each Saffir-Simpson Category (Table 1.2). There were relatively more storms in the period 1990-1997 compared to more recent years in the time series. The seasonal peak in typhoon activity occurs in August through November, with a clear spike in September (Figure 1.22).

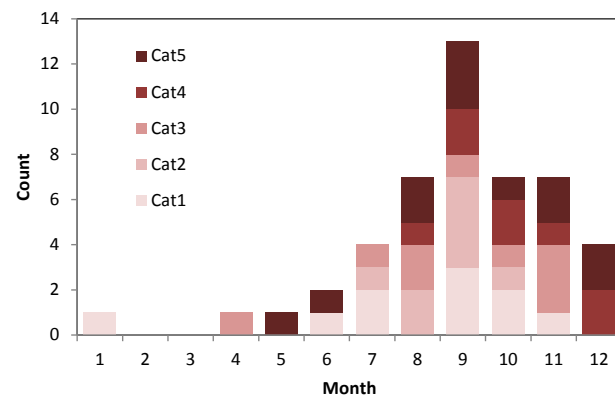
Six drifters passed within 50 km of a typhoon's position. All but one experienced a significant increase in drifter speed during the three days following arrival of the storm (Table 1.3). Increases in speed ranged from 131% to 321% of the pre-arrival velocity. Permutation tests revealed that changes of this magnitude in current speed never occurred by random chance. Every drifter experienced a significant decline in water temperature following arrival of the storm. Decreases ranged from 0.3 to 1° C cooler and could not be explained by drifters simply moving northward. Permutation tests revealed that temperature reductions of these magnitudes had only a 6% to 0% chance of arising randomly.



Guam typhoon.  
Photo credit: NOAA.

**Table 1.2.** Number of typhoons in the Marianas region by year and Saffir-Simpson category.

	Cat1	Cat2	Cat3	Cat4	Cat5	Totals
1990	1	2		1		4
1991		2		1	1	4
1992	2		3	1		6
1993		1				1
1994			1	1		2
1995	2					2
1996	2		1	1		4
1997					6	6
1998						0
1999						0
2000		1				1
2001		1	1		1	3
2002	1		2	1	1	5
2003						0
2004	1			1	1	3
2005	1	1				2
2006					1	1
2007			1			1
2008						0
2009				1	1	2
2010						0
Totals	10	8	9	8	12	47



**Figure 1.22.** Number of typhoons in each Saffir-Simpson category by month in the Marianas region between 1990 and 2010.

Headings were significantly different for four of the six drifters at large in the presence of a typhoon. Differences were not uniform in that some currents showed more variation in headings after the storm and some showed less. The direction of deflection depended on the relative position of the drifter to the storm path.

**Table 1.3.** Typhoon influence on drifter paths. Storm numbers are from NOAA National Weather Service (<http://weather.unisys.com/hurricane/>). Category denotes the Saffir-Simpson value of the storm on the date of drifter presence. Drifter numbers are from the NOAA Global Drifter Program. Drifter speed, heading, and ocean temperature are shown as the mean of the three days before each storm, the mean of the three days after each storm, the difference in these values (bold denotes a significant difference, i.e.  $p < 0.05$ , in either the Mann-Whitney Test for analyses of speed and temperature or Watson-Williams Test for analyses of heading), and if significant, the probability that such a value arose by chance alone in the permutation test for speed and temperature.

Storm	Category	Drifter	Date	Drifter Speed (cm/s)				Ocean Temperature (C°)				Drifter Heading Degrees		
				Before	After	Difference	Permutation	Before	After	Difference	Permutation	Before	After	Difference
1993-23	2	311,977	24-Sep	45	59	14	$p < 0.00$	29.5	29.2	-0.3	$p < 0.06$	11	17	6
1994-35	4	2,012,177	24-Oct	24	65	41	$p < 0.00$	29.1	28.1	-1	$p < 0.00$	177	92	-85
1994-37	2	2,012,177	1-Nov	25	86	61	$p < 0.00$	28	27.2	-0.8	$p < 0.00$	46	22	-24
2002-25	1	34,843	27-Sep	32	49	17	NA	29.8	29.3	-0.5	$p < 0.02$	34	64	30
2004-19	5	39,606	22-Aug	33	106	73	$p < 0.00$	29.3	28.9	-0.4	$p < 0.04$	277	311	34
2004-22	4	36,924	31-Aug	18	53	35	$p < 0.00$	29	28.7	-0.3	$p < 0.06$	48	41	-7

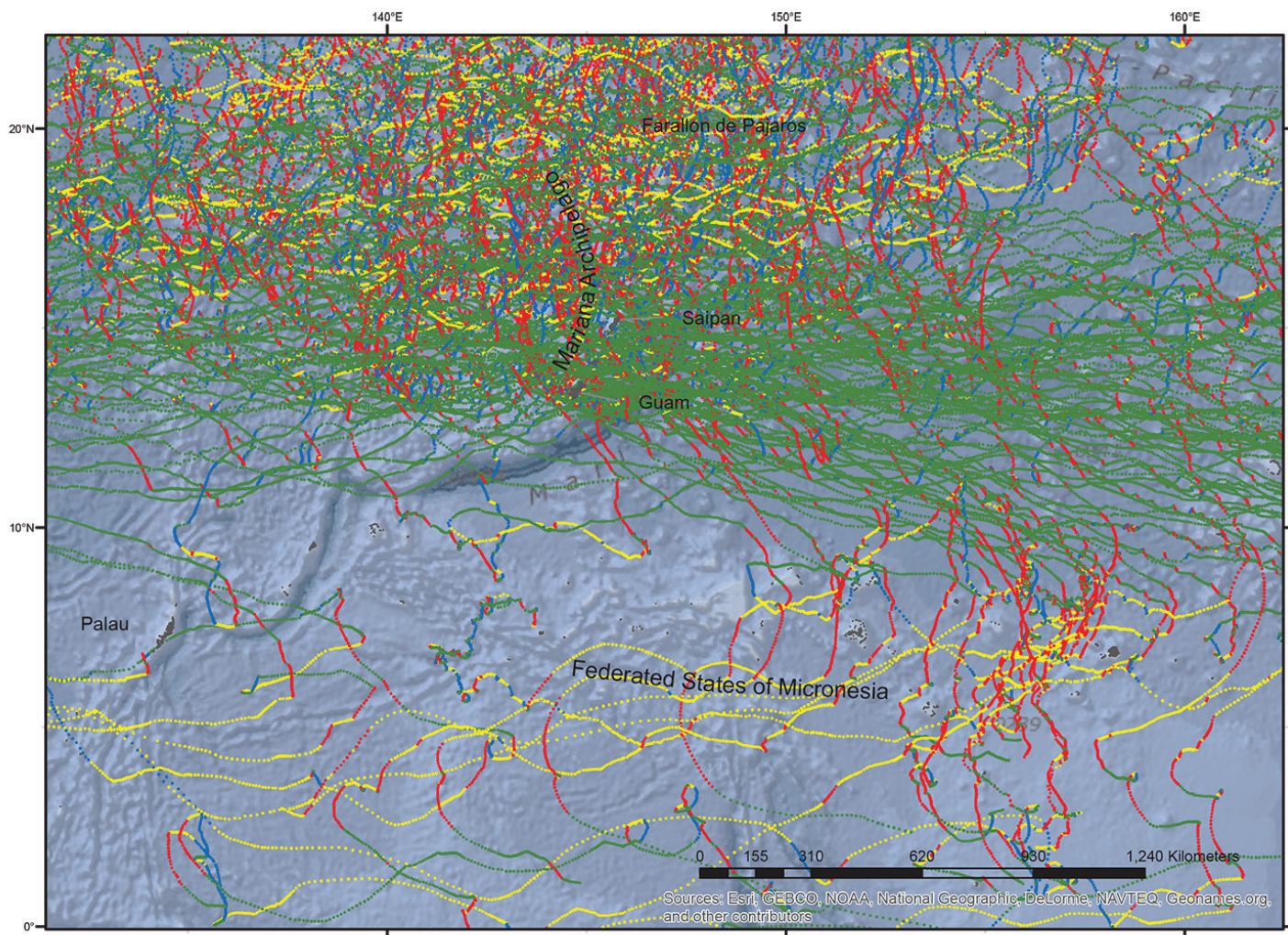
## DISCUSSION

Pelagic larvae in the Mariana region will be subjected to very different transport mechanisms depending on which of the current fields they lie in and potentially the season or year during which they are spawned. Of the four main current fields considered here, the NEC had the least variable speed and heading. The NEC will consistently transport larvae to the west with relatively little variation regardless of season or ENSO state. This current flows across the southern Mariana islands of Guam and Rota, with the northern edge of the current including Saipan and Tinian. The southern edge of the NEC can also include northern islands along the Federated States of Micronesia (FSM), such as the capital island of Yap. This consistent, highly directional flow may regularly sweep larvae away from these islands and result in more predictable transport processes than for larvae in other areas.

Larvae in the NECC will consistently be transported to the east, although with somewhat more variable speed and heading compared to the NEC. Islands in the path of the NECC include the many atolls of Yap, Chuuk, and Pohnpei in the Federated States of Micronesia. Larvae at large in the Fall in the NECC are more likely to be passively transported with greater speed and less variable heading than those in the same area during other seasons. Note that this may include larvae spawned in the Fall and also those spawned during the Summer, provided that they have a long pelagic larval duration that extends their larval life into the Fall months.

Because the NECC and NEC are alongside each other but flowing in opposite directions, there is great potential for eddy formation and looping pathways for larval transport in the region encompassing the northern edge of the Federated States of Micronesia and southern edge of the Marianas (Golbuu et al. 2012). This was particularly evident in the transport of eastward moving drifters from the northern edge of the NECC looping northward into the southern edge of the NEC, and ultimately moving back westward at a higher latitude (Figure 1.23). This mechanism may provide an important pathway of larval connectivity between Micronesia and the Marianas. Interestingly, many drifters were observed to follow this path, but very few went in the opposite direction from the NEC southward to the NECC. For example, in the drifter data used here, between the main islands of Chuuk and Pohnpei, 14 drifters went from the NECC to the NEC (northward), but only 3 went from the NEC to the NECC (southward). The net effect may be that larvae are more likely to go from FSM to the southern Marianas than vice versa. The south flowing Mindanao Current far to the west is the route for most NEC to NECC connections.

In contrast to the relatively consistent direction of the NEC and NECC, those larvae in the regions north of the NEC (i.e. northern Mariana and Bonin Islands) would be subjected to much more variable currents. Larvae there will experience much greater variation in heading regardless of season, ENSO state, and year. These swirling currents may enhance the opportunities for retention of larvae among the islands in the northern part of the Mariana chain and even the Bonin Islands. In contrast to the NEC and NECC however, such connections will be highly variable and unpredictable according to the more random current heading in these northern areas. The meandering currents may also prevent connections among the very wide expanses of open ocean. Whereas the straight flowing NEC may swiftly and directly transport larvae from the Marshalls to the



**Figure 1.23.** Pathways of all drifters passing through the Mariana Archipelago. Drifter headings are color coded where red = northward, blue = southward, green = westward, and yellow = eastward.

Marianas and Marianas to the Philippines, such long distance connections would take much longer and be less likely for larvae in the northern Marianas or Bonin Islands areas.

Collectively, these current patterns correspond well to marine ecoregions and biogeographic classifications that separate the Mariana, Philippine, Caroline, Marshall, and Ogasawara (Bonin) Islands (e.g. Veron 2000, Spalding et al. 2007, Wood et al. 2013). Genetic studies in the region corroborate these patterns as well. For example, gene flow in the crown-of-thorns sea-star, *Acanthaster planci*, relates well to current patterns including the NEC, NECC, Kuroshio, and Mindanao (Yasuda et al. 2009). Genetic population structure of the reef goby, *Bathygobius cocosensis*, in Guam, Ryukyu, and the Bonin Islands corresponds to the connections predicted from the NEC, Kuroshio, and eddy field around the Bonin Islands (Mukai et al. 2009). Further, the genetic population structure of the scribbled rabbitfish, *Siganus spinus*, clusters into distinct groups in agreement with the speed and direction of the NEC, NECC, and eddies in the Mariana and surrounding Islands (Priest et al. 2012).

The season and year during which larvae are spawned can also affect their transport. Larvae spawned into the NEC will experience significantly slower currents in the Summer than in other seasons (Results, Reverdin et al. 1994). Many taxa are documented to have peak spawning activity during Summer in the NEC, including commercially valuable sea cucumbers, such as *Actinopyga mauritiana*, with peak spawning in May-July in Guam (Hopper et al. 1998, Richmond et al. 1996); soft coral, *Sinularia polydactyla*, which has peak spawning in April-June in Guam (Slattery et al. 1999); and perhaps most notably the mass spawning of many coral species in June-August noted in places including Saipan, Guam and the Marshall Islands (Richmond and

Hunter 1990). In contrast, larvae spawned into the NECC will experience significantly slower currents and more northward headings in the Spring than in Summer or Fall (Results, Reverdin et al. 1994). For example, the most extensive mass spawning of corals has been observed in April in Palau (Penland et al. 2004). It has been hypothesized that this seasonal timing is deliberate to minimize transport away from islands and maximize self recruitment in Micronesia (Johannes 1978). Although the northern areas have somewhat faster currents in Summer than in Winter, the high variation in headings may render unpredictable any regular effect of seasonal speed on transport.

Currents in some years had much greater speed or variability than in others. For example, the NEC and northern Mariana regions had currents that were 50-75% faster in 2004-2007 relative to the 4 to 5 years preceding or following. Large interannual differences such as this may result in reliance on external sources of larvae for Mariana islands in some years and self-seeding during others. It may also contribute to the periods of unusually high or low recruitment that have been observed for some taxa among years (e.g. Kami and Ikihara, 1976).

Position and width of currents can vary somewhat, but were kept constant in our analysis for the sake of simplicity. NECC is farther from the equator in January than July (Reverdin et al. 1994), and although just outside our study region, the NEC bifurcation into the Mindanao and Kurshio currents fluctuates in position and strength with the south Asian monsoon and ENSO (Qui and Lukas 1994). Drifter heading and speed showed no differences in ENSO state and few differences among seasons in our study region although we did not vary the current boundaries used for segment extraction based on these variables. There is also a latitudinal salinity front associated with the NEC that cuts through the Mariana archipelago around 15° N (Kimura et al. 2001). It has been gradually moving farther north over the last three decades, with occasional spikes to the south associated with El Niño.

Examining currents more locally within the Mariana archipelagic zones also revealed possible spatial and temporal influences on larval transport. Larvae around Guam, Rota, Tinian, and Saipan experience currents ~ 30% slower than those in the northern zones that are flowing past islands from Agrihan to Farallon de Pajaros. Values were intermediate in the central zones. Any difference in transport distance due to speed may, however, be balanced by variability in headings. Slower currents in the south are highly directional and always westward, whereas faster currents in the north are nearly randomly distributed in their headings. This difference in currents may be partly responsible for differences in reef communities documented gradually along Mariana islands from south to north. Community patterns of many taxa have been shown to vary with island size, habitats, salinity, and even volcanic disturbances (Vermeij et al. 1983, Houk and Starmer 2010). Results here support speculation in those studies that these islands lie along a gradient of differing currents that could impact larval availability. It has been theorized that external recruits may only arrive sporadically to the northern Marianas, perhaps on eddies from the NEC or Kuroshio Current (Kojis and Quinn 2001), a mechanism also likely to play a role shaping biogeographic patterns.

As currents pass by certain islands, eddies can form in their wake which may promote local larval retention. Eddy formation does not always occur and depends primarily on current speed, island size, and relative orientation (Harlan et al. 2002). Where conditions are right, permanent eddies can be attached in an island's wake. In other cases, eddies are periodically spun off or shed downstream. For example, a fine-scale study of ocean currents around Guam in 2000 documented that the westerly flowing NEC results in formation of somewhat stable eddies in the lee of the north and south points of Guam trailing westward (Wolanski et al. 2003). Results here also show that currents passing by the large islands from Guam to Saipan moving from the SE to SW zone experience increased variation in heading. Those eddies in the lee of the islands may re-circulate developing eggs and larvae near their natal reefs and offer repeated opportunity for settlement. This presents an interesting paradox for these islands due to their large size, orientation relative to the NEC, and position near the core of the NEC. Larvae originating from them may be most likely to be swept away westward in the strong center of the NEC, or, on the other hand, possibly entrained in the leeward eddy complex documented here and elsewhere (Suntsov and Domokos 2012), thereby increasing the likelihood of local retention.

The passage of typhoons influences ocean currents in many ways that may affect larval transport. First, altered current speed or direction may simply influence the passive transport of marine larvae. Second, typhoons induce localized upwelling and have a cooling influence on surface waters as was documented here. Cooler waters are known to generally prolong larval development (O'Connor et al. 2007, Heyward and Negri 2010), which may both delay the earliest time that larvae are capable of settlement and also extend their normal larval duration and therefore transport distance. Third, the upwelled water is nutrient rich compared to surface waters and often results in a localized phytoplankton bloom (Fiedler et al. 2013). This may enhance larval feeding, improve development, and reduce both larval and post-settlement mortality. A case study of typhoon effects on the ocean surface was recently conducted for Typhoon Lupit, which formed in October 2009 and passed just south of the Mariana Archipelago (Cheung et al. 2013). Main effects included wind-driven surface currents, a 7° C decline in sea surface temperature, and an increase in chlorophyll-A concentration to bloom levels that were 10 times higher than pre-storm conditions. Width of the path that was influenced along the storm track was positively associated with storm intensity. Given that typhoons of various strengths often pass through this region during fall months, larvae at large during these times may be influenced through the mechanisms noted here. However, any regular effect of typhoons on community connectivity would be difficult to establish given their irregular and unpredictable paths.

# Chapter 2: Patterns of Larval Connectivity and the Influence of Larval Life-History Investigated Through Transport Simulations

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## INTRODUCTION

Coral reefs separated by large expanses of open ocean can actually be connected and dependent on each other due to the transport of larval fish, corals, and other reef invertebrates in ocean currents (Wood et al. 2013, Kendall et al. 2013). Understanding this larval connectivity among reef populations has emerged as a key component of planning sustainable fisheries and effective conservation strategies (Roberts 1997, Botsford et al. 2001, McCook et al. 2009). Regional managers need to identify and coordinate protection of key sources of larvae that sustain reef populations. Connections among reefs must be identified and preserved so that reefs can replenish each other following local disturbance. Indeed, the larval connections among reefs are one element that maintains resilient reefs capable of withstanding and recovering from disturbance (Botsford et al. 2009, Steneck et al. 2009).



*Coral reef community off Mañagaha Beach, Saipan.  
Photo credit: M. Kendall, Biogeography Branch, NOAA.*

A variety of factors can affect transport of larvae among islands. Most obviously it is necessary to understand the speed, direction, and seasonality of the ocean currents by which larvae are transported (described in Chapter 1). It is also necessary to understand how aspects of the larvae themselves can affect their transport. Size of source populations, timing of spawning, duration of the larval period, mortality rates, sensory, and swimming capabilities can all affect the probability that larvae will be transported from a source island to a particular destination (Siegel et al. 2008, Cowen and Sponaugle 2009, Kendall et al. 2013, Sanvicente-Añorve et al. 2013).

Computer simulations that track cohorts of virtual larvae as they are transported in ocean currents offer an effective tool for understanding connectivity and the various biotic and abiotic influences upon it. In this approach, virtual larvae are moved in a direction and distance according to an ocean circulation model that consists of a map of a region’s ocean currents. Life history parameters for larvae (e.g. larval duration, swimming capability) that reflect the characteristics of taxa of interest can be applied to the virtual larvae during or after the simulations (e.g. Black and Moran 1991, Kendall et al. 2013, Johnson et al. 2013). This technique has many useful attributes. For example, a huge number of sources and destinations can be modeled, vast numbers of virtual larvae can be tracked, different years and seasons can be evaluated to easily examine cumulative or temporal aspects of connectivity, rare or threatened species can be investigated without field sampling, and perhaps most importantly, various larval behaviors, life-history parameters, and environmental conditions can be modified in simulations to compare their influence on connectivity. If parameterized properly, transport simulations have proven to be an effective complement to empirically based studies of connectivity (e.g. genetic, mark-recapture, or tracer evidence) for a variety of taxa (e.g. Baums et al. 2006, Yasuda et al. 2009, Christie et al. 2010).

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*Patch reef community off Garapan, Saipan.  
Photo credit: M. Kendall, Biogeography Branch, NOAA.*

In the Mariana Archipelago in particular, the role of ocean currents in supplying the larvae to sustain local populations is suspected to have heightened significance. The islands are oriented perpendicular to the North Equatorial Current (NEC), a dominant current in the region. Some have suggested that local larval production is swept away from, rather than along, the islands in the archipelago due to their position normal to the NEC (e.g. Kojis and Quinn 2001). Indeed, a recent study of mesopelagic plankton found significant differences in communities east and west of the Marianas (Suntsov and Domokos, 2012). While focused more on vertical migrators of the shallow acoustic scattering layer, the study also found some reef fish larvae, and highlights the differences in plankton as the NEC passes the Marianas. In addition, the nearest upstream island neighbors are 400-600 kilometers away, making them potentially unlikely sources of larvae to the Marianas (Quinn and Kojis, 2003).

In this chapter, the fate of virtual larvae originating from each island in the Marianas and surrounding archipelagos is tracked using computer simulations. We have taken the approach of modelling connectivity through a range of life history values and oceanographic seasons in order to compare and contrast the relative influences of these variables on interisland connections. Specifically, our objectives in this chapter were to:

- 1) Describe the overall patterns of connectivity within the Marianas, and regionally throughout surrounding archipelagos.
- 2) Compare the relative influences of larval duration, spawning season, and larval sensory/swimming capabilities on connectivity patterns.
- 3) Evaluate the role of self-seeding, import, and export of larvae at each island in the Marianas.
- 4) Investigate a detailed time series of simulated recruitment at Saipan and Guam, the two most populous islands in the Marianas.

## **METHODS**

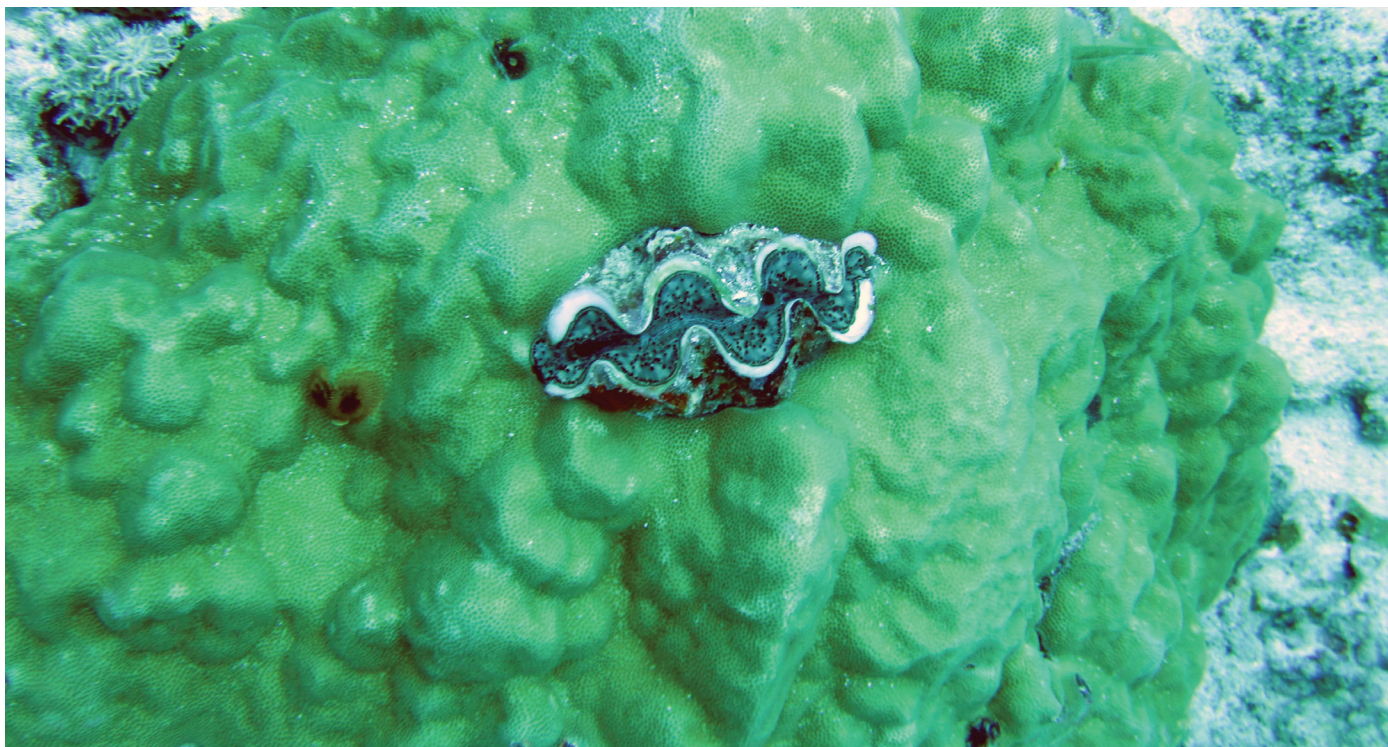
The Hybrid Coordinate Ocean Model (HYCOM) is a three dimensional ocean circulation model (Bleck and Boudra 1981, Bleck and Benjamin 1993, Halliwell et al. 1998) with a 6 hour time step and a horizontal resolution of 1/12 degree (approximately 9 by 9 km grid cells) in our study region. It has been used recently in a number of larval transport studies and has shown good correspondence to results from independent drifter, biogeographic, and genetic datasets (Christie et al. 2010, Kool et al. 2011, Kendall et al. 2013, Sanvicente-Añorve et al. 2013). The current vectors from the Global Hindcast model for the 0-10 m depth layer from



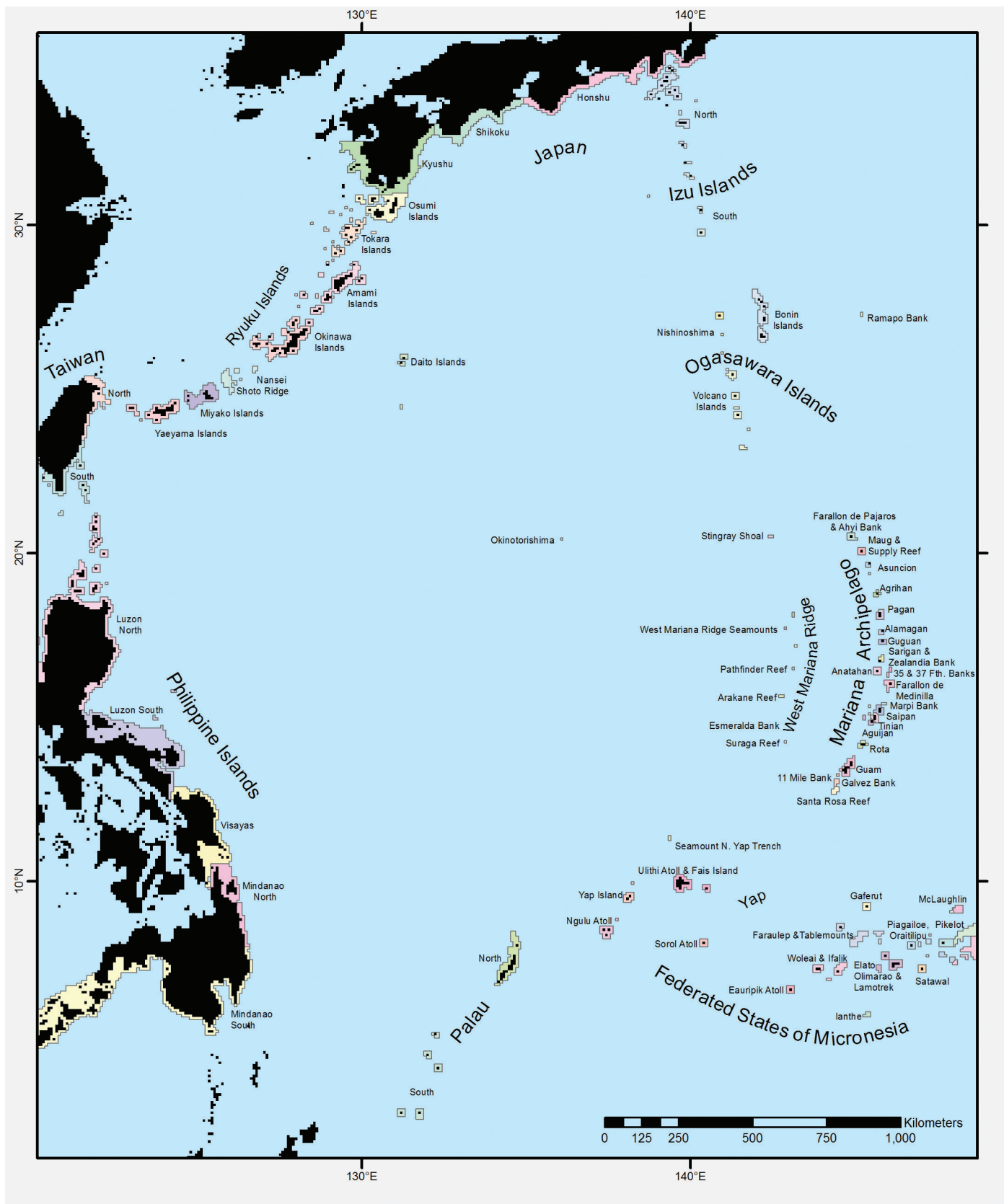
2004-2012 was downloaded in NetCDF format from the HYCOM consortium via the NASA/REASON Ocean Data Portal using Matlab OPeNDAP Toolbox version 2.0 (<http://www.oceanographicdata.org/Toolbox/toolbox.html>). These years represent an eight year period of various El Niño and La Niña conditions. The 9 km grid resolution of HYCOM is not sufficient to capture fine-scale currents close to shore (Swearer et al. 1999, Harlan et al. 2002) and was therefore used only to evaluate broader scales of larval transport among the islands in the study area. Modeled currents from HYCOM have been validated extensively in previous studies and shown to provide an accurate prediction of real transport in ocean currents (Fossett et al. 2012, Kendall et al. 2013).

### Larval Sources

Virtual larvae were started at each of 112 island groups and shallow seamounts in the study area, including 35 in the Marianas and 77 in surrounding archipelagos (Figure 2.1). Islands and seamounts close together were grouped for analysis, especially at the edges of the study region, to simplify and focus presentation of the results on the Mariana Archipelago. The larger islands at the extreme western edge of the study area, including the main islands of Japan, Taiwan, and the Philippines were modelled only as larval destinations since preliminary analysis indicated that larvae spawned from them were very unlikely to reach the Marianas. Larval production was scaled to the area of each island's potential coral reef habitat, defined as the area shallower than the 150 m isobath. This was the best surrogate variable for spawning potential that was available for the entire region. These depths include the approximate depth limits of both photic and meso-photoc coral communities (Mesophotic Coral Ecosystems 2010). The number of starting larvae in each coastal grid cell of HYCOM was assigned based on the proportion of the grid cell with water depths between 0 and 150 m as determined from the General Bathymetric Chart of the Oceans (<http://www.gebco.net>). Those grid cells that were comprised of 100% potential coral reef habitat received 10,000 larvae. Those comprised partly of land and/or deeper water had their number of starting larvae scaled accordingly. Due to scale and alignment differences in the bathymetry and HYCOM grids, depth data could assign larvae to land cells in HYCOM. Such larvae were redistributed among neighboring coastal grid cells, which occasionally resulted in cells with > 10,000 initial larvae, but maintained spawning potential according to bathymetry. Within each coastal grid cell, the assigned number of larvae were randomly distributed. This provided a very large but computationally reasonable number of virtual larvae that could be “spawned” or started moving in transport simulations on any date specified.



*Giant clam and coral in Lighthouse Reef.*  
Photo credit: M. Kendall, Biogeography Branch, NOAA.



**Figure 2.1.** Study area including the Mariana Archipelago and surrounding island chains. Black cells denote land in the HYCOM grid. Colored cells around each island or bank denote the shallow (0-150 m) grid cells that were used as spawning locations at the beginning of transport simulations.

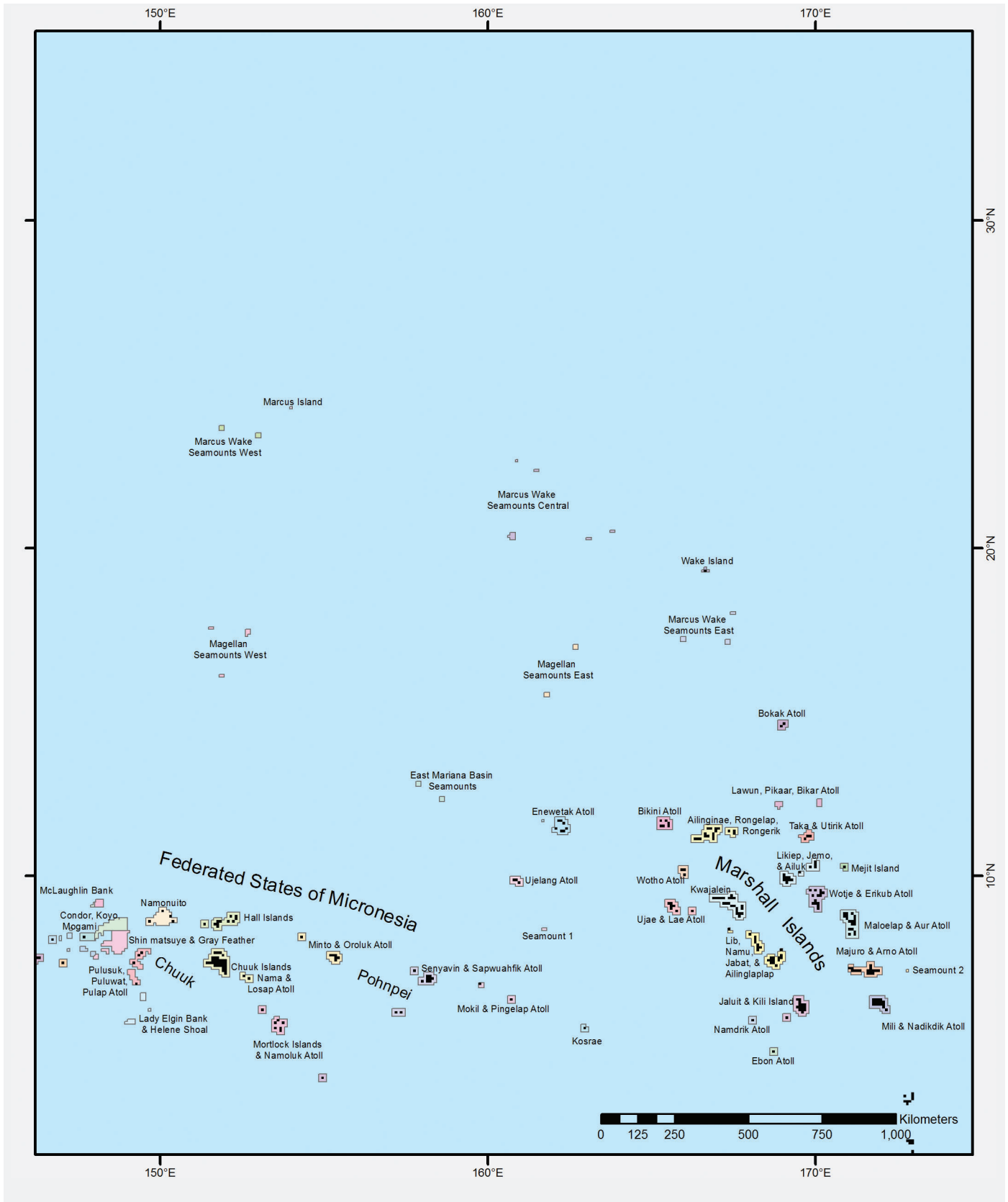


Figure 2.1 cont.

### Start Dates of Larval Transport

Some taxa in the study area spawn throughout the year, whereas others spawn during particular seasonal peaks. For example, most spawning for corals occurs in May-August for Guam, Palau, Yap, and the Marshall Islands (Wallace et al. 1986, Harrison and Wallace 1990, Richmond and Hunter 1990, Slattery et al. 1999, Penland et al. 2004). Most commercially valuable sea cucumber species reproduce in early summer, with a peak in May-June (Richmond et al. 1996, Hopper et al. 1998). Some culturally and commercially important fish species, including Spotcheek Emperor, *Lethrinus rubriperculatus*, and scribbled rabbit fish, *Siganus spinus*, have peak spawning in Spring months (Kami and Ikehara 1976, Chirichetti 1996, Triani 2011). Using a spawning database compiled from multiple sources (Lester et al. 2007), a histogram of spawning months among fish species occurring in the Marianas was created (Figure 2.2). Although far from a complete or representative

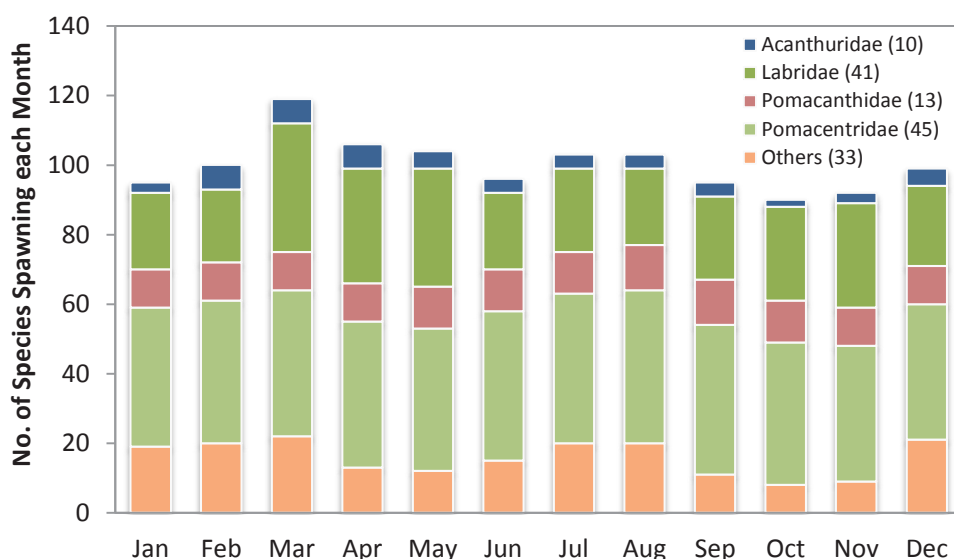
list, the histogram is based on 142 species from 17 families and is useful in conveying the range of spawning seasons among reef fish. This compilation indicates that whereas some taxa have peak spawning seasons, there are a large number of species from diverse fish families that are potentially spawning in any part of the year. This highlights the need to understand the seasonal aspects of connectivity. Also of note, there are some seasonal differences in current speed and heading, especially in the North Equatorial Counter Current (NECC) (Chapter 1). These seasonal aspects in spawning and currents could result in different

connectivity patterns depending on when spawning occurs (Sanvicente-Añorve et al. 2013). To investigate these potential influences on connectivity, we began simulations seasonally, or every three months in each model year (January 1, April 1, July 1, and October 1). It is recognized that spawning dates can vary as much as a month from year to year depending on lunar cycles, for example. However, preliminary tests indicated that transport patterns did not differ substantially when start dates were separated among various phases of the moon, a finding similar to other studies (James et al. 2002) and consistent with time-scales of variation in ocean current patterns within the region (Chapter 1).

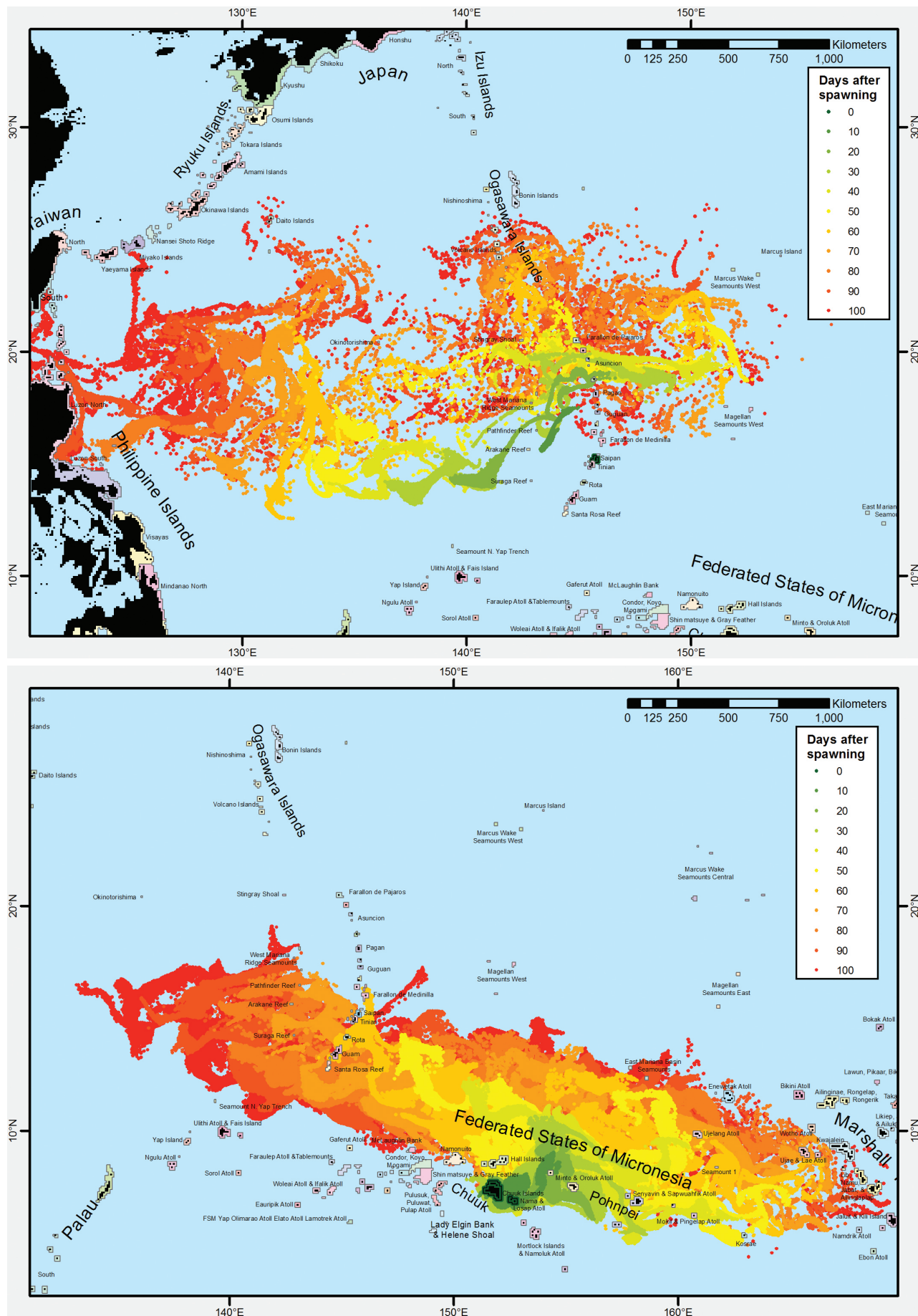
### Larval Transport and Model Uncertainty

In simulations, virtual larvae began at random locations within each coastal grid cell and moved in the direction and speed specified by the corresponding HYCOM vectors for that date and position (Figure 2.3ab). Custom Python scripts were used to implement the larval transport simulations and track positions of the virtual larvae in the General NOAA Operational Modeling Environment (GNOME, version 2) (Zelenke et al. 2012). Preliminary tests indicated that a six hour time step would most appropriately track particle motion based on current velocities in the region and grid dimensions. When virtual larvae encountered islands (edges of null cells with no current vectors in HYCOM), they were refloated at the next model time step to continue drifting.

Random variability in larval paths originating from the same location is an important aspect of connectivity studies (Polovina et al. 1999, Cowen et al. 2000, Siegel et al. 2003, Kobayashi 2006, Chiswell and Booth 2008, Treml et al. 2008, Rudorff et al. 2009, Kendall et al. 2013). GNOME controls random aspects of particle motion at each time step through two variables defined by the user: horizontal diffusivity and uncertainty in current vectors (Zelenke et al. 2012). When properly calibrated, these simulate the stochasticity in larval



**Figure 2.2.** Histogram of number of species spawning by month for fish in the study region summarized from the database used in Lester et al. (2007). Range information was used to select the 142 species from 17 families in the database that are present in the Mariana study region. Number of species by family is noted in parentheses.



**Figure 2.3.** Example results of transport simulations. Plots show position of virtual larvae at 10 day increments following spawning in October 2005 for, a) Saipan, and b) Chuuk.

paths arising from sub-grid scale turbulent processes and random variation. To identify appropriate diffusion and cross- and along-current uncertainty values, actual current path from satellite-tracked drifters were compared to paths predicted in preliminary test simulations for virtual larvae originating at the same date and location as the drifters. Test simulations using diffusion values ranging from 0 to  $106 \text{ cm}^2 \text{ s}^{-1}$  and uncertainty values in current vectors ranging from 0 to 50% of meridional- and zonal-current velocity, were evaluated. Model and drifter paths were compared while recognizing that a given drifter represents only one possible track out of a potential distribution that reflects variation in drift. Using 10% vector uncertainty and a  $100 \text{ cm}^2 \text{ s}^{-1}$  diffusion coefficient encompassed actual drifter tracks and provided reasonable clouds of potential larval pathways. All subsequent model runs were conducted using this realistic level of drift variability. At this stage, all virtual larvae were treated as immortal, non-settling particles. Custom scripts in R were applied to GNOME outputs to simulate the various life history scenarios described in subsequent sections.

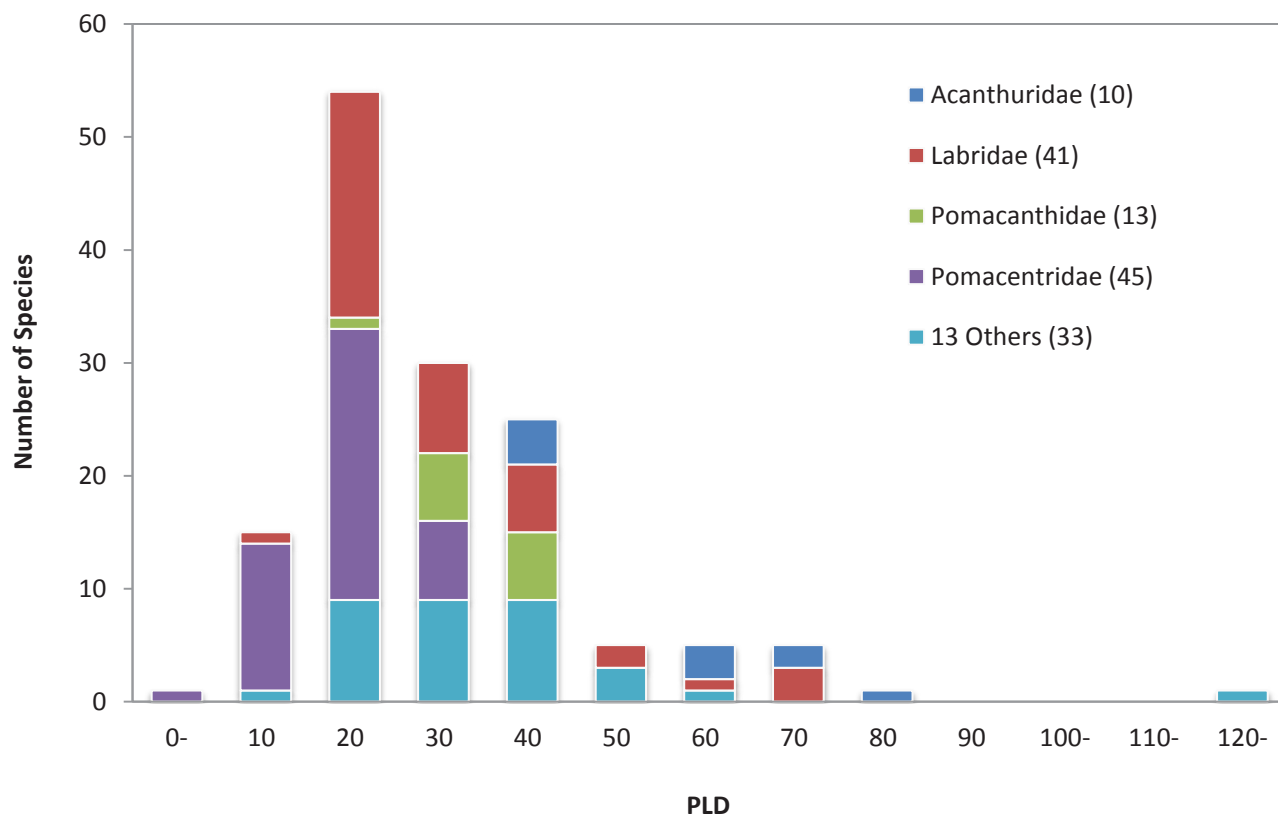
### Precompetency

Spawned gametes, fertilized eggs, and young larvae must spend some time developing and cannot immediately swim or settle even if they encounter suitable habitat (Harrison and Wallace 1990, Fisher 2005). This planktonic phase prior to achieving a body form capable of settlement is termed "precompetency". For a wide variety of reef fish species it is evident that individuals begin to settle once 60-90% of their maximum larval lifespan, termed pelagic larval duration, has elapsed (calculated from values in Victor 1986, Thresher et al. 1989, Wellington and Victor 1989, and Junker et al. 2006). This timing also corresponds to the observation that swimming capability of some larval fish begins to exceed some ocean currents once at least ~50% of their maximum potential larval phase has elapsed (Fisher 2005). Precompetency periods for coral larvae and other taxa are less known and appear somewhat more variable (Harrison et al. 1984, Wilson and Harrison 1998, Miller and Mundy 2003, Graham et al. 2008, Jones et al. 2009). To simulate this developmental period here, virtual larvae were prevented from settlement until a minimum of 60% of their maximum pelagic larval duration (see next section) was completed.

### Pelagic Larval Duration

Pelagic larval duration (PLD) is defined as the period of development spent in the water column as plankton. Total PLD is a composite of broadcast spawning and fertilization, early development, onset of larval behaviors for some taxa (e.g. feeding, vertical migration, swimming), pre-competency, and maximum larval lifespan (see Leis 2006 for a summary of fish larvae and Harrison and Wallace 1990 for coral larvae behaviors). Larvae simply die in the plankton at the end of their maximum PLD if they lack a suitable settlement habitat or energy source. PLD is quite varied among coral reef organisms and can last for days, weeks, or months (e.g. Bonhomme and Planes 2000, Blanco-Martin 2006, Junker et al. 2006, Graham et al. 2008). There can be variability within genera or even among individuals of the same species (Brother et al. 1983, Chirichetti 1996, Wilson and Harrison 1998, McCormick 1999, Junker et al. 2006), with influences such as water temperature and availability of suitable settlement habitat (McCormick and Molony 1995, Munday et al. 2009, Heyward and Negri 2010). In addition, some larvae can lengthen their time as plankton by delaying or partly reversing metamorphosis until a suitable habitat is encountered (McCormick 1999, Richmond 1985).

Although some PLDs over 200 days are documented (e.g. some corals, Graham et al. 2008), these are relatively rare and a large majority of studies have identified PLDs much shorter than 100 days. In a study of several broadcast spawning scleractinian corals in the Pacific, larval energy reserves reached critical levels 100 days after spawning followed by rapidly increased mortality (Graham et al. 2008). Using a PLD database compiled from multiple sources (with permission from Lester et al. 2007) a histogram of PLDs among fish species occurring in the Marianas was created (Figure 2.4). Although far from a representative or complete list, this histogram is based on 142 species from 17 families and is useful in conveying the range of PLD values among reef fish. Mode larval duration was 20-30 days with the majority of species in the 10-50 day PLD range. This compilation and others showed relatively short larval durations of ~15 to 35 days for Pomacentridae and Apogonidae, somewhat longer at 30 to 50 days for Pomacanthidae, longer still for Acanthuridae at ~40 to 80 days, and Labridae the most variable at ~20 to 80 days (Brothers et al. 1983, Chirichetti 1996, Bonhomme and Planes 2000, Lester et al. 2007). Reef invertebrates such as Crown-of-thorns seastars and most commercially valuable species of sea cucumber in Micronesia have larvae that feed on phytoplankton



**Figure 2.4.** Histogram of PLDs for reef fish in the study region summarized from Lester et al. (2007). Range information was used to select the 142 species from 17 families in the database that are present in the Mariana study region. Number of species by family is noted in parenthesis.

and typically complete development in ~10 to 40 days (Lucas 1982, Richmond et al. 1996, Ramofafia et al. 2003).

To compare connectivity among these diverse taxa, we simulated larval transport for maximum PLDs of 10, 20, 50, and 100 days, which encompasses the range of values expected for a wide variety of the fish, corals, and other reef organisms in the region (e.g. summary tables in Bonhomme and Planes 2000, Blanco-Martin 2006, Graham et al. 2008, Jones et al. 2009). This approach enables comparison of connectivity patterns among taxa with different PLDs (Kendall et al. 2013, Sanvicente-Añorve et al. 2013). Note that these are maximum PLD values and that larvae in our simulations are competent to settle any time after 60% of this duration. Therefore, the settlement windows for these maximum PLDs were 6-10, 12-20, 30-50 and 60-100 days. For brevity, these maximum PLD values will hereafter be referred to simply as PLD unless otherwise specified.

### Settlement Zones

Larvae of reef organisms differ widely in their ability to sense, orient toward, and even actively swim to settlement habitat. Coral larvae and those of many invertebrates can be treated essentially as passive particles relative to the speed of ocean currents (Harrison and Wallace 1990, Black and Moran 1991). In contrast, some fish larvae in later stages of development are capable of sustained swimming at rates faster than surrounding currents for distances of several kilometers (McCormick and Milicich 1993, Leis 2002, Fisher 2005, Leis 2007). Although the precise distance at which fish larvae can usefully orient towards reefs and actively overcome ambient currents is debated, it is clear that some larvae need simply to come within a “settlement zone” sufficiently close such that they can sense and swim to the settlement habitat (Atema et al. 2002, Leis and Carson-Ewart 2003, Gerlach et al. 2007). Buffers of appropriate size around suitable habitats are used to represent this “settlement zone” (Lugo-Fernández et al. 2001, James et al. 2002, Cowen et al. 2006, Chiswell and Booth 2008, Kendall et al. 2013). In our simulations, if a larvae passed into an island’s settlement zone after its precompetency period, it was considered to have successfully settled at that island. To reflect these differences in larval capabilities, two settlement rules were used. In one scenario, larvae could only success-

fully settle at a destination cell that contained potential coral reef habitat (i.e. the same cells used as larval sources). This “small” settlement zone best represents larvae with little or no swimming capabilities that must rely entirely on ocean currents to carry them to settlement habitats (representative of coral planulae, other invertebrates, or poor swimming fish larvae). In another scenario, larvae could settle provided that they merely passed close by a cell with potential reef habitat. We defined this “large” settlement zone (representative of strong swimming larvae with good sensory capabilities) as grid cells with potential coral reef habitat plus a buffer of 2 additional grid cells (~18 km).

### **Mortality**

Mortality rate in larval populations has a significant effect on recruitment strength and often varies with larval age and environmental conditions (Cowan et al. 2000, Edmunds et al. 2001, Graham et al. 2008, Connolly and Baird 2010). However, for creating general predictions across the region, mortality rate was kept constant during simulations and applied randomly to individual larvae beginning at the end of precompetency at a rate that would result in 100 % mortality by the end of each maximum PLD considered.

## **DATA ANALYSIS**

### **Role of Season and Settlement Zone Size in Connectivity**

The effect of season and settlement zone size on connectivity were first examined using bar graphs. For these figures we plot cumulative number of settled larvae over all 9 years of simulations. Total number of settled larvae was plotted by PLD and season. In a separate plot, total number of settled larvae is shown by PLD and settlement zone size (small or large). In addition to the number of larvae settled, it is also of use to show the effect of season and settlement zone size on the overall number of interisland connections. In these plots, the number of island pairs with a connection of any strength (cumulative over all 9 years of simulations) was plotted by PLD and season and then in a separate figure by PLD and settlement zone.

### **Connectivity Matrices**

Results from larval transport simulations are often summarized using a connectivity matrix. In this tabular format, islands are listed in both row (larval sources) and column (larval destinations) headers. Cells in the matrix represent the strength of connections made by larvae going from each source to each destination. Cells along the matrix diagonal represent self-seeding, or those that start at and ultimately return to a particular island. The Philippines, Taiwan, and mainland Japan were modeled only as destinations. For each PLD and buffer size we counted the number of simulated larvae released at each source location that travelled to each of the possible destination locations. Values are cumulative over all 9 model years. Matrix cells denote the proportion of larvae from each source (row) that arrived at a given destination (column). Rows thus sum to a number  $\leq 100\%$ . Columns can sum to  $>100\%$ , because it is possible for a high proportion of the larvae produced at several sources to travel to the same destination. Note that connectivity calculated in this way depicts the pattern of larval transport pathways without considering the variation in number of larvae produced at each source due to differences in island size.

Using connectivity matrices, it is easy to visualize groups of connected islands where larval exchange is common, breakpoints between disconnected islands, and directions of larval exchange along island chains. In addition, by comparing matrices created for larvae with different life history traits, the influence of those variables on connectivity patterns can be evaluated (Kendall et al. 2013, Sanvicente-Añorve et al. 2013).

### **Reliance on Self-Seeding in the Marianas**

Self-seeding is the process where locally produced larvae return to their natal islands. It is an important component of larval supply from a management perspective since it offers the most local control. The benefits of local action to sustain spawning populations are locally realized. Focusing only on the islands and banks of the Mariana Archipelago, the proportion of each location’s settlers from self-seeding versus imports from external sources at various PLDs and settlement zone sizes was evaluated using pie charts. All larvae produced from island X and successfully returning there were summed separately for each PLD and settlement zone size. All larvae produced elsewhere but settling at island X were similarly summed. These values were converted to proportions of total settlers at island X from internal and external sources for each PLD and settlement zone. Pie charts display how proportions change with PLD and settlement zone size for each island.



## Island Role as a Source and Destination of Larvae

Each island's role as primarily a source or a destination of larvae is also important to consider. These roles are shown by PLD and settlement zone size using bar charts. The number of larvae produced at island X that successfully settled anywhere else was summed for each PLD. This represents the island's role as a source of larvae. The number of larvae produced elsewhere that successfully settled at island X was similarly summed. This represents the island's role as a destination of larvae. These values were plotted for each island by PLD on the y-axis. Bars extending away to the right of the axis denote each island's role as a source of larvae to other locations and those incoming from the left denote each island's role as a destination so these relative values can be compared. Note that this is different than the previous analysis in that self-seeding is not included in the calculations and actual numbers of larvae are shown to quantify the magnitude of each island's role as a source or destination.

## Time Series at Guam and Saipan

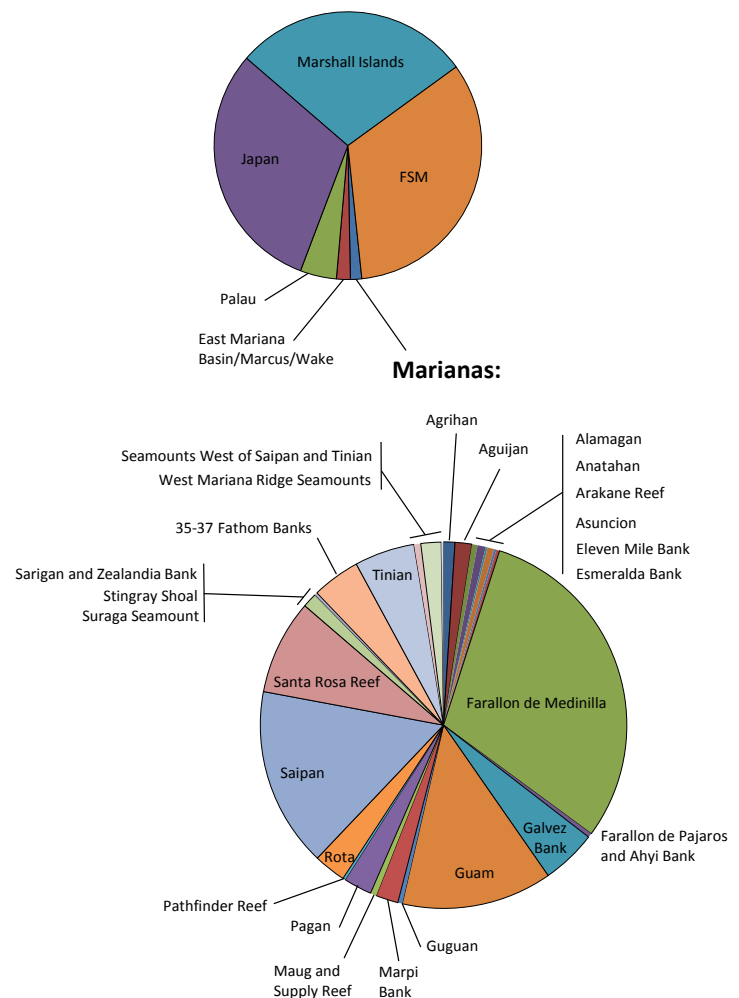
Seasonal and interannual recruitment patterns for Saipan and Guam, the two population centers in the Marianas, were investigated using time series plots of the number of recruiting larvae from each spawning date. The total number of larvae arriving from each spawning event was shown in stacked bar format where recruits were divided into those that were self-seeded and those imported from elsewhere. Separate plots were created for each PLD and settlement zone size to compare the influence of those variables. Multiple-means comparisons were used to evaluate seasonal differences in total number of incoming larvae (JMP v 9).

## RESULTS

Of the approximately 230 billion virtual larvae tracked among all the various model scenarios, only 0.1 to 0.4% of virtual larvae successfully settled in any particular scenario (combination of year, spawning season, PLD, settlement zone). Most larvae simply perished in the ocean. The major sources of starting larvae based on area of potential coral reef ecosystem (0 - 150 m depth) were The Marshall Islands, Federated States of Micronesia (FSM), and Japan (Figure 2.5). Note that this does not include locations such as the Philippines, Taiwan, and the main islands of Japan, which were included only as destinations in our simulations. The Marianas comprised only ~1% of all the starting larvae in the simulations. Within the Marianas, Farallon de Medinilla, Saipan, and Guam were the largest sources of starting larvae (Figure 2.5).

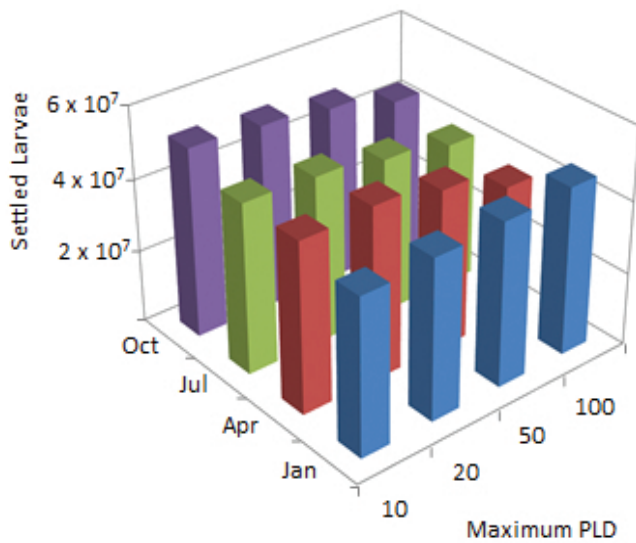


Diver survey at Lighthouse Reef.  
Photo credit: M. Kendall, Biogeography Branch, NOAA.

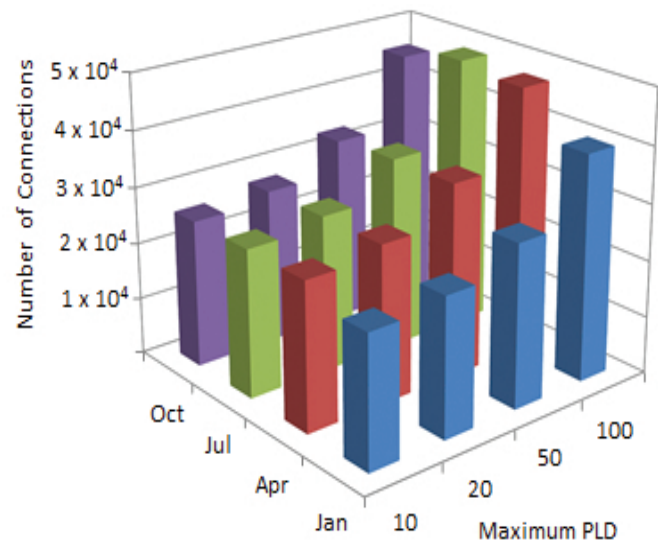


**Figure 2.5.** Proportions of starting larvae by island group (upper pie chart) and by locations within the Marianas (lower pie chart). Values are based on the area of potential shallow coral reef ecosystem (0-150 m) around each island.

Overall, spawning season did not have a strong effect on either the total number of settled larvae (Figure 2.6) or the number of islands that were connected (Figure 2.7) at any PLD. Increasing PLD did not have a large effect on the number of larvae that settled (slight decline with higher PLD), but dramatically increased the number of connections (Figure 2.7). The number of connected island pairs approximately doubled when PLD increased from 10 to 100 days.

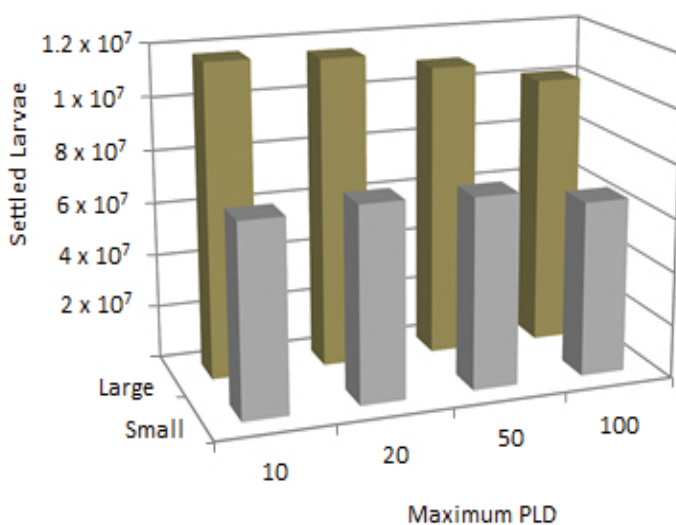


**Figure 2.6.** Cumulative number of larvae in all transport simulations for each PLD and spawning season.

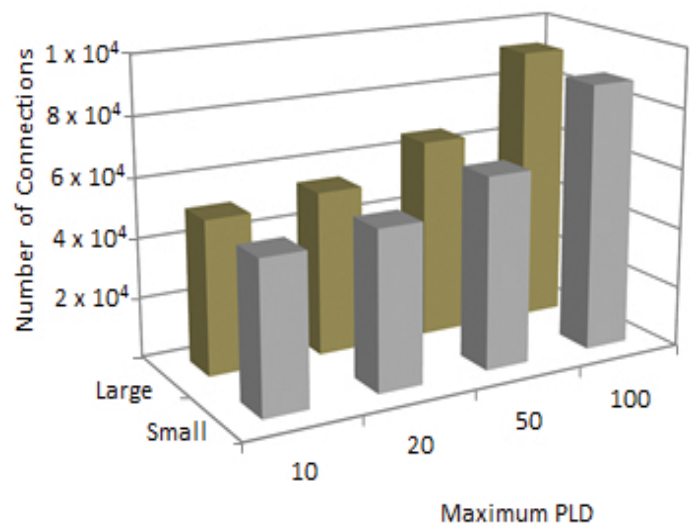


**Figure 2.7.** Cumulative number of island pairs that were connected in all transport simulations for each PLD and spawning season.

Settlement zone size had a large effect on the number of settled larvae (Figure 2.8), but not the number of connections (Figure 2.9). The larger settlement zone enabled almost twice as many larvae to settle at all PLDs. However, because the scale of this effect was localized around each island relative to the scale of interisland connectivity, very few additional island pairs became connected with the larger settlement zone.



**Figure 2.8.** Cumulative number of larvae in all transport simulations for each PLD and settlement zone size.



**Figure 2.9.** Cumulative number of island pairs that were connected in all transport simulations for each PLD and settlement zone size.

## Connectivity Matrices

Individual connectivity matrices for each PLD and settlement zone size are provided in Appendix A. A composite overlay of all PLDs (Figure 2.10) demonstrates how the spatial extent of connectivity increases with PLD. Virtual larvae with a 6-10 day PLD rarely settled beyond a few neighboring islands away. Those with 12-20 day PLD showed moderate connectivity among islands within each archipelago, but generally not to destinations in other archipelagos. The 30-50 day PLD enabled broad connectivity among many islands within each archipelago, but maintained separation of archipelagos with a few exceptions. Once PLDs reached 60-100 days, a majority of islands within each archipelago were exchanging larvae and many archipelagos became interconnected. Enlarging the size of the settlement zone had little effect on which islands each source could reach, but did increase the strength of most connections.

### *6-10 day PLD*

Specifically in the Marianas for the 6-10 day PLD and for larvae with poor swimming capabilities (small settlement zone), there was a clear breakpoint in connectivity along the northern edge of the NEC at the latitude of Guam and Rota (Appendix A.1). Guam and the banks south of it had much larval exchange among each other but none with the Marianas to the north apart from minor exchange with Rota. Rota and the islands and banks north of it to Farallon de Medinilla also had much larval exchange among each other, but virtually none with the Marianas to the south. Beginning at Farallon de Medinilla was another breakpoint in the pattern of connectivity. Larvae from Farallon de Medinilla up to Farallon de Pajaros could settle anywhere ~150-200 km north or south of their position along the Marianas. Larvae from the Marianas only seldom made the connection to destinations along the West Mariana Ridge. When the size of the settlement zone was increased, the strength of these connections was increased for neighboring islands, but the overall distance and direction of possible transport was nearly unchanged (Appendix A.2). At this short PLD, virtually no larvae were successfully exported from or imported to adjacent archipelagos.

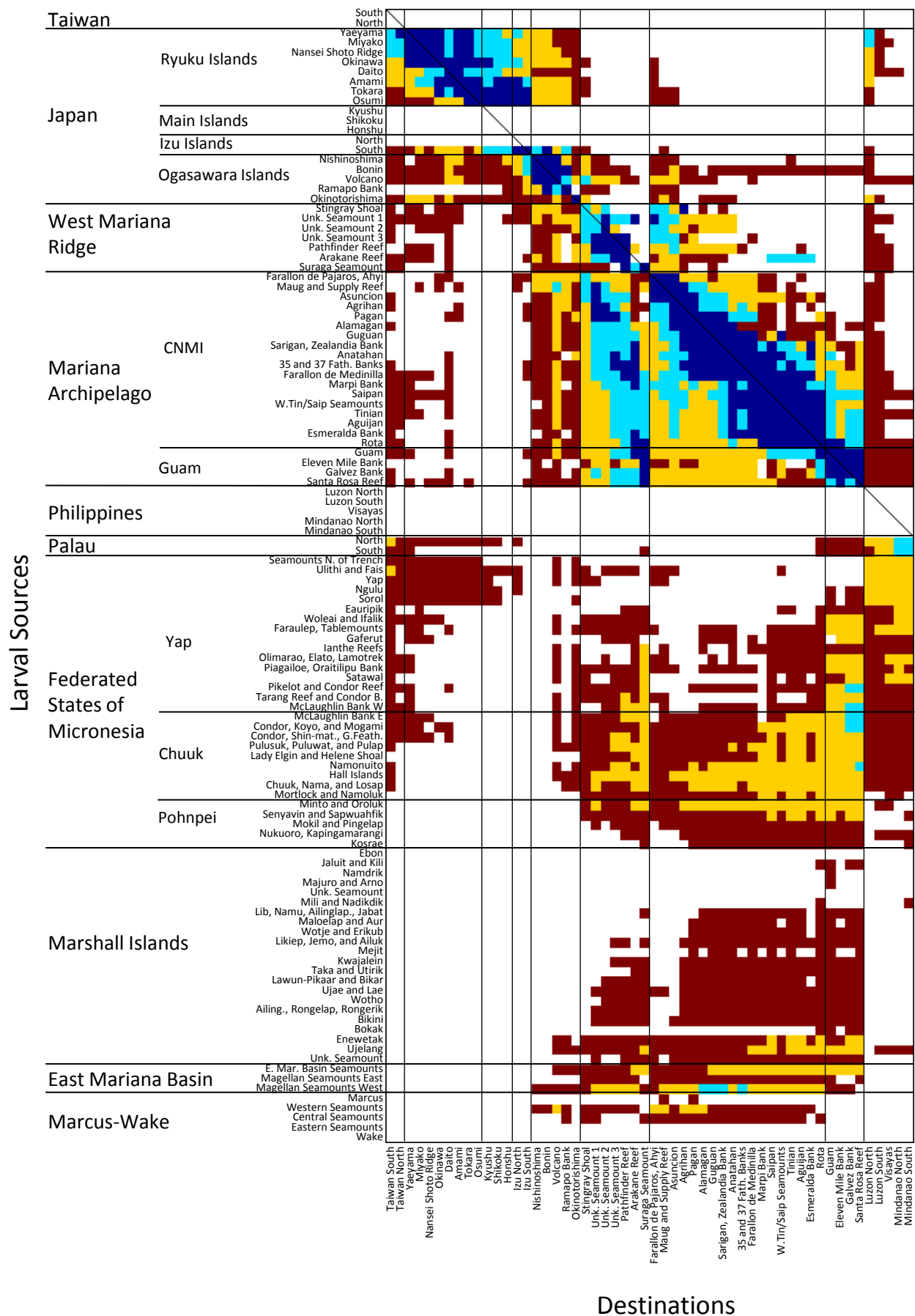
### *12-20 day PLD*

For the 12-20 day PLD there was still a breakpoint in connectivity along the northern edge of the NEC between Rota and Guam (Appendix A.3). Guam only occasionally sent a small number of larvae to destinations northward of this latitude, whereas Rota and islands to the north only occasionally sent larvae to the south. Between Rota and Farallon de Pajaros, sources could send larvae to destinations ~150-200 km south or 300-400 km north of their position. Also of note for this PLD, connections were much more likely between the islands in the Marianas and some of the submerged banks along the West Mariana Ridge. This transport occurred in the NEC from the southern Marianas or in the eddy field north of it in the higher latitudes. Increasing the size of the settlement zone greatly increased the strength of connections to the West Mariana Ridge and between neighboring islands (Appendix A.4). For this PLD, larvae successfully reaching other archipelagos from the Marianas and vice versa were extremely rare.

### *30-50 day PLD*

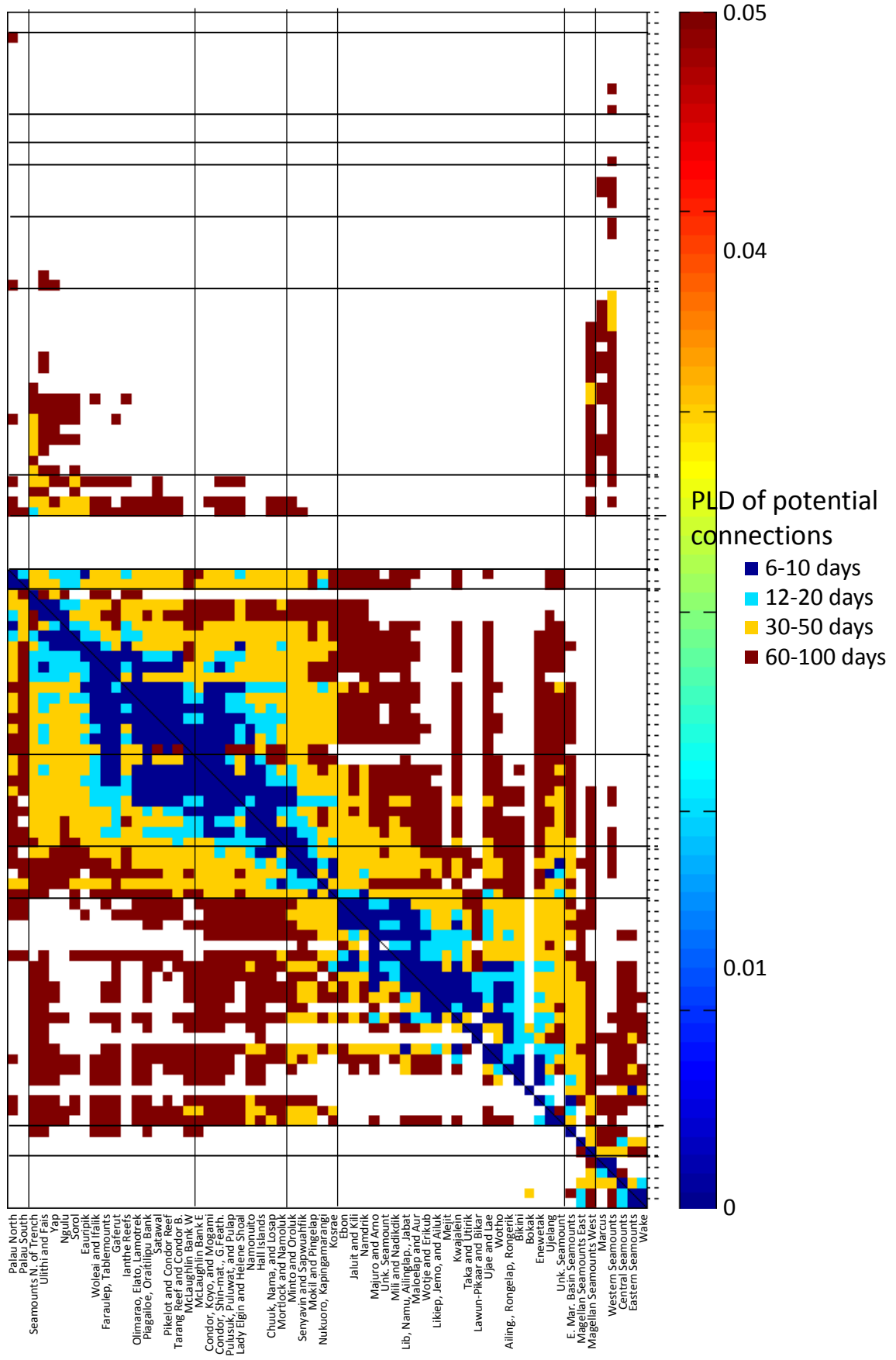
For the 30-50 day PLD, connectivity patterns along the Mariana Archipelago lacked the clear divisions seen for shorter PLDs (Appendix A.5). Instead, larvae with this longer PLD appeared capable of settling at locations anywhere in the Marianas north of their starting point or along the West Mariana Ridge. For example, larvae from Guam could self-seed, settle at Farallon de Pajaros, or anywhere in between. There was a northward bias in this transport however, in that larvae tended not to travel quite as far southward. For example, larvae from Agrihan went only as far south as Farallon de Medinilla and larvae from Guguan went only as far south as Rota. The mechanism for this northward bias appears to be the eddies spun off the northern edge of the NEC (Chapter 1). These gradually drift north and westward through the Marianas. When size of the settlement zone was increased, the northward bias in connectivity strength was greater within the Marianas as well as to destinations in the West Mariana Ridge (Appendix A.6).

The 30-50 day PLD also enabled several, low strength connections between the Marianas and the islands to the south in the Caroline Archipelago. Specifically, larvae from Yap and Chuuk could arrive in the Marianas regularly at Guam and the banks to its south. Larvae from Chuuk could also arrive at many locations between Rota and Farallon de Medinilla and in some cases as far north as Asuncion. These larvae were entrained in the current loops connecting the eastward flowing NECC at the latitude of FSM to the westward flowing NEC



**Figure 2.10.** Presence/absence of larval connections by PLD. This connectivity matrix depicts the potential connections among larval sources and destinations for all PLDs considered. Colored cells indicate those sources and destinations that were linked by any level of larval connection without regard to strength. The matrices are stacked with longest PLDs on the bottom to visualize how increasing PLD broadens the extent of potential connections among islands. With few exceptions, the connections possible at shorter PLDs

(larval sources continued from facing page)



(text continued from previous page) also occurred at longer PLDs but not vice versa (e.g. cells showing a connection at the 6-10 day PLD also were connected at all other PLDs). This overlay was based on the results for the small settlement zone only. The larger settlement zone (i.e. small zone plus 18 km buffer) shows nearly the same presence/absence pattern of connectivity and only differs in connection strength which is not shown in this format.

at the latitude of the southern Marianas. Larvae from some locations in the southern Marianas (e.g. primarily between Rota and Santa Rosa Reef) could reciprocate this transport and arrive at some of the islands and atolls to the west in Yap via the NEC and its eddies spun off to the south. Low strength connections were also observed between the Marshalls and the southern Marianas.

#### 60-100 day PLD

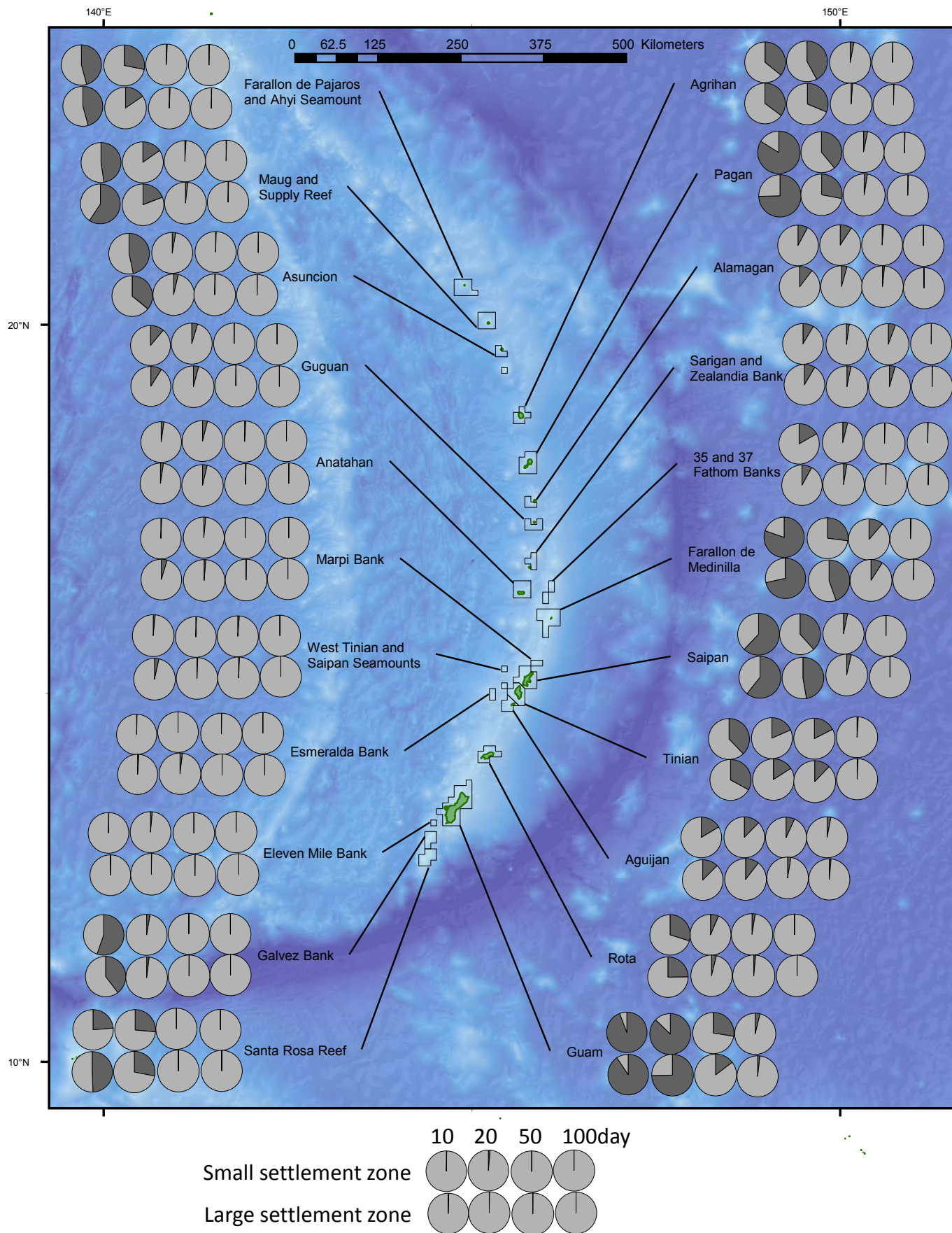
For the 60-100 day PLD, the longest considered in this study, there was widespread connectivity within the Marianas (Appendix A.7). Larvae from any Mariana source could settle at any other Mariana destination to the north, anywhere along the West Mariana Ridge, and even as far north as the Ogasawara Islands of Japan. Again, there was a northward bias in this pattern in that larvae could settle anywhere northward of their source island but almost no larvae from north of Alamagan went south of Tinian. At these long PLDs, connections between the Carolines and Marianas were more routine. Larvae from anywhere in Chuuk, Pohnpei, and parts of Yap could arrive nearly anywhere in the Marianas or the West Mariana Ridge via the NECC to NEC current loops. Larvae from the Marianas south of Farallon de Medinilla also had a stronger connection to Yap and could arrive at low levels at places in Chuuk and occasionally northern Palau. Also of note, for this very long PLD, larvae from islands in the NW region of the Marshall Islands could arrive at locations throughout the Marianas at least at low strength and from the Marianas to Luzon and other locations in the Philippines. These long distance connections were made possible by the straight line transport of the fast flowing NEC that connects these distant islands along this latitude. When size of the settlement zone was increased, connections with notably higher connection strength included the northward bias in transport within the Marianas, from the Marianas to the Volcano Island group in Japan, and from the Marshall Islands to Guam (Appendix A.8).

#### Self-seeding Versus Import in the Marianas

Increasing the size of the settlement zone around each island had very little effect on the proportions of larvae that were self-seeded versus imported (Figure 2.11). Increasing the settlement zone size often reduced the fraction from self-seeding, but only by a few percentage points. Only a few islands obtained half of their larval supply from self-seeding and even then only for short PLDs. These included Guam and its southern banks, Saipan, Farallon de Medinilla, and islands north of Pagan. All islands relied on an increasing proportion of larvae from external sources for longer PLDs. For example, Saipan's arriving larvae were >50% self-seeded when PLD was 10 days, <5% when PLD was 50 days, and <1% when PLD was 100 days. Only Guam relied on self-seeding for more than ~15% of its larval supply for PLDs of 30-50 days. At PLDs of 60-100 days, imports dominated such that Guam had the highest proportion of self-seeding of any location in the Marianas at a mere ~3%. With few exceptions, submerged banks and seamounts were almost totally reliant on larvae arriving from external sources at all PLDs and settlement zone sizes. Exceptions were based on very few larvae.



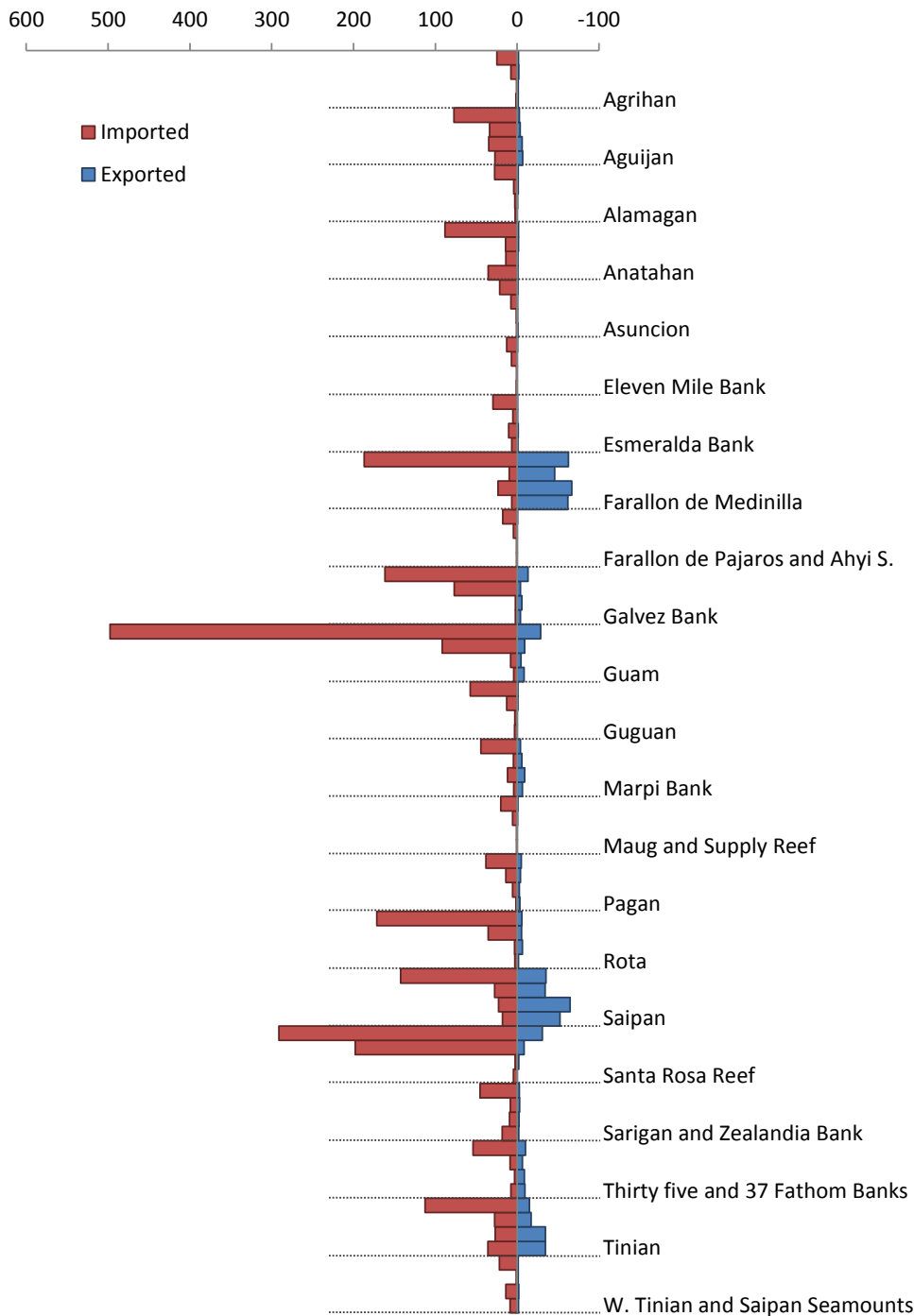
Sea cucumber in Lao Lao Bay, Saipan.  
Photo credit: M. Kendall, Biogeography Branch, NOAA.



**Figure 2.11.** Proportions of larvae settling at each island that are from self-seeding (dark grey) versus imported (light grey). Eight pie charts are shown for each location for each combination of PLD and settlement zone size. Maximum PLDs from left to right next to each island are 10, 20, 50, and 100 days. Upper row denotes results for the small settlement zone and the lower denotes results for the large settlement zone.

### Import and Export at the Marianas

The magnitude of import and export values roughly doubled when the larger settlement zone size was used; however, the relative pattern among islands and PLDs was quite similar (Figure 2.12). Therefore, only the small settlement zone results are shown. In general, most locations imported more larvae than they exported and the number of larvae imported declined for shorter PLDs. Longer PLDs enabled more larvae to arrive from distant locations. Exceptions were Farallon de Medinilla, Saipan, and Tinian, which often exported more larvae than they imported for PLDs under 100 days. Examining the annual model outputs revealed that the high exports from Farallon de Medinilla were due to larvae sent to its island neighbor to the northwest, Anatahan during many years, but also to Arakane Reef and neighboring banks. The high export from Saipan was due to transport of larvae with short PLDs to its neighbors including Tinian and Farallon de Medinilla in various years. The largest import of larvae was for the 50 and 100 day PLDs arriving at locations between Santa



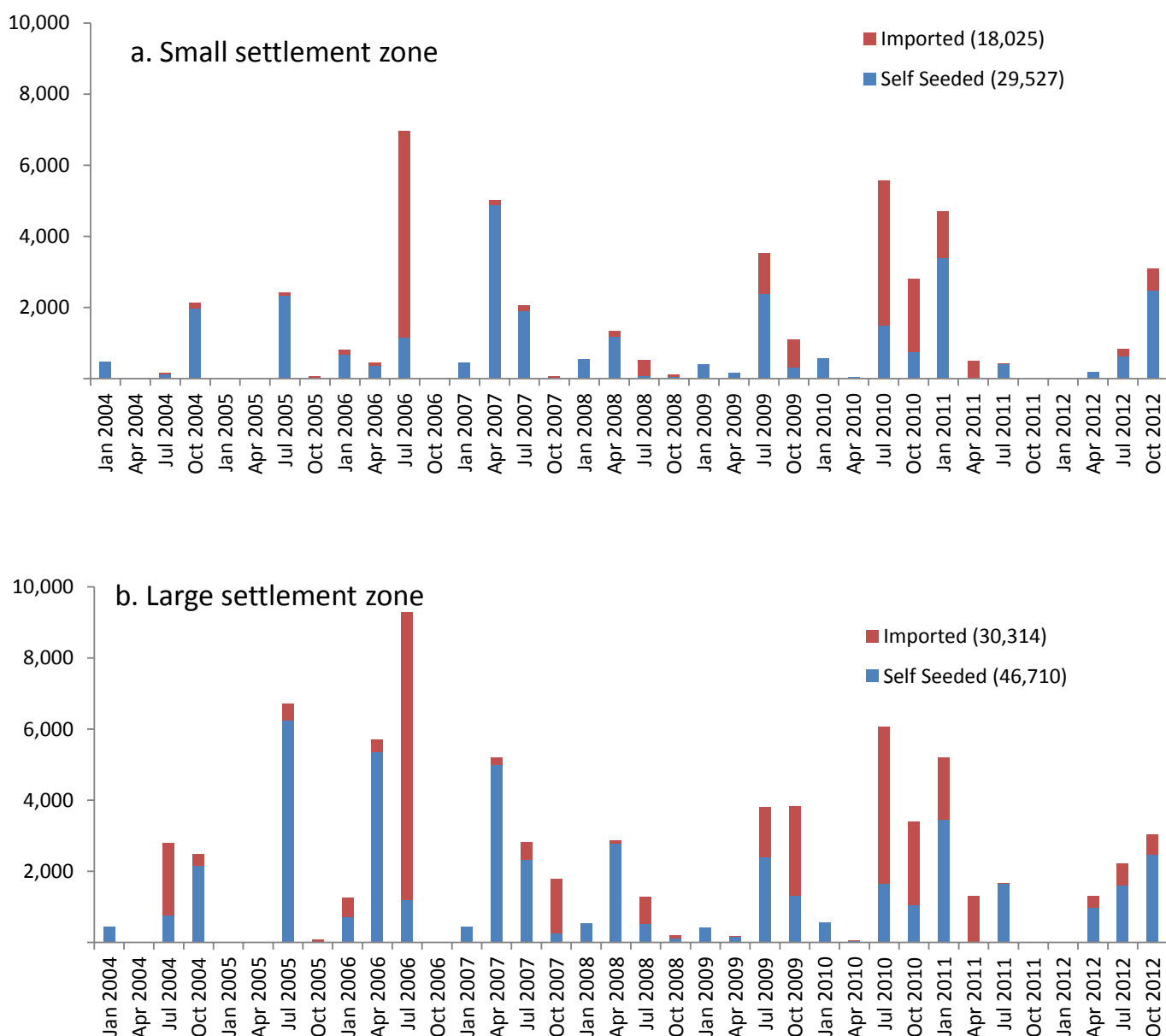
**Figure 2.12.** Number of virtual larvae that are imported and exported from each island in simulations with the small settlement zone size. Bars within each island denote the 100, 50, 20, and 10 day maximum PLDs arranged from top to bottom. All values are in thousands.



Rosa Reef and Farallon de Medinilla. Guam was the single largest importer (almost twice as many imported as the next highest importer), probably due to its large size and position centrally in the NEC. Larvae arriving at these locations were primarily from Chuuk in the FSM and Bikini and Enewetak Atolls in the Marshalls.

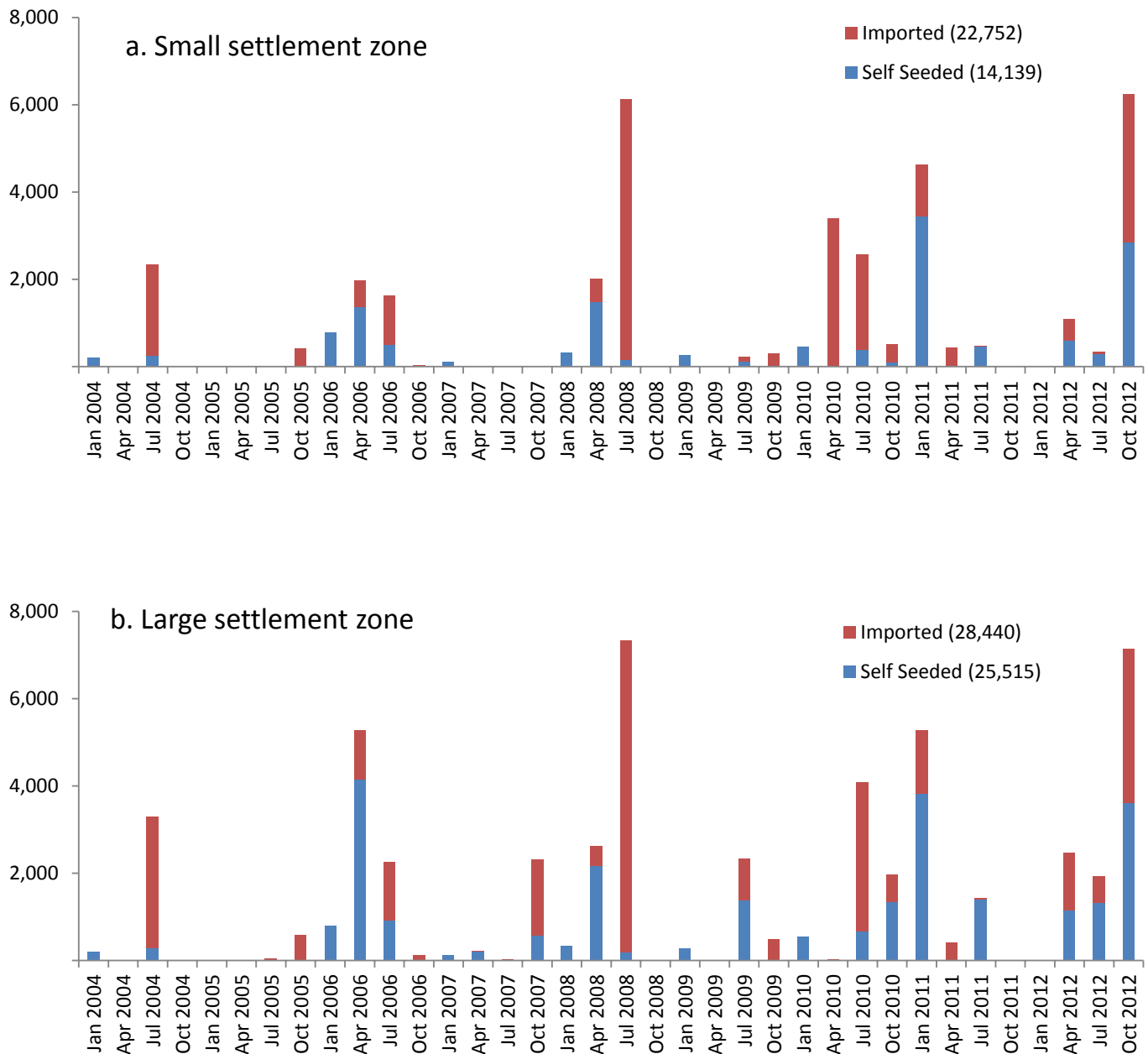
### Time Series of Recruitment Strength at Saipan and Guam

There were no seasonal differences in the number of larvae arriving at Saipan with a 6-10 day PLD. There was almost total recruitment failure at Saipan in approximately 1/3 of the simulated spawning events. At the opposite extreme, spikes in larval supply occurred irregularly among seasons, years, and ENSO conditions. Spikes in self-seeding occurred in April 2007, July 2009 and January 2011 (Figure 2.13a). There was also a spike in larval imports in July 2006 and around October 2010. These larvae arrived primarily from Farallon de Medinilla in 2006 via an eddy north of the NEC and from Tinian in 2010. These were the only times when imports comprised a greater proportion of incoming larvae than self-seeding. Overall, self-seeding accounted for ~60% of arriving larvae. When size of the settlement zone was increased, the overall pattern was similar although the magnitude of recruitment values increased for most simulations (Figure 2.13b). Total arriving larvae increased by a factor of 1.6 with the larger zone. Also of note, self-seeding was dramatically higher on two occasions (July 2005, April 2006) when the larger settlement zone was used.



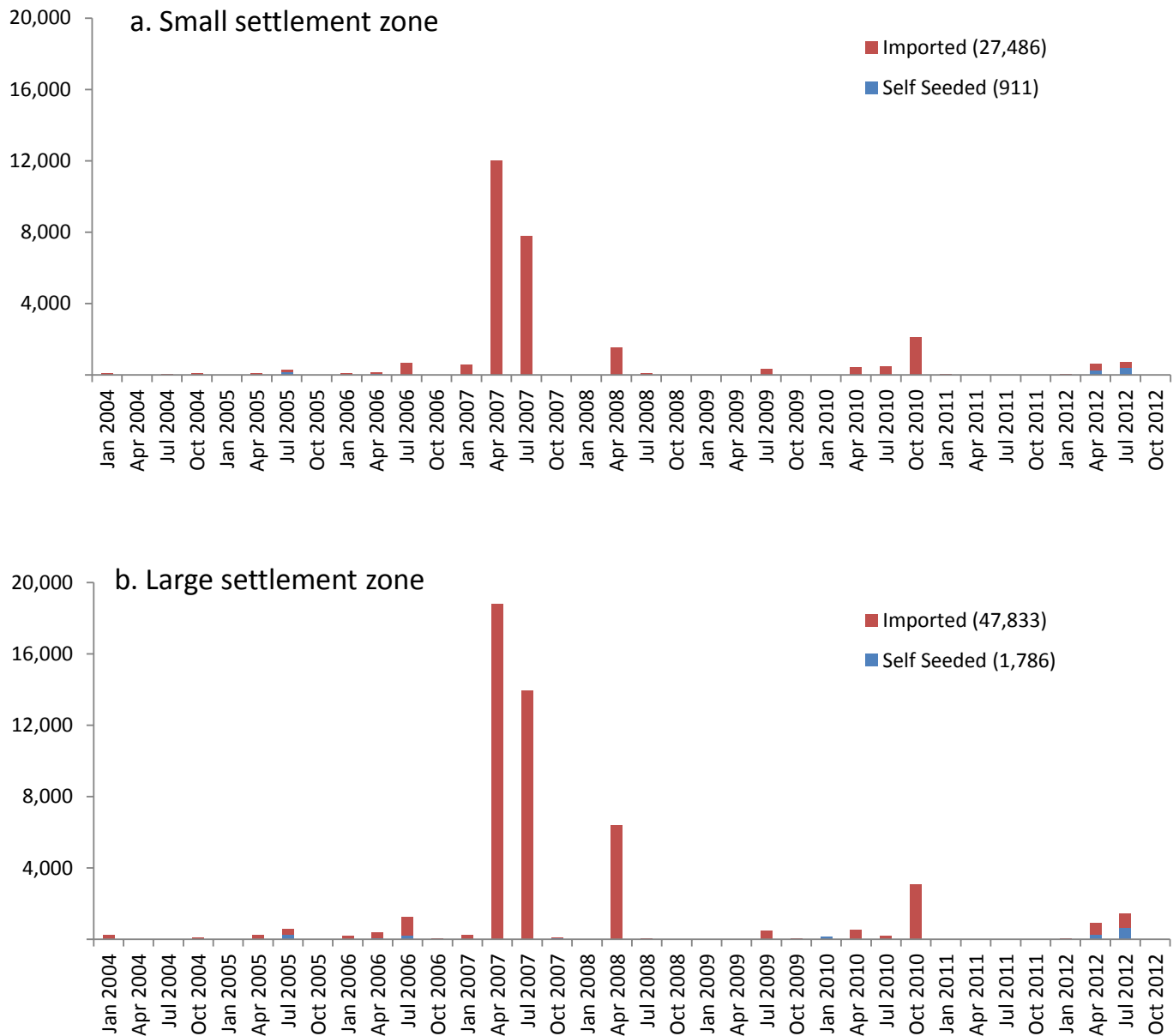
**Figure 2.13.** Time series of imported and self-seeded larvae arriving at Saipan with a 6-10 day PLD within the: a) small settlement zone, b) large settlement zone. Values in parentheses denote the total number of larvae arriving from import and self-seeding.

For the 12-20 day PLD there were still no seasonal differences in number of larvae arriving at Saipan (Figure 2.14a). The number of spawning dates with recruitment failure increased compared to the 6-10 day PLD scenario. Recruitment peaks occurred on different dates than seen for the 6-10 day PLD as well. Self-seeding showed peaks around April 2006 and 2008, January 2011, and October 2012. Imports also showed peaks around these dates as well as July 2004. Overall, imports accounted for ~60% of arriving larvae. Imported larvae were from Farallon de Medinilla in July 2008 and April 2010, and from Tinian in October 2012. When size of the settlement zone was increased, the overall pattern was similar although the magnitude of many self-seeding and import values often increased (Figure 2.14b). Total arriving larvae increased by a factor of 1.5 with the larger zone.



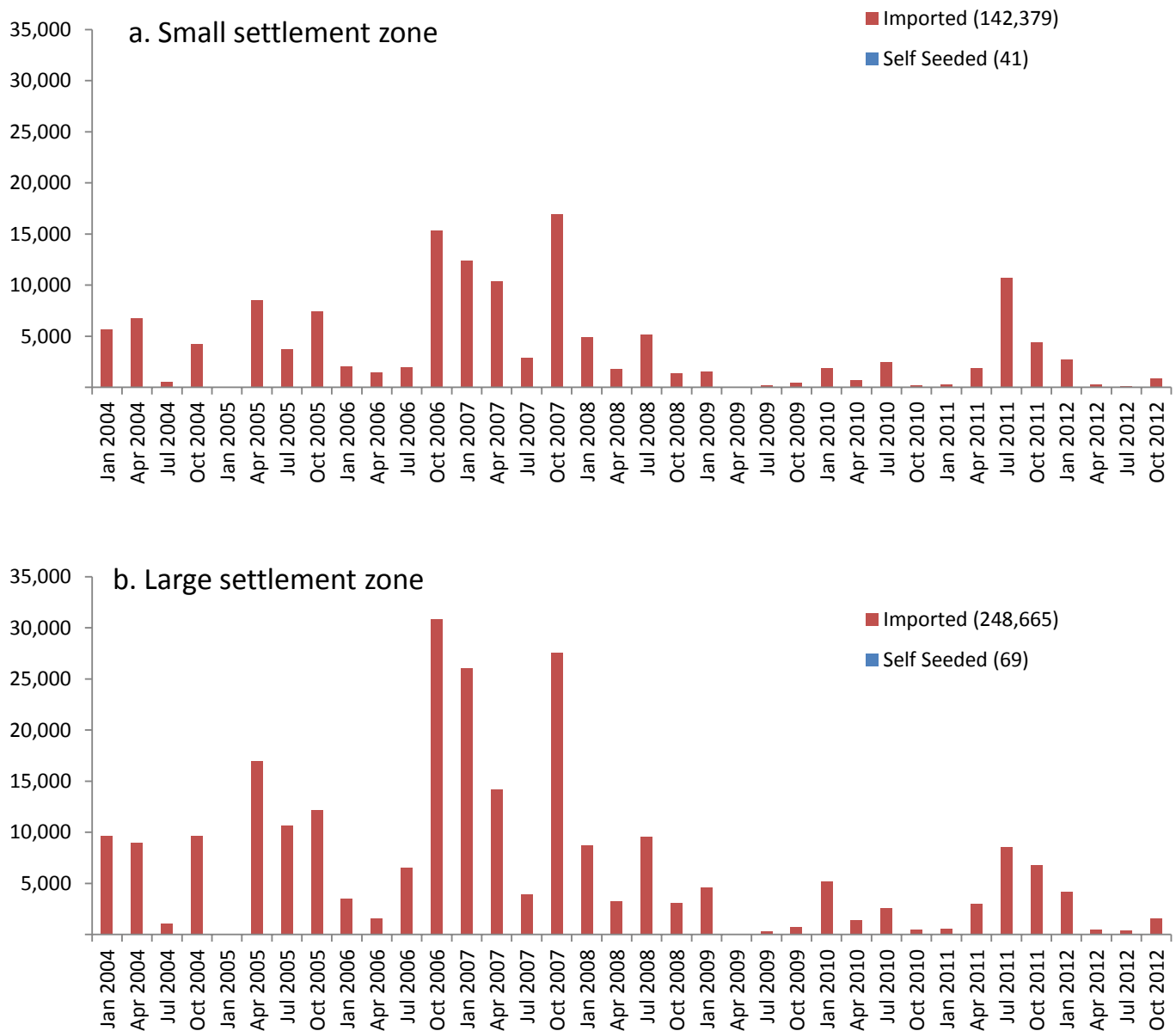
**Figure 2.14.** Time series of imported and self-seeded larvae arriving at Saipan with a 12-20 day PLD within the: a) small settlement zone, b) large settlement zone. Values in parenthesis denote the total number of larvae arriving from import and self-seeding.

For the 30-50 day PLD, self-seeding in Saipan practically vanished, accounting for only 3% of total settlement. Currents almost never returned larvae to Saipan in the 30-50 day timeframe (Figure 2.15a). In fact, most season/year combinations received no larvae at all. This PLD was in a temporal range wherein locally produced larvae have all been swept away, but larvae from elsewhere have not yet arrived regularly. Settlement at Saipan was almost entirely from imports, especially in April and July of 2007. These larvae were from Chuuk via the NECC to NEC transport loops. Again, these few settlement peaks occurred in various seasons. When size of the settlement zone was increased, recruitment dates were very similar although the magnitude of imports was higher by a factor of 1.7 overall (Figure 2.15b).



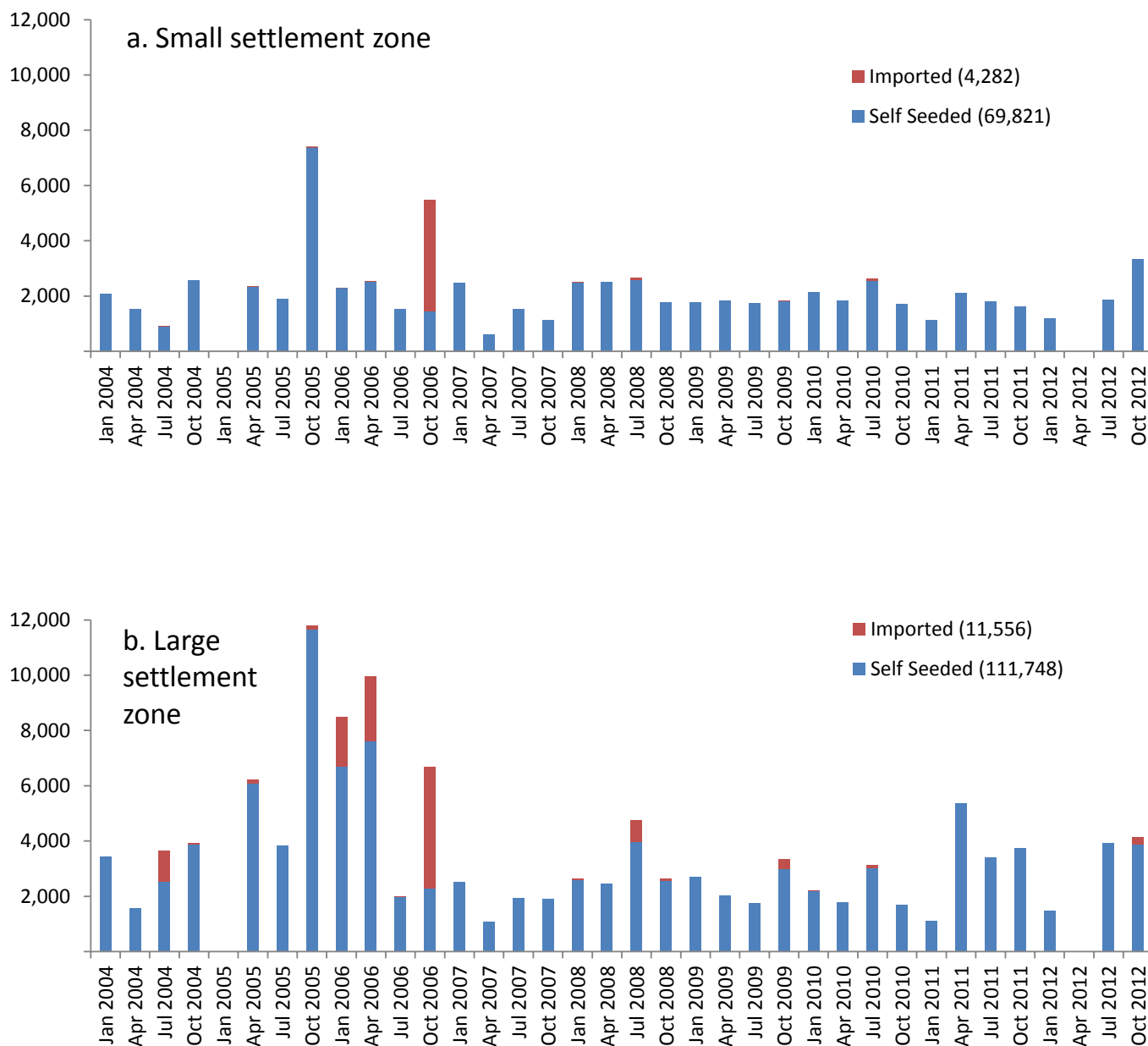
**Figure 2.15.** Time series of imported and self-seeded larvae arriving at Saipan with a 30-50 day PLD within the: a) small settlement zone, b) large settlement zone. Values in parenthesis denote the total number of larvae arriving from import and self-seeding.

For the 60-100 day PLD, larvae arriving at Saipan were still totally dominated by imports in all season/year combinations (Figure 2.16a). There was no difference in settlement among seasons. A period of especially strong import occurred from October 2006 through October 2007. This was due to incoming larvae from locations in the Marshall Islands via the NEC and Chuuk and Pohnpei via the NECC to NEC current loops. The NEC had highest median current speeds of any year during 2007, which would facilitate those connections (Chapter 1). There was also a period of especially low recruitment from April 2009 to April 2011, years when NEC current speeds were very low. This illustrates that a year of remarkably good recruitment can be followed soon after by one of relatively low recruitment due entirely to ocean circulation patterns. When size of the settlement zone was increased, recruitment patterns were very similar although the magnitude of imports increased in many dates such that overall recruitment increased by a factor of 1.7 (Figure 2.16b).



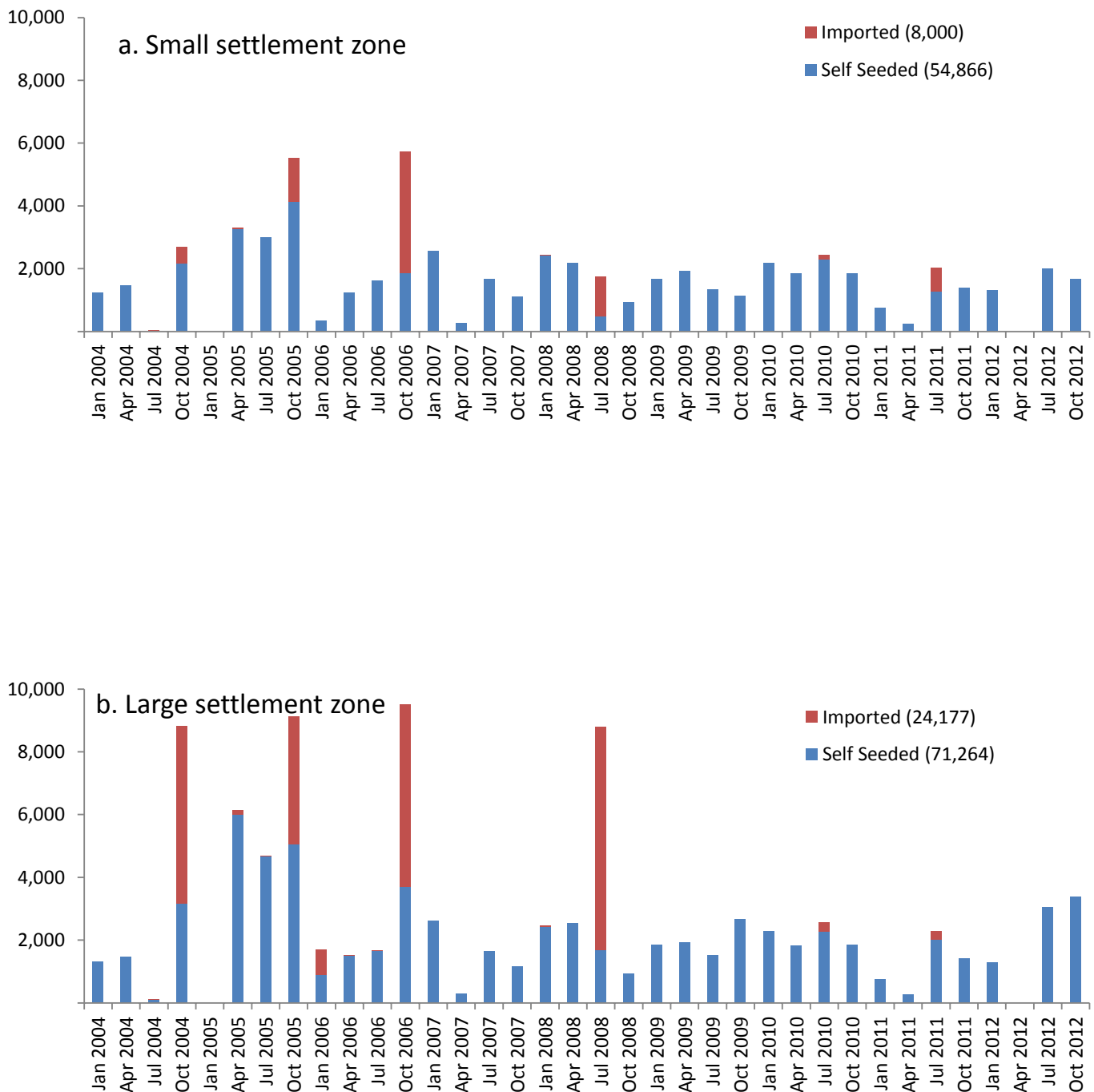
**Figure 2.16.** Time series of imported and self-seeded larvae arriving at Saipan with a 60-100 day PLD within the: a) small settlement zone, b) large settlement zone. Values in parenthesis denote the total number of larvae arriving from import and self-seeding.

Larvae arriving at Guam with PLDs of 6-10 days were almost entirely from self-seeding which accounted for 94% of total settlement (Figure 2.17a). The number of self-seeded larvae was quite regular with the exception of October 2005, which experienced a spike in self-seeding 4 times higher than typical levels. The mechanism for this appears to be a clockwise eddy spun off the northern edge of the NEC. Also of note, in October 2006 there was a one-time influx of larvae from Guam's southern neighbor, Galvez Bank, which tripled the number of arriving larvae. This was the only spawning date out of 35 simulations with significant larval import from outside of Guam. There were no differences among seasons. When size of the settlement zone was increased, recruitment patterns were overall very similar but with a broader peak of self-seeding in 2005-2006 (Figure 2.17b). Total arriving larvae increased by a factor of 1.7 with the larger zone.



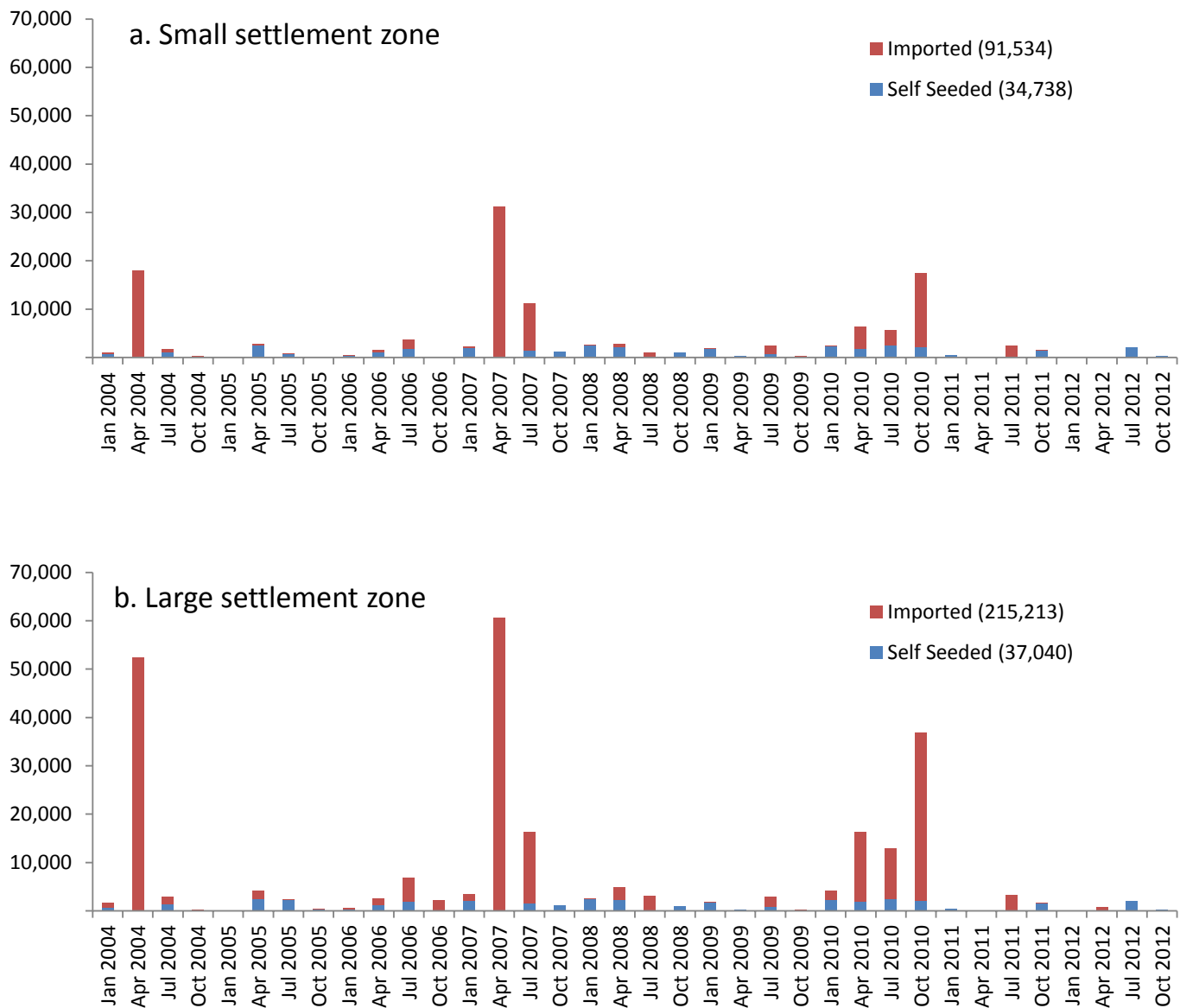
**Figure 2.17.** Time series of imported and self-seeded larvae arriving at Guam with a 6-10 day PLD within the: a) small settlement zone, b) large settlement zone. Values in parenthesis denote the total number of larvae arriving from import and self-seeding.

For the 12-20 day PLD, the spike in imported larvae to Guam from Galvez Bank in October 2006 was still apparent as was the increase in self-seeding in October 2005 (Figure 2.18a). Total settlement was still dominated by self-seeding which accounted for 87% of all recruits. The most noticeable effect of increasing the size of the settlement zone was that the magnitude of the rare larval imports was increased and showed four clear peaks. Three occurred following October spawning in 2004, 2005, and 2006 and another in July 2008 (Figure 2.18b). These larvae were from Galvez Bank (2005, 2006, 2008) and Saipan (2004). Even with these increases in import, self-seeding still dominated recruitment accounting for 75% of all settling larvae. There were no seasonal differences. Total arriving larvae increased by a factor of 1.5 with the larger zone.



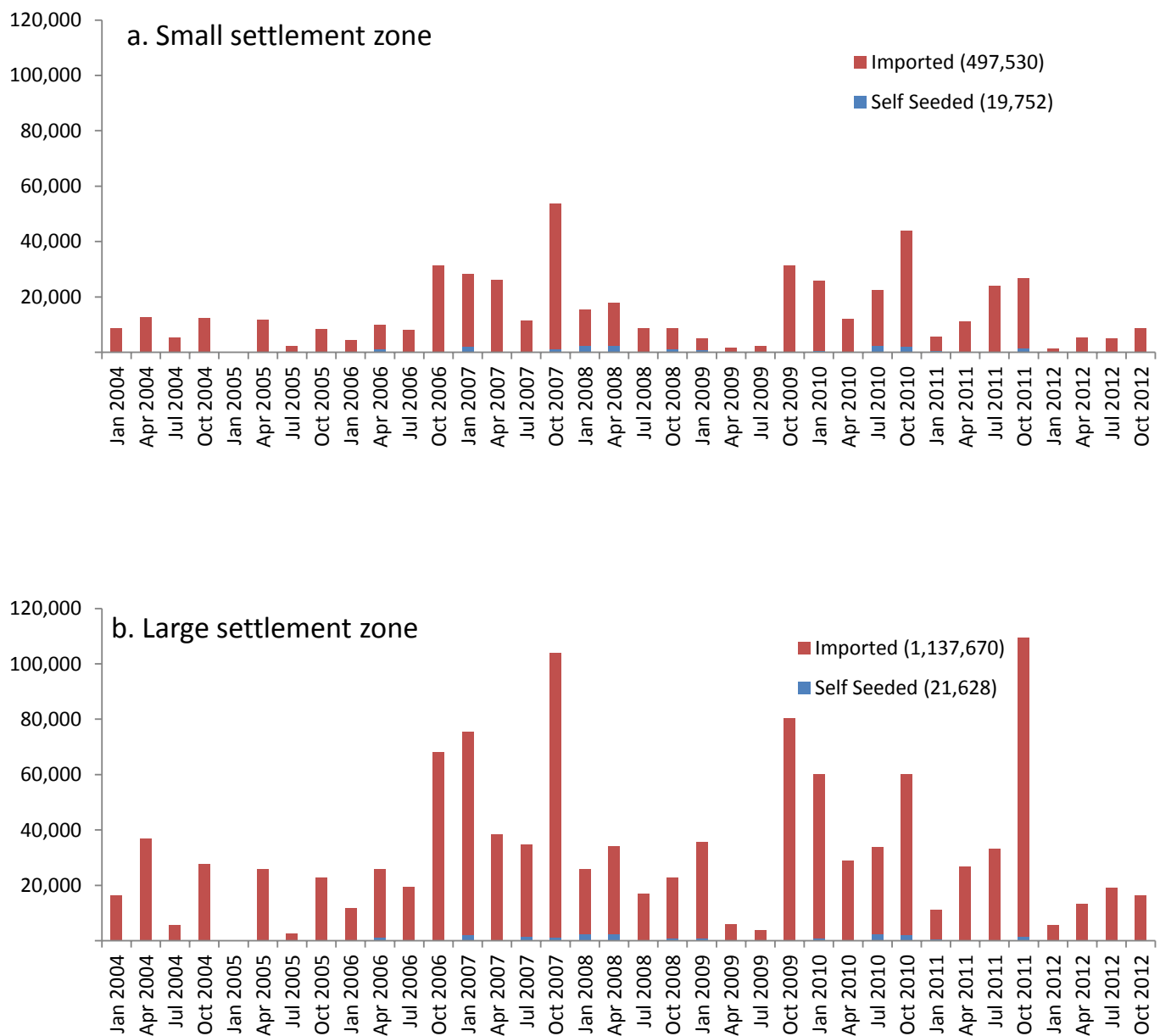
**Figure 2.18.** Time series of imported and self-seeded larvae arriving at Guam with a 12-20 day PLD within the: a) small settlement zone, b) large settlement zone. Values in parenthesis denote the total number of larvae arriving from import and self-seeding.

For the 30-50 day PLD, self-seeded larvae still arrived regularly at Guam but were small in number (~30% of total recruits) compared to the rare but huge number of larvae arriving from elsewhere (Figure 2.19a). There were no seasonal differences. Three import spikes dominated larval recruitment following multiple spawning events in 2004, 2007 and 2010. These were from Chuuk and arrived due to a northward shift in the loops connecting the NECC to the NEC. These events occurred in various ENSO states and because there were only three events statistical analyses were not attempted. When settlement zone size was increased, the basic pattern of recruitment remained consistent but the magnitude of spikes in imported larvae was dramatically affected. Overall, twice as many larvae arrived, primarily from Chuuk, due to the larger settlement zone (Figure 2.19b).



**Figure 2.19.** Time series of imported and self-seeded larvae arriving at Guam with a 30-50 day PLD within the: a) small settlement zone, b) large settlement zone. Values in parenthesis denote the total number of larvae arriving from import and self-seeding.

For the 60-100 day PLD, recruitment at Guam was heavily dominated by imports (96% of all recruits) which occurred regularly in all years (Figure 2.20a). There also appeared to be regular seasonal peaks in recruitment from Chuuk and Pohnpei following October spawning for several years including 2006, 2007, 2009, 2010, and 2011. The multiple-mean comparison test indicated that recruitment from October spawning was significantly higher than from April and July spawning and was driven by larval import. This represented the only significant seasonal pattern in recruitment for Guam or Saipan. This connection could be facilitated by the higher speed and more northward trajectory of the NECC during Fall and Winter (Chapter 1) when larvae with this PLD would be at large. There were two years of especially heavy import from the Marshall Islands and Chuuk. These were in 2007 and 2010 and began in October of the preceding years. Current speeds of the NEC were high during 2007, but not in 2010 (Chapter 1). In contrast, especially low recruitment was seen in early 2009 and 2012. The NEC was relatively slow in 2009 (Chapter 1, no data available for 2012), and did not transport larvae from the Marshall Islands quickly enough to reach Guam in those years. When settlement zone size was increased, the basic pattern of recruitment remained consistent but the magnitude of spikes in imported larvae could be more than doubled (Figure 2.20b). Overall, recruitment increased by a factor of 2.2 for the larger settlement zone.



**Figure 2.20.** Time series of imported and self-seeded larvae arriving at Guam with a 60-100 day PLD within the: a) small settlement zone, b) large settlement zone. Values in parenthesis denote the total number of larvae arriving from import and self-seeding.



## DISCUSSION

Coral reef organisms can be locally depleted through fisheries extraction, natural or anthropogenic disturbance, or regular cycles of meta-population dynamics. Understanding which islands serve as sources of larvae to themselves and others is crucial component of managing reef ecosystems and fisheries that are resilient to disturbance. Simulations in this report document interconnected webs of larval exchange within and among archipelagos of the NW Pacific that vary in size with PLD. Along with traditional fisheries management and reduction of land-based stressors, the information in this report can be used to devise a more complete strategy for ecosystem management.



*Corals in Lao Lao Bay, Saipan.  
Photo credit: M. Kendall, Biogeography Branch, NOAA.*

The connectivity matrices illustrate how PLD affects the spatial extent and geographic pattern of connectivity. The speed, direction, and variability of ocean currents identified in Chapter 1 explained much of the pattern in the matrices. The position of the NEC through the southern Marianas and the eddy field along the Marianas to the north were primarily responsible for connectivity patterns in the Marianas for taxa whose larvae have a maximum PLD up to about 50 days. Geographic break points in connectivity fell along the interface of these currents approximately at the latitude of Rota. The mechanism for the northward skew in transport at higher latitudes appears to be the eddies spun off the northern edge of the NEC (Chapter 1). These gradually drift north and westward through the Marianas, often spinning clockwise although the exact position, size and duration are highly variable. Broader scales of connectivity among archipelagos for larvae with PLDs of 50-100 days were also explained by the regional ocean currents described in Chapter 1. Connections from FSM to the southern Marianas were enabled by the eastward NECC picking up larvae as it flowed through the FSM, the northward current loops that transport larvae in the NECC to the NEC, and the westward flow of the NEC that may deposit those larvae to the southern Marianas. The distance and current speed along this pathway regularly enable this connection for taxa with longer PLDs of 50-100 days but generally not for those with shorter PLDs. For the longest PLD, the straight and fast flowing NEC could transport larvae from the Marshall Islands in the east to the southern Marianas, and from the southern Marianas to the Philippines. There are few, if any, locations to act as stepping stones between these islands to enable larvae with shorter PLDs to make these transits, even over multiple generations.

Increasing the settlement zone size by 18 km around each model grid cell containing potential reef habitat had a doubling effect on the number of larvae settling. Larvae of some fish may have sufficient orientation, speed, and endurance capability to connect from even farther offshore, which could further increase the number of settlers. When considering the implications of our findings for connectivity of fish taxa, it is important to recognize that while PLD is often determined by counting the number of days until a settlement mark is observed on an otolith, some taxa may develop sufficiently to be considered nekton rather than plankton at an earlier day, perhaps only 50% of their maximum PLD (Fisher 2005). After this point, they may be able to keep pace with ocean currents near settlement habitat until they mature to a settlement stage. For these taxa, it may be more appropriate to consider the shorter duration of only the truly planktonic portion of their PLD in our results, rather than their total PLD. In contrast to the increase in number of settlers, the larger settlement zone did not enable many more island pairs to be connected and had little effect on the spatial pattern of connectivity for any PLD. This is because the scale of the settlement zone effect is localized around each island relative to the scale and distances of interisland connectivity. Reducing transit distance by 18 km (width of the large settlement zone) does not affect connectivity for islands hundreds of kilometers apart.

Spawning season did not have a large effect on either the total number of successful larvae or the number of interisland connections. This was somewhat surprising given the seasonal differences in the region's ocean currents (Chapter 1) and that many organisms have well defined seasonal peaks in spawning activity (e.g.

Kami and Ikehara 1976, Richmond and Hunter 1990, Hopper et al. 1998). Presumably, seasonal spawning is selected for at least in part, to set larvae adrift at times favorable for transport (Triani 2011, Sanvicente-Añorve et al. 2013). The lack of seasonal differences in results here could be due to several factors. Seasonal differences in ocean currents may not be that large compared to the interannual variation in currents or stochastic parameters (i.e. diffusivity and variance in current vectors) used in transport simulations. These sources of variation accumulated over 9 years of simulations may overwhelm any seasonal signal. It could also be that seasonal spawning has less to do with optimizing times for physical transport and more to do with other factors such as better development conditions for larvae, optimal gonad development, or synchrony of reproductive effort to maximize fertilization success or mating opportunities. None of those factors were considered in our study, which kept reproductive output and larval mortality rates constant in all seasons. Individual taxa often have reproductive seasons but in composite when many species are considered together, there did not appear to be one dominant group of months in which most spawning occurred (e.g. Figure 2.2). It is also important to keep in mind that seasonal effects were primarily investigated at the scale of the entire study area. Smaller groups of islands within those currents that may be most affected by season (e.g. NECC is faster and more northward in winter, Chapter 1) should be the focus of additional analyses to determine if such areas are more sensitive to seasonal aspects of transport.

Several analyses in this chapter examined the relative roles of self-seeding versus reliance on external sources of larvae. A few islands in the Marianas, most notably the human population centers of Guam and Saipan, relied upon their own reef communities to supply 50-90% of their arriving larvae for short PLDs. The proportion of each island's larval supply that comes from self-seeding has special importance from a management perspective. If an island gets most of its larvae from its own reef communities, local management actions take on a heightened significance. Where local spawning stocks are maintained at healthy levels, the benefits of larval production will be locally rewarded. Where local spawning stocks are depleted through overfishing, habitat destruction or environmental degradation, the consequences will be reduced local recruitment to maintain fisheries and less resilient reef communities. In contrast, many islands were reliant on larval imports to sustain their local reef communities. In such cases, local management decisions may be less important than identifying the upstream sources of arriving larvae and promoting responsible management at those sites.

If an island is heavily dependent upon larval imports to sustain local populations (e.g. many places in the Marianas for taxa with short PLDs and essentially everywhere in the Marianas including Guam and Saipan for taxa with long PLDs), it does not mean that its local communities can be harvested or allowed to decline without consequence. Even though a location may not self-seed, it may be an important or even critical source of larvae to some destination downstream. For example, three islands in the Marianas: Saipan, Tinian, and Farallon de Medinilla, bear the responsibility of being the source of many larvae to other locations in our simulations.

Thus far discussion has been primarily on the cumulative patterns of connectivity among all seasons and years of simulation data. The time series of recruitment at Saipan and Guam for each discrete seasonal spawning event over 9 years offers additional insight into the temporal trends and variation in larval transport. When examined as consecutive spawning and recruitment events, connectivity can be seen as a much more volatile and variable process than when data are examined cumulatively. Individual seasons and years of high recruitment can be followed by periods of low or no recruitment. This is borne out in the boom or bust cycles of some organisms in the Marianas such as rabbitfish harvest and COTS outbreaks, both of which are addressed specifically in the next chapter. Such variability highlights the need to examine not just one or two years of connectivity data, even when they are believed to be "representative", but to analyze many years during a variety of oceanographic conditions (e.g. ENSO) to truly understand connectivity patterns. Another observation made possible by the time series of recruitment events is that even relatively closely spaced islands such as Saipan and Guam can have quite different temporal patterns of settlement. A strong recruitment event in Saipan is not necessarily going to be matched with a strong event in Guam on the same month/year combinations and vice versa.



Lao Lao Bay Marine Protected Area.  
Photo credit: M. Kendall, Biogeography Branch, NOAA.

## APPLICATIONS

The best way to apply the information in this report will depend on specific management or scientific needs, and may not be covered in the limited set of analyses presented thus far. For example, scientists can use the results to inform sampling strategies or field surveys. Where might study organisms be predicted to have strong or weak recruitment? Geneticists can use model results to optimize allocation of field samples and set-up hypothesis tests based on predictions from the connectivity matrices. Specific recruitment events observed in field surveys can be tested against results from specific season/year simulations. Fisheries managers can identify locations of key spawning stocks and understand where larvae that sustain local fisheries ultimately arrive from. On Guam for example, there is speculation that a significant proportion of larval supply comes from nearby banks. This and other hypotheses can be addressed using the results from our simulations.

A key management application of model results is in the assessment of existing marine protected areas (MPA) and placement of new ones. Appropriately sized and spaced MPAs are one of the tools known to help conserve, manage, and maintain coral reef ecosystems. Like in other areas, MPAs in the Marianas have been devised based on consideration of best available scientific information, local objectives, and of course political feasibility. As of 2013 there were a total of 22 MPAs in the Marianas created with a variety of goals, sizes, and use restrictions. An understanding of larval connectivity across the region was not available at the time most were established. Clearly, for MPAs with an emphasis on natural resource and fisheries management, MPA placement decisions can be enlightened by understanding which locations provide the greatest return to Mariana reef communities. Where does larval production from each MPA go? What proportions of larval production self-seed home islands, drift to an adjacent island, benefit adjacent nations, or become lost at sea? Where does larval production that sustains MPAs arrive from? Many individual MPAs in the Marianas are quite small and have an average marine area of <math><3\text{ km}^2</math> (excluding the Marianas Trench Marine National Monument). These small MPAs represent only a fraction of the total larval pool for their host island. Our results, however, only offer insight at the scale of the host island for those MPAs. For larger MPAs such as the Islands Unit of the Marianas Trench Marine National Monument, which encompasses the entire islands of Asuncion, Maug, and Farallon de Pajaros, our results are more directly comparable (Presidential Proclamation 8335, 2009). Our simulations may be especially useful in understanding potential interconnections in MPA networks for the region. Protecting 30% of the regions near-shore marine resources is encouraged

through the Micronesia Challenge ([www.micronesiachallenge.org](http://www.micronesiachallenge.org)) and our results should be used as part of the planning process to select the most beneficial sites to include.

In addition to MPAs, traditional fisheries management tools such as regulations on gear use, minimum and maximum size limits, and temporary harvest moratoria can also be a very effective means of improving brood stocks. For example, CNMI has had a ban on the use of scuba for spear fishing for well over a decade, resulting in a depth refuge with increasing size of conspecifics with depth (Lindfield et al. 2014). The benefit of such a regulation is in the overwhelmingly larger area as a refuge compared to the small MPAs. Whereas the shallow-water MPAs capture small and specific (human-selected) segments of coast, the deep-water refuge offered by the scuba ban circles every island and includes a broad diversity of deeper habitats. Other fisheries management tools, such as the temporary moratoria on Trochus (aliling tulompo) and Sea Cucumber (balati) harvest can be imposed to rebuild brood stocks until populations rebound (<http://www.cnmi-dfw.com/>). The benefits of these regulations will differ spatially as demonstrated by findings in this report.

Larval production was scaled to potential area of coral reefs around each island in our simulations. Of course, the distribution of reef fish and corals is not uniform among islands and is correlated with variables including size of nearby human population, MPA presence, geomorphology, depth, and temperature (e.g. Houk and Starmer 2010, Richards et al. 2012, Taylor et al. 2012, Gove et al. 2013). These factors will affect the reproductive output of the spawning population at each island independently of reef area. Unfortunately, population size structure and density information is not available for all islands or all taxa throughout the study area and therefore was not included in this analysis.

Constant mortality rates corresponding to each PLD were used here to generate connectivity matrices. It is recognized that, in reality, mortality rates vary among taxa and environmental conditions. Survival curves estimated for larvae of many reef organisms broadly show a constant mortality rate throughout larval development (Cowen et al. 2000, Graham et al. 2008, Schnitzler et al. 2012, Connolly and Baird 2010) but varies for others often depending on environmental conditions (Graham et al. 2008, Connolly and Baird 2010, Schnitzler et al. 2011). Sensitivity of connectivity patterns produced here due to various survival curves and mortality rates will be an important next step in future analysis especially in the context of climate change and future environmental conditions. Post-settlement mortality can also be a major controlling factor on population structure (Houk and Starmer 2010) but was not considered here.

It is important to note that all results are primarily based on multiyear-composite of transport unless otherwise noted. Looking at recruitment intensity resulting from particular spawning dates for Guam and Saipan shows the large volatility in number



Local fish for sale in Saipan.

Photo credit: M. Kendall, Biogeography Branch, NOAA.

of arriving larvae. This highlights the need to look at many years of recruitment patterns to understand the temporal aspects of connectivity. Results would have differed had just one or a few years been analyzed even if they were suspected to be “representative” of typical conditions.

Also of note, connections spanning multiple generations are not explicitly included in any outputs shown here. At first glance, locations far from each other may seem completely disconnected. For example, the Philippines and Marshall Islands are at opposite sides of our study region and never exchanged even a single larva in any of our simulations. However, it is possible for long lived larvae from the Marshalls to make it to the Marianas, and then in the next generation, make it from the Marianas to the Philippines. Considered in the context of multiple generations, the connections mapped here can take on a new dimension.

The entire database of simulations performed here could be the subject of extensive additional analyses. We only examined a few regional-scale values and only looked more closely at the time-series of recruitment at two out of 116 locations. Results were not thoroughly evaluated for correlations with ENSO or subregional effects due to season. Analysis of drifter data in Chapter 1 indicated some differences in heading and velocity of regional currents among La Niña, neutral, and El Niño years. Linking those patterns to results of the transport simulations will require careful analysis of the timing of ENSO effects (e.g. lag in ENSO state and response in ocean current), corresponding spawning dates used in simulations, and PLD values which may span multiple seasons and ENSO conditions. Such complexity was beyond the scope of our study, however such an analysis may provide useful insight into the role of ENSO on larval connectivity.

The outputs could also be subjected to additional modification in future analyses. Number of starting larvae could be rescaled at various islands based on regional field surveys, or to examine effects of hypothetical management scenarios. Number of arriving larvae could be used to rescale each island’s starting larvae in successive generations to examine the compounding effect of connectivity on each island over many years. Virtual MPAs could be evaluated wherein an island’s spawning stock and number of larvae is increased to evaluate the effect on regional connectivity. Another important avenue of future research would be to use current vectors from an ocean circulation forecast model (rather than from a hindcast model as was used here) in larval transport simulations to generate predictive models of future connectivity.

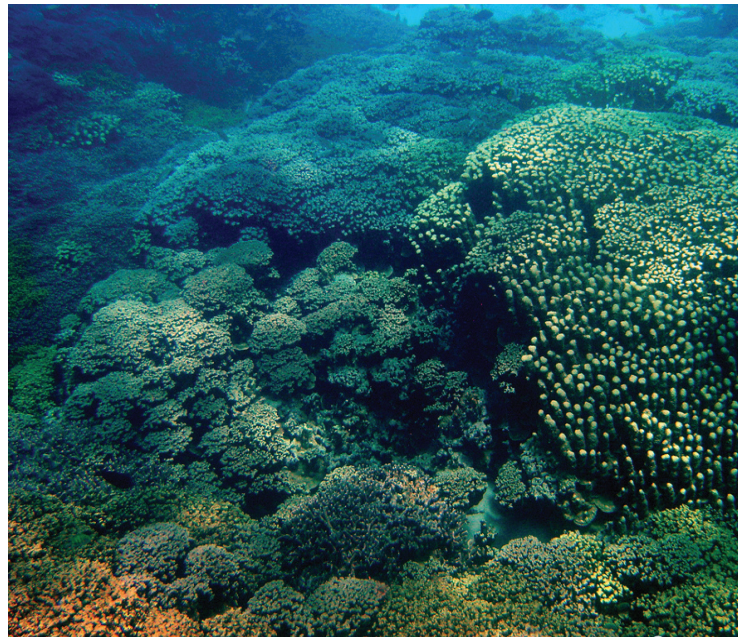


# Chapter 3: Patterns of Larval Connectivity for Priority Species

Matthew S. Kendall<sup>1</sup>, Matthew Poti<sup>1,2</sup>, Peter Houk<sup>3</sup>

## INTRODUCTION AND METHODS

There are several coral reef taxa in the Marianas that are of special significance due to their role in the ecosystem, importance in local fisheries and culture, or extreme rarity or abundance. Such high priority species were subjected to further customized simulations and analysis. Local managers and scientists in CNMI and Guam provided an initial list of 12 suggested taxa. Beginning with these, literature search and consultation with experts were used to determine if the larval life-history parameters needed for computer simulations had been published, were known anecdotally, or could be reasonably assumed. At a minimum, spawning season(s) and larval duration are needed for modelling. Of the 12 taxa of interest, only 6 had sufficiently known larval life-history parameters to enable taxon-specific larval transport simulations (Table 3.1).



A Guam reefscape.  
Photo credit: Used with permission from David Burdick, guamreeflife.com

Published literature, consultation with local experts, and in some cases, fisheries data from CNMI<sup>1</sup> and Guam<sup>2</sup> agencies were used to create life-history summaries for larvae of the priority taxa. These summaries included information on their spawning season(s), larval duration, and settlement season if known. This information was used to set parameters for transport simulations specific to each taxon using the same general methodology described in Chapter 2. All transport simulations were based on HYCOM currents for the years 2004-2012. HYCOM grid cells with potential reef ecosystem were used as the settlement zone for simulations involving invertebrate larvae. A two cell buffer (18 km) around this was added as a settlement zone for simulations involving fish larvae due to their presumably better sensory and swimming capabilities. Larval mortality was constant and applied randomly to individual larvae beginning at the end of pre-competency at a rate that resulted in 100% mortality by the end of the PLD for each taxon. Lunar phases corresponding to spawning for each taxon were drawn from the

**Table 3.1.** List of key taxa and their significance to the Mariana Archipelago region.

Taxon	Importance
Mass spawning corals [multiple species]	Reef building corals.
Post-larval Yellowfin Goatfish <i>Mulloidichthys flavolineatus</i>	Consistently among the top harvested species (DAWR Fisheries Reports). Newly settling larval fish are caught in schools as they recruit.
Post-larval Scribbled Rabbitfish <i>Siganus spinus</i>	Culturally significant fisheries species (Kami and Ikehara 1976, DAWR Fisheries Reports). Newly settling fish larvae are caught in schools as they recruit.
Humpead wrasse <i>Cheilinus undulatus</i>	Fisheries and culturally important species. Listed as "vulnerable" by the World Conservation Union.
Bluespine unicornfish <i>Naso unicornis</i>	Consistently among the top harvested species (DAWR Fisheries Reports).
Crown-of-thorns seastar <i>Acanthaster planci</i>	High ecological significance. Major controlling factor on coral cover.

<sup>1</sup> NOAA/NOS/NCCOS/CCMA/ Biogeography Branch

<sup>2</sup> NOAA/NOS/NCCOS/CCMA/Biogeography Branch and Consolidated Safety Services, Inc., Fairfax, VA, under NOAA Contract No. DG133C07NC0616

<sup>3</sup> University of Guam Marine Lab

Footnote 1. CNMI's Division of Fish and Wildlife (DFW) provided creel survey data for the years 2005 - 2011. These data are spatially restricted to the Saipan lagoon and are missing various months in several years due to logistical constraints. These issues prevented inference of larval life-history characteristics or robust statistical comparisons of catch patterns with our modelling results. Therefore, CNMI/DFW survey data is discussed only generally.

Footnote 2. Guam's Department of Agriculture/Division of Aquatic and Wildlife Resources (DAWR), provided creel survey data (1985-2011), fisheries reports (1963-2000), and fishing permit information (2007-2012).

National Aeronautic and Space Administration's online lunar calendar. Objectives for this chapter were to describe regional connectivity patterns for each taxon using:

- Connectivity matrices depicting the overall scope of interisland connections. Matrices display the fraction of larvae released at each source that settles at each destination,
- Pie charts summarizing the relative importance of self-seeding verses reliance on external sources of larvae to sustain populations at each location in the Marianas,
- Bar charts summarizing the total number of larvae imported and exported by each island in the Marianas to quantify their role as a source or destination of successfully settled larvae, and
- Depending on data availability, additional analyses specific to each taxon to examine variation in recruitment strength among years and evaluate modelled recruitment patterns in the context of available fisheries data.

## LARVAL PROFILES

**Taxon:** Mass-spawning of scleractinian corals.

Many coral species are involved in the mass-spawning event. A few of the more commonly occurring species include *Goniastrea retiformis*, *Acropora surculosa*, *Acropora abrotanoides*, *Favia matthaii*, *Favia stelligera*, and *Platygyra pini* (Richmond and Hunter 1990, P. Houk pers. comm.).

**Spawning season:** The commonly known peak spawning period for corals on Saipan and Guam is 5-10 days after the full moon in July (pers. comm. P. Houk, S. Johnson, L. Raymundo). These dates were determined for our model years based on the full moon in July plus seven days. Estimated spawning dates used to begin transport simulations for mass-spawning corals are provided in Table 3.2.

**PLD:** Multiple coral taxa with various PLDs take part in mass-spawning. Therefore, we evaluated connectivity patterns separately for larvae with maximum PLDs of 10, 20, 50, and 100 days. A list of species and their PLDs is not compiled here due to the multitude of coral species in the Marianas and lack of larval duration studies on the majority of them at present.

**Settlement season:** Variable due to multiple taxa.

**Taxon:** Yellowfin Goatfish (*Mulloidichthys flavolineatus*); common name on Guam is "ti'ao".

**Spawning season:** Peak spawning is in March, but activity occurs all year at low levels (Davis 1991). Individuals with spent ovaries can only be found during the last lunar quarter. Based on this, spawning dates to begin transport simulations were identified for each year as approximately the mid-point between the last quarter of the lunar cycle and the new moon in March (i.e. new moon date minus three days) (Table 3.3).

**PLD:** 70 to 90 days (B. Tibbatts pers. comm., DAWR) based on inference from monthly gonad index values and recruitment dates for settling larvae.

**Settlement season:** Guam's Department of Agriculture/Division of Aquatic and Wildlife Resources (DAWR) creel surveys (1985 to 2011) for *M. flavolineatus* recruits were summarized by month to identify recruitment season (Figure 3.1). Peak settlement begins in June, followed by declining catch through the fall, and lowest but still measureable catch in the Spring months. DAWR Fishing Permit data (2007-2012) also matched this seasonal pattern (Figure 3.2). Permits are issued for access to Guam MPAs when post-larval *M. flavolineatus* and *S. spinus* are observed arriving in strength at inshore habitats. Peak season for permit requests begins in May for most years, remains high through summer months, and then falls off sharply in October. Survey data for Saipan lagoon from DFW also showed evidence of higher catch beginning around May or June, but with secondary peaks occurring as late as November and December in some years. These fisheries data match the pattern predicted for a species with peak spawning beginning in March, a PLD of ~70-90 days, but may also spawn all year at a lower levels.

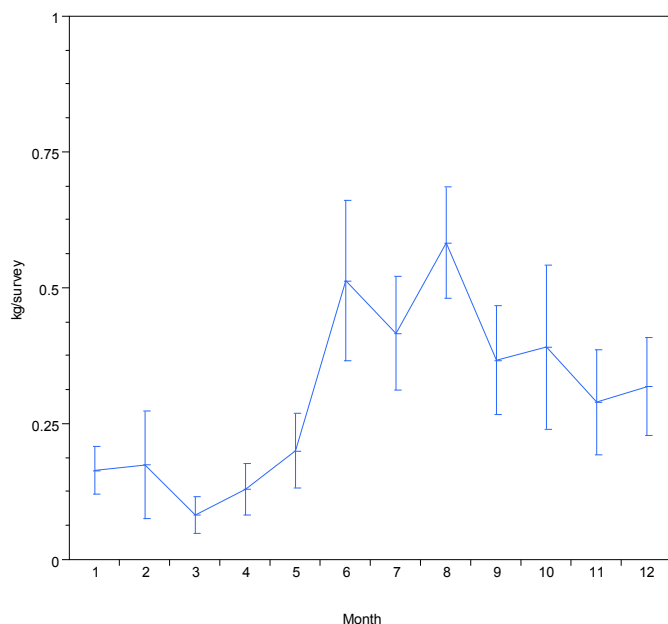
**Table 3.2.** Dates used for mass-spawning event of corals. Dates are based on known life-history information and the lunar calendar (i.e. mass spawning annually observed 7 days after the full moon in July).

Year	Simulation Spawning Date
2004	July 9
2005	July 28
2006	July 18
2007	August 6
2008	July 17
2009	July 14
2010	August 3
2011	July 22
2012	July 10

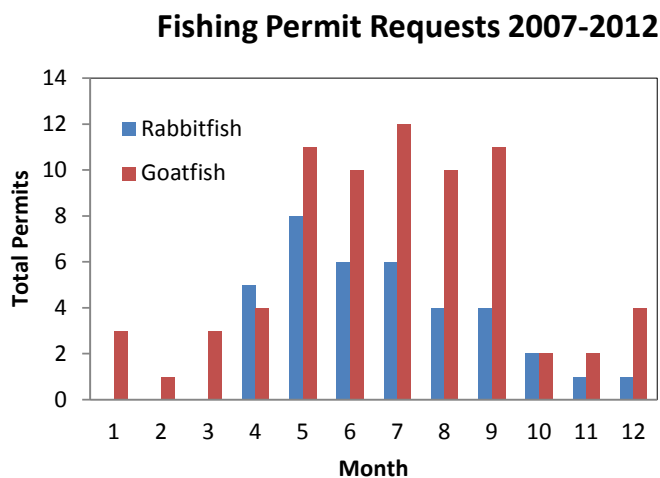
**Table 3.3.** Estimated spawning dates used to begin transport simulations for *M. flavolineatus*. Dates are based on published life-history information and the lunar calendar from the National Aeronautical and Space Administration.

Year	Simulation Spawning Date
2004	March 17
2005	March 7
2006	March 26
2007	March 16
2008	March 4
2009	March 23
2010	March 12
2011	March 31
2012	March 19





**Figure 3.1.** Mean catch per survey (+/- 95% CI) by month for *M. flavolineatus*. Summarized from Guam DAWR creel surveys from 1985 to 2011.



**Figure 3.2.** Number of Guam DAWR permit requests for *M. flavolineatus* and *S. siganus* by month. Summarized from 2007-2012.

**Taxon:** Scribbled Rabbitfish (*Siganus spinus*); common name on Guam is “mañahak”.

**Spawning season:** Peak spawning occurs in spring between the 17th and 25th day of the lunar month (Chirichetti 1996, B. Tibbatts DAWR pers. comm.). DAWR harvest permits are requested in April and again in May nearly every year. Additional spawning occurs over the summer and fall, however, the March and April events capture peak activity. Based on the PLD, dates of permit requests, and lunar calendars, dates were identified to start transport simulations in March and April of each model year (Table 3.4).

**PLD:** 30 day minimum, 33 day maximum PLD based on an otolith study at Guam (Chirichetti 1996). However, see Soliman et al. (2010) for PLD in the Philippines. Mariana values were used in our simulations.

**Settlement season:** Settlement occurs very predictably in April and May +/- 2 days around the last quarter of the moon in the Marianas (Kami and Ikehara 1976, Chirichetti 1996, B. Tibbatts DAWR pers. comm.). Highest settlement is also observed in April and May in the Philippines, but within 1-2 days of the new moon (Soliman et al. 2010). In some years, a small third and fourth run may occur in June and October (Kami and Ikehara 1976). DAWR Permit request dates for rabbitfish recruits corroborate these studies (Figure 3.2). Requests begin in April, peak in May, and then taper off through the rest of the year. In general, there was also excellent correspondence (within 0 to 3 days) between date of DAWR permit requests and the predicted dates of spawning based on the lunar calendar and PLD (Chirichetti 1996).

**Table 3.4.** Estimated spawning dates used to begin transport simulations for *S. spinus*. Dates are based on published life-history information, dates of harvest permit requests, and the lunar calendar.

Year	Simulation Spawning Dates
2004	March 13, April 12
2005	March 03, April 01
2006	March 22, April 21
2007	March 12, April 10
2008	March 29, April 28
2009	March 18, April 17
2010	March 08, April 07
2011	March 27, April 26
2012	March 14, April 13

**Taxon:** Bluespine unicornfish (*Naso unicornis*)

**Spawning season:** Mature or spent females are seen August through October in Guam (unpublished data noted in Mcllwain et al. 2012). Spawning in Saipan, CNMI probably occurs in July through October (unpublished data noted in DeMartini et al. In Press). Spawning may specifically peak during the new and full moon phases (Arai and Sato 2007 cited in Mcllwain et al. 2012). Based on these studies and the lunar calendar, the full and new moon dates were identified for each model year to start transport simulations during September, the core month of the spawning season (Table 3.5).

**PLD:** Identified as 75 days average PLD, with most 68 to 80, and a total range of 67 to 94 days (Planes et al. 2002, B. Tibbatts DAWR pers. comm.). These parameters were used to define precompetency in our simulations as 67 days after spawning, and the maximum larval duration as 94 days.

**Settlement season:** Settlement has been observed June – October in Guam (Horne et al. 2013), suggesting at least some earlier spawning by 1-3 months for this or other source locations. This was not a study of seasonality of spawning and it is not known if other months were sampled.

**Taxon:** Humphead wrasse (*Cheilinus undulatus*)

**Spawning season:** Spawning may occur year-round in Palau and during any lunar phase (Colin 2010). Based on this and the observation that recruitment occurs at least at low levels year-round, transport simulations were begun at regular intervals in all seasons (i.e. on the first of the month in January, April, July, and October) in each model year.

**PLD:** Approximately 25 days is estimated as the end of pre-competency and the earliest that larvae could settle based on behavior of hatchery-reared larvae (Slamet and Hutapea 2005). Assuming this is at least 60% of the maximum larval duration based on the composite of other reef fish (see Chapter 2), an estimated maximum PLD of 42 days was estimated. This general estimate is based on the best available information. More detailed knowledge of this species' larval life-history is needed to provide more specific parameters for future models.

**Settlement season:** Settlement occurs year-round, but has been described as bimodal in some years, with peaks in May and October in Palau (Tupper 2007). Stronger recruitment has also been observed in Guam and Kosrae in Fall and late Spring, possibly due to more conducive oceanographic conditions (M.Tupper pers. comm.).

**Taxon:** Crown of Thorns Seastar (COTS) (*Acanthaster planci*)

**Spawning season:** In the Ryukyu Islands, south of the main islands of Japan, *A. planci* spawns annually in June, with a possible secondary spawning in October (Yamazato and Kiyon 1973, Yokochi and Ogura 1987). Similarly, in Palau spawning occurs in April to May and also September (Idip 2003). Spawning in the Marianas is believed to correspond to these patterns, with the main peak in April, and possibly secondarily in September (Houk pers. comm.). April 15 was therefore used as the spawning date for each model year in transport simulations since this is believed to encompass the main spawning period for this species.

**PLD:** Approximately 14 days is the minimum pre-competency period in lab experiments (Lucas 1973, 1982, Olson 1987). Maximum PLD has been shown to vary between 20 to over 40 days depending on diet, temperature, and other factors (Lucas 1982). We used 14 and 40 days as our pre-competency period and maximum PLD.

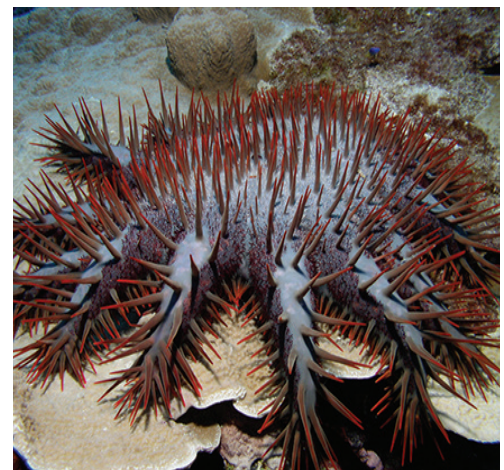
**Settlement season:** No information available

**Table 3.5.** Estimated spawning dates used to begin transport simulations for *Naso unicornis*. Dates are based on best available life-history information and the lunar calendar.

Year	Simulation Spawning Dates
2004	September 14 and 28
2005	September 3 and 18
2006	September 7 and 22
2007	September 11 and 26
2008	September 15 and 29
2009	September 4 and 18
2010	September 8 and 23
2011	September 12 and 27
2012	September 16 and 31



Young humphead wrasse (*Cheilinus undulatus*).  
Photo credit: Used with permission from David Burdick, [guamreeflife.com](http://guamreeflife.com)



Crown of thorns seastar (*Acanthaster planci*)  
Photo credit: Used with permission from David Burdick, [guamreeflife.com](http://guamreeflife.com)

## RESULTS AND DISCUSSION

### Mass spawning corals

When virtual larvae were attributed with the life history characteristics of corals, connectivity patterns were heavily influenced by larval duration (Figure 3.3a-d). Coral larvae with a 6-10 day PLD seldom settled beyond neighboring islands throughout the study area. Those with 12-20 day PLD showed moderate connectivity among islands within each archipelago, but generally not to destinations in other archipelagos. The 30-50 day PLD enabled broad connectivity among many islands within each archipelago, but maintained separation of archipelagos with a few exceptions. For longer PLDs of 60-100 days, a majority of islands within each archipelago were exchanging larvae and many archipelagos became connected. In general, the results in matrices for mass spawning corals showed similar but slightly more constrained dispersal compared to those from the same PLD in Chapter 2. This was due to two factors, including: 1) mass spawning corals were only subjected to summer currents, whereas results in Chapter 2 were based on the greater diversity of currents in all four seasons which would spread out dispersal clouds to more locations; and 2) mass spawning simulations occurred once each year, whereas in Chapter 2 there were 4 start dates each year which provided 4 times as many larvae and, therefore, potentially more diverse clouds of transport.

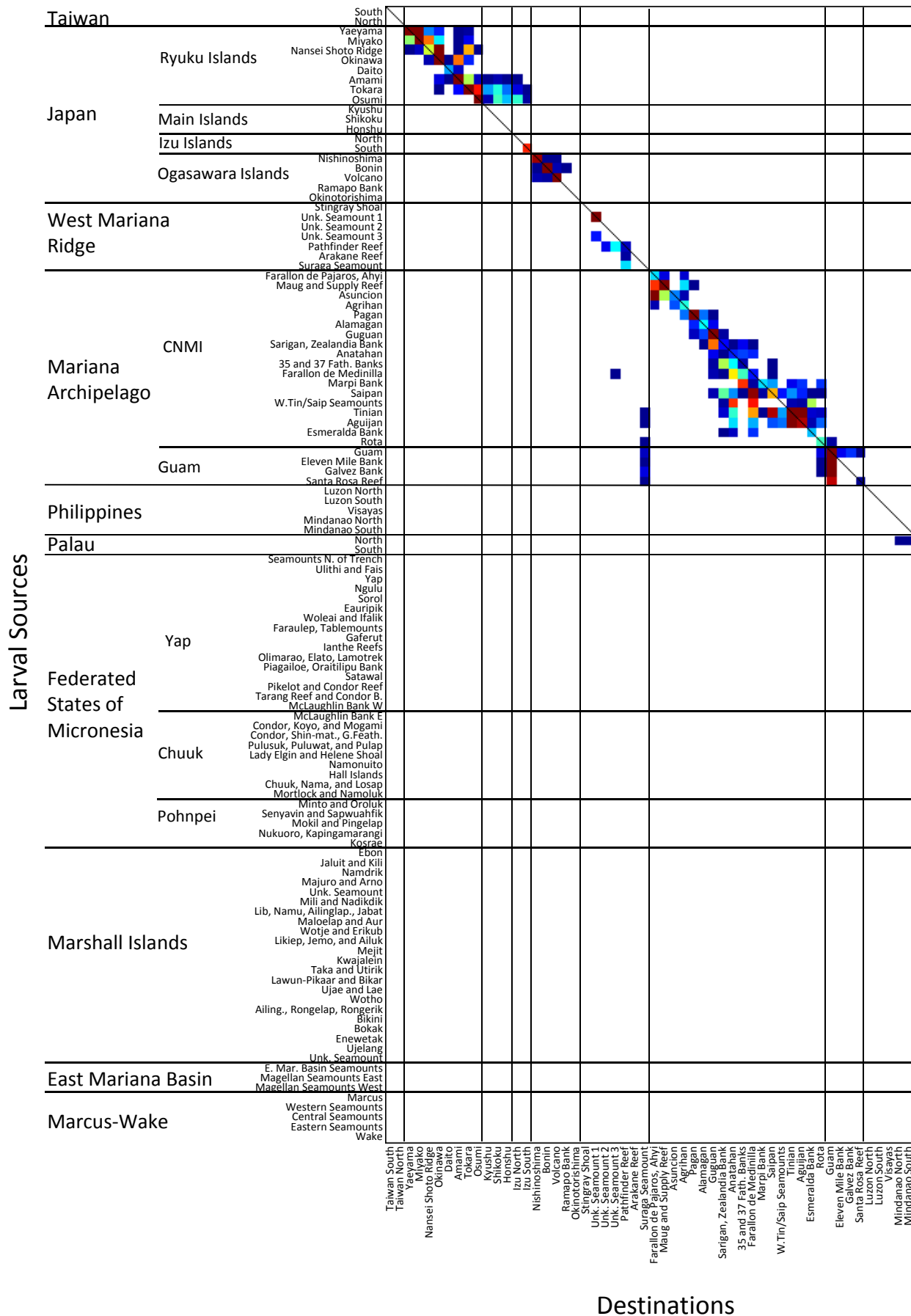
Specifically in the Marianas, for coral larvae with a 6-10 day PLD, there was a breakpoint in connectivity along the northern edge of the NEC at the latitude of Rota (Figure 3.3a). Rota and the islands and banks south of it had some larval exchange but none with Marianas to the north. From Rota to Marpi Bank north of Saipan, sources had much larval exchange among each other but none with Marianas to the south. Farallon de Medinilla was at another geographic breakpoint in connectivity. There was much larval exchange between it and Mariana Islands northward to Guguan, but not southward past Saipan. Last, there was a block of interconnected islands exchanging larvae from Agrihan northward to Farallon de Pajaros. Each of these sections of the Marianas experienced virtually no larval exchange with islands or banks to the north or south in the archipelago.

For the 12-20 day PLD, as virtual coral larvae began travelling farther, the breakpoints of larval connectivity in the Marianas became less distinct and showed more overlap (Figure 3.3b). For example, there was much exchange among islands and banks from Santa Rosa Reef in the south to Saipan in the north. This region had some overlap with another block of connectivity among islands from Aguijan to Pagan. Last, there was another block of connectivity for locations between Pagan and Farallon de Pajaros. Also of note, at this PLD connections were possible between the islands in the Marianas and some of the submerged banks along the West Mariana Ridge. This transport occurred most notably in the NEC from the southern Marianas, but also in the eddy field north of the NEC at higher latitudes.

For the 30-50 day PLD, connectivity patterns along the archipelago lacked the clear divisions seen for shorter PLDs (Figure 3.3c). Instead, larvae with this longer PLD appeared capable of settling at locations approximately 700 km north to 400 km south along the archipelago from any particular source. For example, larvae from Guam could settle anywhere to the north up to Maug. There was northward bias in the settlement pattern in that larvae from Pagan went southward but not as far as Rota, and there was generally a lower probability of a southward connection. The mechanism for this northward bias appears to be the eddies spun off the northern edge of the NEC. These gradually drift north and westward through the Marianas, often spinning clockwise, although the exact position, size and duration are highly variable. Also of note, there was widespread but low-strength connectivity at this PLD between Marianas islands south of Agrihan and the submerged banks along the West Mariana Ridge.

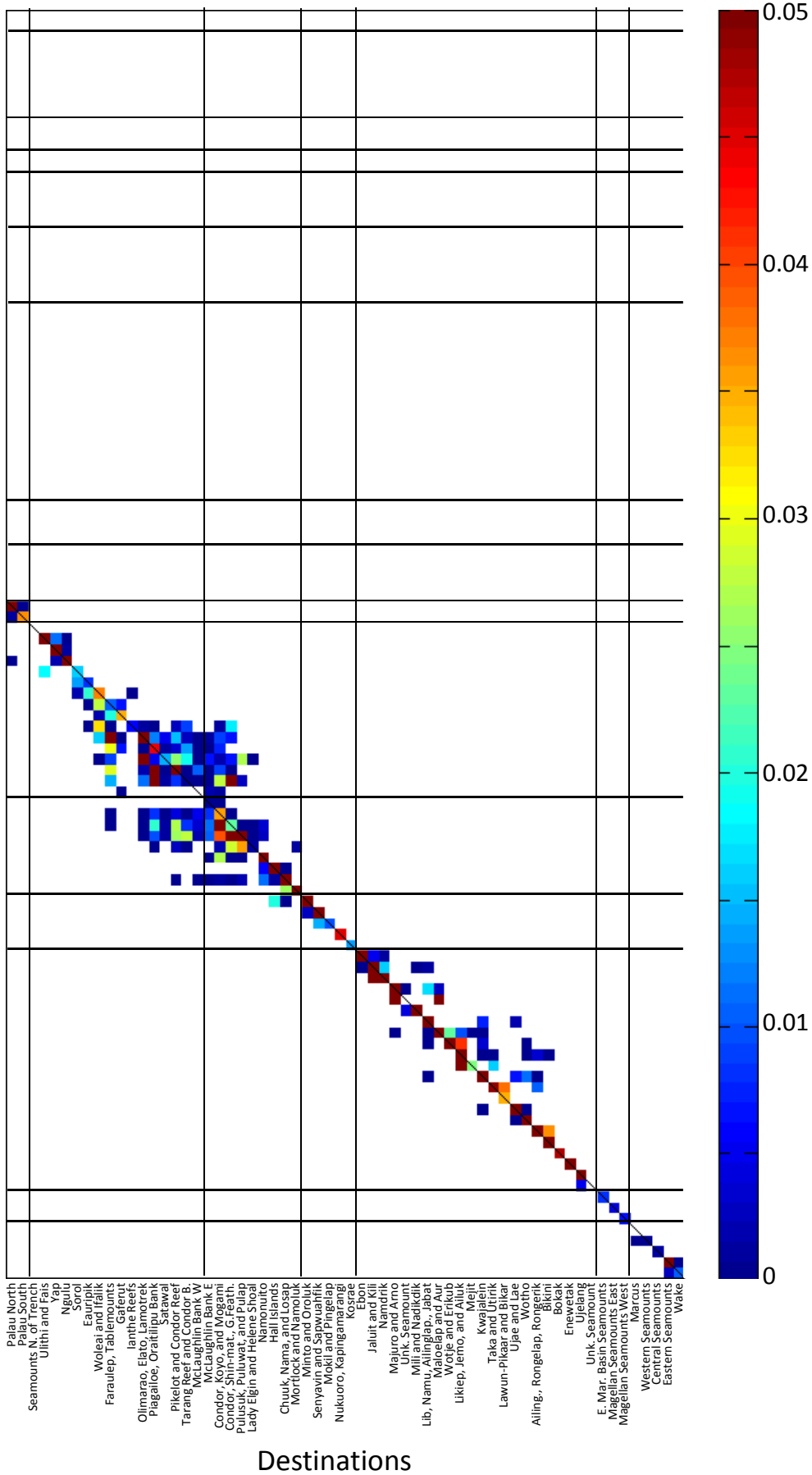
The 30-50 day PLD also enabled some low-strength connections between the Marianas and the islands to the south in the FSM. Specifically, larvae from Yap could arrive in the Marianas at low abundance between Santa Rosa Reef in the south to Saipan in the north, and in some cases larvae from Chuuk arrived as far north as Pagan. These larvae were entrained in the current loops connecting the eastward flowing NECC at the latitude of FSM to the westward flowing NEC at the latitude of the southern Marianas. Larvae from some locations in the southern Marianas (up to Saipan) could also arrive at many of the islands and atolls to the west in Yap via the NEC and its eddies spun off to the south.

For the 60-100 day PLD (Figure 3.3d), the longest considered in this study, there was widespread connectivity within the Marianas. Larvae from any Mariana source could settle at any of the other Mariana Islands to the north, any-



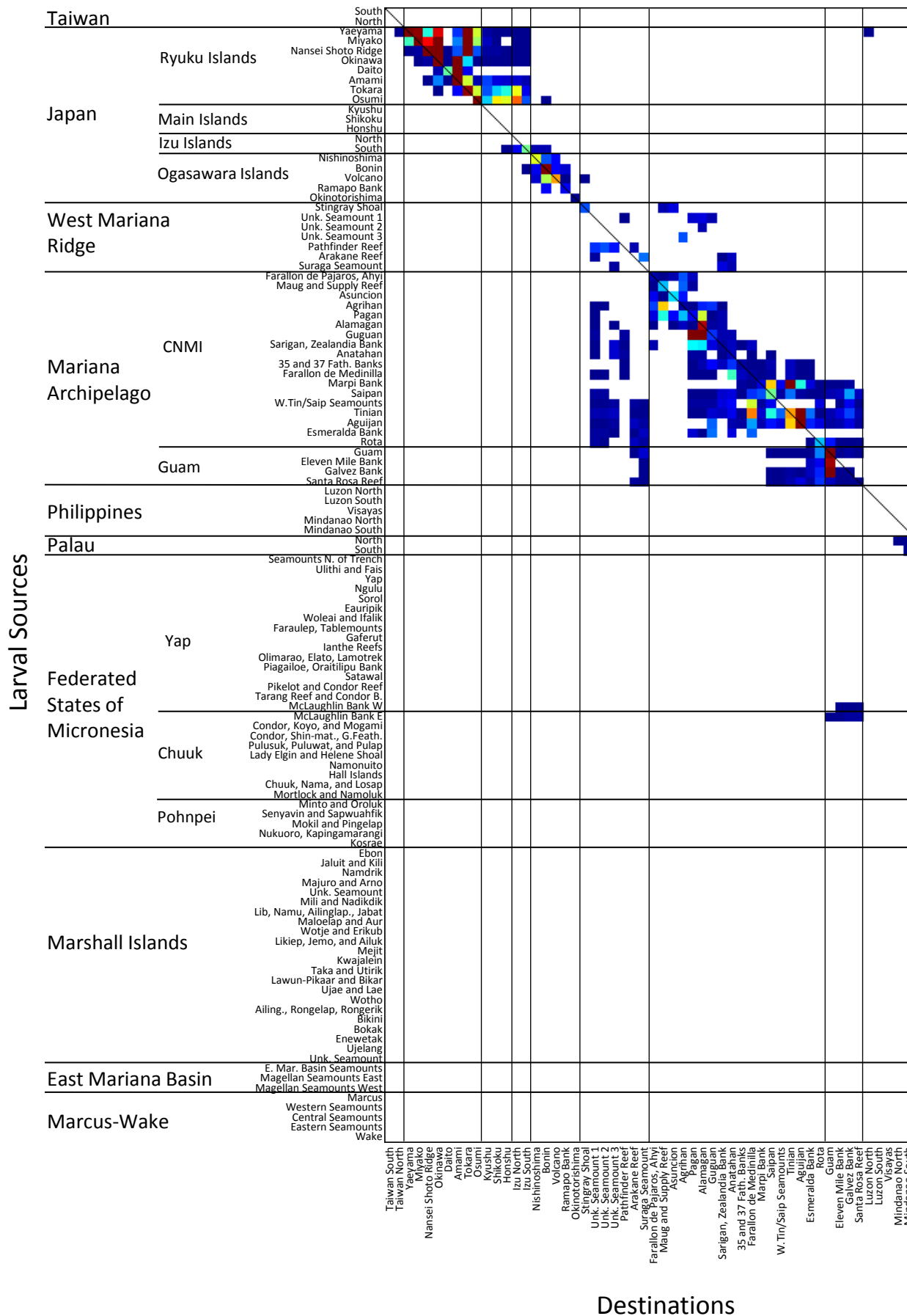
**Figure 3.3a.** Connectivity matrices for mass spawning corals for a 6-10 day PLD. Cumulative connectivity for 2004-2012. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for 2004-2012.

(larval sources continued from facing page)



Fraction of larvae from source settled at destination

Figure 3.3a cont.



**Figure 3.3b.** Connectivity matrices for mass spawning corals for a 12-20 day PLD. Cumulative connectivity for 2004-2012. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for 2004-2012.

(larval sources continued from facing page)

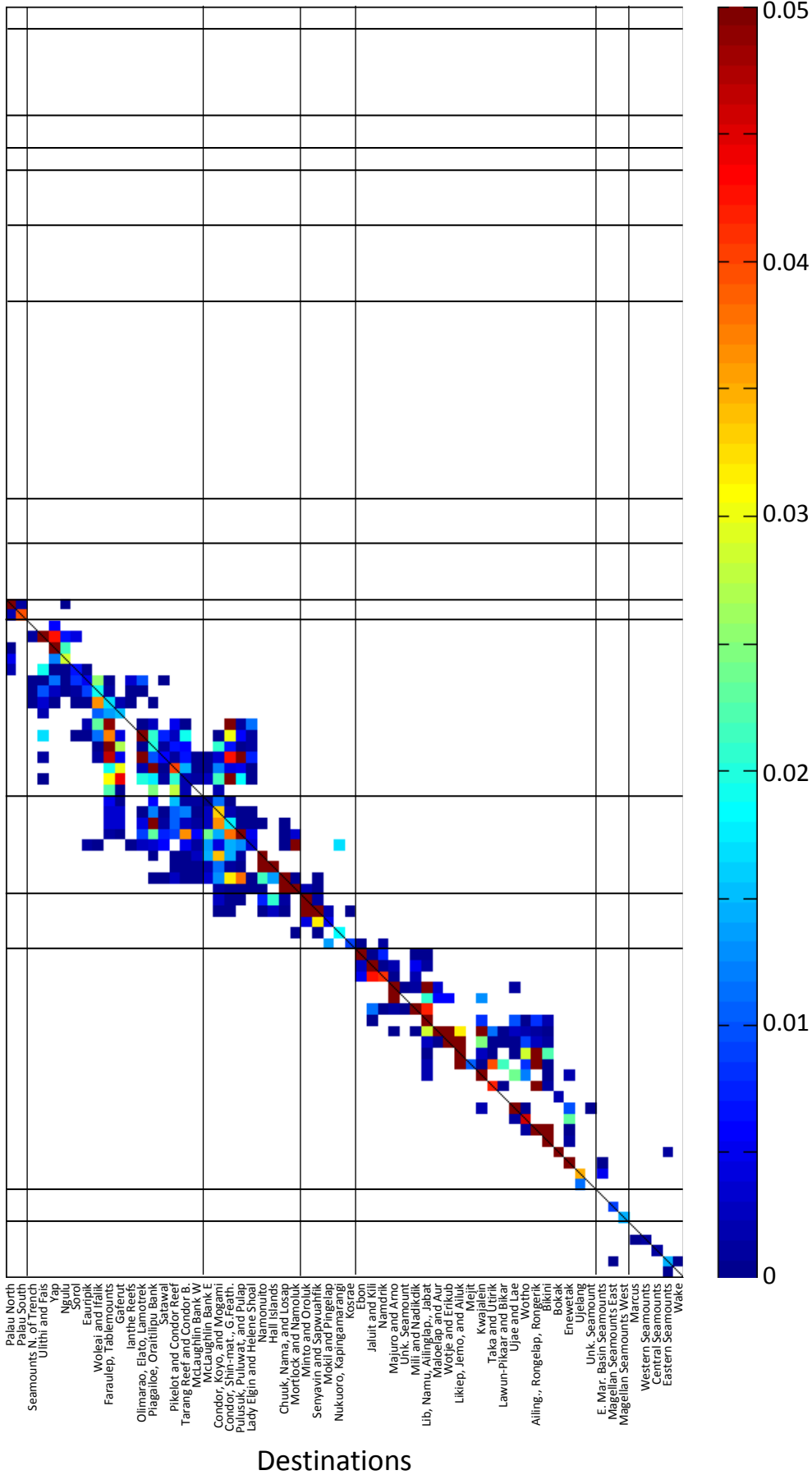
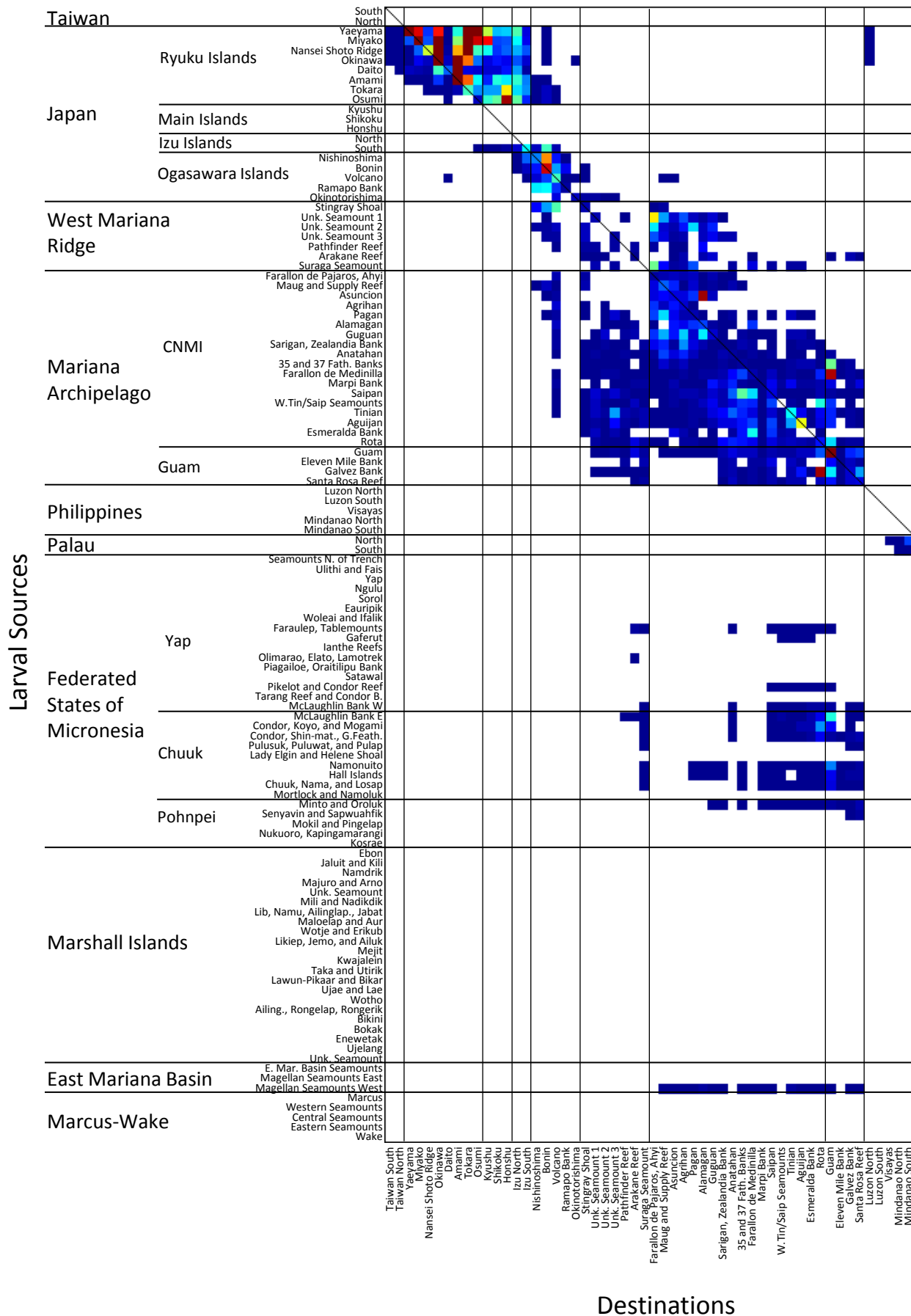


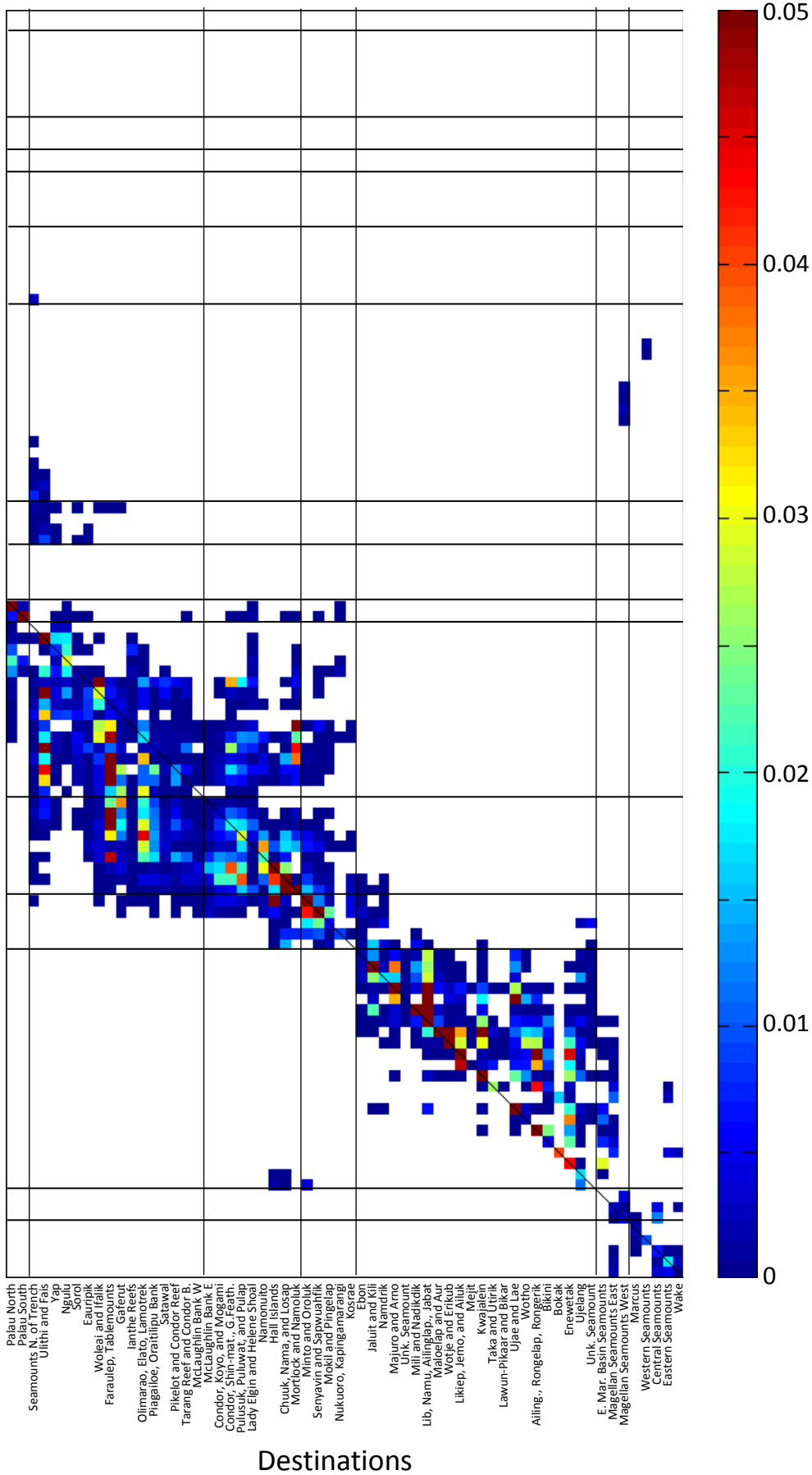
Figure 3.3b cont.



**Figure 3.3c.** Connectivity matrices for mass spawning corals for a 30-50 day PLD. Cumulative connectivity for 2004-2012. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for 2004-2012.

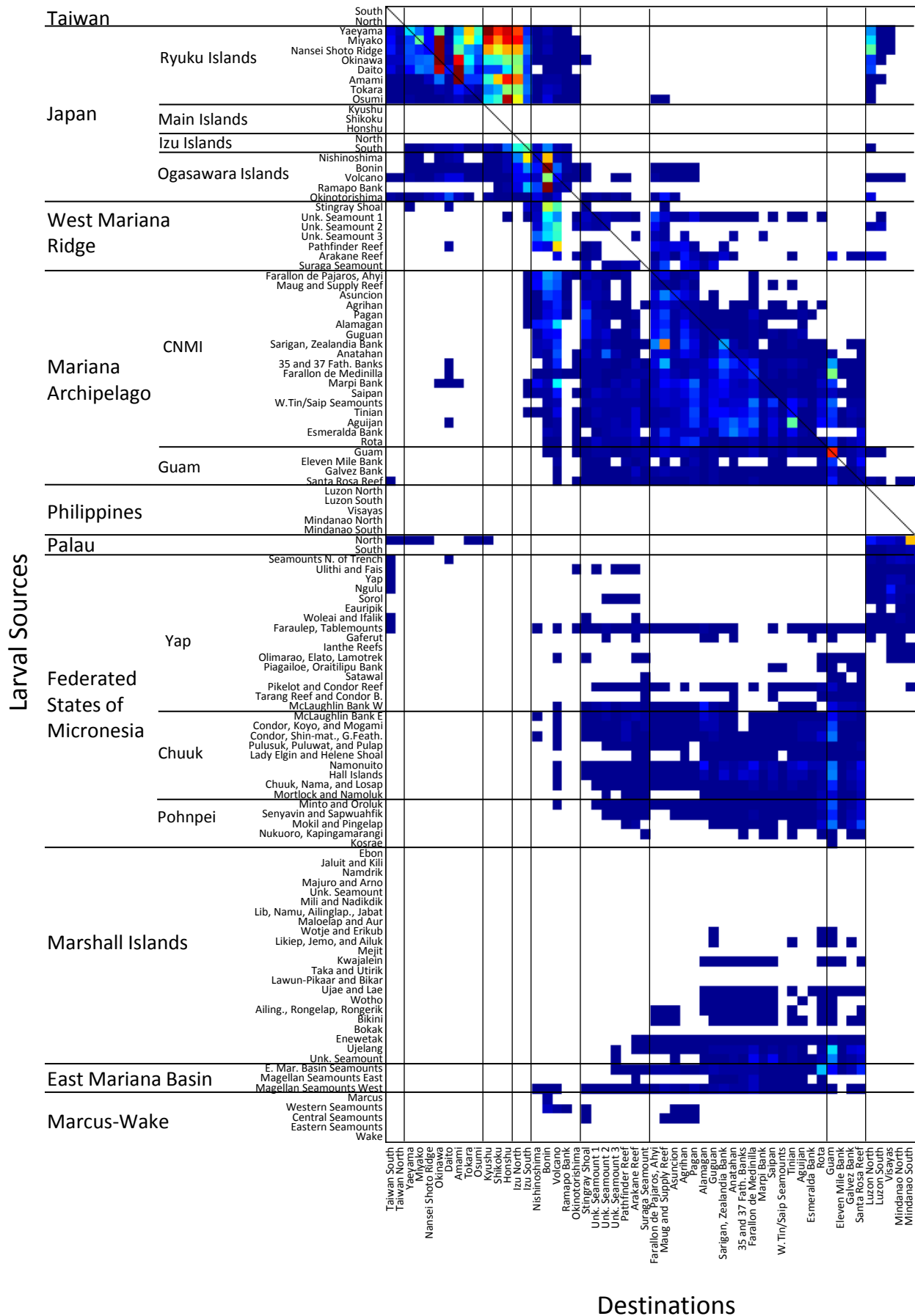


(larval sources continued from facing page)



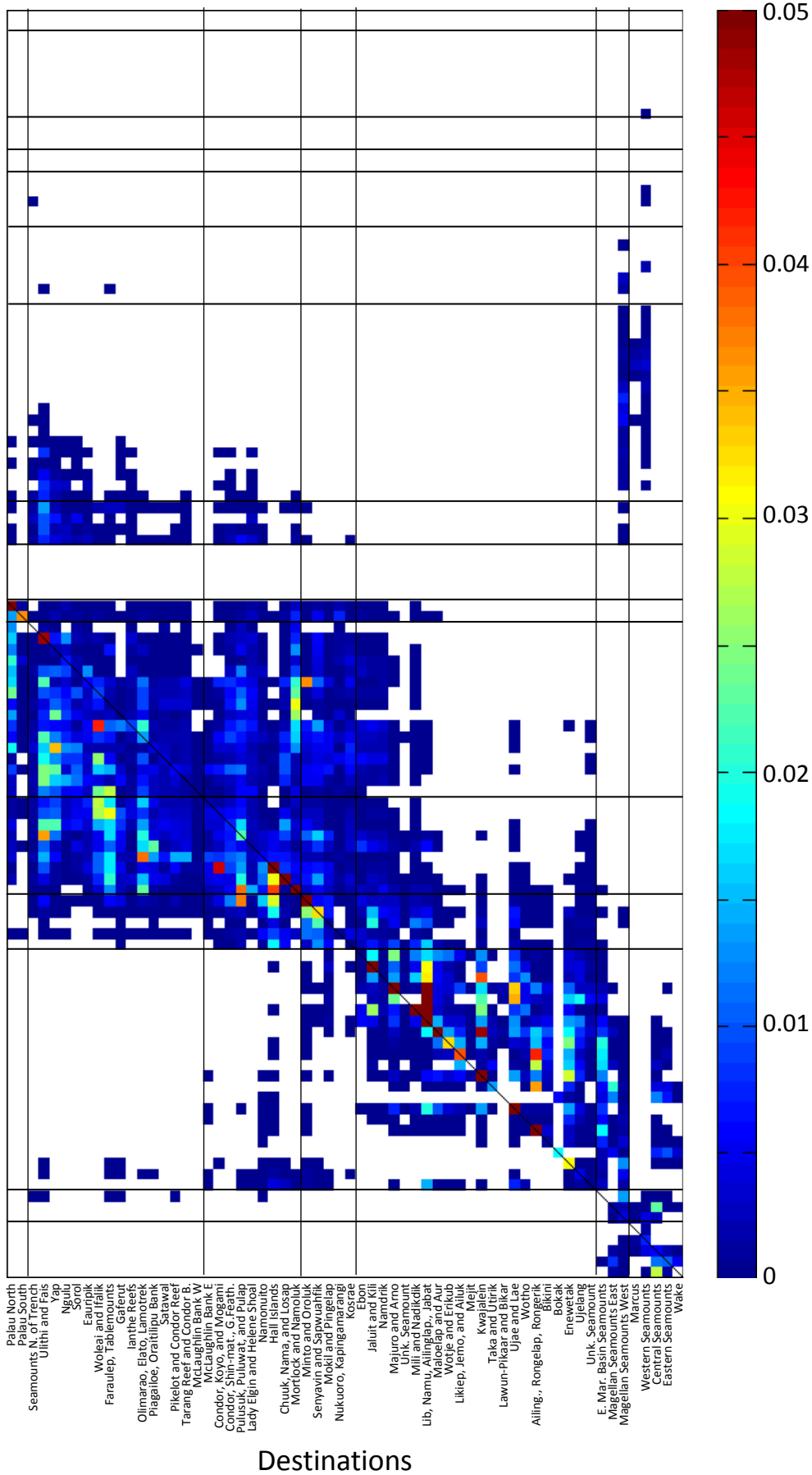
Fraction of larvae from source settled at destination

Figure 3.3c cont.



**Figure 3.3d.** Connectivity matrices for mass spawning corals for a 60-100 day PLD. Cumulative connectivity for 2004-2012. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for 2004-2012.

(larval sources continued from facing page)



Fraction of larvae from source settled at destination

Figure 3.3d cont.

where along the West Mariana Ridge, and even as far north as the Ogasawara Islands of Japan. Again, there was a northward bias in this pattern in that larvae did not travel as far southward along the archipelago and there was a generally lower probability of southward connections. For these long PLDs, connections between FSM and the Marianas were more common. Larvae from Chuuk and Pohnpei could arrive nearly any place in the Marianas or the West Mariana Ridge via the NECC to NEC current loops. Larvae from the Marianas south of Farallon de Medinilla also had stronger connections to Yap and could arrive at low levels at places in Chuuk. Also of note for this very long PLD, larvae from islands in the NW region of the Marshall Islands could arrive at locations throughout the Marianas, at least at low strength. This was made possible by the straight line transport of the fast flowing NEC that connects these distant islands along this latitude.

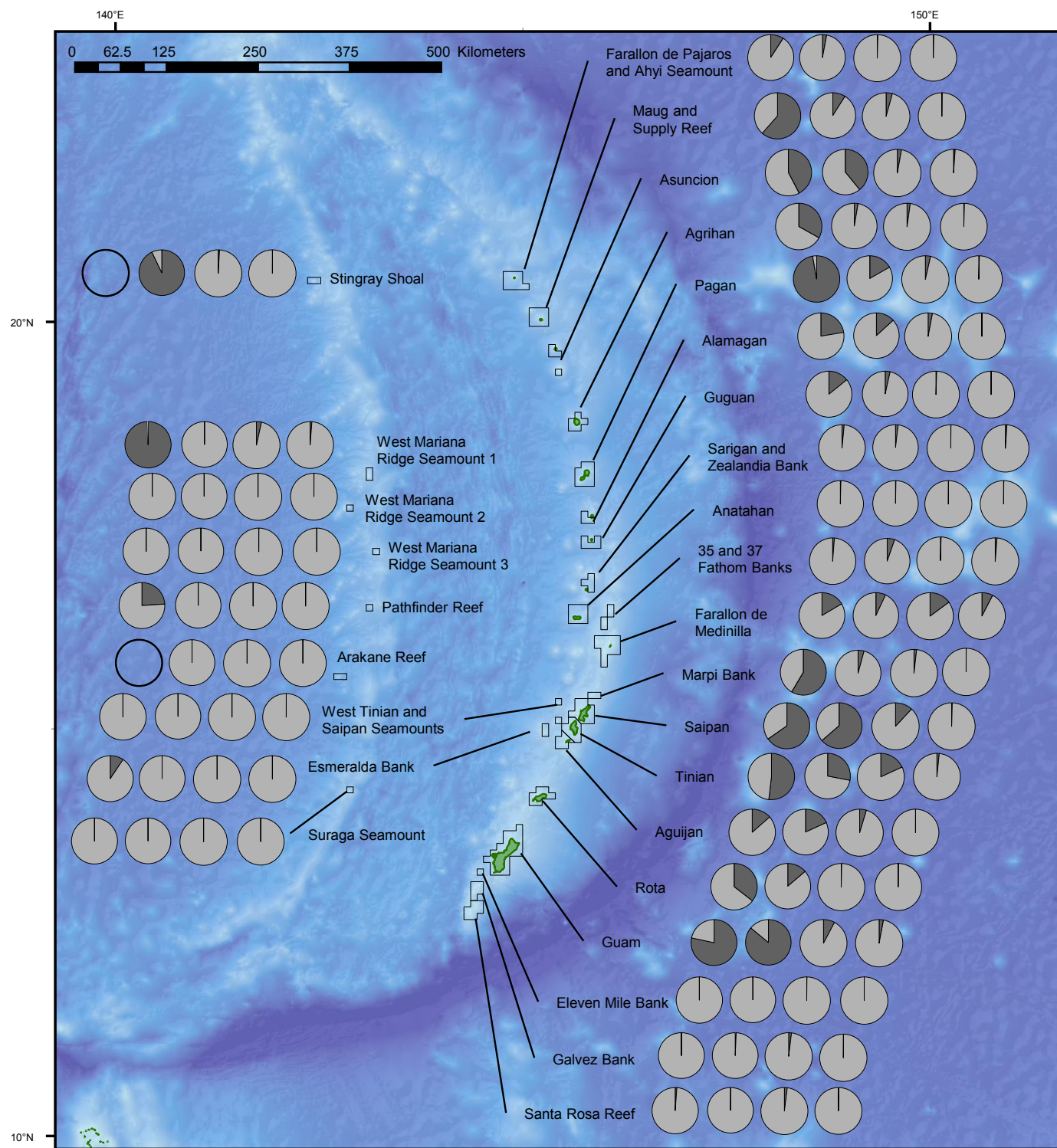
The proportions of coral larvae arriving at each island or bank that were self-seeded versus imported are shown as pie charts by PLD. Only a few islands, including Guam, Saipan, and a few others obtained more than half of their



*Corals off Tanguisson Beach, Guam.*

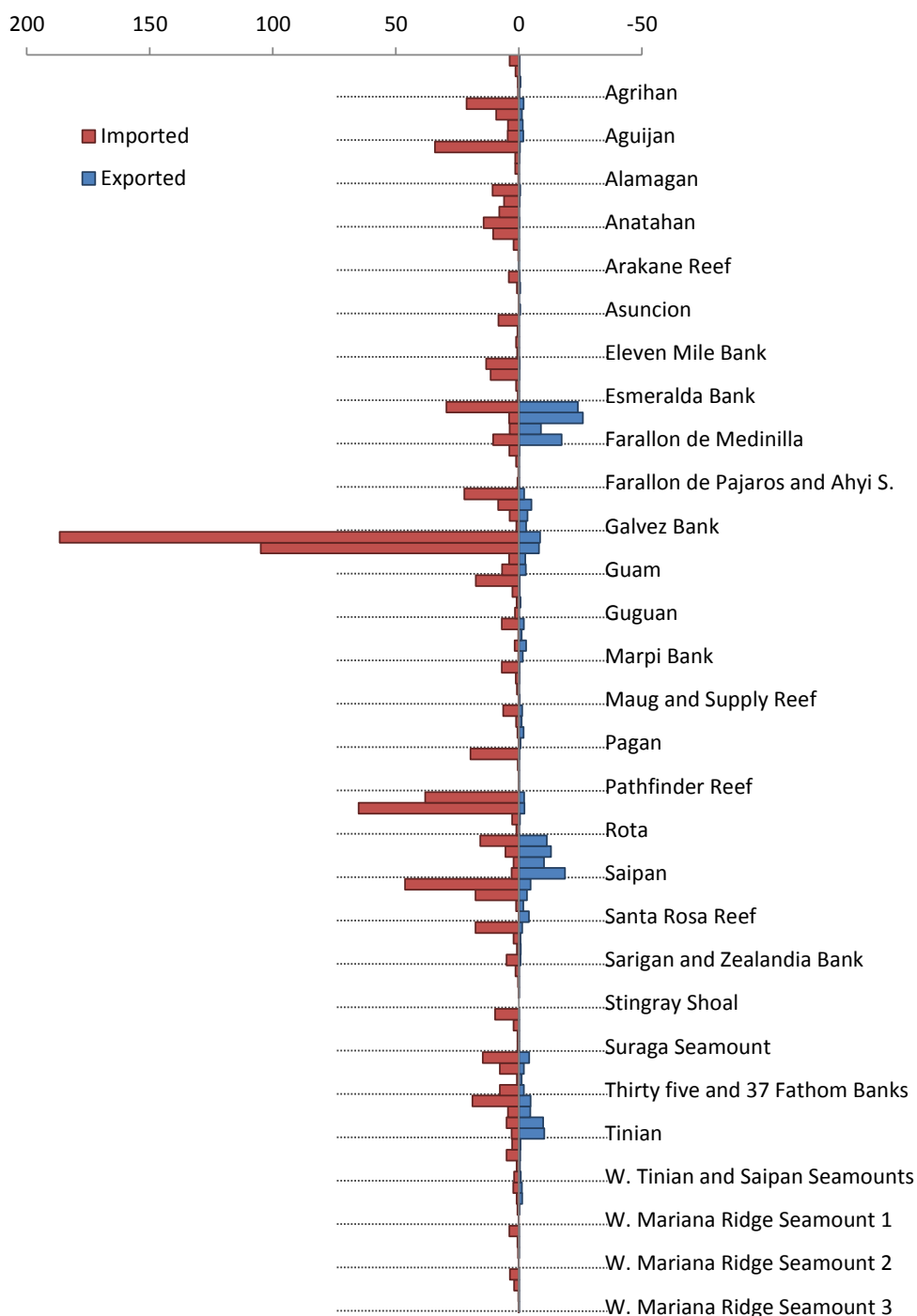
*Photo credit: Used with permission from David Burdick, guamreeflife.com*

larval supply from self-seeding, and then only for short PLDs (Figure 3.4). Islands relied on an increasing proportion of larvae from external sources for longer PLDs. For example, Saipan's arriving larvae were ~60% self-seeded when PLD was 10 days, 7% when PLD was 50 days, and <1% when PLD was 100 days. No place in the Marianas relied on self-seeding for more than 20% of their larval supply for PLDs of 50 days. At PLDs of 100 days, imports dominated such that Farallon de Medinilla had the highest proportion of self-seeding of any location in the Marianas at a mere ~5%. With few exceptions, submerged banks and seamounts, including the locations in the West Mariana Ridge, were almost totally reliant on larvae arriving from external sources at all PLDs. Exceptions were based on very few larvae.



**Figure 3.4.** Proportions of larvae from mass coral spawning settling at each island that are from self-seeding (dark grey) versus imported (light grey). Maximum PLDs from left to right next to each island are 10, 20, 50, and 100 days.

In general, most locations imported more larvae than they exported and the number of larvae imported declined with shorter PLDs (Figure 3.5). Longer PLDs enabled more larvae to arrive from distant locations. Exceptions were Farallon de Medinilla, Saipan, and Tinian, which exported more larvae than they imported for most PLDs. Examining the annual model outputs revealed that the high exports from Farallon de Medinilla were due to larvae sent to its island neighbor to the northwest, Anatahan during many years, but also an anomalous but very strong recruitment to Guam following spawning in 2006 when maximum PLD was 50 to 100 days. The high numbers from Saipan were due to transport of larvae with short PLDs to Farallon de Medinilla and nearby destinations in various years. The largest importers of larvae were Guam and Rota for PLDs of 50 and 100 days. Larvae arriving at Guam and Rota at these PLDs were primarily from Chuuk in the FSM, with especially large recruitment events in 2010 and 2011.

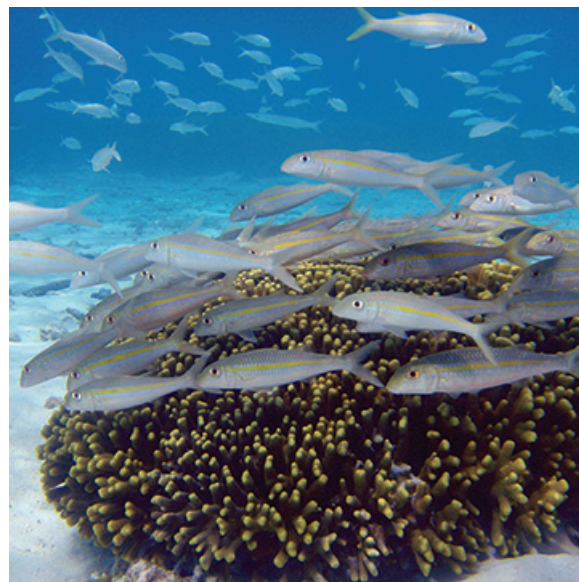


**Figure 3.5.** Number of larvae from coral mass-spawning events that are imported and exported from each island. Bars within each island denote the 100, 50, 20, and 10 day maximum PLDs arranged from top to bottom. All values are in thousands.

Corals are the foundation for the reef ecosystem. Several authors have speculated on the role that ocean currents have in governing their distribution and the resilience of reefs in the Marianas (e.g. Kojis and Quinn 2001, Houk and Starmer 2010). Findings here demonstrate that the PLD of each coral species will dramatically affect their connectivity with neighboring islands and archipelagos. Corals with 10-20 day PLDs will be almost entirely restricted to transport within their native archipelagos. For these species, many islands in the Marianas will be dependent upon healthy local sources of larvae to sustain their populations. In such cases, local management will play the greatest role in promoting resilient populations. For corals with 50-100 day PLDs, all islands in our simulations were strongly dependent upon larvae imported from other locations, including other archipelagos. Resilience of such populations is dependent upon the health of neighboring islands and highlights the importance of coordinated regional management and the role that inter-island networks of MPAs, for example, can play in promoting regional ecosystem stability. Key exporters of larvae are identified in the connectivity matrices and could be prioritized for protection.

### **Yellowfin Goatfish (*M. flavolineatus*)**

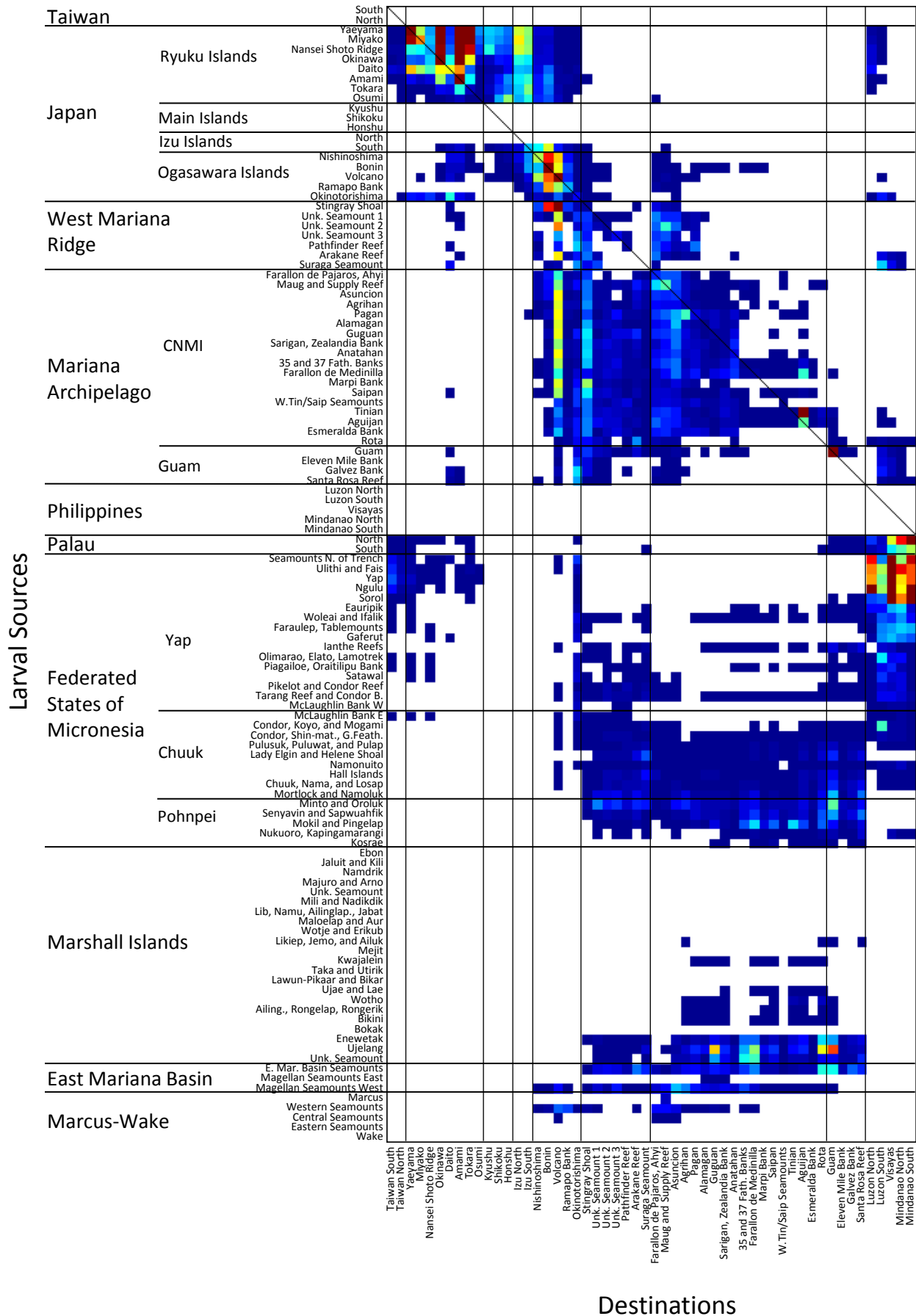
When virtual larvae were attributed with the life history characteristics of *M. flavolineatus*, there was broad connectivity among islands within each archipelago, and moderate exchange of larvae among some archipelagos (Figure 3.6). In the Marianas, there were several distinct clusters of connectivity. For the southernmost sources of Santa Rosa Reef, Galvez, and Eleven Mile Bank, there was no self-seeding and larvae were only rarely connected to the very northernmost Marianas and reefs of the West Mariana Ridge. Guam was somewhat isolated at a transition point with strong self-seeding. It received no larvae from sources north or southward along the archipelago and sent few larvae elsewhere in the Marianas, and then only at low levels to the islands north of Farallon de Medinilla. Islands from Aguijan to Farallon de Medinilla exchanged larvae with locations elsewhere in the Marianas to the north and south. From Anatahan to Farallon de Pajaros was another block of interconnected islands exchanging larvae. Reefs along the West Mariana Ridge could receive larvae at low levels from almost any of the Marianas. Destinations for West Mariana Ridge larvae included transport to locations north of Pagan.



*Yellowfin goatfish (M. flavolineatus).*  
Photo credit: Used with permission from David Burdick, [guamreeflife.com](http://guamreeflife.com)

There was some exchange of *M. flavolineatus* larvae between the Marianas and other archipelagos as well. Larvae from the West Mariana Ridge and even southern Marianas between Rota and Santa Rosa Reef could occasionally arrive as far away as the Philippines. This is a direct line along the route of the NEC. Larvae from the Marianas between Aguijan and Farallon de Pajaros could arrive eastward at Marcus Island or the Magellan Seamounts on the eddies common to this latitude. Larvae from nearly any place in the Marianas could also arrive in the Ogasawara Islands of Japan, especially those from islands north of Tinian, which showed a strong connection to the Volcano Islands. Although virtually no larvae from the Marianas went to the FSM, larvae arriving in the Marianas could come from many sources in FSM. These travelled in the feedback loops connecting the NECC at the latitude of the FSM to the NEC at the latitude of the southern Marianas. Palau had low level transport to the southern Marianas between Rota and Santa Rosa Reef. Larvae from anyplace in Chuuk could arrive, at least at low levels, at any destination throughout the Marianas and the West Mariana Ridge. Strongest connections were between sources in Pohnpei and destinations in the southern Marianas. Larvae could also arrive in the Marianas from many of the atolls in the Marshall Islands. Connections were most common from the northwestern Marshalls such as Ujelang and Enewetak Atolls with occasionally strong connection to Guam and Rota. This was made possible by the straight flowing NEC that connects these locations.

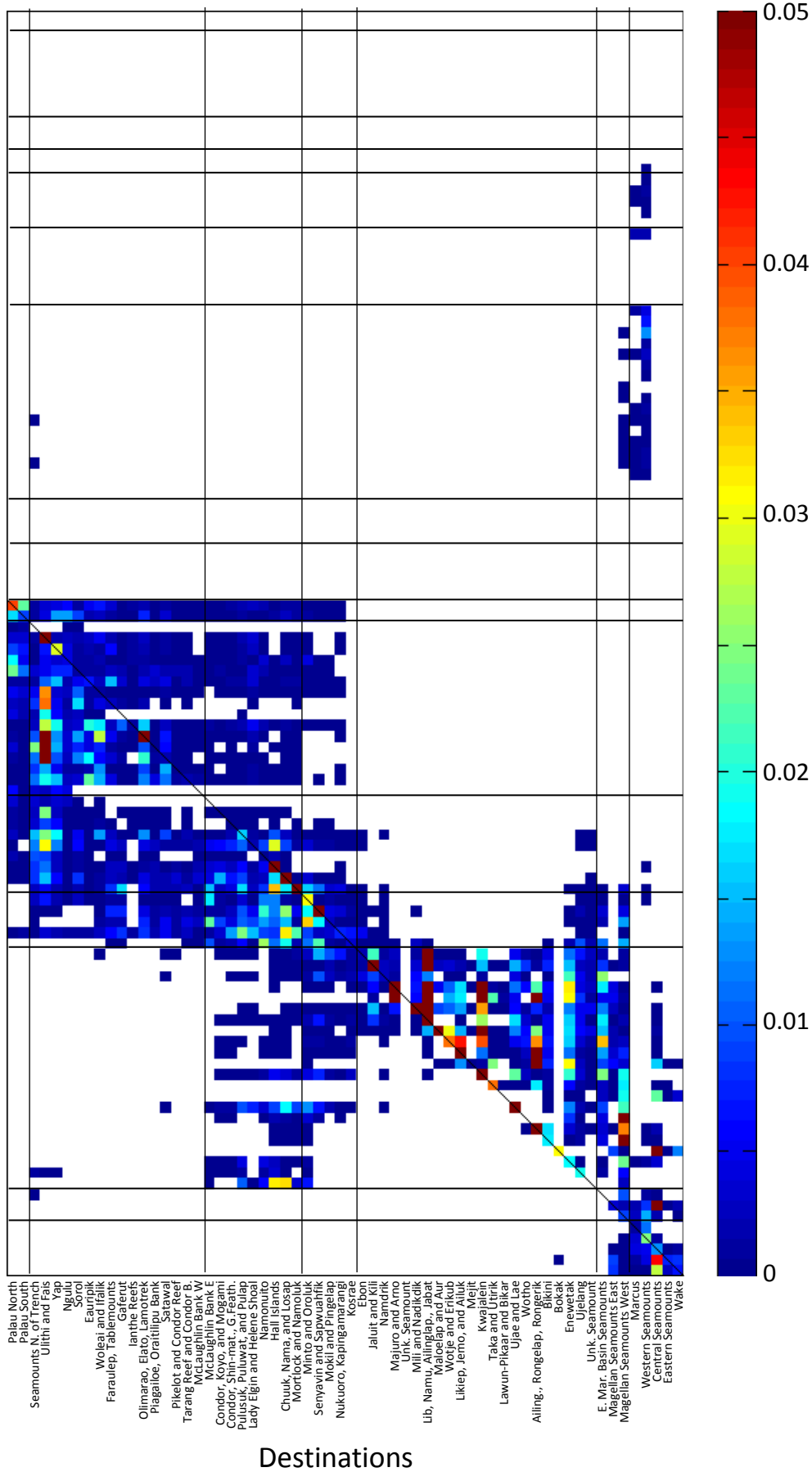
The proportions of *M. flavolineatus* larvae arriving at each island or bank that were self-seeded versus imported were similar to those observed for mass spawning corals with a 100 day maximum PLD (Figure 3.3d), and therefore separate figures are not provided. All locations throughout the Marianas and West Mariana Ridge imported 95-100% of their larval supply. Only 5% of larvae arriving at Guam were self-seeded, and this was the highest value of self-seeding in the Marianas.



**Figure 3.6.** Cumulative connectivity (2004-2012) for *M. flavolineatus* larvae. Color scale indicates the fraction of simulated larvae released at source settling at destination.



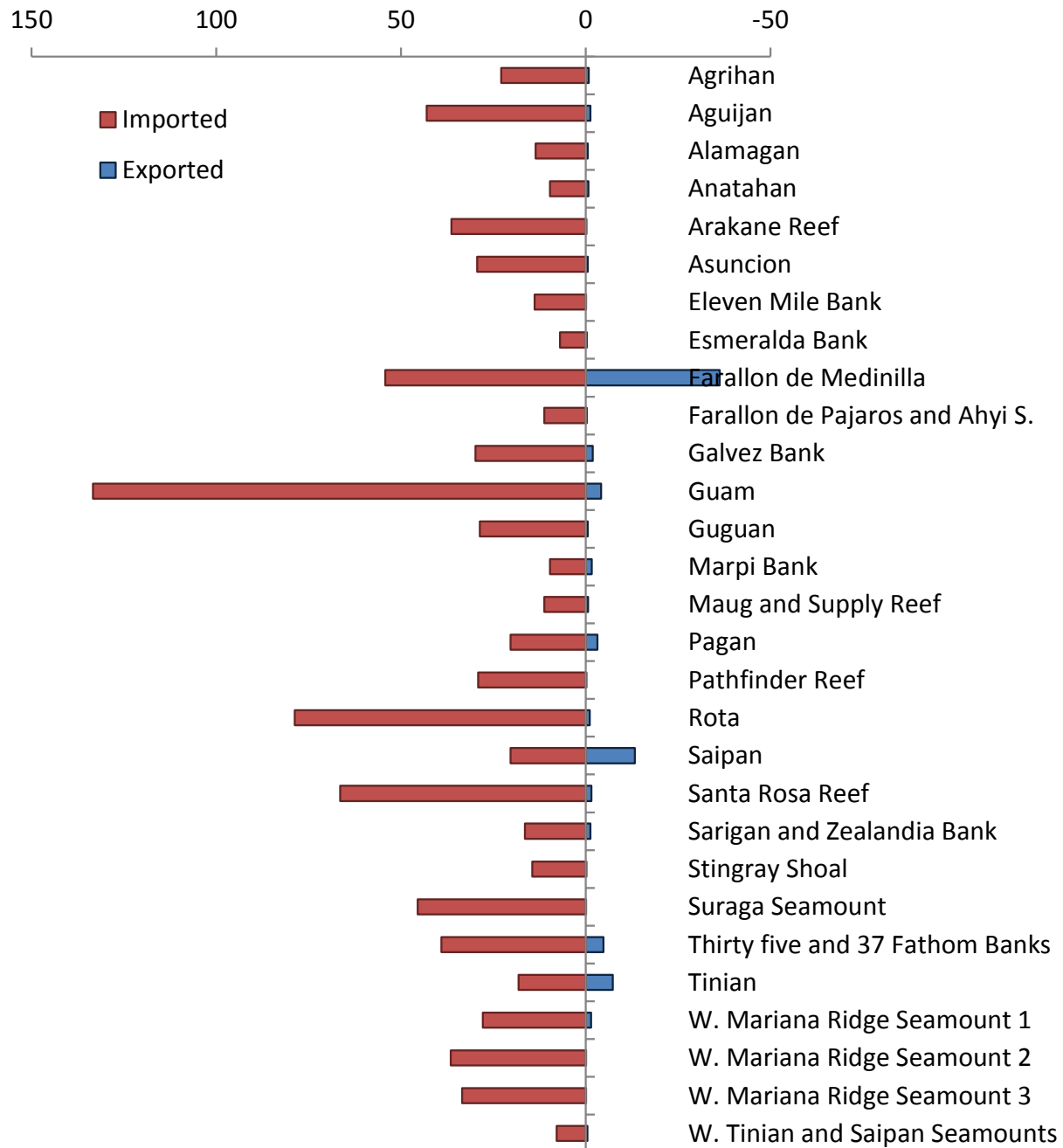
(larval sources continued from facing page)



Fraction of larvae from source settled at destination

Figure 3.6 cont.

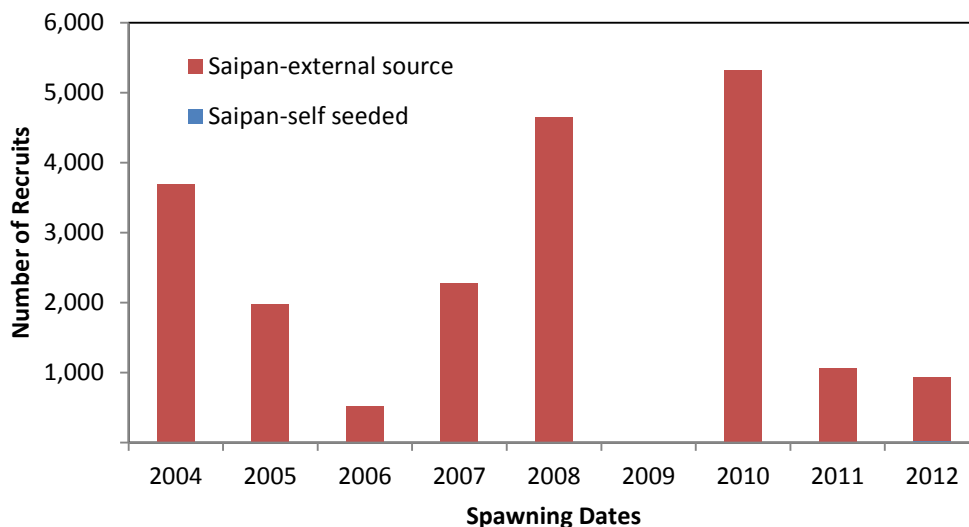
The number of *M. flavolineatus* larvae imported exceeded the number exported for all locations (Figure 3.7). The largest number of larvae arrived at Guam, likely due to a combination of its size and position in the archipelago. First, it is simply a large settlement target relative to the rest of the Marianas. Second, its position in the NEC makes it the recipient of virtual larvae from FSM and even the Marshall Islands given the long PLD of *M. flavolineatus* and current loops connecting the NECC to the NEC. Large numbers of larvae also arrived at the much smaller locations of Rota and Santa Rosa Reef positioned to the north and south of Guam. These larvae were also primarily from FSM (via the NECC) and the Marshalls (via the NEC). Tiny Farallon de Medinilla, located close to the mid-point northward along the Mariana Archipelago, also received many larvae. These were also primarily imported from the Marshalls and FSM. The only locations that exported many successful larval settlers were Farallon de Medinilla and Saipan. Examining the model outputs revealed that these spikes were largely due to larval exports from Saipan to the West



**Figure 3.7.** Number of *M. flavolineatus* larvae that are imported and exported from each island. Values are in thousands.

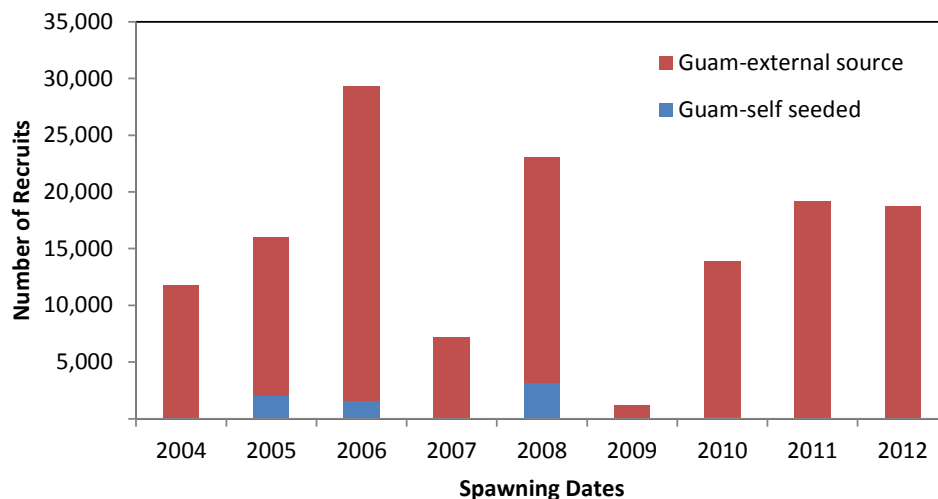
Mariana Ridge and Volcano Islands of Japan. Larval exports from Farallon de Medinilla went to Aguijan, the Volcano Islands, and several of its close island neighbors.

Looking more closely at patterns of simulated recruitment of *M. flavolineatus* in Guam and Saipan revealed some volatile settlement events among years. In Saipan, nearly all settling larvae were from external sources (Figure 3.8). In three model years, there were spikes in recruitment (2004, 2008, and 2010). These dramatically higher periods of larval recruitment were the product of large and rare contribution of larvae arriving at Saipan from Chuuk in 2004, Pohnpei in 2008, and Enewetak in the Marshalls in 2010.



**Figure 3.8.** The total number of *M. flavolineatus* larvae arriving at Saipan for each spawning date that were self-seeded (blue) or arrived from an external source (red).

Guam also experienced dramatic fluctuations in strength of recruitment events (Figure 3.9). Alternating years of high and low recruitment occurred from 2006 to 2009. Self-seeding at Guam was a small but measurable component of larval supply only in 2005, 2006, and 2008. Peak settlement in 2006 and 2008 was due to larvae arriving from sources in FSM.



**Figure 3.9.** The total number of *M. flavolineatus* larvae arriving at Guam for each spawning date that were self-seeded (blue) or arrived from an external source (red).

The spikes in recruitment occurred in different years for Guam and Saipan, with only 2008 showing a high value at both islands. This suggests that incidents of high recruitment are independent events on each island. In addition, it should be emphasized that the observed variability in virtual recruitment occurred solely as a result of variations in ocean currents. Important aspects of larval biology such as variation in interannual larval production and larval mortality rate were kept constant in our simulations but would certainly add other dimensions to levels of actual recruitment.



Young yellowfin goatfish (*M. flavolineatus*).  
Photo credit: Used with permission from David Burdick, [guamreeflife.com](http://guamreeflife.com)

The intermittent spikes in simulated larval recruitment caused by occasional but strong connections to larval sources in FSM are also consistent with what is observed in catch records. DAWR's Annual Fisheries Reports revealed a highly variable pattern of recruitment strength for *M. flavolineatus* in Guam. However, attempts to relate creel survey data from DAWR for *M. flavolineatus* to simulation results were inconclusive. Simulated recruitment strength at Guam from each model year was plotted against catch values during peak settlement times. The overall pattern was as expected in that catch values were typically higher in years when simulations predicted high recruitment; however, the relationship was not statistically significant in a linear regression (Figure 3.10). Reasons for this lack of significance could include poor statistical power due to the low number of years ( $n = 8$ ) with both catch and simulation data, as well as several

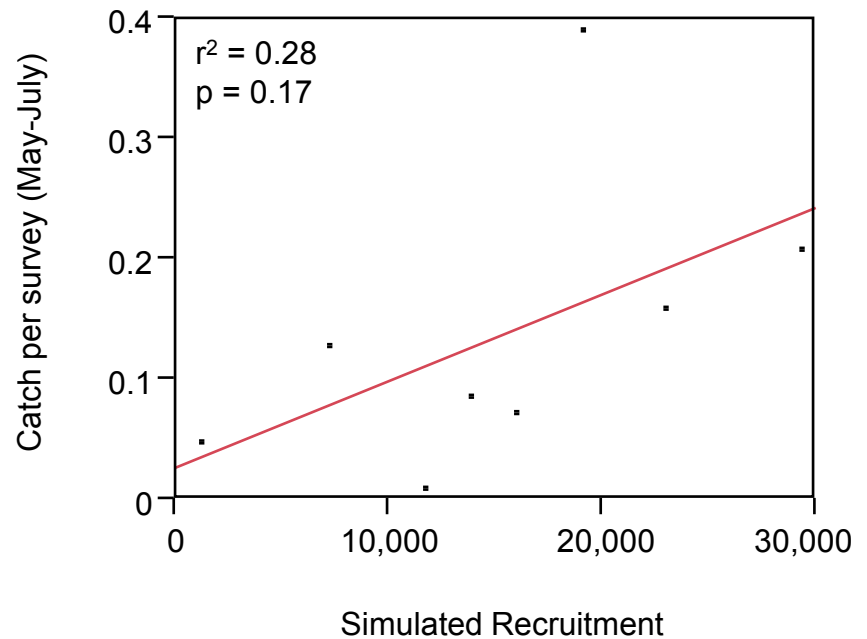
aspects of both the fisheries and model data. Fisheries survey data does not cover all of Guam, effort is highly variable among years, and there are a large number of zeros in reported catch (even in months when fishing permits were requested, an indication that *M. flavolineatus* are being fished). Unfortunately, model results can't be scaled down to only those coastal regions with creel survey sites. It will be useful to compare future simulation data with additional fisheries records as more data become available to improve these comparisons.

Recruiting *M. flavolineatus* post-larvae are an important fisheries and cultural resource in the Marianas (Davis 1991, DAWR Fisheries Reports). Findings from simulations here demonstrate that due to its long PLD, a large proportion of larvae arriving at each island in the Marianas is likely to be imported from elsewhere, with significant contributions from outside the archipelago. Unfortunately, this may leave little incentive to protect local stocks at each island, because local larval production may not be locally rewarded. Coordinated management decisions between CNMI and Guam in the Marianas, and with Chuuk and Pohnpei in FSM, would be especially useful for promoting sustainable fisheries of this species throughout the region.

### Scribbled Rabbitfish (*S. spinus*)

Because *S. spinus* is a shallow-water species, submerged banks and seamounts were excluded from the analysis. When virtual larvae were attributed with the specific traits of *S. spinus* larvae, islands within each respective archipelago often exchanged larvae but were seldom transported from one archipelago to another (Figure 3.11). Within the Marianas, the cloud of larval transport around each source island tended to skew northward, such that each island seeded most of the Marianas north of its position within the archipelago, but only ~3-6 islands along the chain to the south.

Islands in the FSM showed a strong tendency for self-seeding, but they also could be strongly connected to neighboring islands. Transport could be eastward or westward along the FSM, but strength of connections tended to be higher for destinations west of each source island (warmer tones of Figure 3.11). The eastward and westward transport is a product of the NEC and NECC current shear that occurs in the region where many of these islands lie. Larval transport from Yap tended to skew more westward, likely a consequence of its more northerly position at the southern edge of the westward flowing NEC. Transport from Palau tended to skew more eastward likely due to its more southern position under stronger influence of the typically eastward flowing NECC. In the Marshall Islands, self-seeding was again a strong aspect of transport, however, there was also a strong northward tendency. Island sources in the Marshalls generally did not, or only weakly, transport larvae to their neighbors south and east along the chain. In-



**Figure 3.10.** Number of virtual larvae arriving at Guam plotted against the corresponding year of catch data from DAWR (kg/survey during *M. flavolineatus* settlement period in May- July).

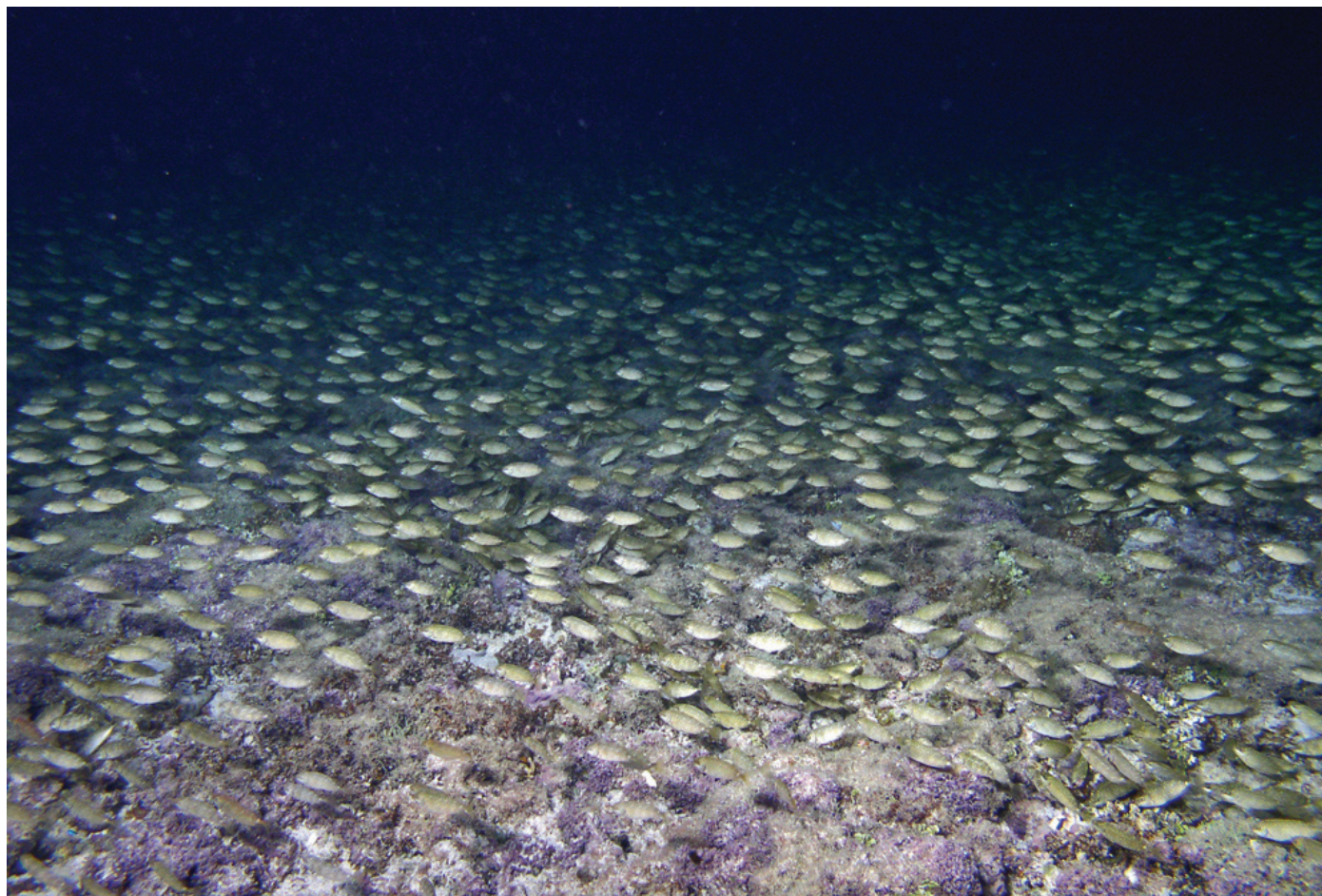
stead, there were often strong connections from Marshallese atolls to all the other destination atolls to their north and west. This is a region of strong feedback loops from the NECC northward into the NEC. Both the Ryukyu Islands and Ogasawara Islands of Japan were also quite isolated from other archipelagos. Transport along these islands tended to follow expected patterns along the strong influence of the Kuroshio Current. There was barely measurable exchange between the Japanese Islands in the Volcano group and the very northernmost islands in the Marianas.



*Scribbled rabbitfish (S. spinus).*

*Photo credit: Used with permission from David Burdick, guamreeflife.com*

There were other rare but noteworthy exchanges of larvae between different archipelagos. For example, during some years, islands and atolls in the Chuuk region of FSM could be sources of larvae that were carried northward in the NECC loops to the NEC and successfully settled in the southern Marianas between Saipan and Guam. During the spring months of high rabbitfish spawning and recruitment modelled here, drifter data demonstrate that the NECC has significantly more northward transport than would occur in Summer or Fall. Consequently, the Chuuk to southern Marianas connection may be less likely for taxa spawning at other times of the year.



*Recently settled cohort of rabbitfish.*

*Photo credit: Used with permission from David Burdick, guamreeflife.com*

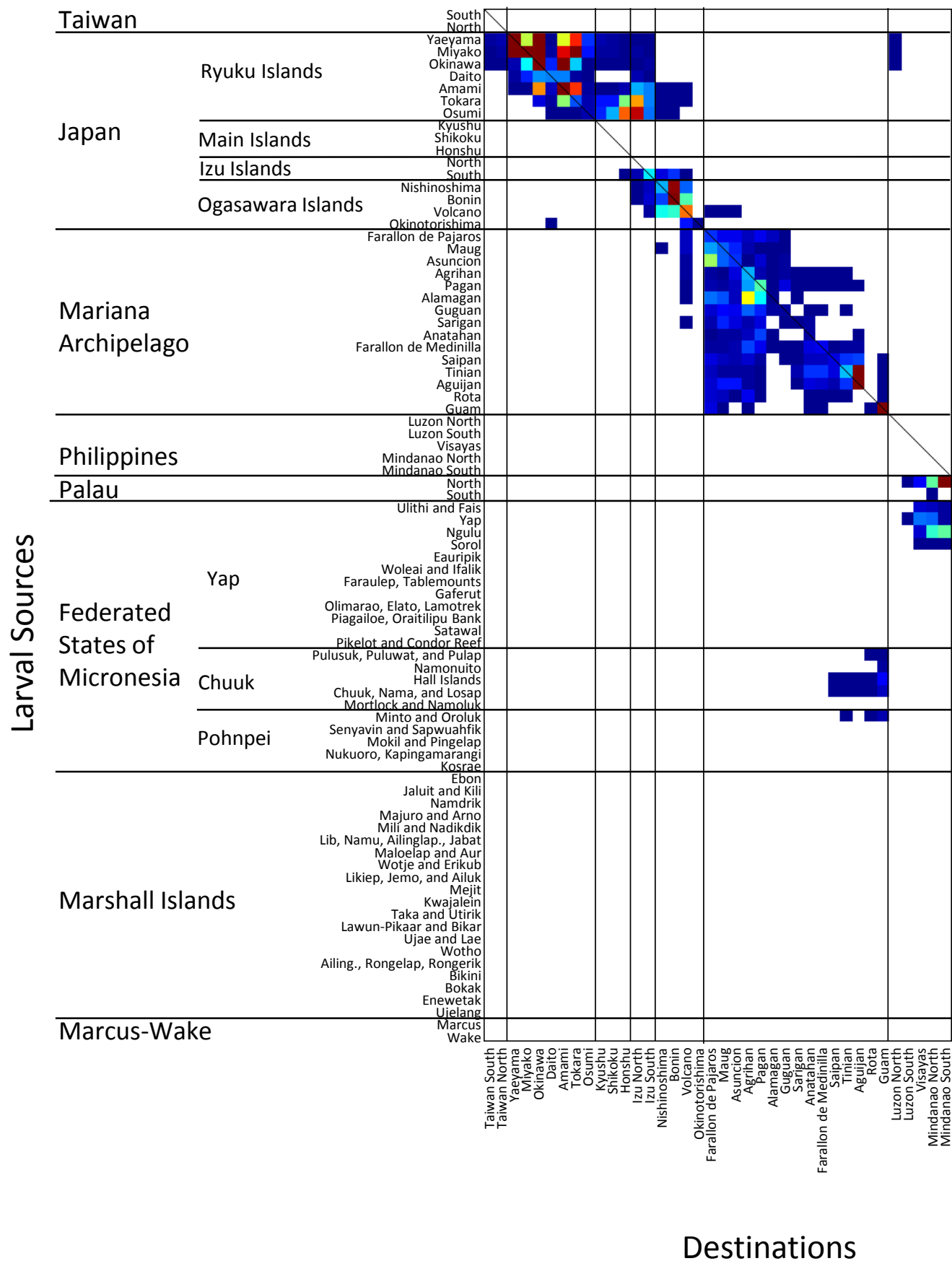
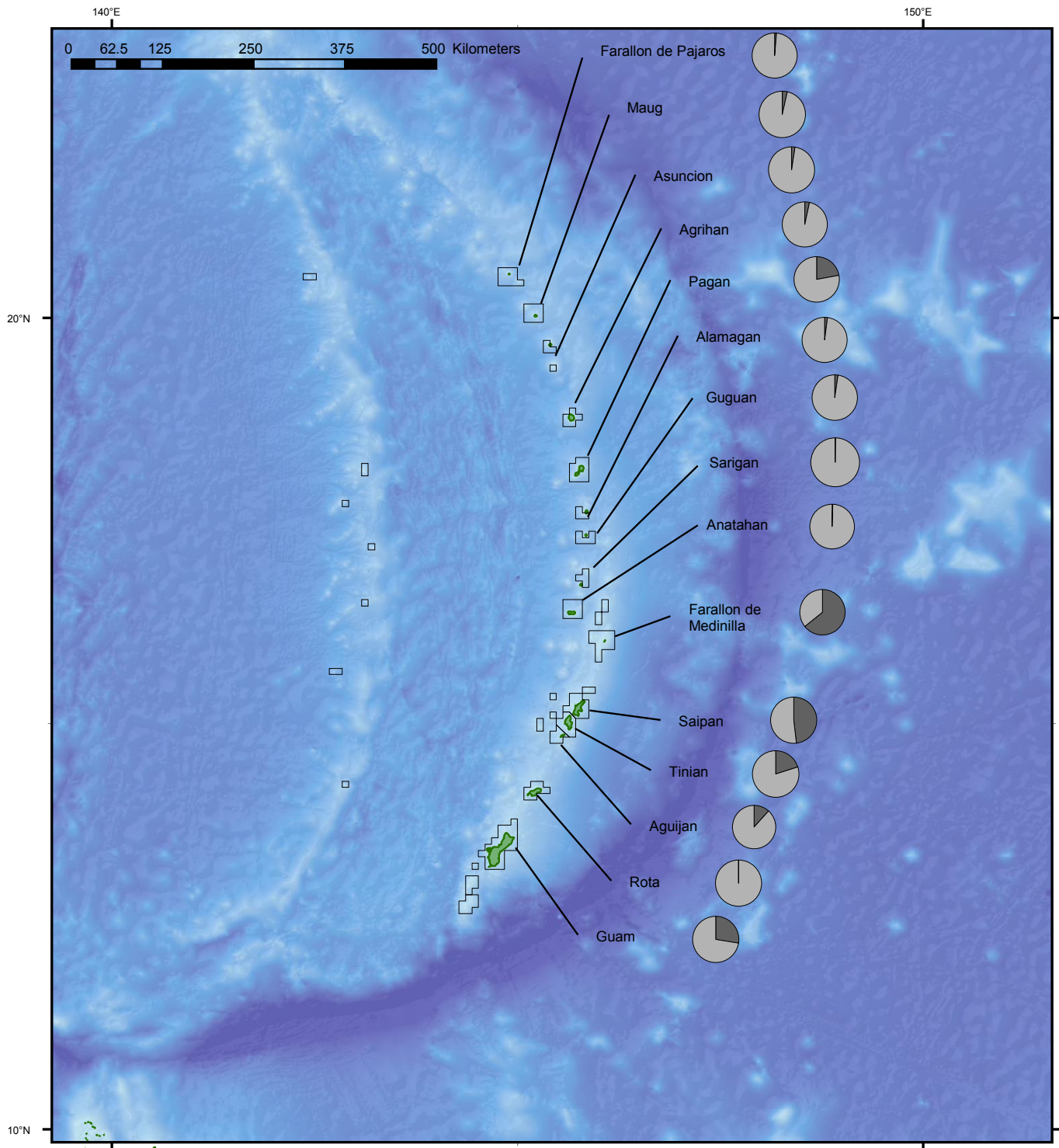


Figure 3.11. Cumulative connectivity (2004-2012) for *S. spinus* larvae. Color scale indicates the fraction of simulated larvae released at source settling at destination.



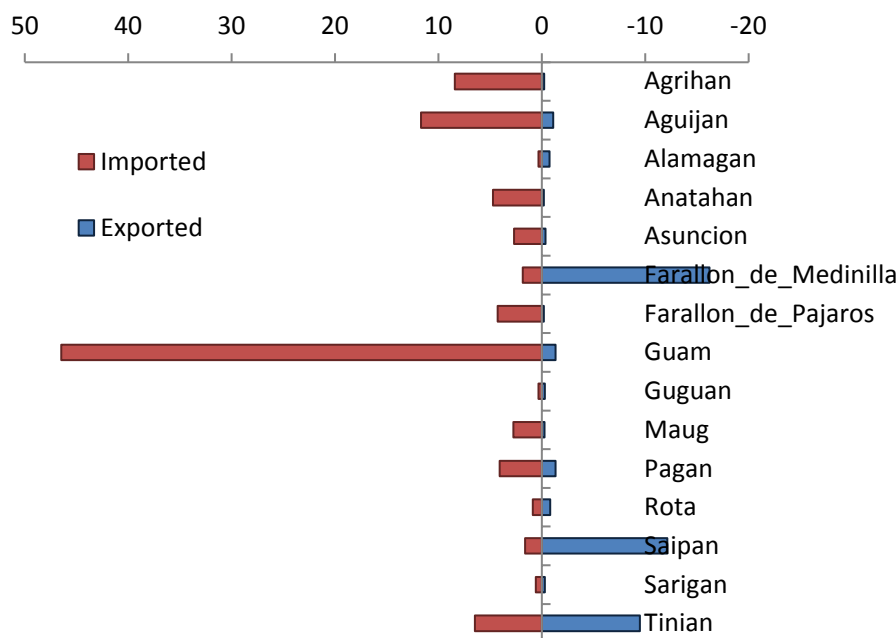
Most locations in the Marianas imported more larvae than they retained (Figure 3.12). Only Saipan and Farallon de Medinilla relied upon self-seeding for more than ~50% of their total incoming larvae. Guam, Tinian, and Pagan self-seeded 25% of their larvae. Most of the smaller islands in the Marianas relied on imports for 90-100% of their larval supply.



**Figure 3.12.** Proportions of *S. spinus* larvae settling at each island that are from self-seeding (dark grey) versus imported (light grey).

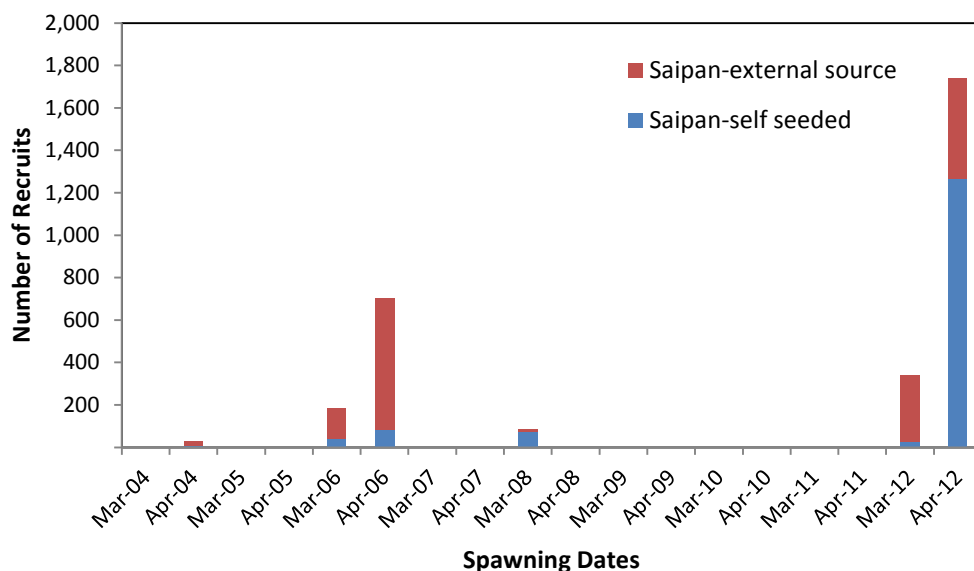


Most locations in the Marianas imported more *S. spinus* larvae than they exported (Figure 3.13). Exceptions were Farallon de Medinilla and Saipan, which exported many times more larvae than they imported. Exports were slightly greater than imports for Tinian as well. Examining annual model outputs revealed that the high numbers from Farallon de Medinilla were due to larvae sent to Agrihan and other island neighbors to the north. The high numbers from Saipan were due to larvae sent to Tinian and Aguijan, its close island neighbors to the south. The largest numbers of arriving larvae were seen at Guam. Larvae arriving at Guam were primarily from Chuuk in the FSM during recruitment events in 2007.



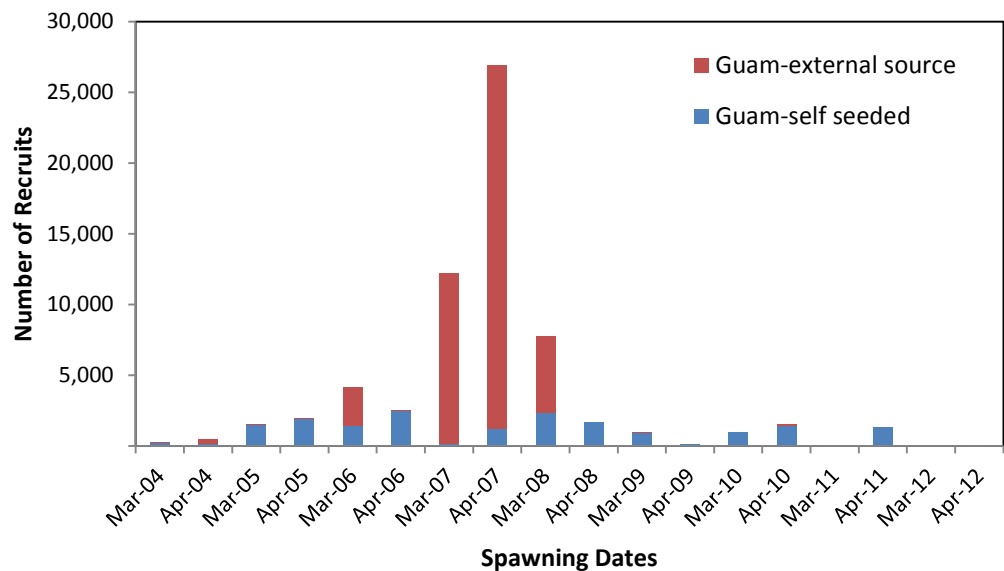
**Figure 3.13.** Numbers of *S. spinus* larvae that are imported and exported from each island. Values are in thousands.

Looking more closely at patterns of simulated recruitment of *S. spinus* in Guam and Saipan revealed some highly variable events among years. In Saipan, there was low or no recruitment of virtual larvae following many spawning dates (Figure 3.14). On four model dates, however, there were pulses in recruitment (March and April 2006, March and April 2012). These periods of high larval recruitment were primarily the product of a large and rare contribution of larvae arriving at Saipan from other sources. Major outside contributors of larvae to Saipan on those dates primarily included nearby islands in the Marianas, but also, in April 2006, a large number of recruits arriving from Chuuk in the FSM. The single largest simulated recruitment event occurred in April of 2012 and was the result of a massive increase in self-seeding due to an eddy returning larvae to Saipan at the critical moment for rabbitfish settlement.



**Figure 3.14.** The total number of *S. spinus* larvae arriving at Saipan for each spawning date that were self-seeded (blue) or arrived from an external source (red).

Guam also experienced dramatic fluctuations in strength of recruitment events (Figure 3.15). On many model dates, virtual larvae that were self-seeding Guam arrived at a generally consistent strength (1000-2000 larvae). Following some spawning dates, however, recruitment spiked 3-12 times higher than levels typically seen (March 2007, April 2007, March 2008). This was entirely due to the rare pulses of larvae arriving at Guam from various locations in Chuuk.

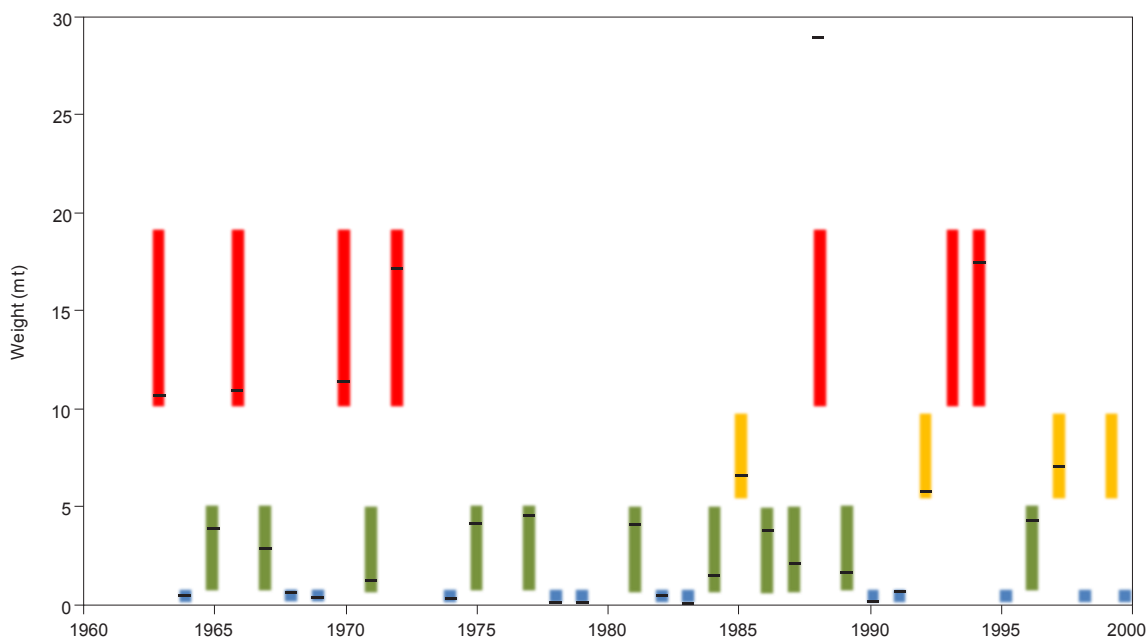


**Figure 3.15.** The total number of *S. spinus* larvae arriving at Guam for each spawning date that were self-seeded (blue) or arrived from an external source (red).

Also of note, the dates for these spikes in recruitment differed for Guam and Saipan. This suggests that incidents of high recruitment and catch are independent events on each island. In addition, it should be emphasized that the observed volatility in virtual recruitment occurred solely as a result of variations in ocean currents. Important aspects of larval biology, such as variation in interannual larval production and larval mortality rate, were kept constant in our simulations, but would certainly add other dimensions to levels of actual recruitment.

The high variability of simulated larval recruitment caused by occasional but strong connection to larval sources in FSM is also consistent with the intermittent spikes observed in catch records (Kami and Ikehara 1976). DAWR's Annual Fisheries Reports reveal a highly variable pattern of recruitment strength for *S. spinus* in Guam (Figure 3.13) (Tsuda et al. 1974). Reports were available for most years from 1963 to 2000 and include either catch weight or qualitative assessment of recruitment strength (e.g. "poor", "average", "exceptional"), and often both. Effort in collecting catch data varied over this long dataset which introduced an uncontrolled source of variation, and therefore values must be interpreted cautiously. To provide a relatively continuous depiction of catch over these years, the time series of catch information was plotted using a semi-quantitative approach to graph recruitment strength (Figure 3.16). Using years where both a quantitative measure (catch weight converted to metric tons) and qualitative description (using the adjectives above) of catch were provided, semi-quantitative categories were created based on the following breakpoints: Exceptional catch = > 10 mt, High = > 5 but < 10 mt, Medium = > 1 but < 5 mt, Low = < 1 mt. Catch ranged between ~0 and 29 mt annually for the time period when records were kept between 1963 and 2000, and there was no temporal trend (non-significant linear regression). Catch was not reported and could not be inferred in 3 out of the 37 years (1973, 1976, and 1980). The most striking observation about catch records is their extreme variability. Catch was variously described as "poor" and "exceptional", sometimes in adjacent years. The erratic catch patterns have been examined for trend and regular cycling during a period from 1963 to 1975 and found to not differ significantly from randomness (Kami and Ikehara 1976). The similar pattern found here in simulated recruitment, although for a different time period, offer one possible explanation and mechanism (i.e. variation in transport) to explain such high variability in catch. Unfortunately, the creel surveys for *S. spinus* were discontinued by 1999 in Guam to avoid potential conflict with fishermen, and therefore could not be directly compared to our simulation results which began in 2004.

Arriving post-larval *S. spinus* are an important fishery and cultural resource in the Marianas (Kami and Ikehara 1976). Results in the connectivity matrix correspond well to recent genetic evidence of population partitioning among archipelagos (Priest et al. 2012). Locations from Chuuk and Pohnpei in FSM are connected in both studies, presumably via the NECC, as were locations in Yap, Palau, and the Philippines via the NEC. Findings here suggest that the occasional spikes in recruitment at Saipan and Guam may differ in their origin and may not be synchronized among even nearby islands. The high variability in both source and timing makes it challenging to predict recruitment and



**Figure 3.16.** DAWR creel survey data for *S. spinus* catch summarized by year. Breakpoints are based on descriptions in fisheries reports. Exceptional catch (red) = > 10 mt, High catch (yellow) = > 5 but < 10 mt, Medium catch (green) = > 1 but < 5 mt, Low catch (blue) = < 1 mt.

select reasonable catch limits to promote a sustainable fishery among years and locations. Simulations suggest that such strong recruitment events in Saipan, for example, may be a product of enhanced self-seeding as well as enhanced imports. Maintaining local larval production is therefore partly what allows the rare but spectacular levels of recruitment in some years. At Guam, locally produced larvae are also important to maintain baseline levels of recruitment, but played little role in the rare, but dramatic recruitment spikes. For both locations, coordinated regional management of adequate spawning stock within the Marianas and with Chuuk is the best approach for maintaining baseline levels of recruitment and for preserving the potential for the rare, but occasionally large recruitment events (Priest et al. 2012).

### Bluespine Unicornfish (*N. unicornis*)

When virtual larvae were attributed with the life history characteristics of *N. unicornis*, there was broad connectivity within and among archipelagos (Figure 3.17). In the Marianas, there was a northward and westward bias in larval exchange among islands. The northward bias was evident in that larvae from any source in the Marianas could be transported to nearly any place in the Marianas to the north of it (e.g. larvae from Guam could arrive at Farallon de Pajaros or anyplace in between). Southward transport was more limited in that larvae could only reach destinations ~500 km to the south of their starting points (e.g. larvae from Pagan could only arrive as far south as Aguijan). Westward bias was evident in that larvae from anywhere in the Marianas could arrive nearly anyplace in the West Mariana Ridge but not vice versa. There was broad exchange of *N. unicornis* larvae between the Marianas and other archipelagos. Larvae from the southern Marianas, between Rota and Santa Rosa Reef, could arrive in strength as far away as the Philippines via the NEC. There was also widespread but lower level transport from the southern Marianas to many places in Yap in the FSM. Larvae from nearly any place in the Marianas could also arrive in the Daito Islands of Japan, and a few larvae from the Saipan/Tinian region even arrived in Taiwan. Larvae arriving in the southern Marianas, particularly Guam, could come from many sources in FSM via loops from the NECC to the NEC. This connection is probably enhanced in Fall and Winter when *N. unicornis* larvae are at large. NECC headings are more northward and currents are fastest during Fall/Winter compared to other seasons. Strongest connections were between sources in Chuuk and



*Bluespine Unicornfish (N. unicornis).*  
Photo credit: Used with permission from David Burdick, [guamreeflife.com](http://guamreeflife.com)

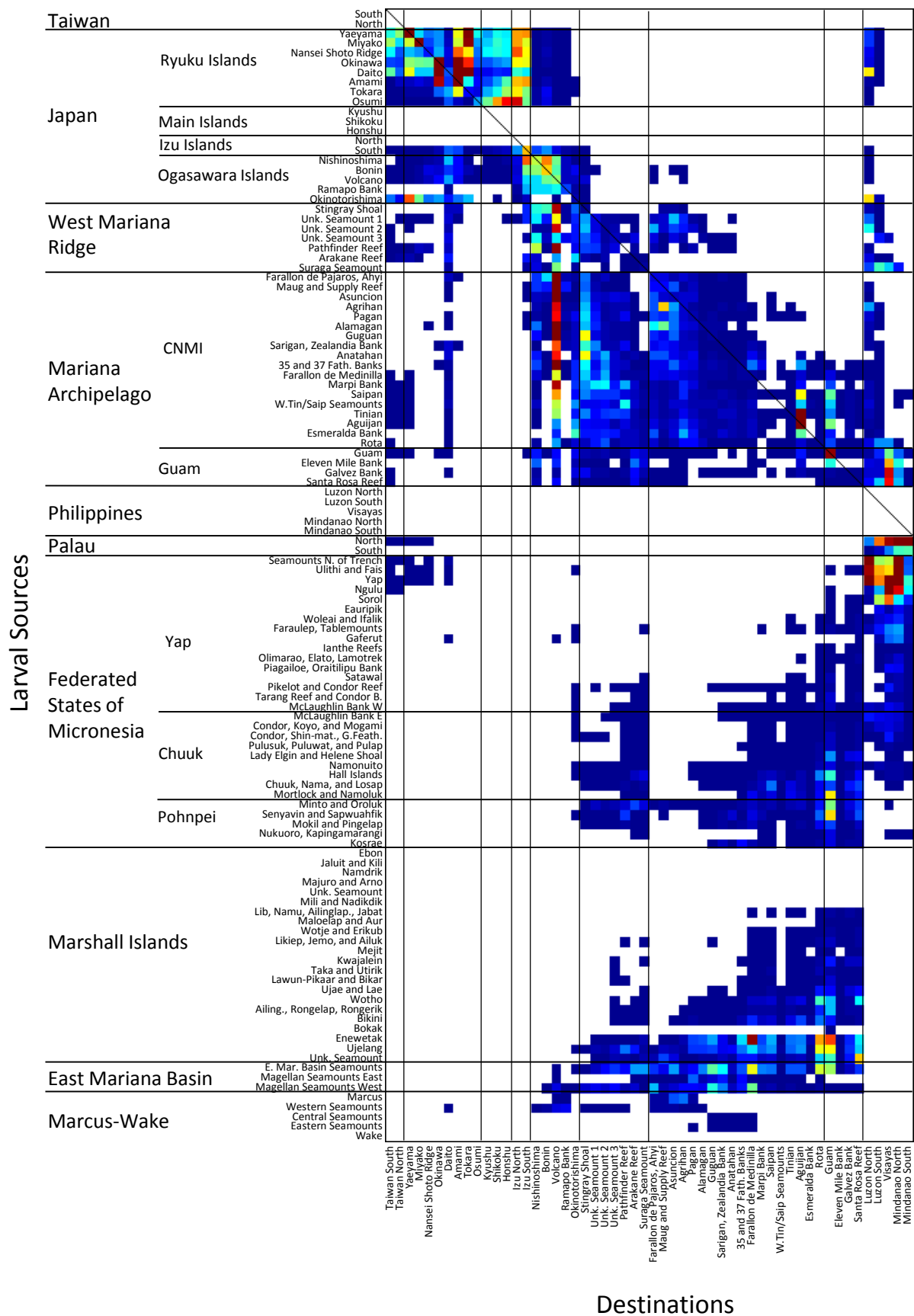


Figure 3.17. Cumulative connectivity (2004-2012) for *N. unicornis* larvae. Color scale indicates the fraction of simulated larvae released at source settling at destination.

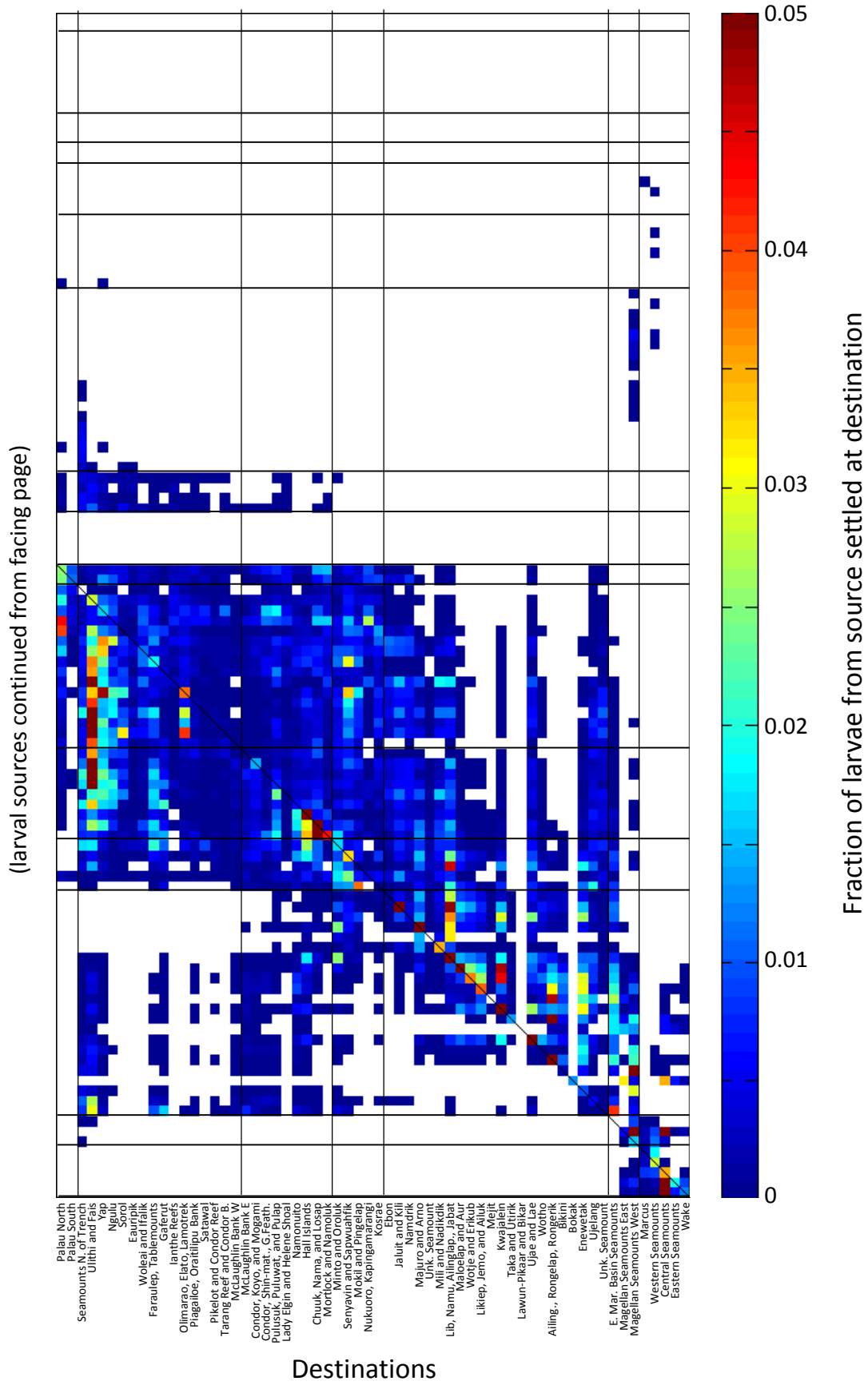
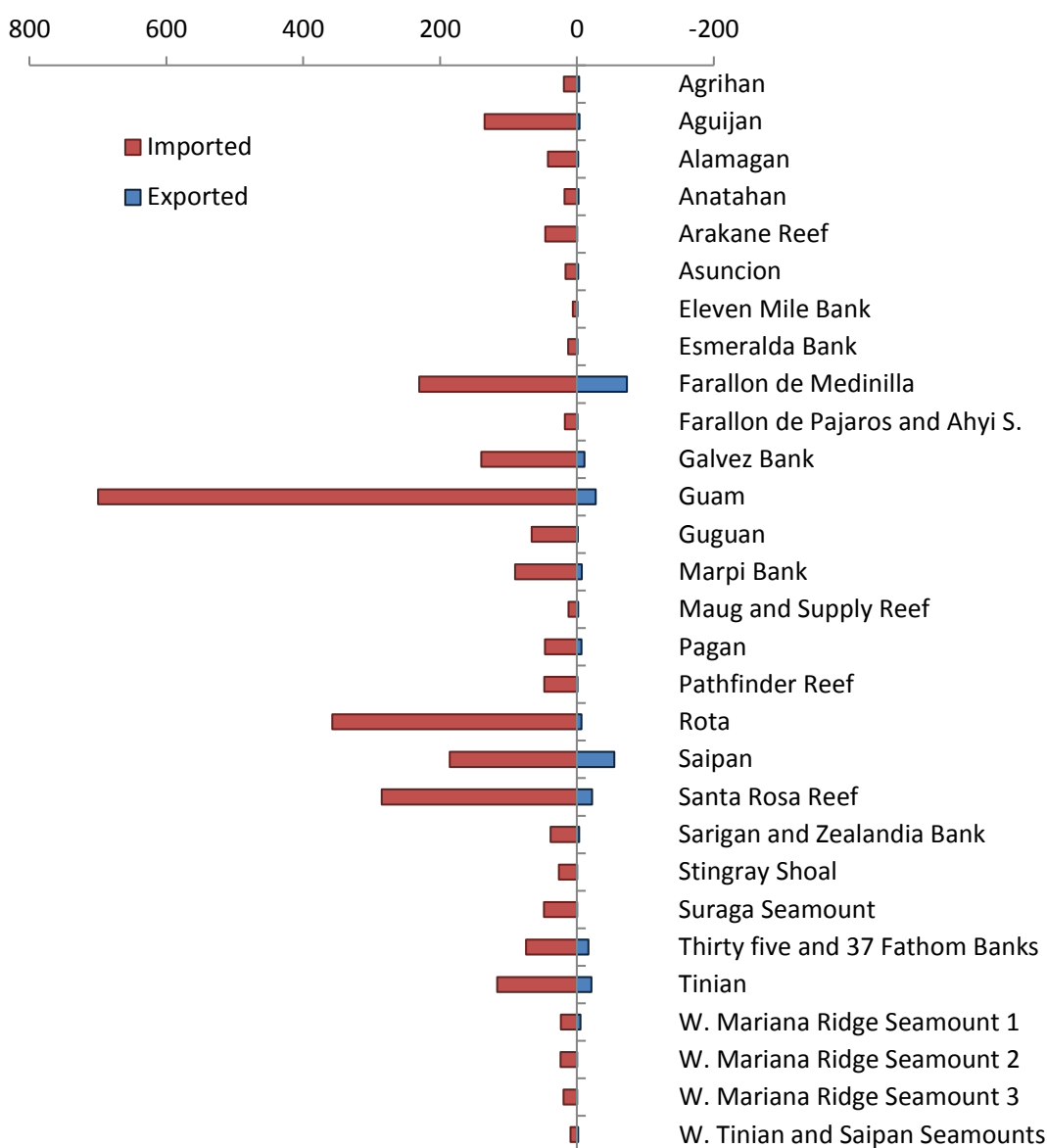


Figure 3.17 cont.

Pohnpei to destinations in the southern Marianas. Connection strength gradually diminished northward along the Marianas and westward along the FSM such that larvae from Yap rarely arrived north of Tinian. Larvae could also arrive in the Marianas from many of the atolls in the Marshall Islands. Strongest connections were from the northwestern Marshalls, such as Enewetak to Guam and Rota. These connections are via the NEC, which has peak speed and most consistently westward headings at this time of the year.

The proportions of *N. unicornis* larvae arriving at each island or bank that were self-seeded versus imported were similar to the 100 day PLD for corals (Figure 3.3d). All locations in the Marianas imported 98-100% of their larval supply. Only 2% of Guam's larvae were self-seeded, and this was the highest value in the Marianas.

The number of *N. unicornis* larvae imported exceeded the number exported for all locations in the Marianas (Figure 3.18). The largest number of imported larvae arrived at Guam, likely due to a combination of its size and position in the archipelago. First, it is simply a large settlement target relative to the rest of the Marianas. Second, its position in the NEC makes it the recipient of virtual larvae from FSM and even the Marshall Islands given the long PLD of *N. unicornis*. Large numbers of larvae also arrived at the much smaller locations of Rota and Santa Rosa Reef positioned to the north and south of Guam. These larvae were also primarily from FSM and the Marshalls. Tiny Farallon de Medinilla, located close to the mid-point northward along the Mariana Archipelago, also received many larvae.



**Figure 3.18.** Number of *N. unicornis* larvae that are imported and exported from each island. Values are in thousands.

These were primarily imported from the Enewetak region of the Marshalls during a single recruitment event following spawning in September 2009. The only locations that exported many successful larval settlers were Farallon de Medinilla and Saipan. These spikes were due largely to larval exports to Aguijan, the West Mariana Ridge, and the Volcano Islands of Japan.

Bluespine unicornfish are among the top fisheries species on the reefs of the Marianas (Horne et al. 2013, DAWR Fisheries Reports). Genetic evidence from recruiting *N. unicornis* at Guam and Saipan reveal a genetically homogeneous and mixed suite of arriving larvae, and possibly even the identification of sibling larvae arriving at islands 250 km apart (Horne et al. 2013), which is in agreement with the broad and far dispersal clouds simulated here. Like other species with a long PLD, simulation results suggest that a large proportion of larvae arriving at each island in the Marianas is imported from elsewhere. Long distance transport among archipelagos is probably also enhanced for this species due to the timing of Fall spawning and seasonal aspects of ocean currents. The NEC has peak speed and highly directional flow in Winter, offering the best opportunity for connecting the Marshall Islands to the Marianas. Similarly, the NECC has more northward headings that probably promote connections from the FSM to the Marianas. This widespread interdependence among archipelagos in larval supply enhances the need for coordinated management throughout the study area to maintain sustainable fisheries for this species (Horne et al. 2013).

#### **Humphead Wrasse (*C. undulatus*)**

When virtual larvae were attributed with the life history characteristics of *C. undulatus*, there was broad exchange of larvae among islands within archipelagos and little exchange of larvae from one archipelago to another (Figure 3.19). Within the Marianas, there was a northward and westward bias in larval exchange among islands. The bias was evident in that larvae could be transported to destinations nearly any place northwards of their starting point (e.g. Guam could transport larvae as far north as Farallon de Pajaros), but larvae went southward along the Marianas only 300-500 km (e.g. larvae from Farallon de Pajaros could reach only as far south as Farallon de Medinilla). The westward bias was evident in that the West Mariana Ridge could receive larvae from nearly any place in the Mariana Archipelago. There was also a greater proportion of larval export to the north than to the south. Few *C. undulatus* larvae were exchanged with locations outside the archipelago except the low-level exchange among islands of the Bonin and Volcano Islands of Japan with the northernmost Marianas. The southernmost banks in the Marianas (Santa Rosa Reef and Galvez) were sources of some larvae to Yap via the NEC. The islands of Chuuk and even Yap were sources of some larvae arriving at the southern Marianas from Santa Rosa Reef to approximately Farallon de Medinilla.



*Humphead Wrasse (C. undulatus).*

*Photo credit: Used with permission from David Burdick, guamreeflife.com*

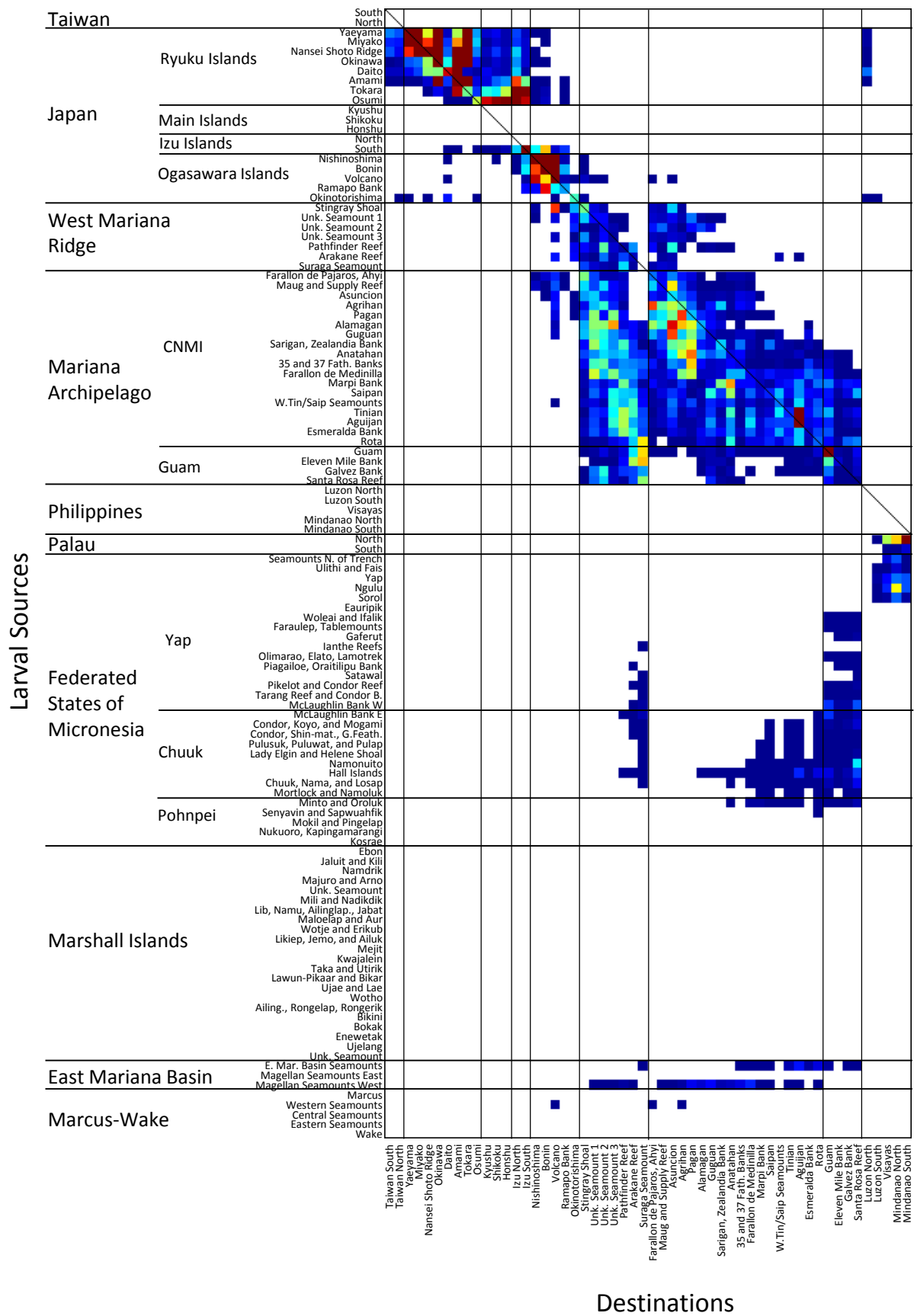


Figure 3.19. Cumulative connectivity (2004-2012) for *C. undulatus* larvae. Color scale indicates the fraction of simulated larvae released at source settling at destination.



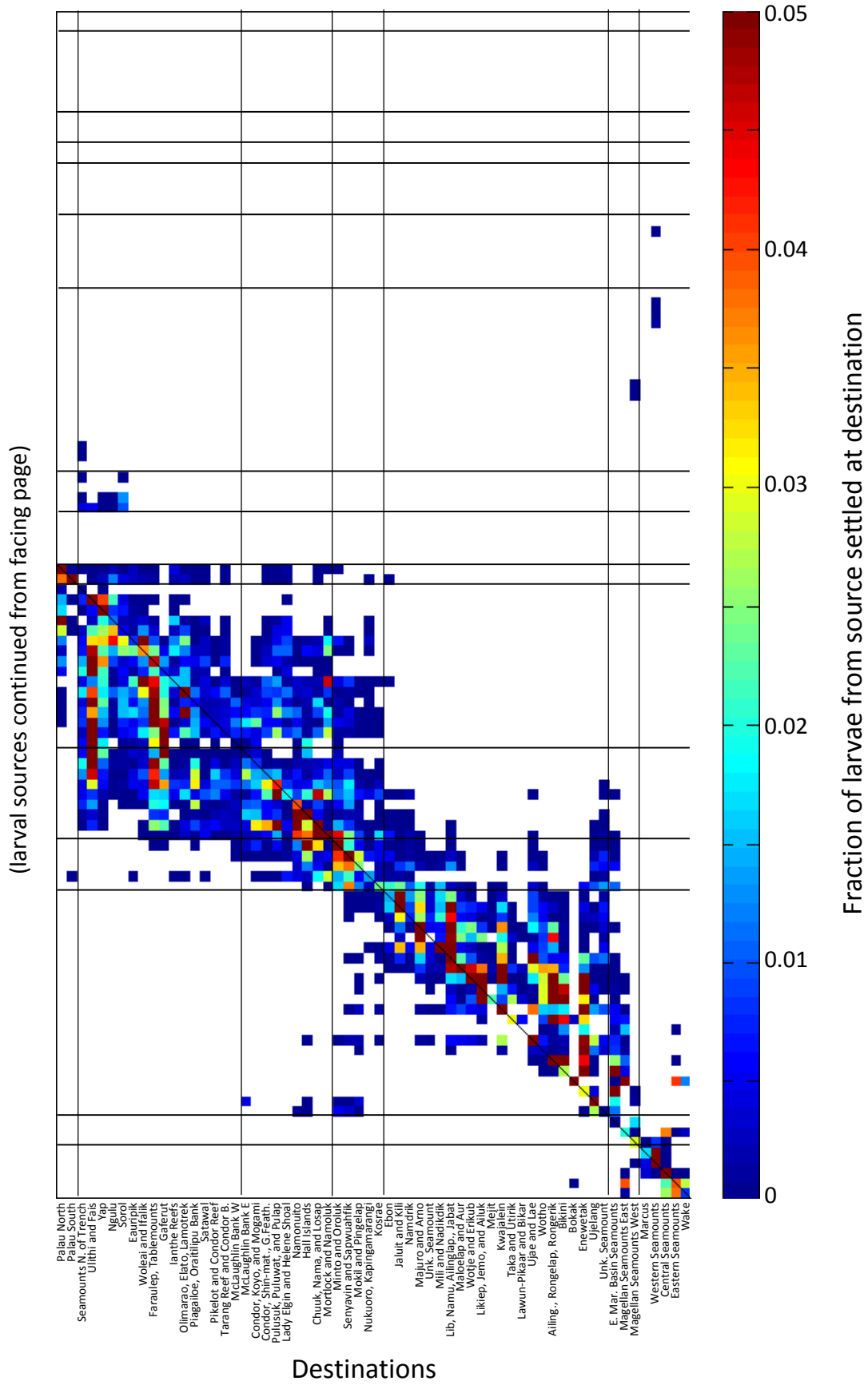
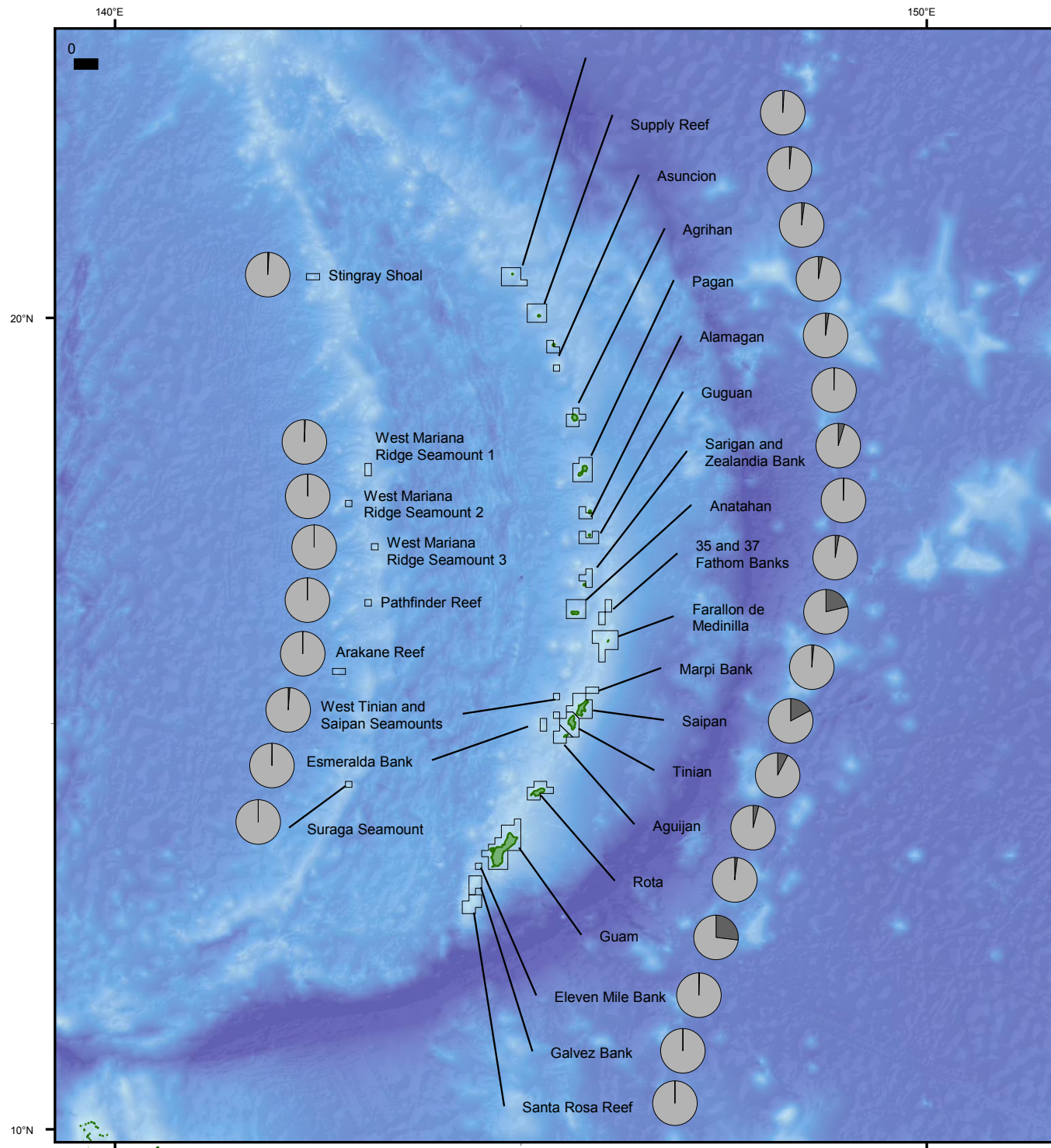


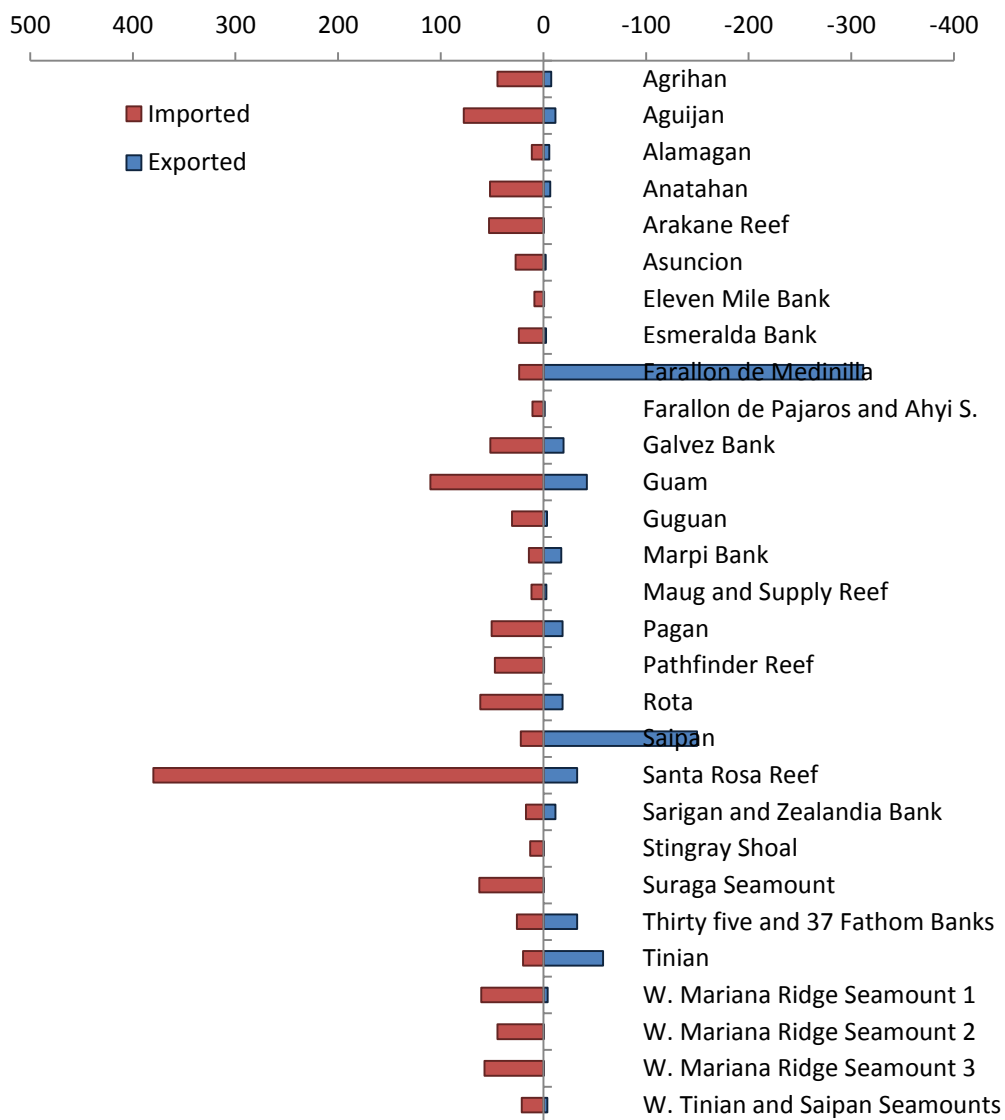
Figure 3.19 cont.

All locations in the Marianas imported more *C. undulatus* larvae than they retained (Figure 3.20). Only Guam, Saipan, and Farallon de Medinilla relied upon self-seeding for more than ~5% of their total incoming larvae. Most of the smaller islands in the Marianas relied on imports for over 95% of their larval supply. Submerged banks, including all the locations in the West Mariana Ridge, were almost totally reliant on larvae arriving from external sources.



**Figure 3.20.** Proportions of *C. undulatus* larvae settling at each island that are from self-seeding (dark grey) versus imported (light grey).

Most locations in the Marianas imported more *C. undulatus* larvae than they exported (Figure 3.21). Exceptions were Farallon de Medinilla, Saipan, Tinian, as well as Marpi, Thirty-Five, and Thirty-Seven Fathom Banks. In the case of Saipan and Farallon de Medinilla, successfully exported larvae drastically outnumbered imported larvae. Examining the annual model outputs revealed that high numbers of larvae from Farallon de Medinilla arrived at Pagan following spawning in April 2011, and to West Mariana Ridge destinations during many years. The high numbers of larvae from Saipan were due to larvae spread widely among diverse Mariana and West Mariana Ridge destinations during many years. Also of note, the largest number of arriving larvae was seen at tiny Santa Rosa Reef. This was due to heavy recruitment in several years from locations in Chuuk in FSM.



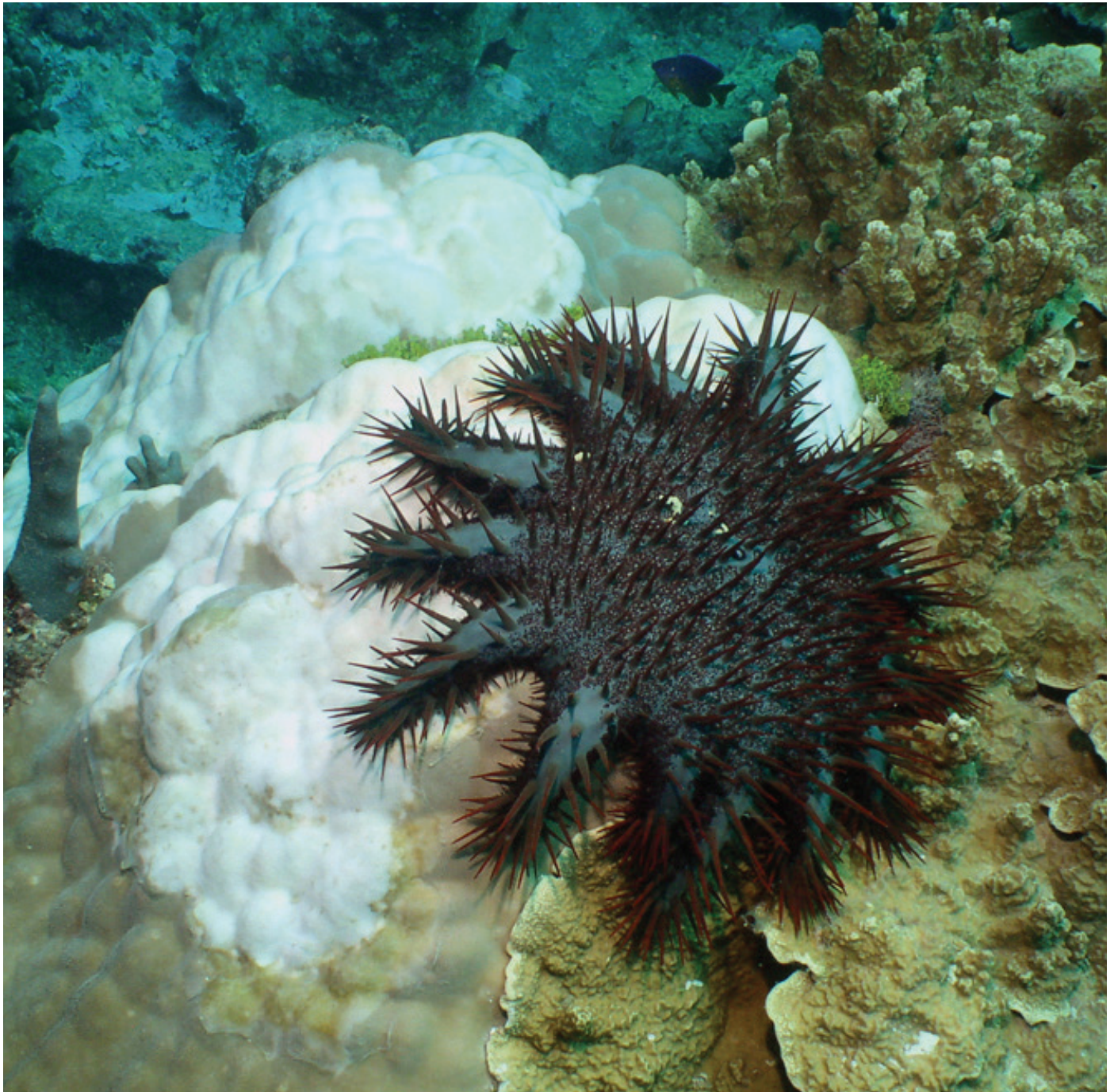
**Figure 3.21.** Number of *C. undulatus* larvae that are imported and exported from each island. Values are in thousands.

Humphead wrasse are rare. In recent years, *C. undulatus* has been listed as a “species of concern” by NMFS, “endangered” by IUCN and in Appendix II of CITES. As a long-lived hermaphrodite, it is susceptible to overfishing. Understanding larval connectivity is an important part of devising the recovery strategy for any threatened species. Depending on their location, some spawners will contribute more to local or regional recovery of populations than others. Although in need of protection wherever they exist until populations rebound, simulations here identify important sources of larvae, such as Saipan, which may be especially vital to maintain. Some islands, such as Saipan and Guam, are also reliant on self-seeding for a significant proportion of their larval supply. These islands have an espe-

cially high self-interest in maintaining local spawning stocks. Elsewhere in the Marianas, many locations are more reliant on imported larvae. However, due to the relatively short PLD, these larvae are mostly arriving from elsewhere in the Marianas rather than imported from outside the archipelago. Coordinated management between CNMI and Guam would have the greatest benefit for this species in the Marianas.

#### **Crown-of-Thorns Seastar (*A. planci*)**

When virtual larvae were attributed with the life history characteristics of *A. planci*, islands within each archipelago often exchanged larvae, but larvae seldom made the connection from one archipelago to another (Figure 3.22). In the Marianas, several interesting patterns emerged. Larvae from Guam and the submerged banks to its south (Santa Rosa Reef, Eleven Mile, and Galvez Banks), could settle at destinations in the West Mariana Ridge but almost nowhere else in the Mariana Archipelago. Rota represented a geographic transition point in *A. planci* connectivity



*Crown-of-Thorns Seastar in Guam.*

*Photo credit: Used with permission from David Burdick, guamreeflife.com*

potentially due to its position along the northern edge of the NEC. Larvae from Rota were primarily transported to Mariana destinations to the north, as well as along the West Mariana Ridge. Sources from Rota north to Anatahan showed a block of larval exchange among the islands between them and could also seed destinations at any of the Marianas to the north and along the West Mariana Ridge. From Anatahan to Alamagan, transport was entirely to the northward within the archipelago and to destinations along the West Mariana Ridge. The pattern shifted again with larvae from Pagan and Agrihan being transported both south and north along the archipelago. Unidirectional transport of larvae was evident from sources in Chuuk to the southern Marianas from Santa Rosa Reef to Farallon de Medinilla via NECC/NEC loops.

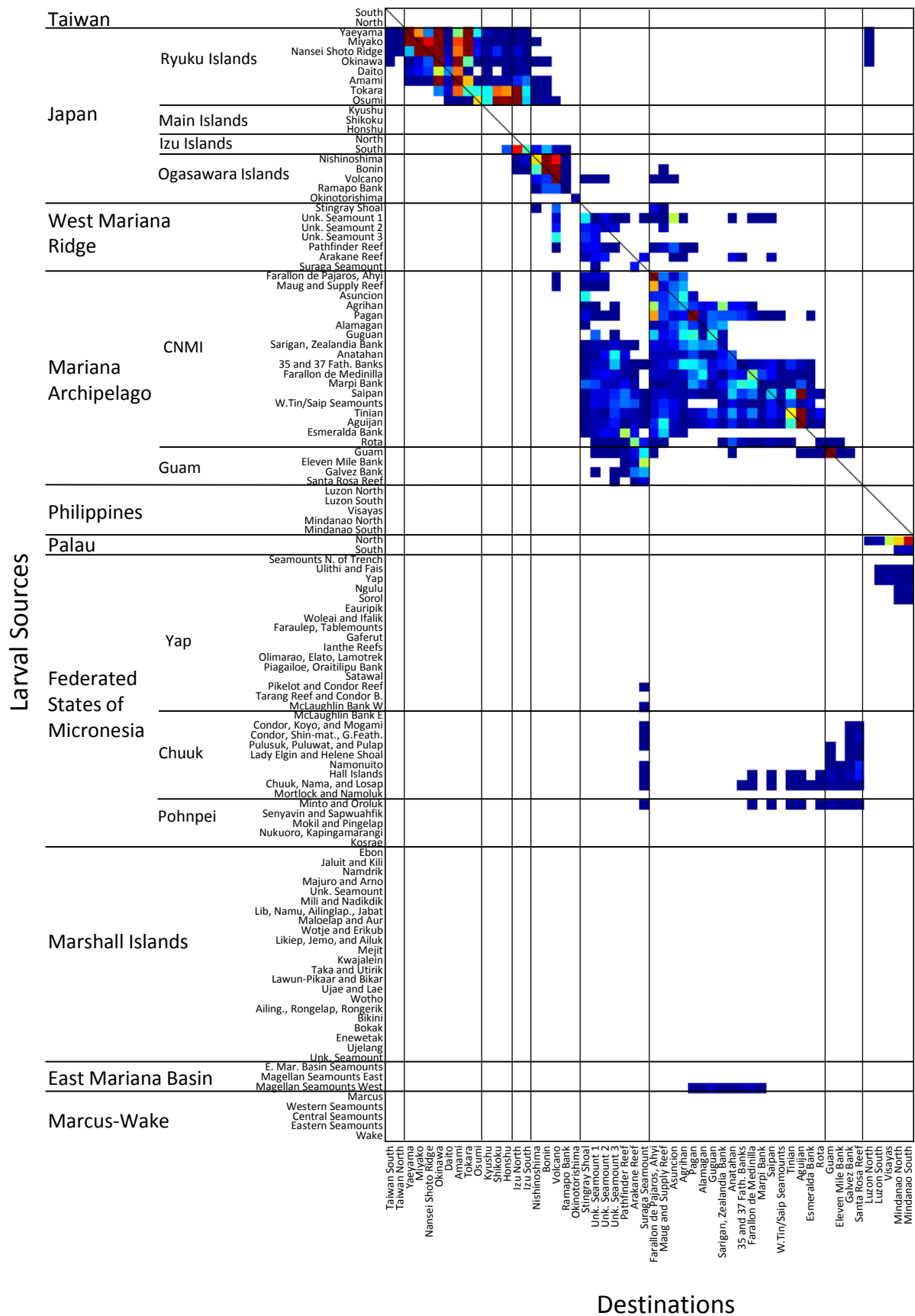


Figure 3.22. Cumulative connectivity (2004-2012) for *A. planci* larvae. Color scale indicates the fraction of simulated larvae released at source settling at destination.

(larval sources continued from facing page)

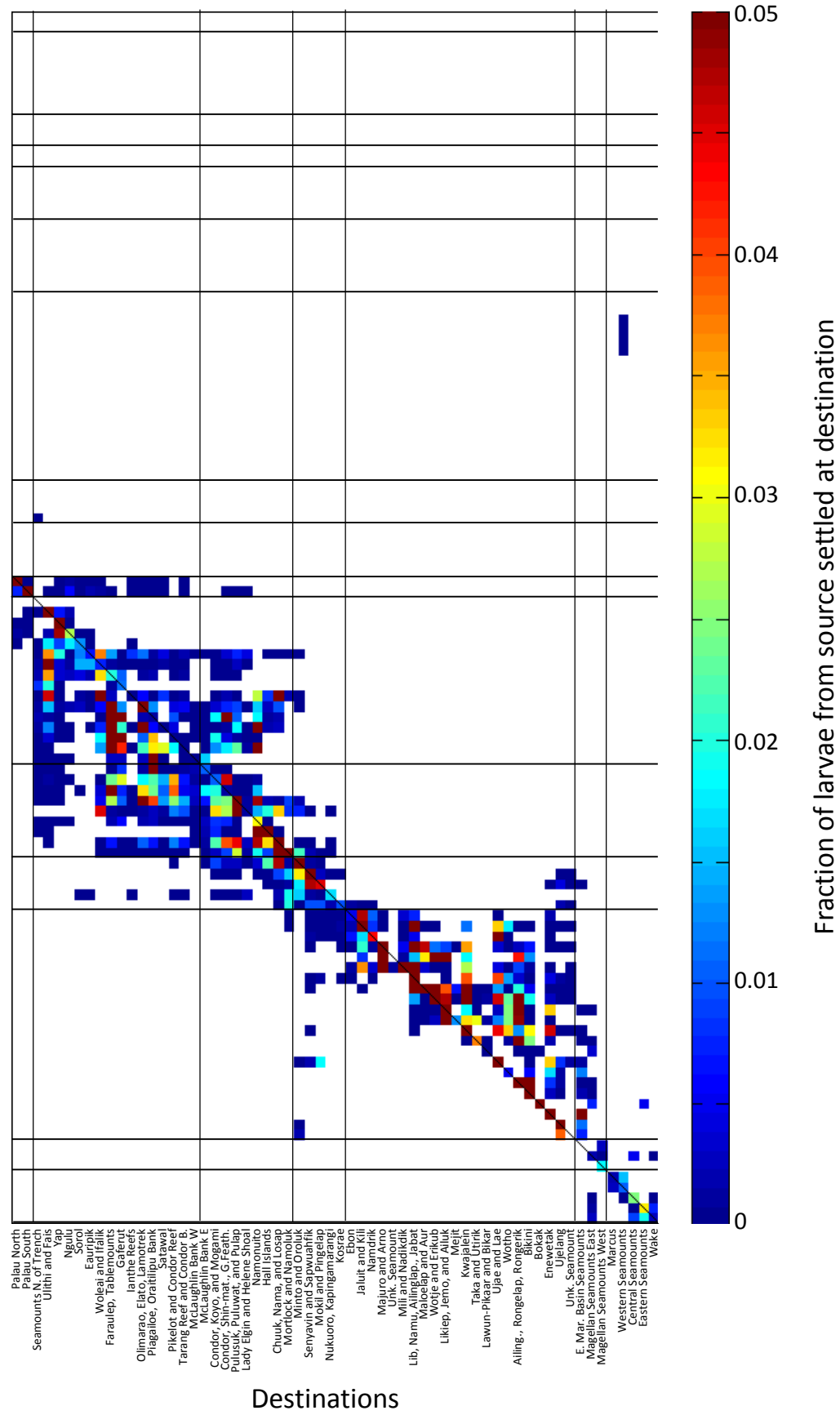


Figure 3.22 cont.

Most locations in the Marianas imported many more larvae than they retained (Figure 3.23). Only Guam and Farallon de Medinilla self-seeded a majority of their arriving larvae. Saipan, Pagan, and Tinian self-seeded 25-50% of their arriving larvae. Most small islands and submerged banks, including all the locations in the West Mariana Ridge, were almost totally reliant on larvae arriving from external sources.

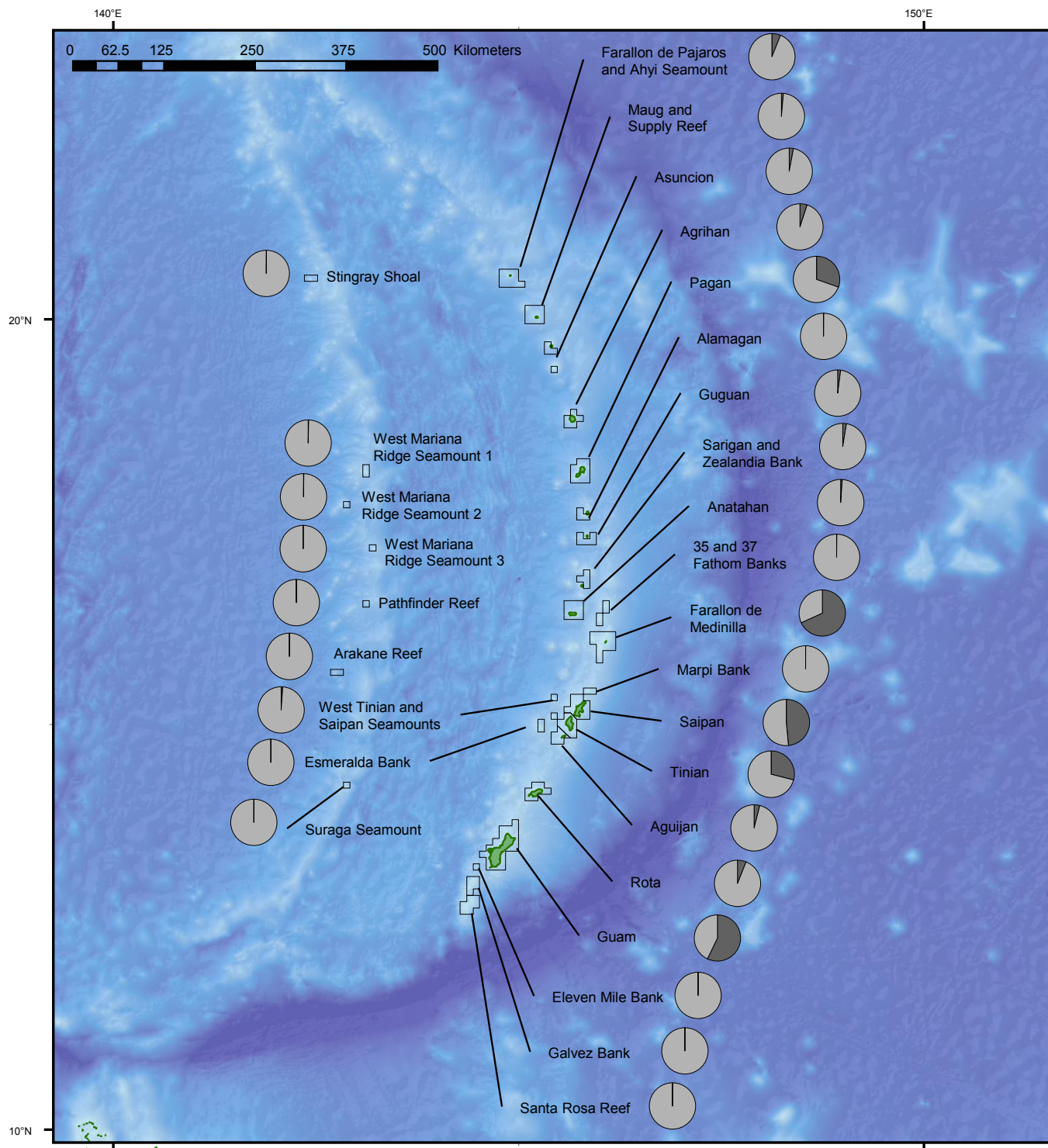


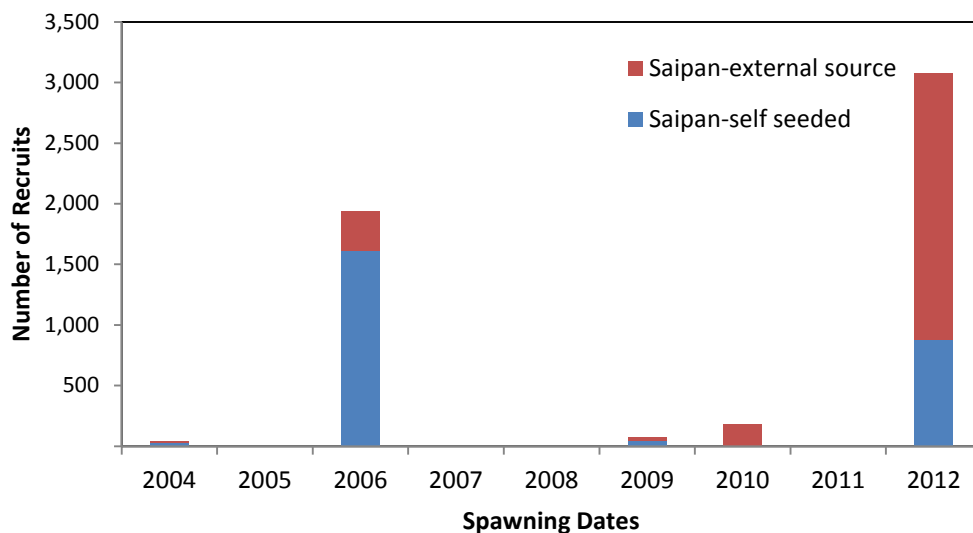
Figure 3.23. Proportions of *A. planci* larvae settling at each island that are from self-seeding (dark grey) versus imported (light grey).



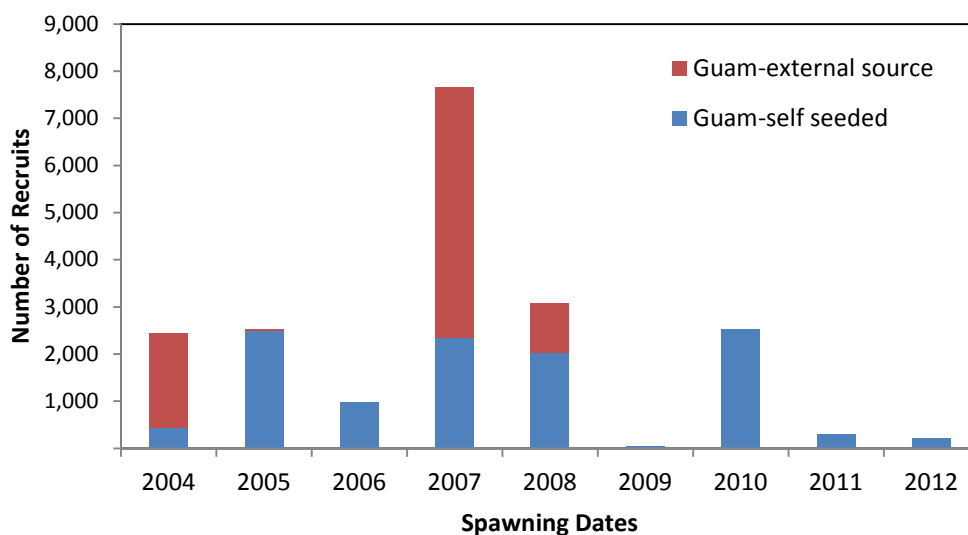
Because COTS outbreaks can be a major control on live coral cover and reef condition, it was of interest to examine the interannual variability of recruitment strength (Figure 3.24 and 3.25). It should be emphasized here that results are based on a regular supply of larvae in each spawning event, whereas in reality there are environmental triggers that cue very different levels of larval output and survival (Timmers et al. 2012). Those important sources of variability were controlled in these results. Number of larvae arriving at Saipan was highly variable among model years. Very few larvae arrived at Saipan in 7 of the 9 modeled years. In 2006 and 2012, however, the number of arriving larvae experienced dramatic spikes. In 2006, this was due to self-seeding, whereas in 2012 it was due to both increased self-seeding and also incoming larvae from surrounding islands. Examining the sources of these larvae in the model outputs revealed that a large number of larvae arrived from Farallon de Medinilla. Number of larvae self-seeding at Guam was somewhat more consistent among model years. The most notable exception was

2007, when the number of arriving larvae more than doubled the amount seen in typical years. This was due to a spike in incoming larvae primarily from the islands and Atolls of Chuuk in the FSM. In other years, such as 2009, 2011, and 2012, almost no larvae arrived at Guam from any source. These highly variable recruitment due to simulated transport processes events may play a role in the periodic outbreaks of COTS that can devastate corals in these islands. It should be noted that, although these islands lie relatively close to each other, the spikes in recruitment occurred in completely different years. As with rabbitfish, it should be emphasized that the observed volatility in virtual recruitment was solely a function of variation in ocean currents, not due to differences in initial larval supply or mortality rates, which play a large role in numbers of incoming larvae.

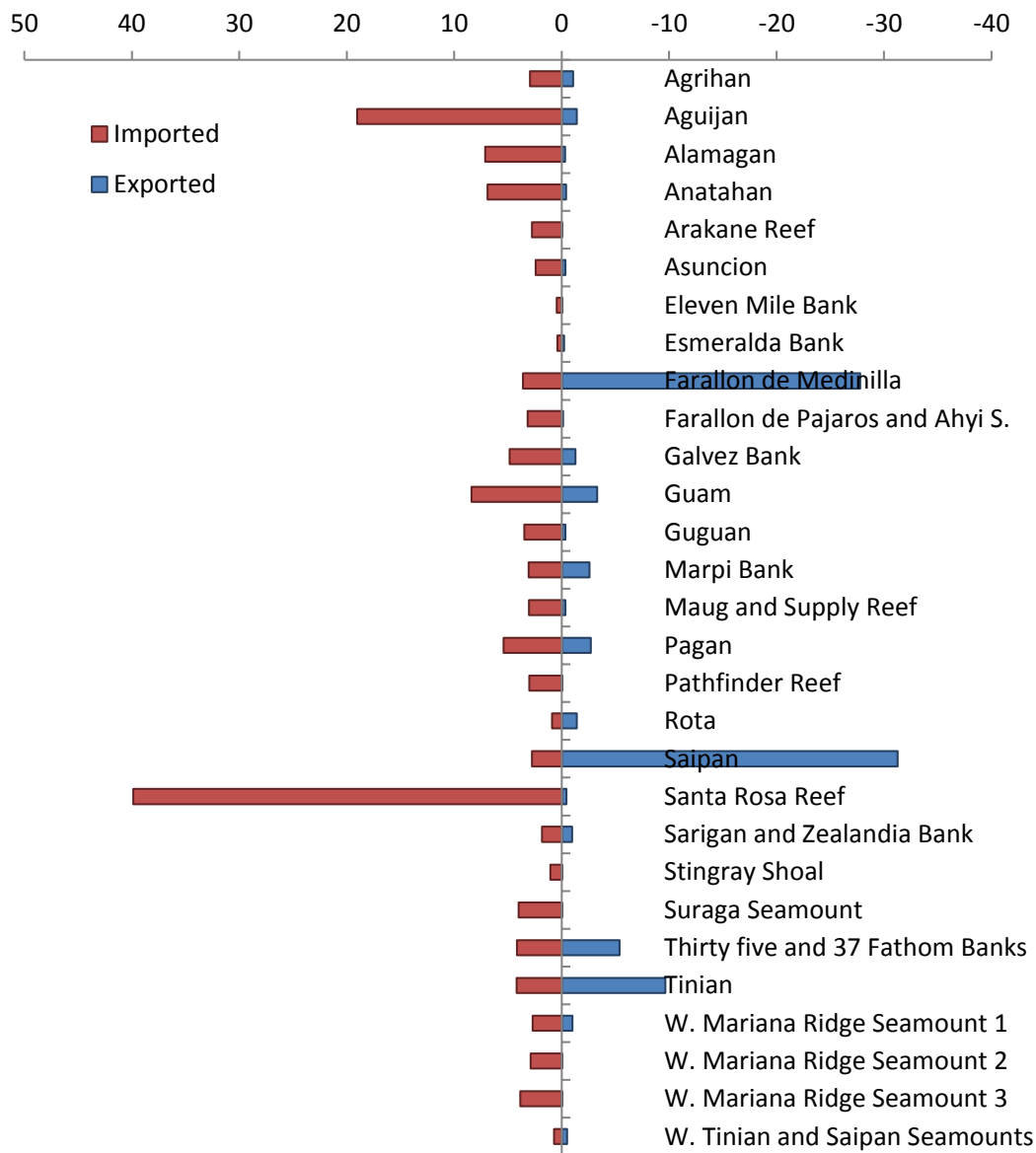
Most locations in the Marianas imported more *A. planci* larvae than they exported (Figure 3.26). Exceptions were Farallon de Medinilla, Saipan, Tinian, and Thirty-Five and Thirty-Seven Fathom Banks. In the case of Saipan and Farallon de Medinilla, successfully exported larvae drastically outnumbered imported larvae. The high numbers for these islands were for large recruitment events from Farallon de Medinilla advected northward to neighboring islands in 2005 and 2012. Saipan was the source of a massive number of larvae to Aguijan in 2008. Tinian also exported many larvae to Aguijan, its small island neighbor to the south. The largest numbers of arriving larvae were seen at



**Figure 3.24.** Number of COTS larvae arriving at Saipan by model year. Stacked bars represent larvae from Saipan (blue) and from all external sources (red).



**Figure 3.25.** Number of COTS larvae arriving at Guam by model year. Stacked bars represent larvae from Guam (blue) and from all external sources (red).



**Figure 3.26.** Number of *A. planci* larvae that are imported (red) and exported (blue) from each island. Values are in thousands.

Santa Rosa Reef and secondarily at Aguijan. In the case of Santa Rosa Reef, larvae came entirely from Chuuk in the FSM. Larvae settling at Aguijan were largely from Saipan and Tinian in 2008 and 2012.

Outbreaks of COTS are one of the main controlling factors on live coral in the study area (Goreau et al. 1972). Previous attempts to use transport simulations to explain COTS distribution and outbreaks have proven effective in other regions (Dight et al. 1990, Black and Moran 1991). Results here correspond well to recent genetic evidence. For example, Yasuda et al. (2009) document population mixing via the NECC from FSM to the Marshall Islands, and a stronger relationship of Palau populations to those in the Philippines than those in the FSM. Timmers et al. (2012) document the mixing of populations within the Marianas and the general separation of populations among sampled archipelagos in the region, such as between the Marianas and Yap. These studies were based on genetic samples from different sets of locations, and many fewer islands than were possible in our simulation study. Despite this, there is clear agreement among the results of these very different approaches.

Transport simulations here also suggest that variations in current patterns alone can result in a dramatic increase in local recruitment events of COTS over typical years. Outbreaks that are partly caused by these variations in ocean currents are not synchronized among years even for nearby islands, and the dominant sources of incoming larvae

can vary among outbreaks. Unfortunately, this makes for a challenging mix of variables in predicting COTS outbreaks and planning any preventive or control measures.

An important caveat in the results of COTS simulations is that a uniform mortality rate was used in all model years. In reality, mortality rates are variable by region, season, and even among larval stages, which could have a major influence on recruitment strength. Temperature, as well as variety and concentration of phytoplankton diet during development, will affect mortality rates differently among COTS larval stages (Lucas 1973, 1982, Olson 1987). There is some evidence that mass emergence of adults and spawning may be timed to coincide with conditions especially conducive to larval survival (Houk and Raubin 2010). When these ideal survival and transport environments coincide, especially large settlement events and subsequent outbreaks may occur.



*A Guam reefscape.*

*Photo credit: Used with permission from David Burdick, guamreeflife.com*

## CONCLUSIONS

Connectivity patterns vary widely among taxa. There is no single best advice to provide managers interested in conserving larval sources to promote sustainability and resiliency of reef communities. For the relatively short lived larvae of humphead wrasse, rabbitfish, COTS and corals with short PLD, each archipelago was relatively isolated from its neighbors. Larvae sustaining those populations on many islands may primarily come from self-seeding or their immediate island neighbors within the same archipelago. Local activities may be most rewarding for managing such stocks because the benefits will be locally realized.

For the relatively long-lived larvae of unicornfish, goatfish, and corals with a long PLD, there was widespread exchange of larvae among more distant islands and archipelagos. This offers a greater safety net for recovery following localized disturbance since larvae may arrive from widespread locations, many of which will probably not have been impacted by sub-regional stressors. However, the management challenges are greater since they will involve more coordinated decision-making and cooperation among island nations. Those conservation actions implemented locally may have a large proportion of their benefits realized elsewhere for species with long PLDs.

Although individual taxa differed widely in their patterns of connectivity, a few key patterns emerged. Geographic breakpoints in connectivity were detected for several taxa between the southern and northern Marianas along the northern edge of the NEC. This occurred variously between Guam, Rota and Saipan across the model years. There was also a consistent northward bias to transport within the Marianas. Activities that preserve spawning stock in the northern portions of the archipelago may have less benefit to the Marianas than those undertaken in the southern portions of the archipelago. A similar northward bias was seen for several taxa in the Marshall Islands. Lastly, there was some connectivity, even at short PLDs in some years, to the Southern Marianas from islands in Chuuk and from the southern Marianas to Yap. This circular connection from Yap to Chuuk, Chuuk to the Marianas, and the Marianas back to Yap could be a focus of international coordination efforts between these jurisdictions. This connectivity loop takes multiple generations to complete a cycle, and therefore the benefits of coordinated protection would not be realized for several years. Such a regional initiative may, however, be critical for maintaining the overall stability and productivity of the coral reef ecosystems among these archipelagos.



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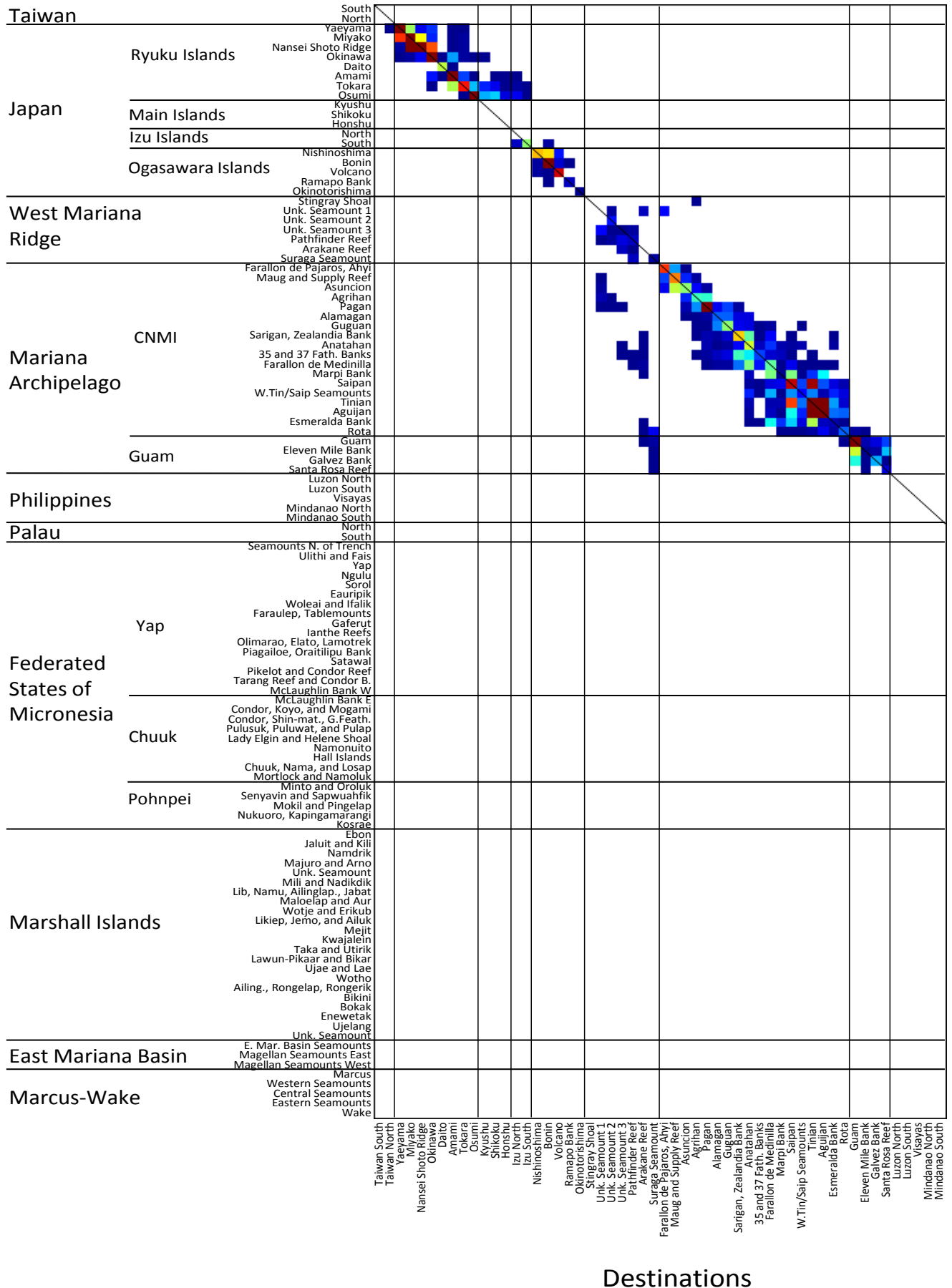
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## Appendix A. Connectivity Matrices

Larval Sources

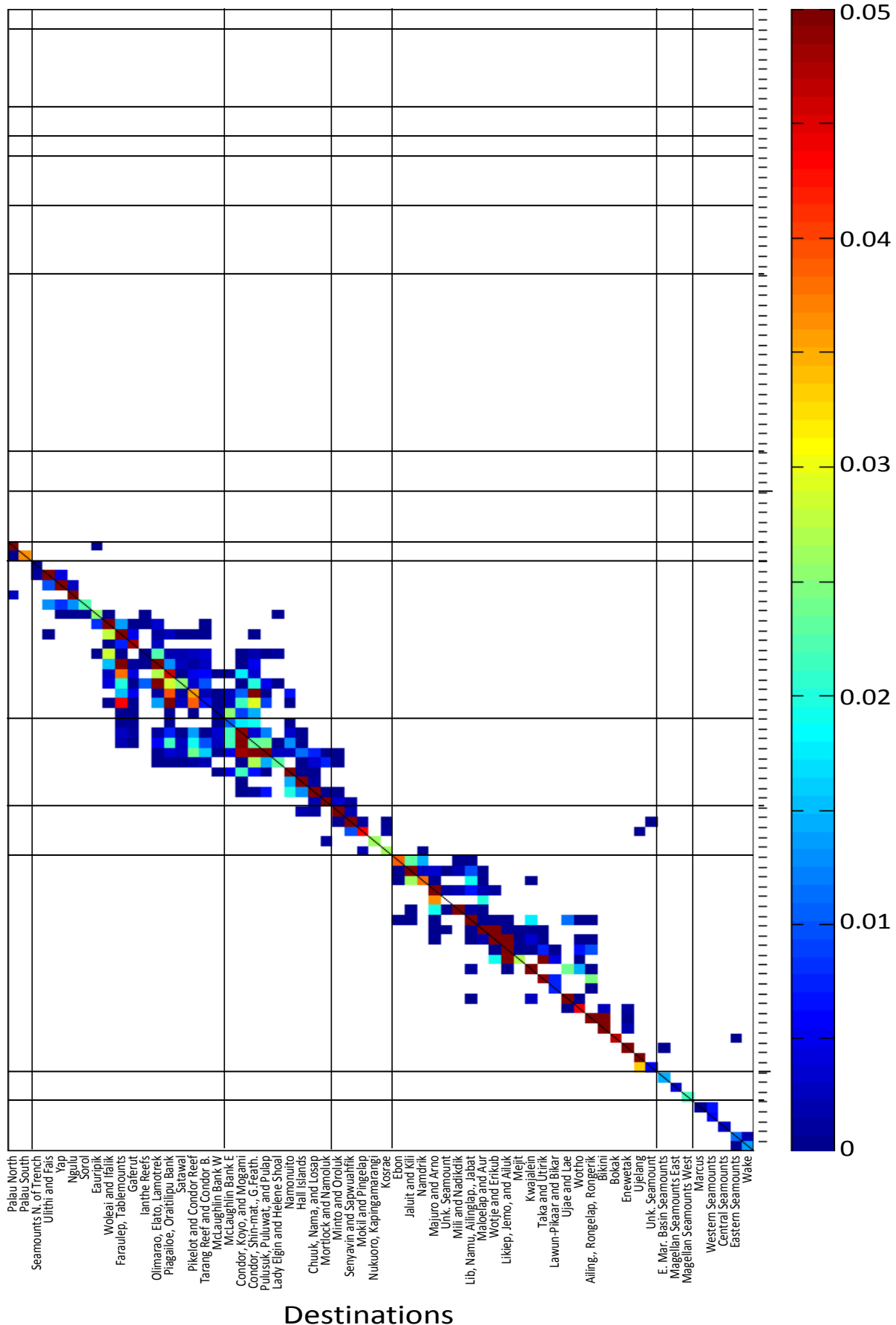


Destinations

Figure A1. Connectivity matrix for virtual larvae with a **6-10 day** PLD and **small** settlement zone. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for all seasons and years (2004-2012).



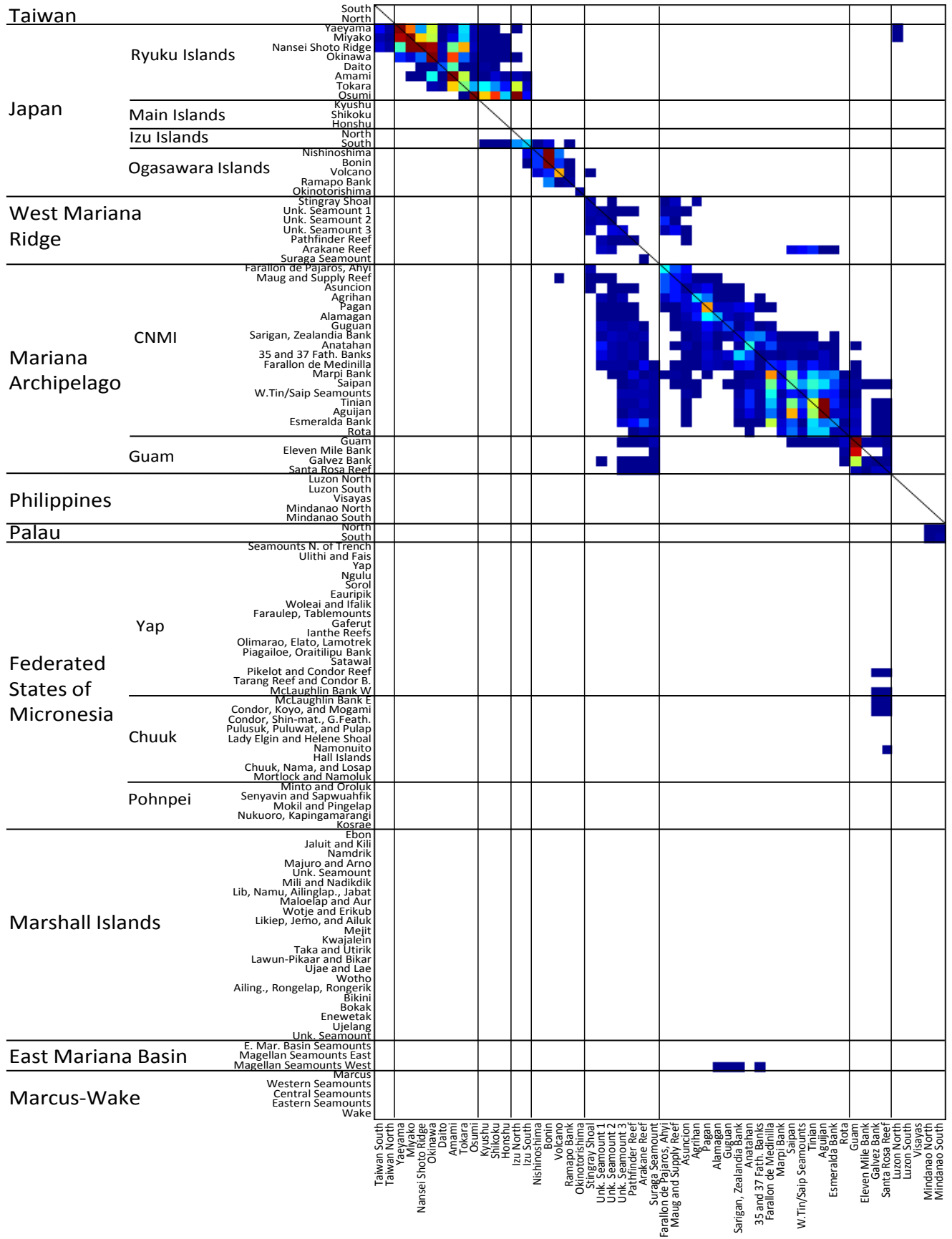
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Fraction of larvae from source settled at destination

Figure A1 cont.

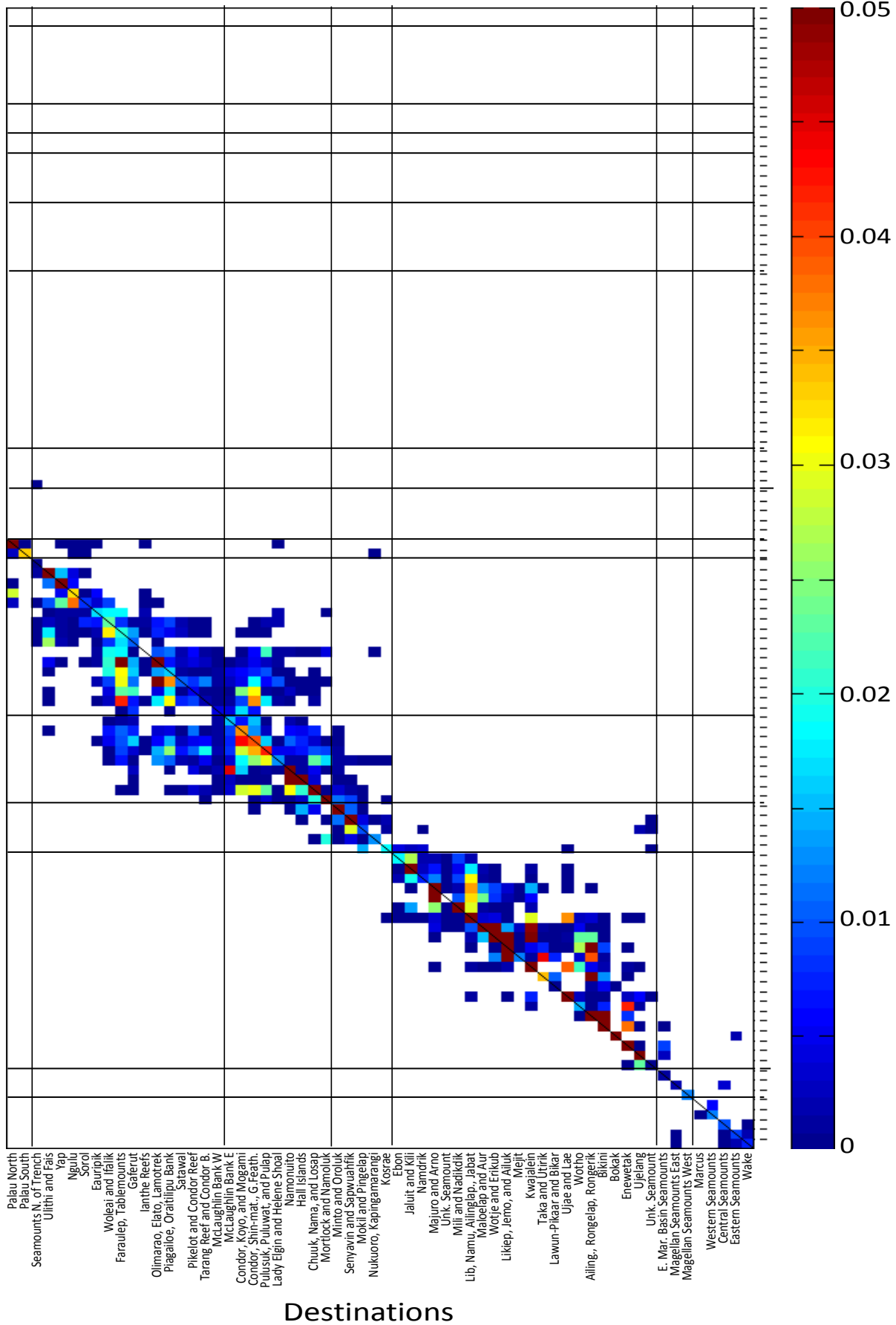
Larval Sources



Destinations

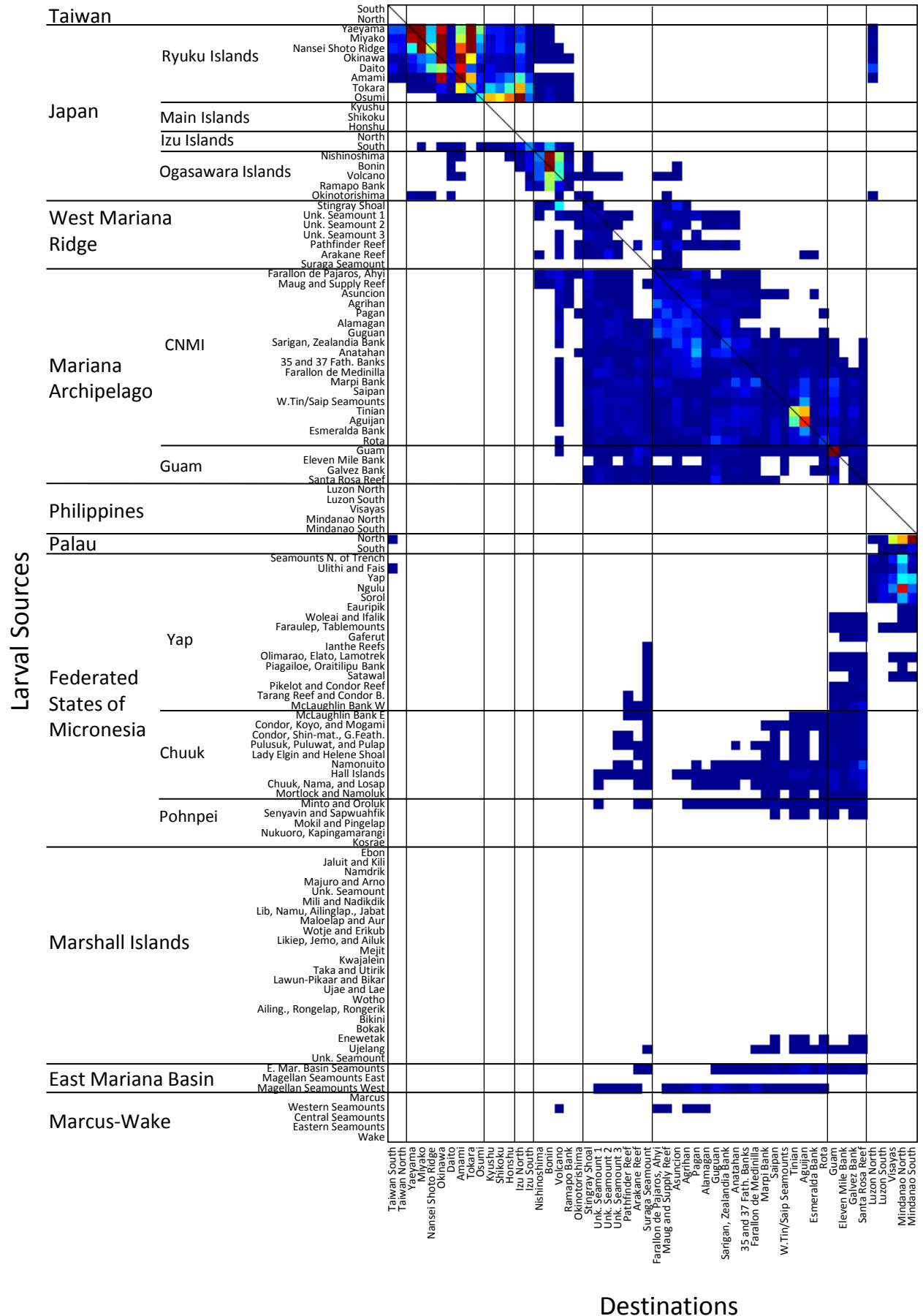
Figure A2. Connectivity matrix for virtual larvae with a **12-20 day** PLD and **small** settlement zone. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for all seasons and years (2004-2012).

(larval sources continued from facing page)



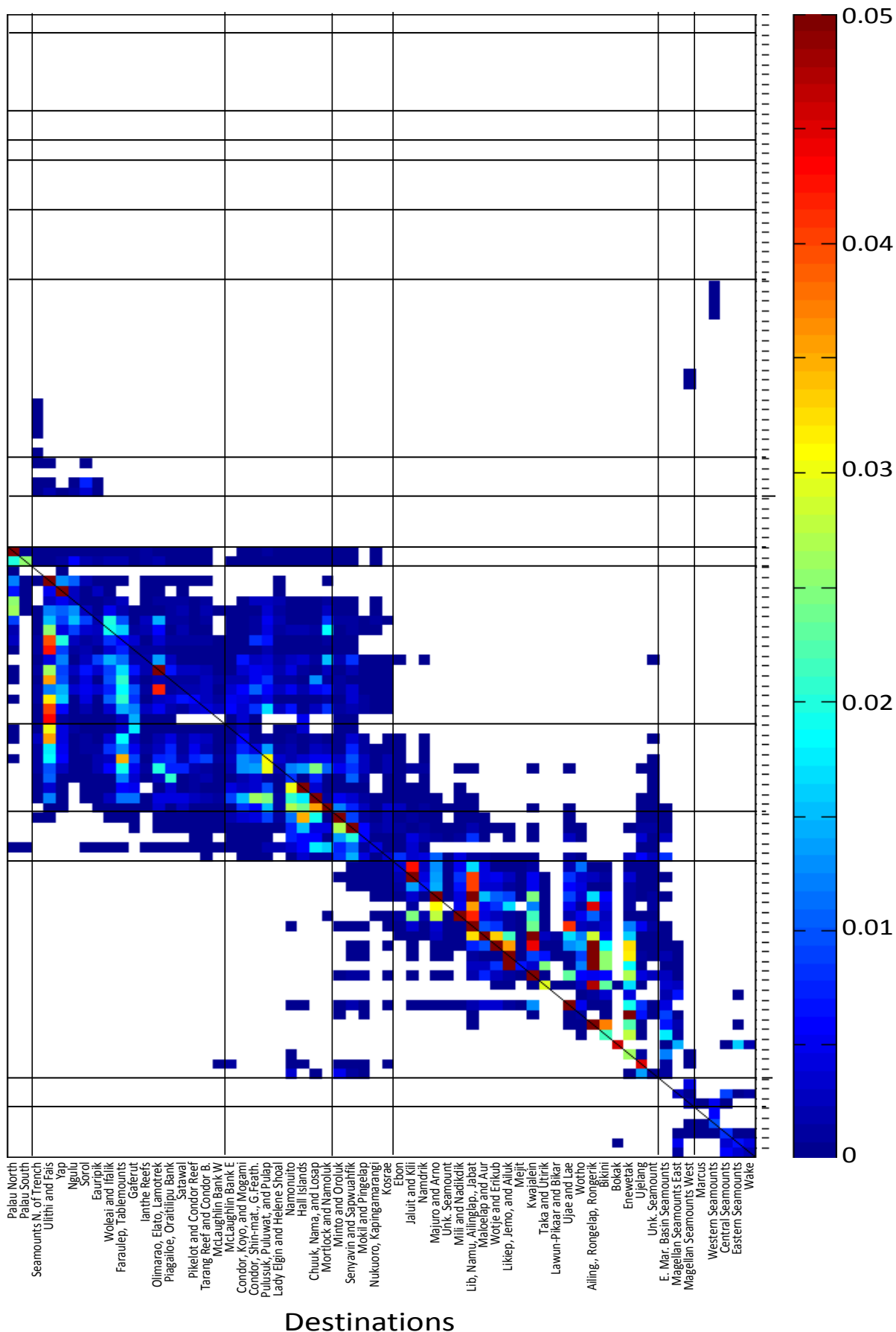
Fraction of larvae from source settled at destination

Figure A2 cont.



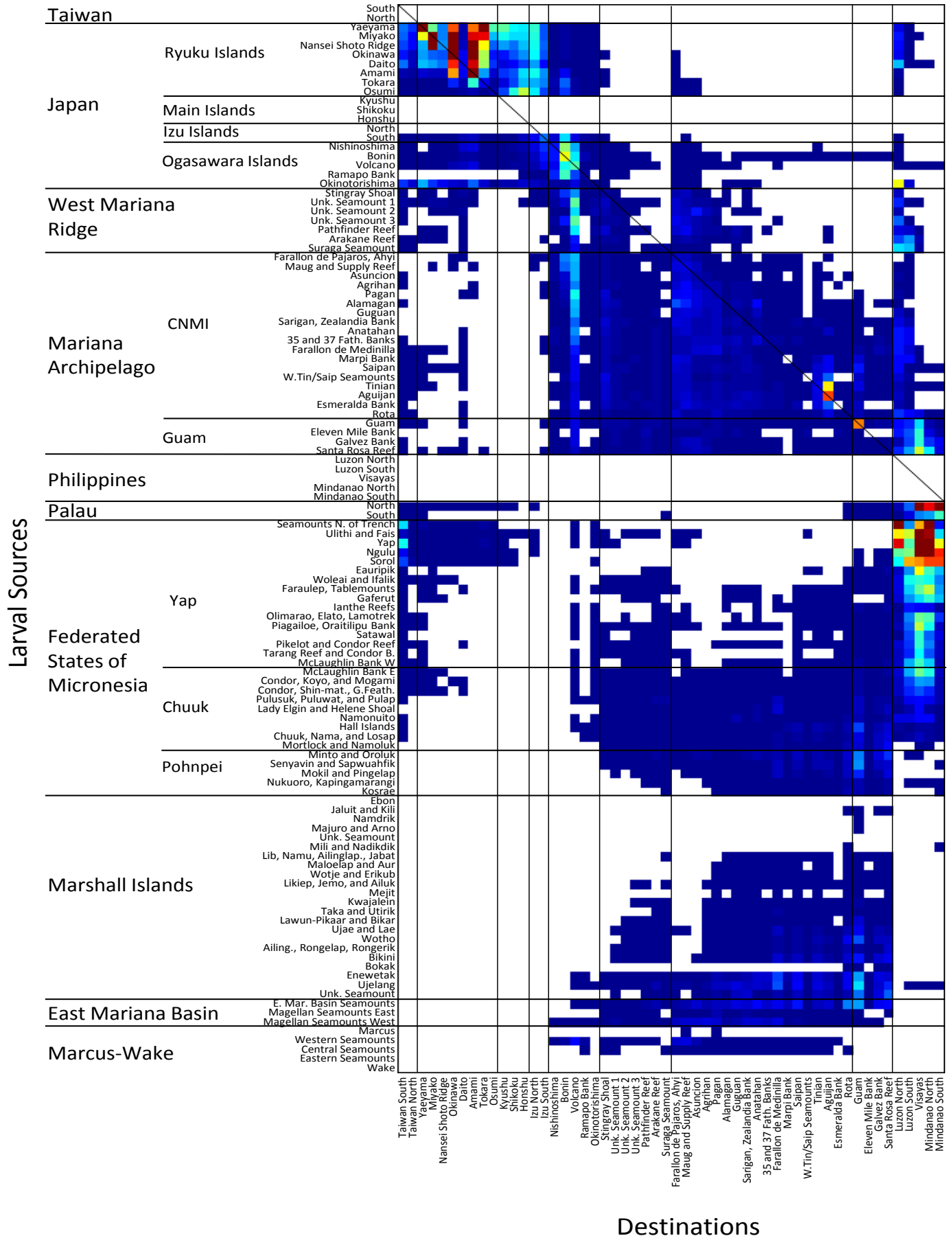
**Figure A3.** Connectivity matrix for virtual larvae with a **30-50 day** PLD and **small** settlement zone. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for all seasons and years (2004-2012).

(larval sources continued from facing page)



Fraction of larvae from source settled at destination

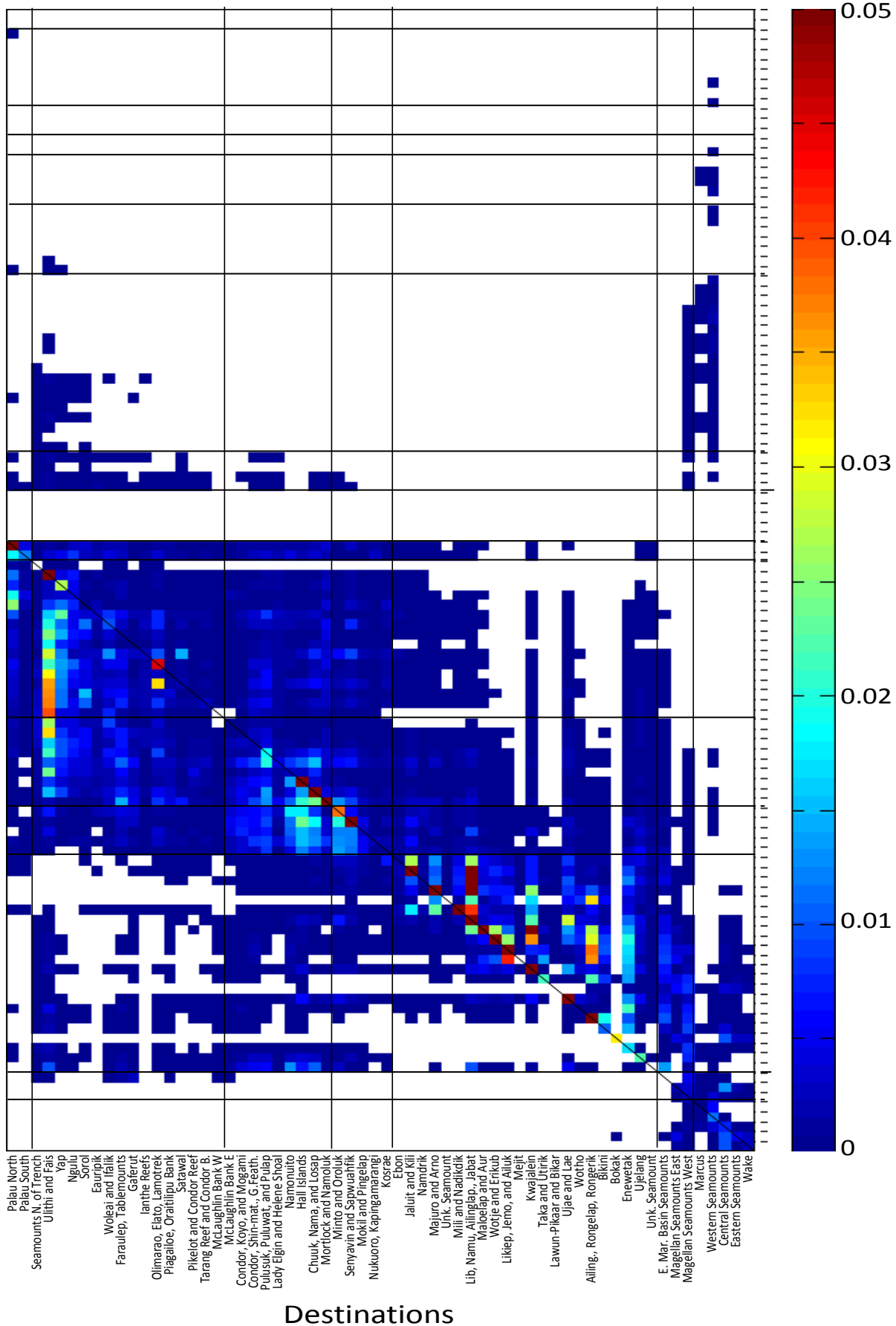
Figure A3 cont.



Destinations

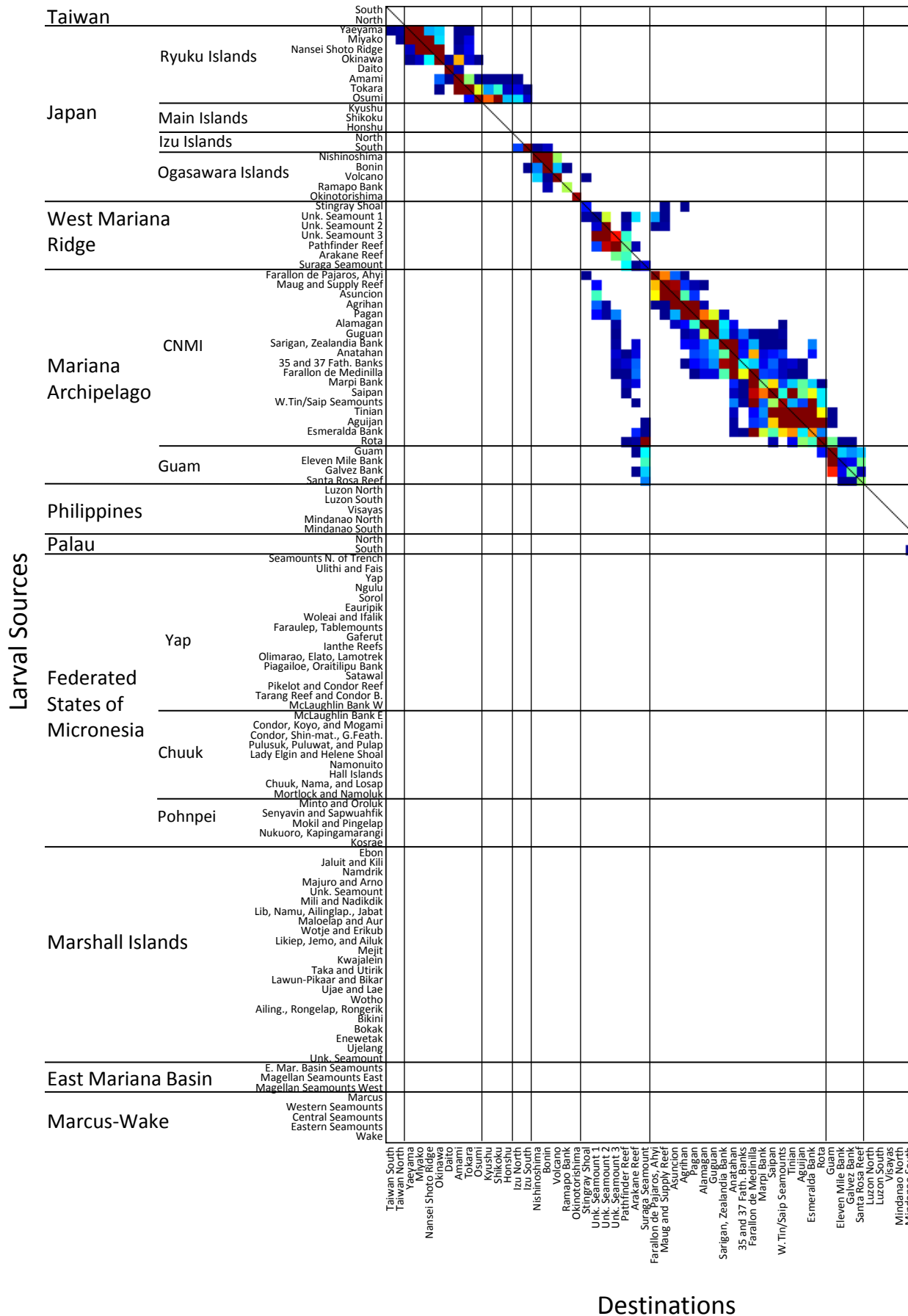
Figure A4. Connectivity matrix for virtual larvae with a **60-100 day** PLD and **small** settlement zone. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for all seasons and years (2004-2012).

(larval sources continued from facing page)



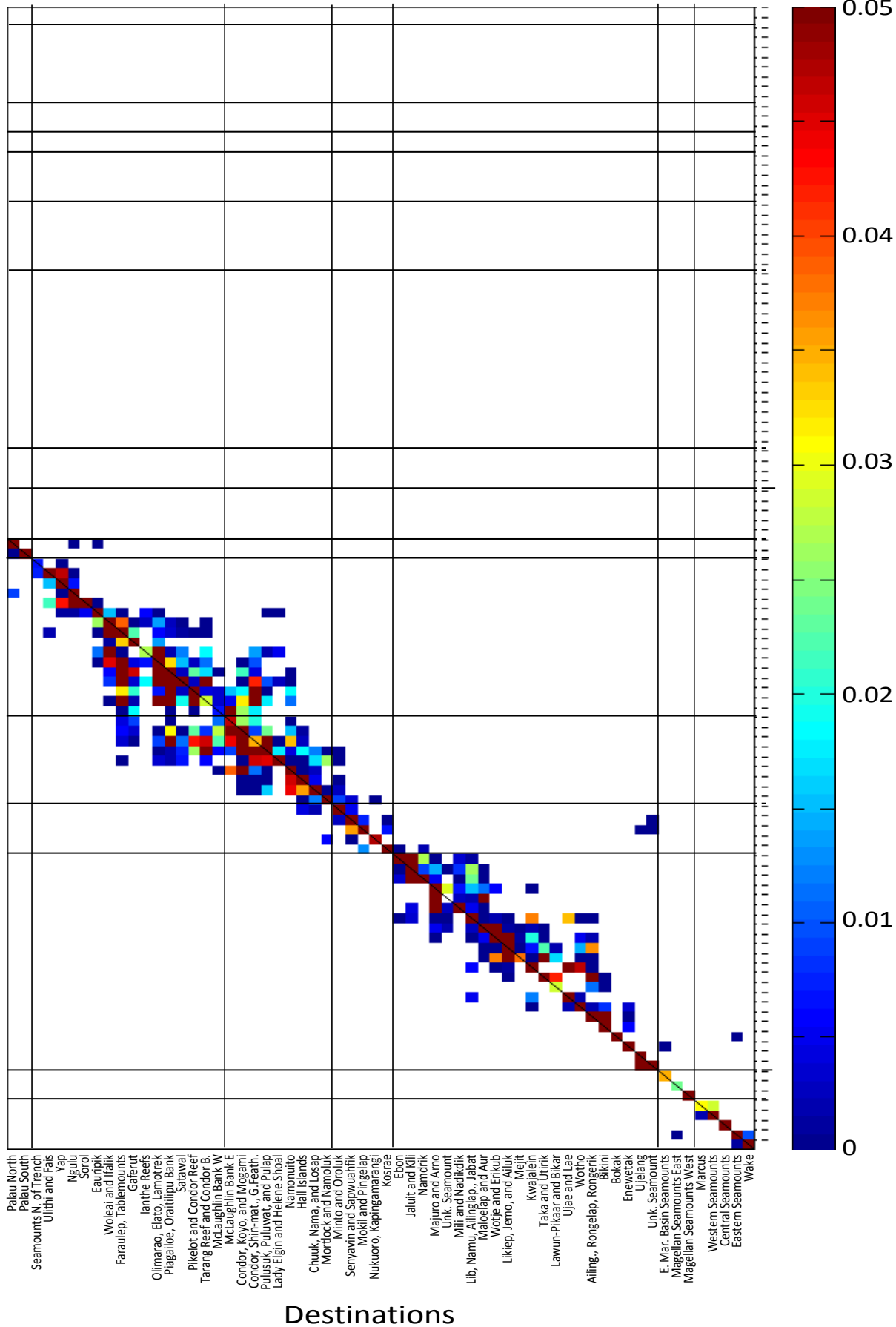
Fraction of larvae from source settled at destination

Figure A4 cont.



**Figure A5.** Connectivity matrix for virtual larvae with a **6-10 day** PLD and **large** settlement zone. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for all seasons and years (2004-2012).

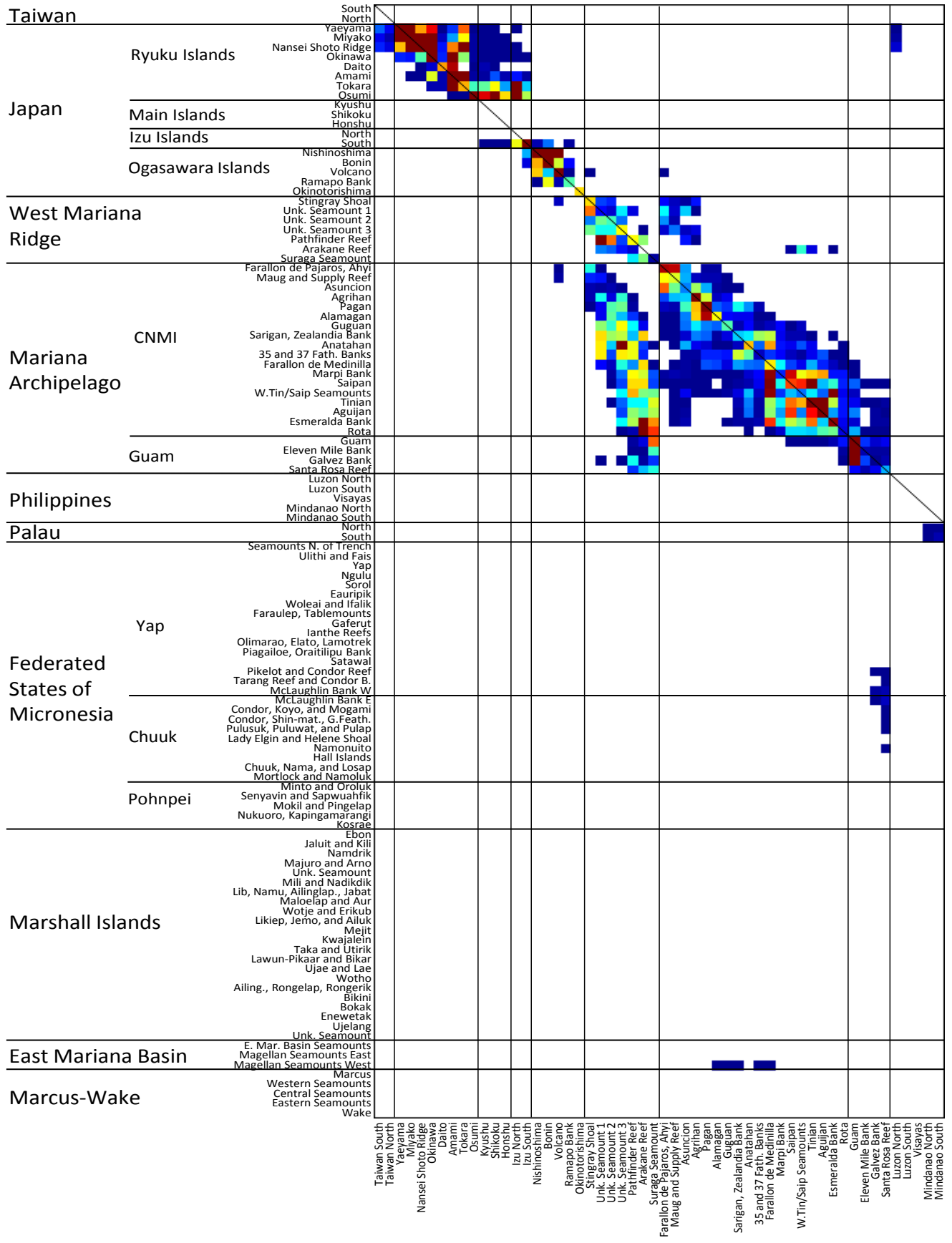




Fraction of larvae from source settled at destination

Figure A5 cont.

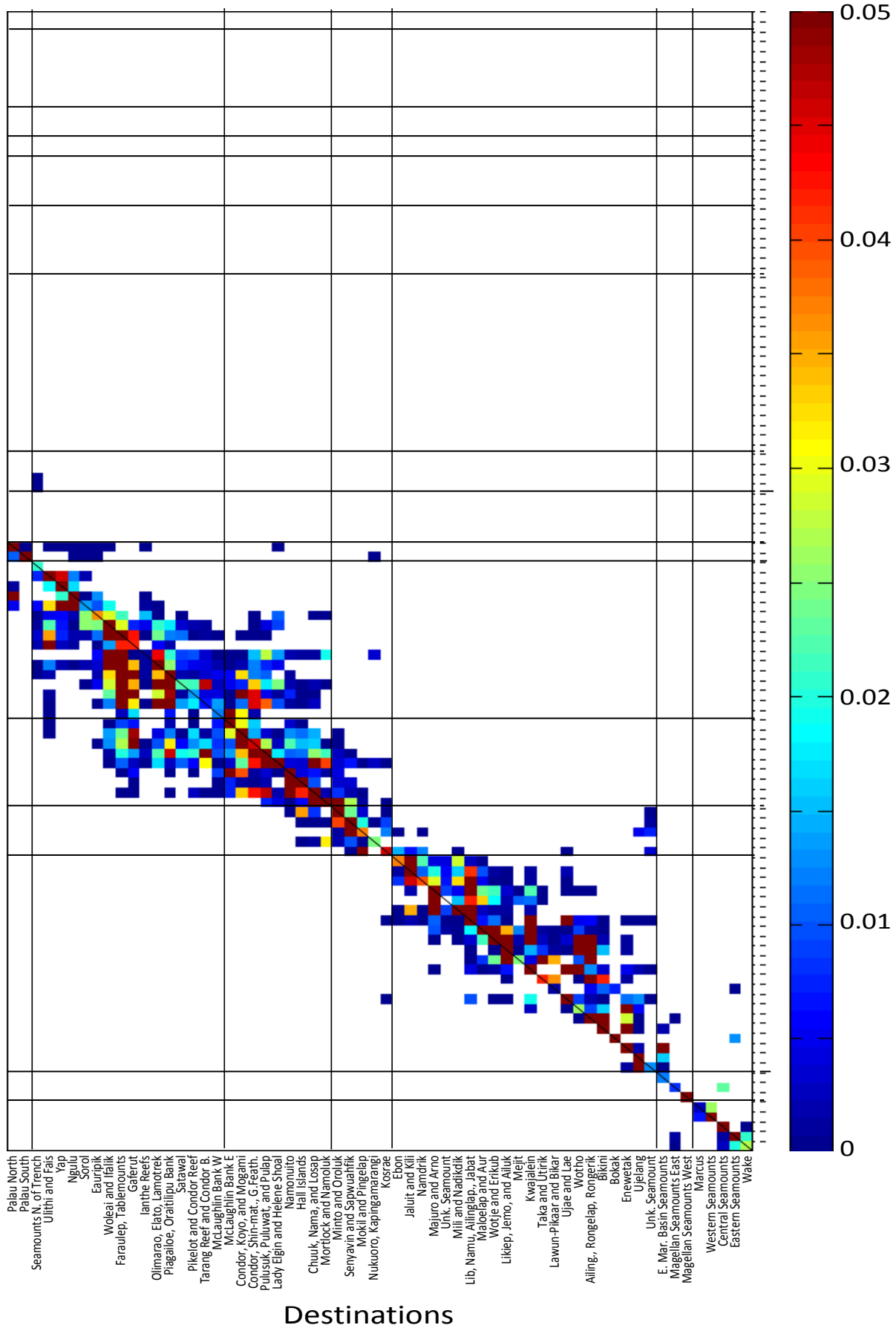
Larval Sources



Destinations

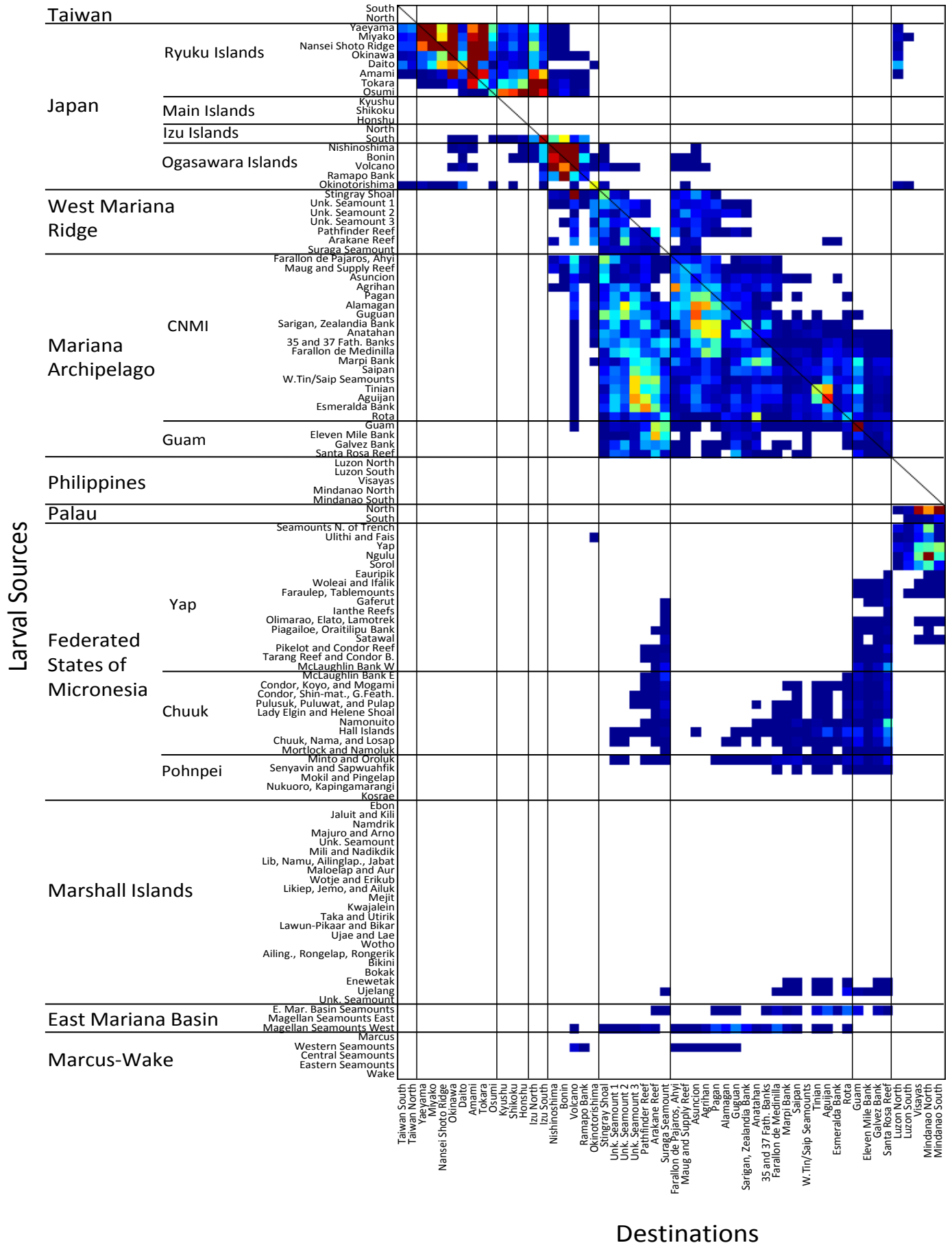
**Figure A6.** Connectivity matrix for virtual larvae with a **12-20 day** PLD and **large** settlement zone. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for all seasons and years (2004-2012).

(larval sources continued from facing page)



Fraction of larvae from source settled at destination

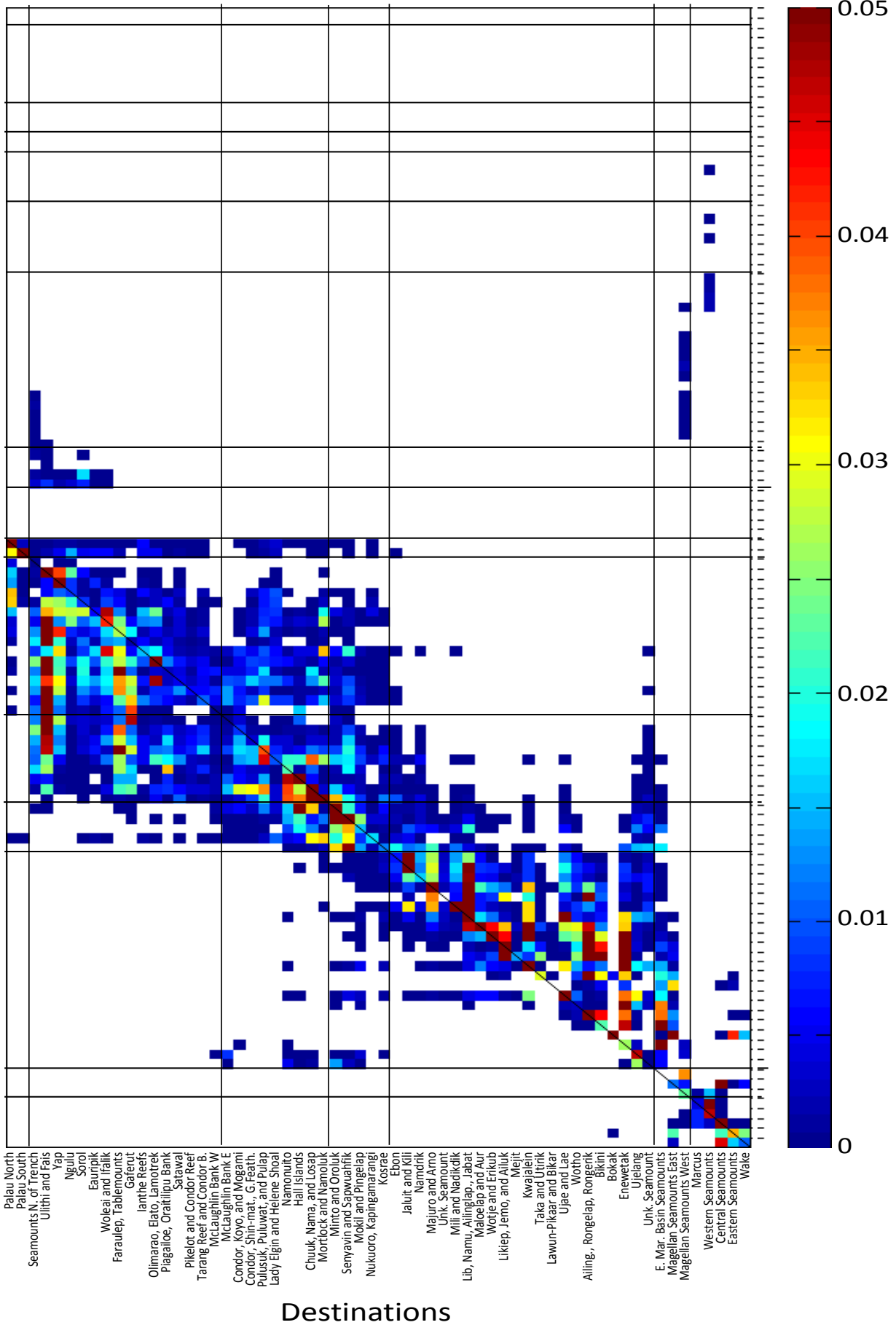
Figure A6 cont.



Destinations

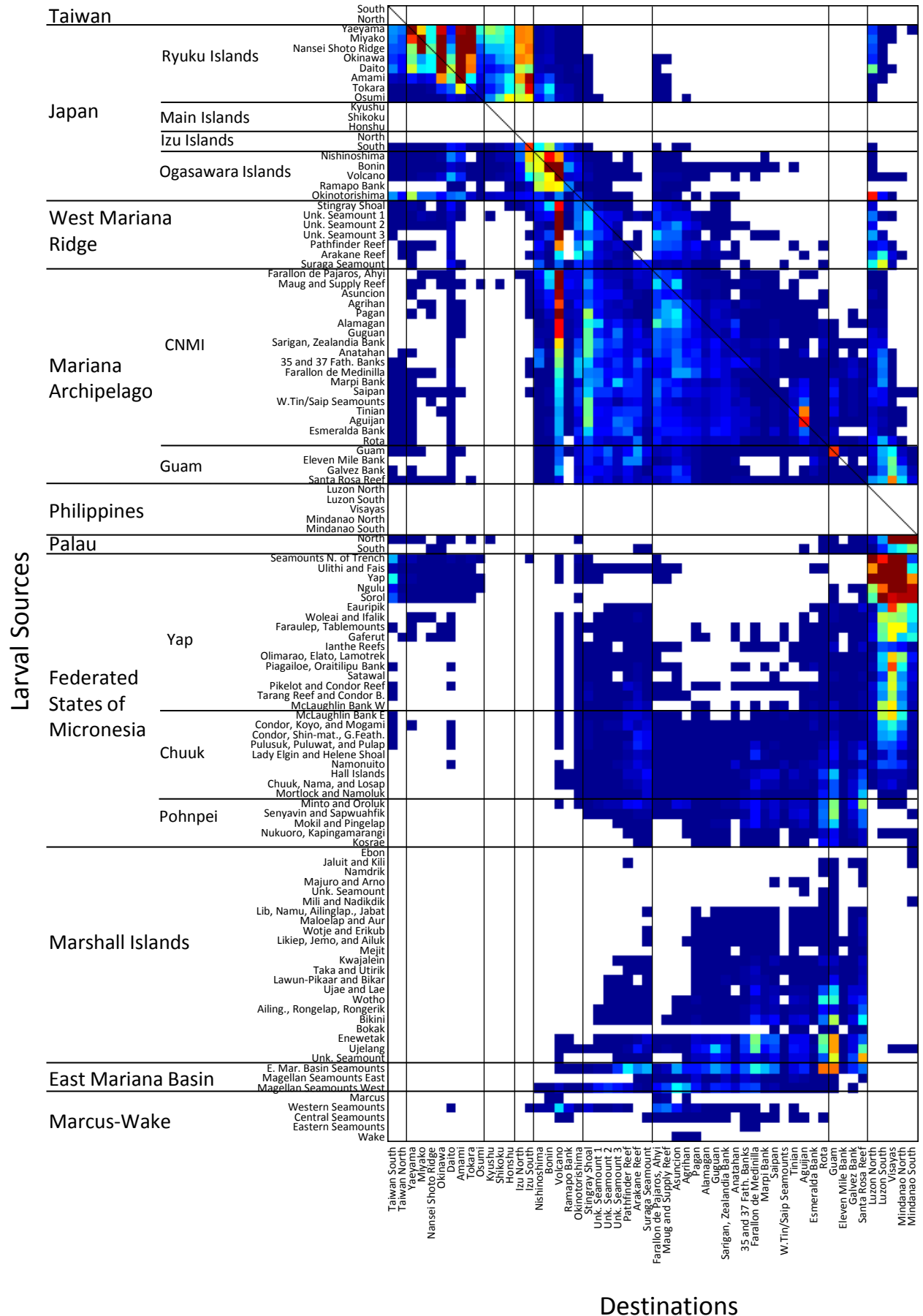
Figure A7. Connectivity matrix for virtual larvae with a **30-50 day** PLD and **large** settlement zone. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for all seasons and years (2004-2012).

(larval sources continued from facing page)



Fraction of larvae from source settled at destination

Figure A7 cont.



**Figure A8.** Connectivity matrix for virtual larvae with a **60-100 day** PLD and **large** settlement zone. Color scale indicates the fraction of simulated larvae released at source settling at destination. Values are cumulative for all seasons and years (2004-2012).

(larval sources continued from facing page)

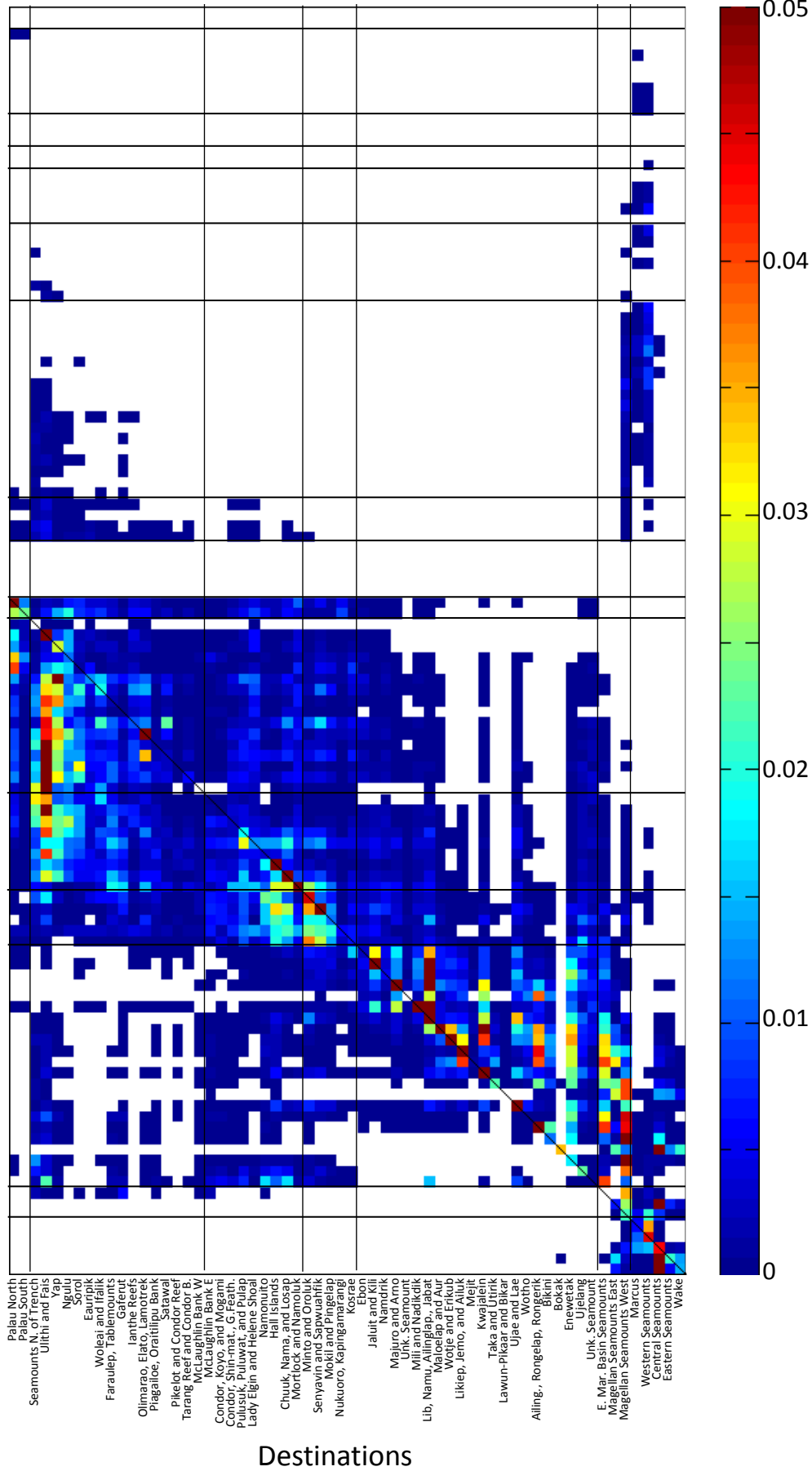


Figure A8 cont.









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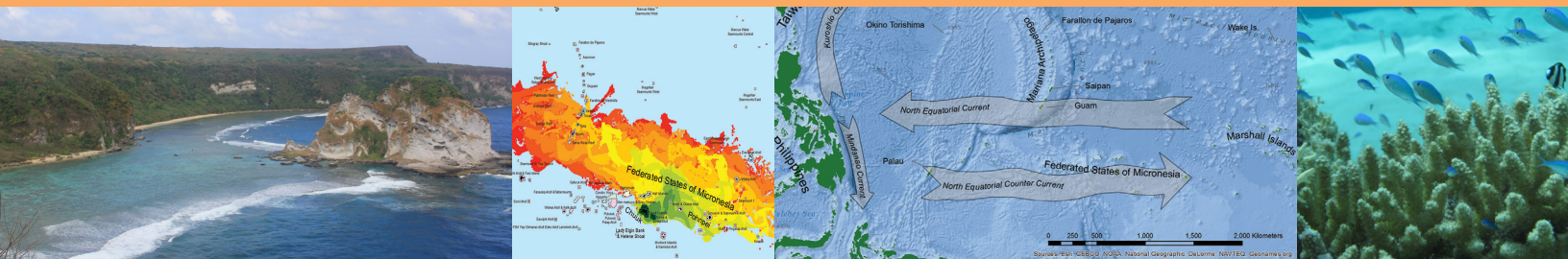
**Penny Pritzker**, *Secretary*

National Oceanic and Atmospheric Administration

**Kathryn Sullivan**, *Under Secretary for Oceans and Atmosphere*

National Ocean Service

**Russell Callendar**, *Acting Assistant Administrator for National Ocean Service*



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