

Connectivity and Integrated Ecosystem Studies

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INTRODUCTION

Population connectivity is the exchange of individuals among geographically separated subpopulations. Defining the scale of connectivity among marine populations and determining the factors driving this exchange are critical to our understanding of the population dynamics, genetic structure and biogeography of reef fishes (Cowen et al., 2006). Although larvae have the potential for long-distance dispersal, evidence is mounting that larval dispersal may be limited and marine subpopulations may be more isolated over smaller spatial scales than previously thought (Cowen et al., 2007). The rates, scale and spatial structure of successful exchange, or connectivity, among local populations of marine organisms drive population replenishment and, therefore, have profound implications for population dynamics and genetics of marine organisms, spatially oriented resource management (e.g., marine protected areas) and the spread of invasive species. Despite the importance of this issue in understanding population dynamics and effectively managing these species or areas (e.g., Crowder et al., 2000; Valles et al., 2001), larval connectivity in the Northwestern Hawaiian Islands (NWHI) is relatively unknown. The uniquely endemic fish and other marine faunas of the Hawaiian Archipelago (Hourigan and Reese, 1987) and the extreme expression of endemism in the NWHI (DeMartini and Friedlander, 2004) make such information critically important for the Hawaiian Archipelago and specifically the Papahānaumokuākea Marine National Monument (PMNM).

LARGE-SCALE POPULATION CONNECTIVITY MODELS FROM OCEAN CURRENTS

For many marine species, population connectivity is determined largely by ocean currents transporting larvae and juveniles between distant patches of suitable habitat. To evaluate the patterns in connectivity throughout the Hawaiian Archipelago, a spatially explicit biophysical model was used to simulate coral dispersal between reefs spanning the archipelago for three different years (a strong El Niño year- 1997, a strong La Niña year- 1999, and a neutral year- 2001; Trembl et al., 2008). Simulated connectivity was summarized seasonally and across years.

This two-dimensional Eulerian advection–diffusion model of coral dispersal incorporates realistic surface current velocity data and estimates of planktonic larval duration (PLD). In this model, the probability of potential dispersal to a reef is the product of: 1) the hydrodynamic arrival probability, 2) larval mortality and 3) the settlement probability. The spatially explicit hydrodynamic model and resultant arrival probabilities incorporate reef topology, ocean current variability and spawning location.

Summary of Patterns Across Hawaii with Reference to Spatial Data

Results indicate that the scale of dispersal is on the order of 50-150 km, which is consistent with recent studies in the Caribbean (Cowen et al., 2006). On average, the Main Hawaiian Islands (MHI) appear to be consistently connected and well mixed at levels above 1/10,000 per season for hypothetical larvae with a PLD of 60 days (Figure 9.1). The northwestern most atolls (Kure, Midway, and Pearl and Hermes) are also constantly and strongly connected throughout the dispersal scenarios. The entire Hawaiian archipelago appears completely

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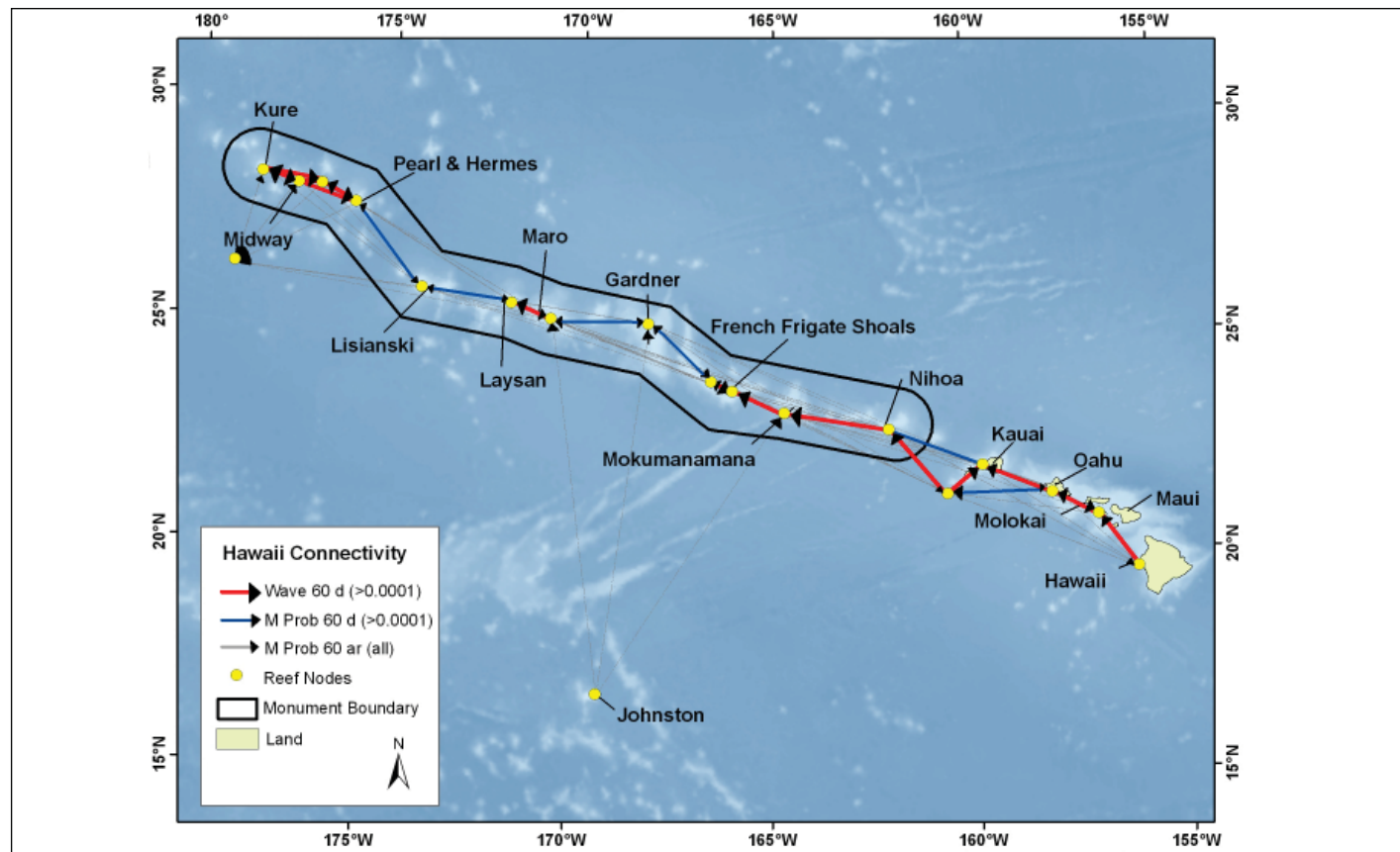


Figure 9.1. Dispersal pathways in the Hawaiian Archipelago based on Eulerian advection-diffusion models (adapted from Trembl et al., 2008). Coral reef habitat is represented by nodes within the graph framework. When larvae from a source reef reach a downstream reef site, a dispersal connection is made. This dispersal connection and direction is represented by an arrow, or 'edge' within the graph. The thickness of the arrow reflects the strength of connection. Source: Trembl, unpublished data; map: L. Wedding.

connected at similar levels for at least one season out of the years modeled, albeit predominately in a north-westerly direction. For connectivity via rafting and for those organisms that have a longer PLD or higher survival while dispersing, the hydrodynamics around the Hawaiian Islands provide opportunity for dispersal and mixing throughout. In addition, long distance larval dispersal from Johnston Atoll to the mid-Hawaii archipelago appears to be possible during unique seasons: La Niña, July – September and October – December; neutral years, July – September, with the strongest connection in October – December during La Niña years.

Larval Retention Versus Larval Subsidy

Metapopulation connectivity in the Hawaiian Archipelago is poorly understood, and this hinders effective management and assessment of living marine resources in the region. Pelagic transport was investigated using high-resolution ocean current data and computer simulation (Kobayashi, in review). Adjacent strata in the archipelago appeared well connected via simulated pelagic larval transport regardless of larval duration, while connectivity of more distant strata appear mediated by larval duration (Figures 9.2-9.8). Retention (defined as the return of natal propagules) is contrasted with reception or subsidy (the influx of propagules from other sources). These two processes appear to be decoupled based on examination of archipelago-wide simulations. Single-generation and multigeneration effects of connectivity were considered using a simple population dynamics model driven by the dispersal kernel probability estimates. The PMNM appears to be largely self-sustaining based on these results, with differential input to certain inhabited islands farther southward in the archipelago depending on the pelagic larval duration.

Retention rate (as a fraction of propagules released) ranged from a low of 0.39% at Lanai, to a high of 17.24% for the island of Maui (Figure 9.8). When retention and subsidy were pooled to estimate total settlement per unit of habitat, settlement ranged from a low of 6,288 settlers per pixel at Kure Atoll to a high of 149,192 settlers per pixel at Northampton. The high settlement rate at the relatively small Northampton is attributed mostly to subsidy.

The biological significance of the PMNM to the entire Hawaiian Archipelago can be considered from the connectivity probabilities and the metapopulation analysis. The equilibrium metapopulation composition predicted after many generations can be useful in understanding the importance of adjacent or even nonadjacent geographic strata. For organisms with short larval duration (15 days), a relatively narrow transitional region including Nihoa, Middle Bank, Niihau and Kauai is composed of settlers from both the PMNM and MHI regions. Areas farther north and south have negligible crossover. However, at longer PLDs (90 days), nearly all regions throughout the MHI have some component of the settlers derived from the PMNM, whereas most of the PMNM is self-seeding until approximately Mokumanamana is reached.

While the effects of Maro and Gardner can be attributed to their relatively large reproductive output in the simulations, other large areas do not contribute similarly to the equilibrium composition, which is a model consequence of dispersal kernel probabilities operating over many generations. When the effect of habitat size is removed by scaling total retention and reception by habitat pixel counts, this yields evidence of a decoupling of retention and reception processes. This implies that there is very little, if any, physical (geographic or oceanographic) relationship between factors which promote effective natal larval retention and factors which promote influx of outside larval reception. Settlement and recruitment studies which ignore propagule origins may have difficulty in relating observed patterns to oceanographic features for this very reason. Since neither measure is a strong proxy for the other, the futility of understanding transport dynamics given the single aggregated measure is readily apparent. The need for additional genetics studies and other stock identification markers for sourcing of incoming propagules is urgent (e.g., Bernardi et al., 2002; Schultz et al., 2007).

Clearly since the connectivity measures appear high for adjacent habitats, over evolutionary time the genetic connectivity might be more pronounced than inferred here. This could be particularly important at the southern boundary of the PMNM, with a protected spawning source able to effectively seed areas to the south over time via a “stepping stone” effect, not immediately apparent from examining the pair-wise connectivity values. This gradual diffusive process could lead to much more connectivity than that described by a single generation.

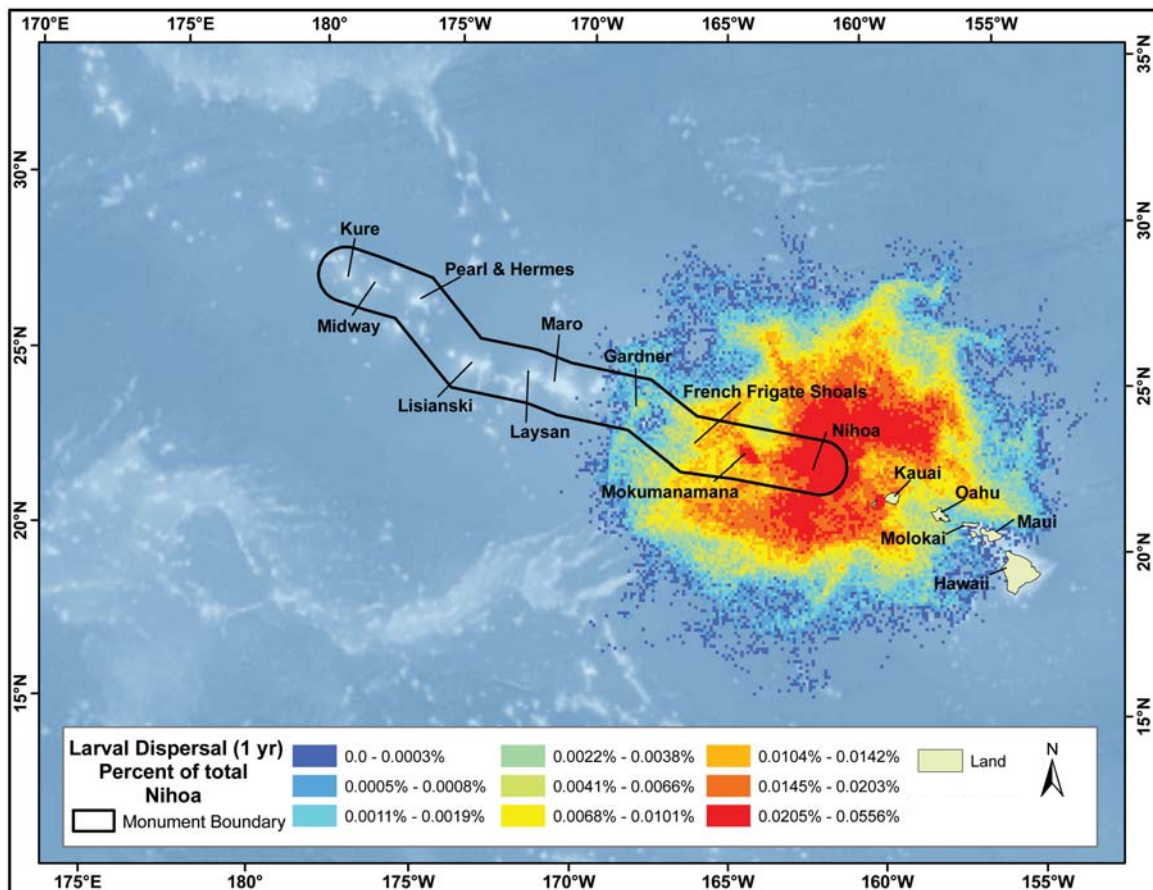


Figure 9.2. Larval dispersal (45 day PDL) one year after being released from Nihoa Island. Source: Kobayashi, in review; map: L. Wedding.

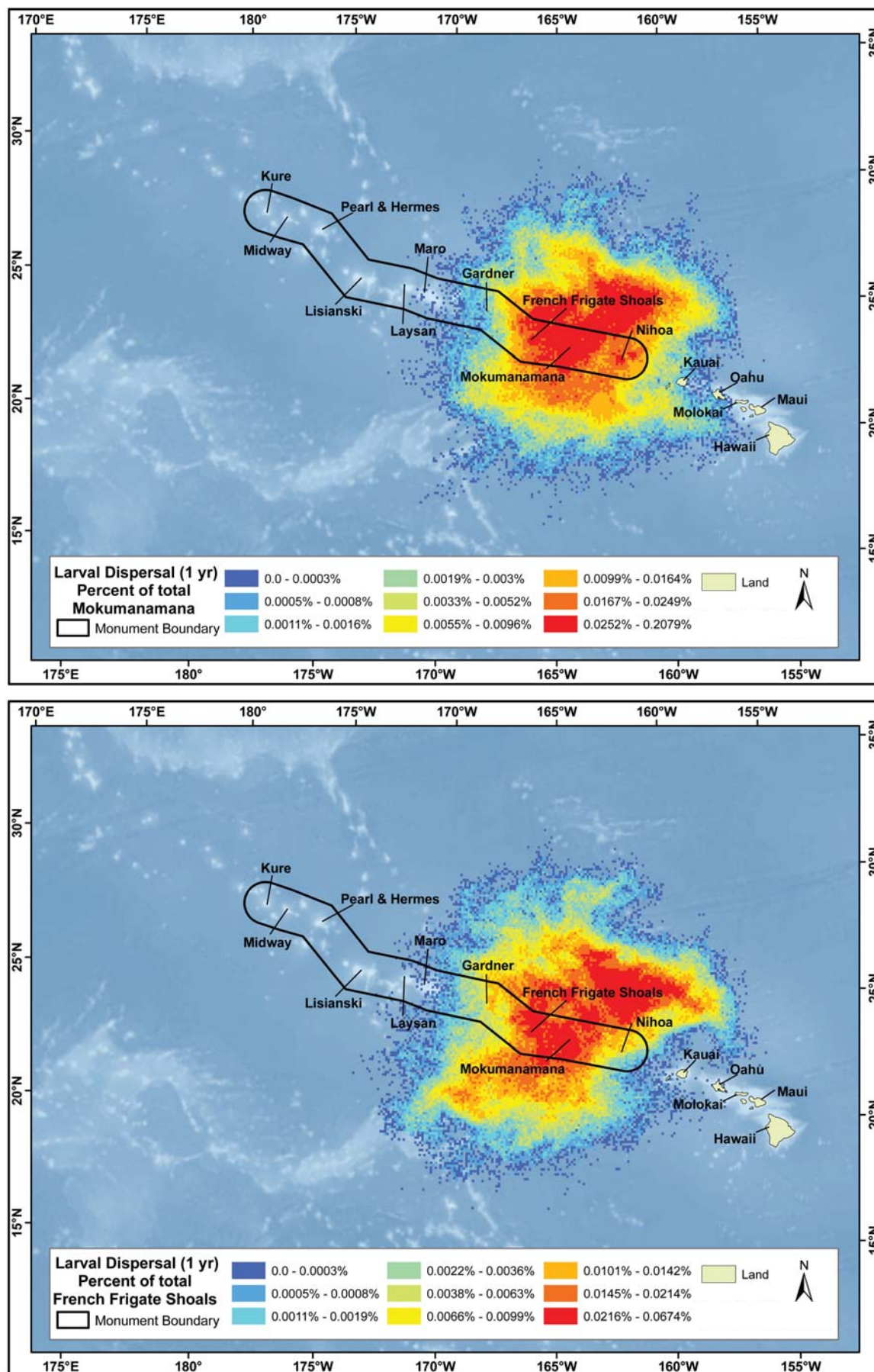


Figure 9.3. Larval dispersal (45 day PDL) one year after release from Mokumanamana (top) and French Frigate Shoals (bottom). Source: Kobayashi, in review; maps: L. Wedding.

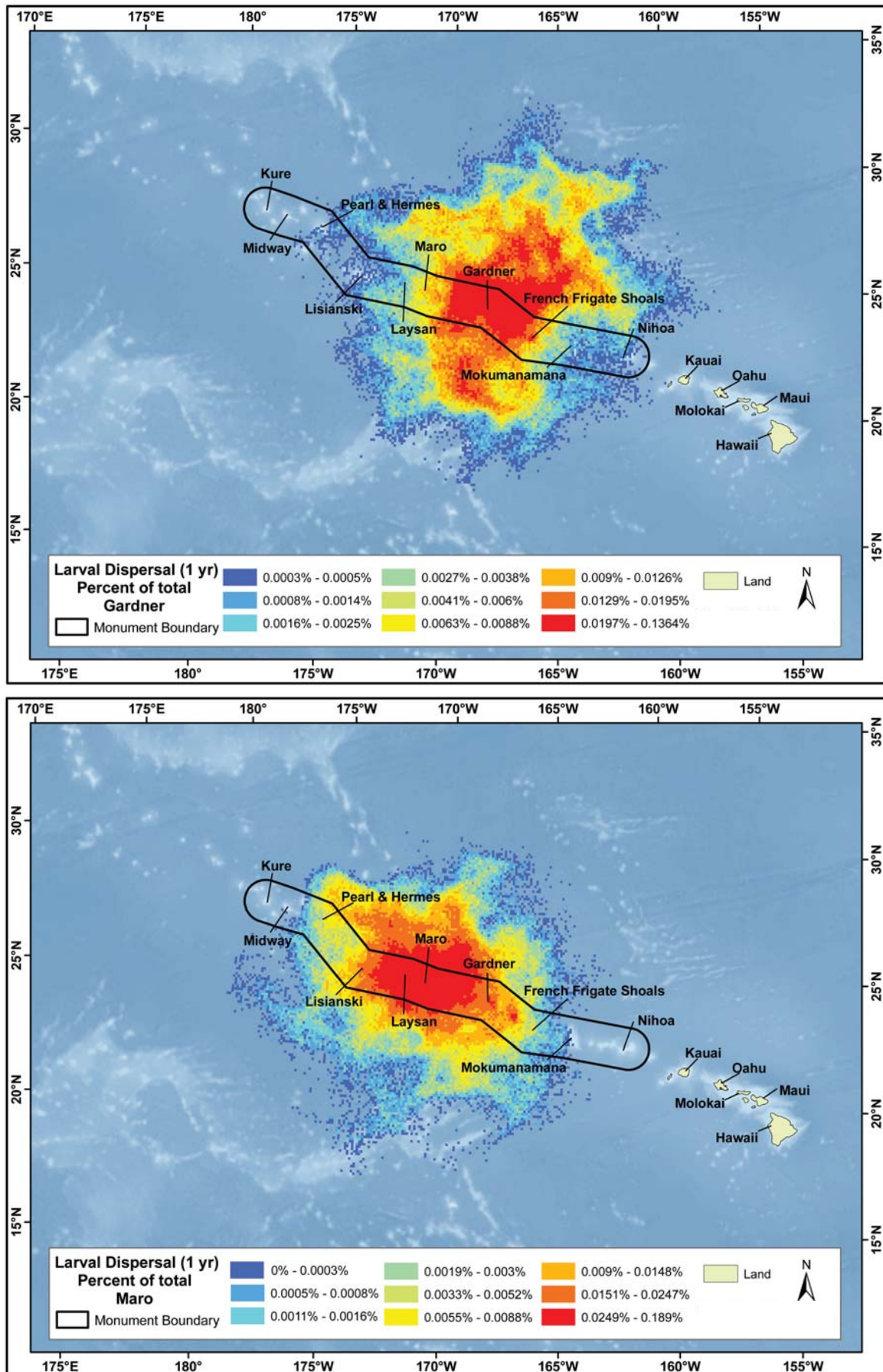


Figure 9.4. Larval dispersal (45 day PDL) one year after release from Gardner Pinnacles (top) and Maro Reef (bottom). Source: Kobayashi, in review; maps: L. Wedding.

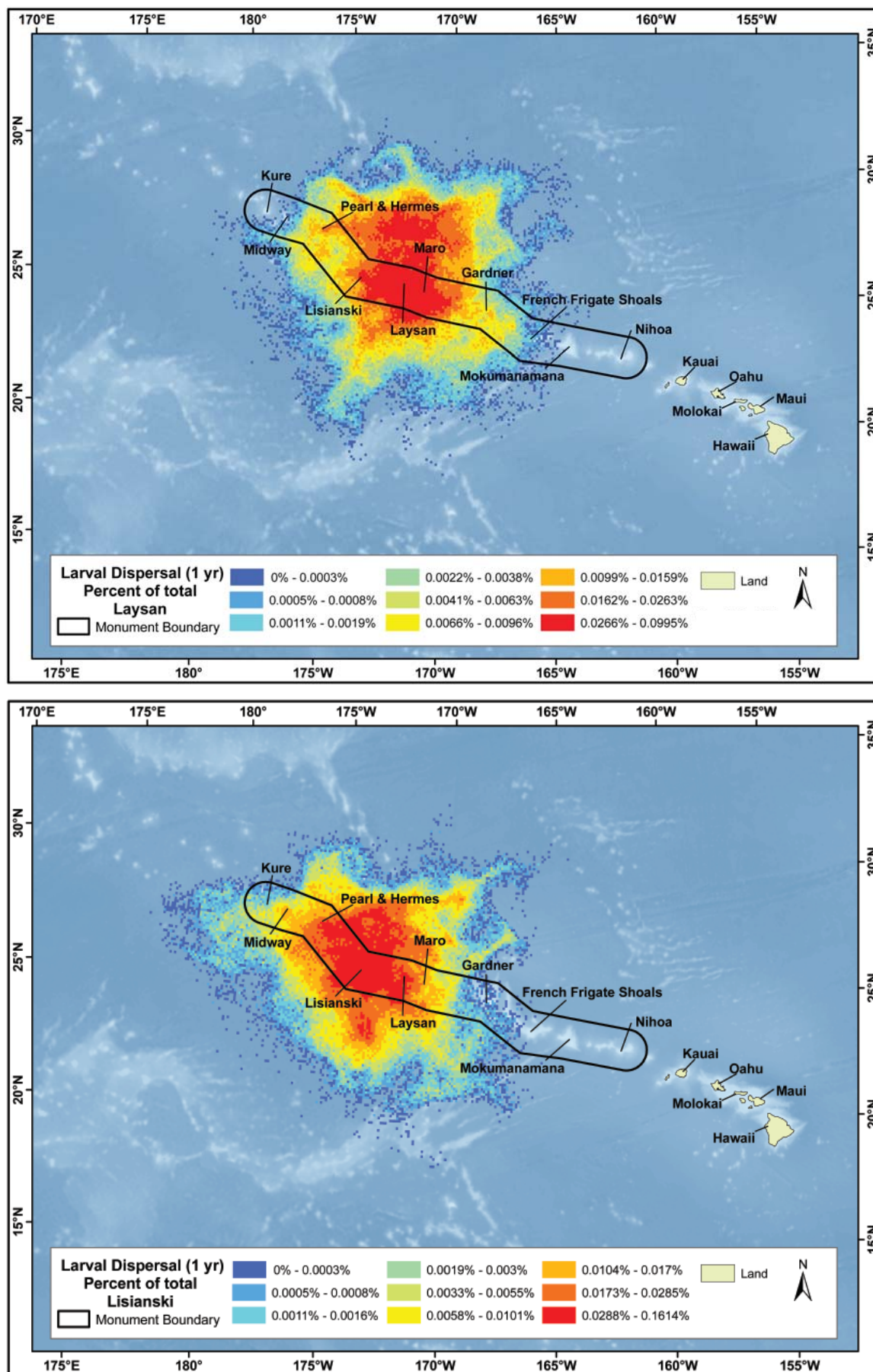


Figure 9.5. Larval dispersal (45 day PDL) one year after release from Laysan Island (top) and Lisianski Island (bottom). Source: Kobayashi, in review; maps: L. Wedding.

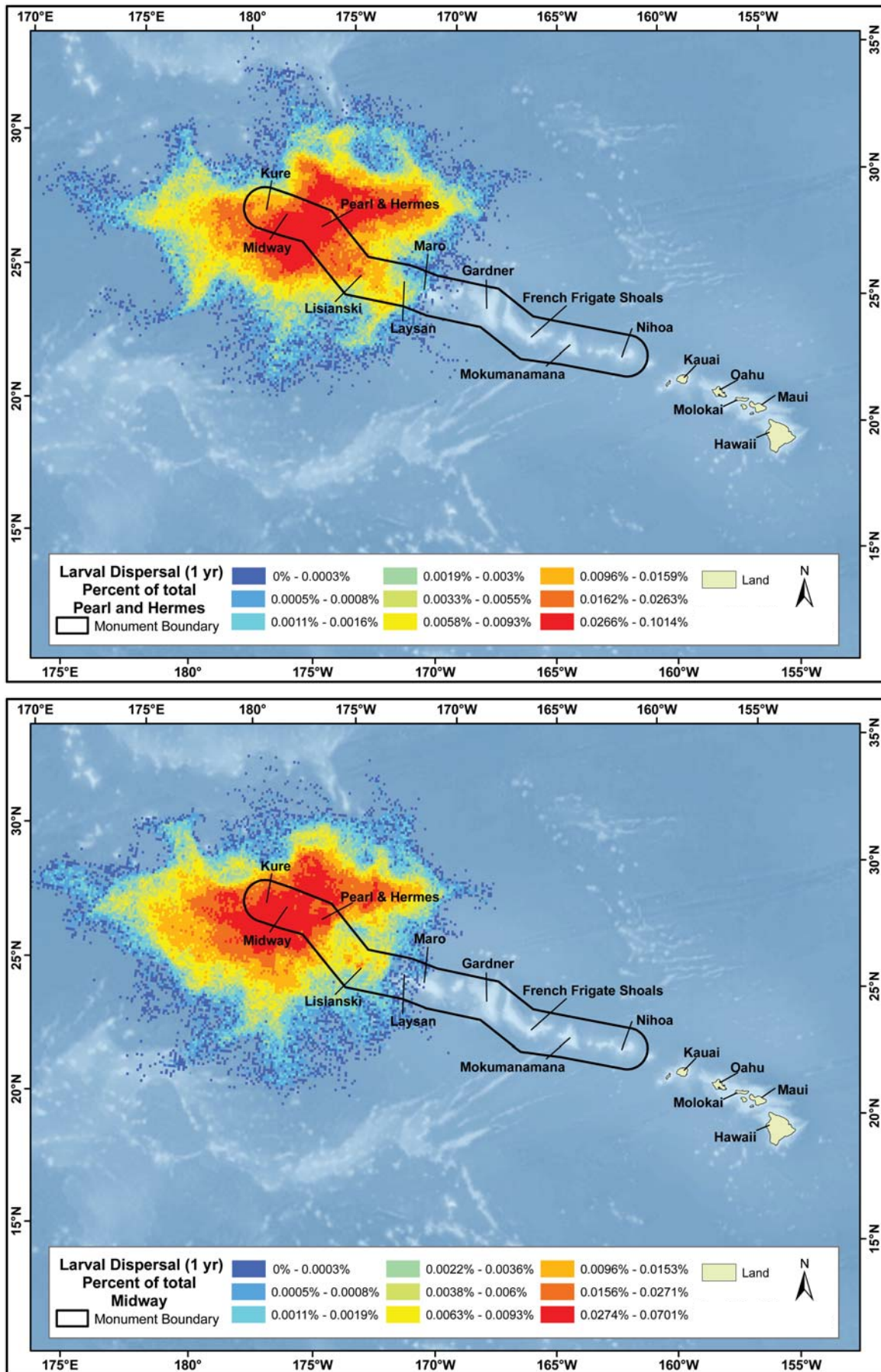


Figure 9.6. Larval dispersal (45 day PDL) one year after release from Pearl and Hermes Atoll (top) and Midway Atoll (bottom). Source: Kobayashi, in review; maps: L. Wedding.

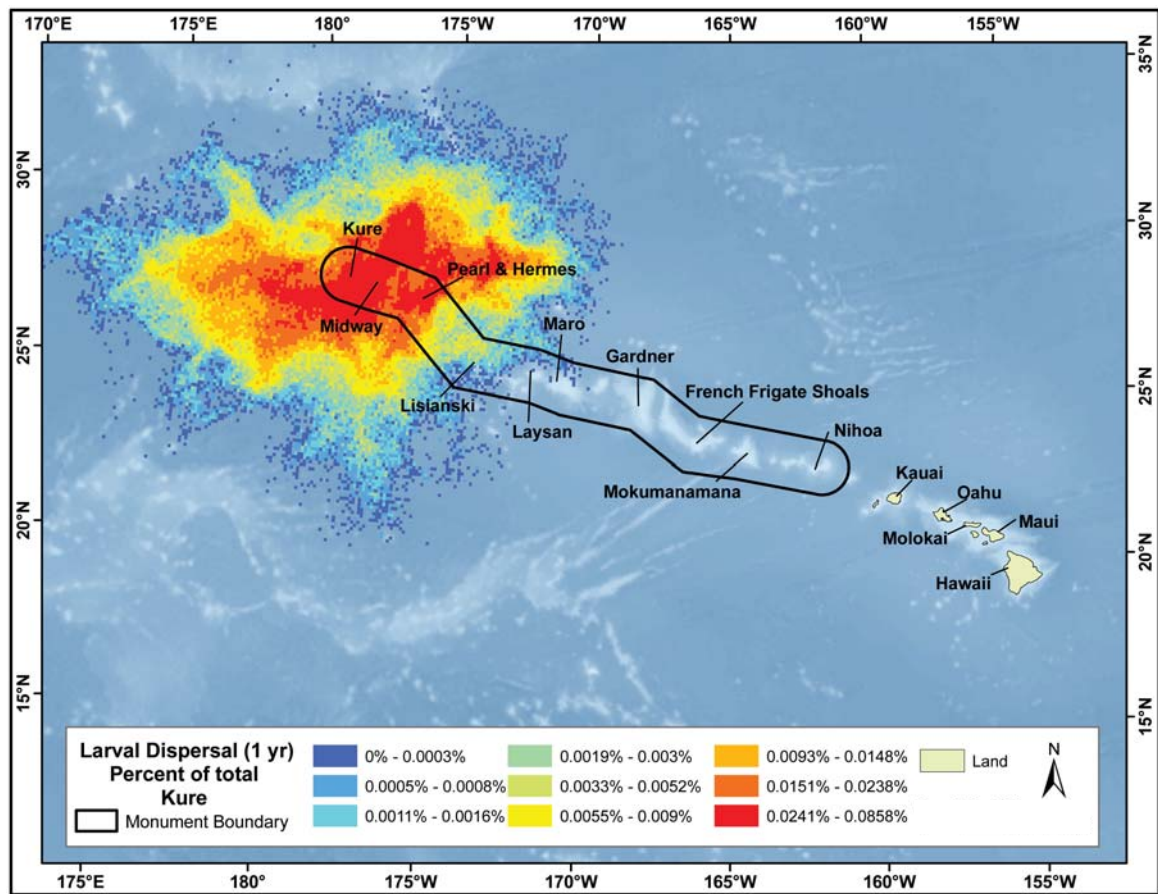


Figure 9.7. Larval dispersal (45 day PDL) one year after being released from Kure. Source: Kobayashi, in review; map: L. Wedding.

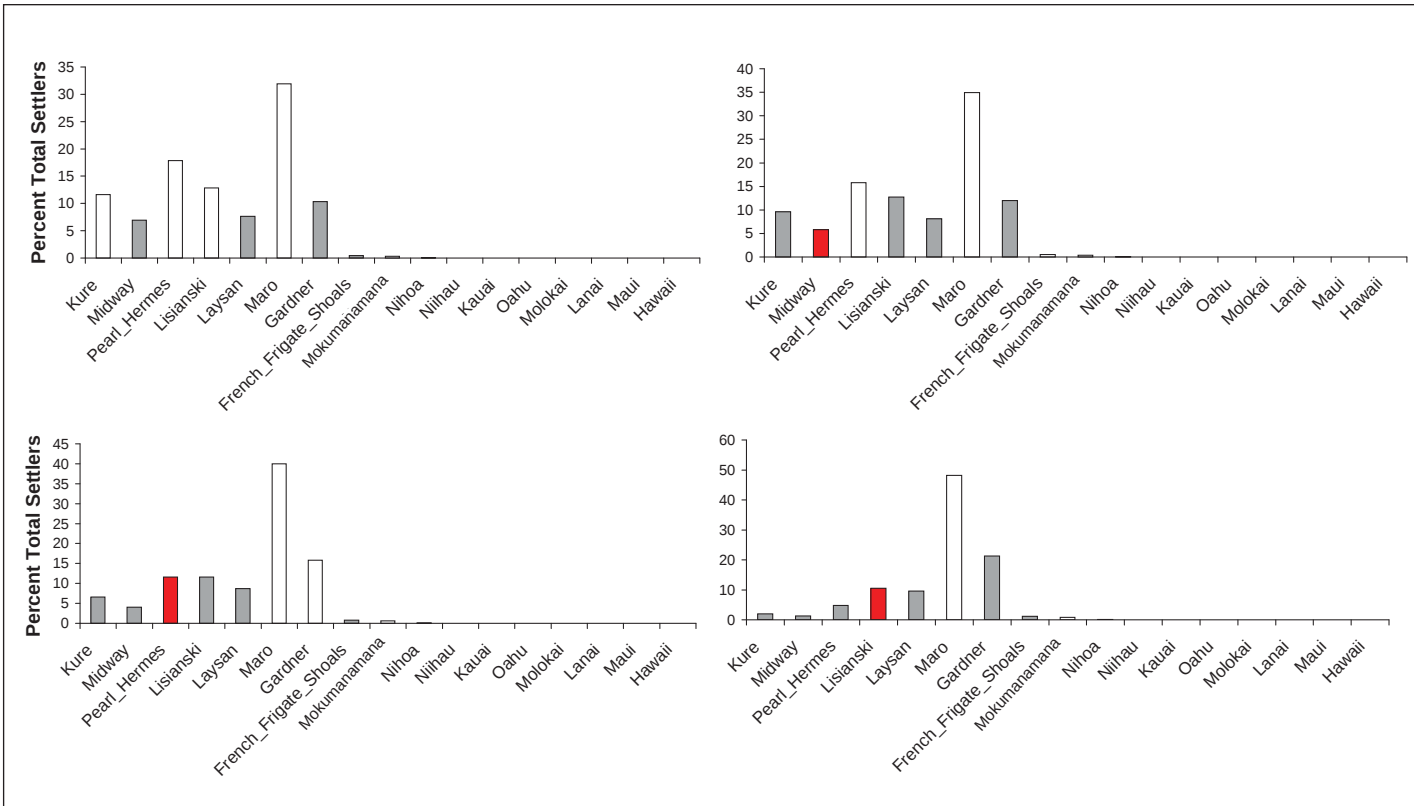


Figure 9.8: Larval retention for propagules released at each of 10 islands/atolls. The red bars in each graph indicate the island or atoll from which the larval propagules were initially released. Source: Kobayashi, unpublished data.

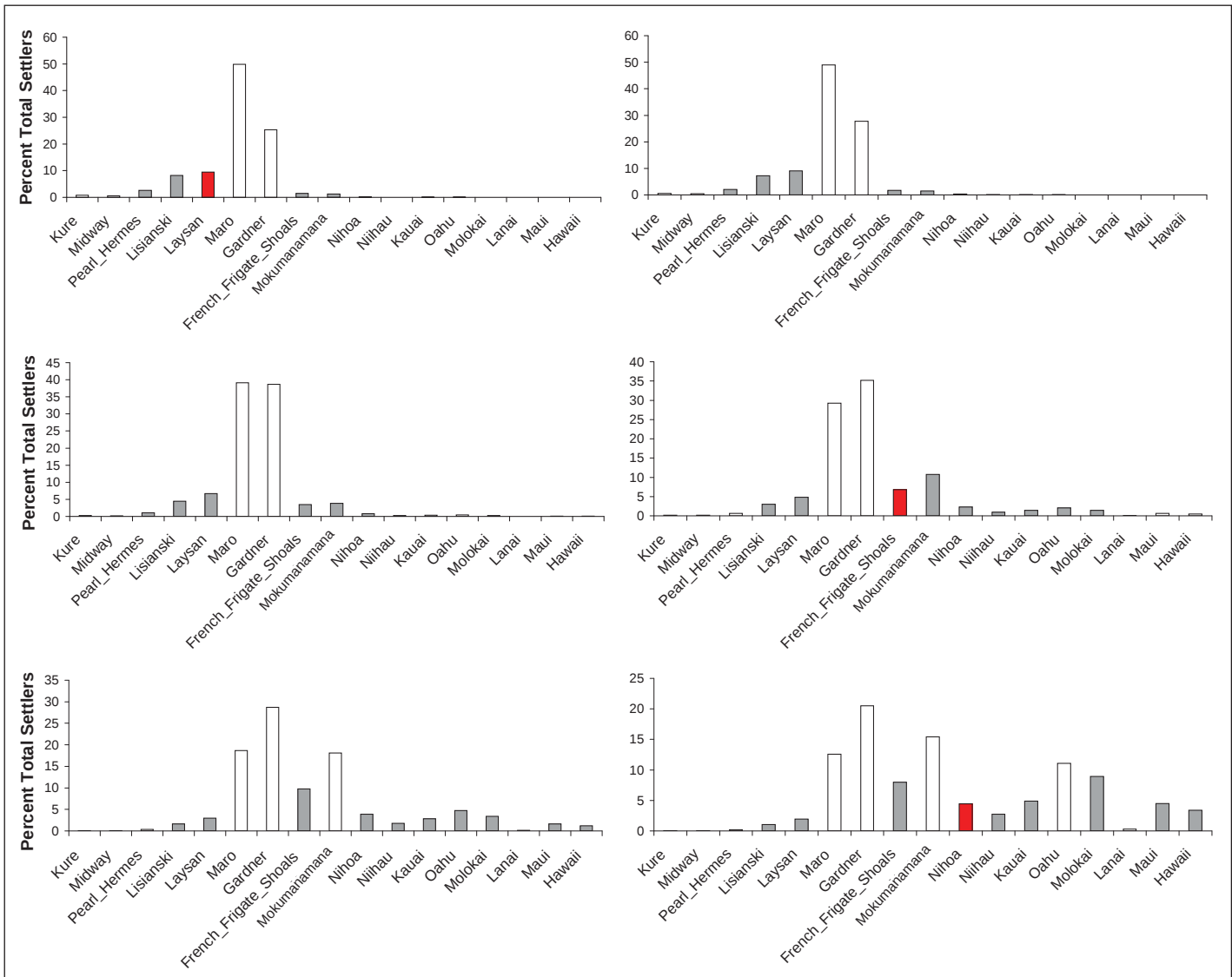


Figure 9.8 (continued): Larval retention for propagules released at each of 10 islands/atolls. The red bars in each graph indicate the island or atoll from which the larval propagules were initially released. Source: Kobayashi, unpublished data.

Directed Movements of Adult Fishes—Connectivity at the Scale of the Individual

Acoustic telemetry of giant trevally (white ulua, *Caranx ignobilis*; Figure 9.9) and jobfish (uku, *Aprion virescens*; Figure 9.9), large-bodied apex predators on Hawaiian reefs, revealed each to be site attached and home ranging (Meyer et al., 2007a,b; Figure 9.10). No inter-atoll movements were detected but animals were site attached to core activity areas where they exhibited diel habitat shifts and made periodic atoll-wide excursions up to 29 km. Movements to seasonal mating aggregations were identified in the summer during specific phases of the moon for each species.



Figure 9.9. Giant trevally (left) and jobfish (right) are both large, top predators in the NWHI coral reef ecosystem. Photos: J. Zamaow and J. Maragos.

Giant Trevally Movement

A large proportion of giant trevally from French Frigate Shoals were caught at La Perouse Pinnacle, and these fish all showed high detections/day at this location, verifying their strong site fidelity to a core area (Figures 9.11). The lower detection/day at East and Tern Islands also suggests that these locations are on the periphery of the fish's home range (none of the fish detected at East or Tern were tagged at those locations). The large number of fish detected at Rapture Reef suggests this site provides important habitat for giant trevally at French Frigate Shoals, as fish tagged throughout the atoll made seasonal excursions to this reef. The arrival and departure times of fish were strongly correlated with each other and in turn with the lunar cycle. Coupled with anecdotal diver observations, the acoustic data indicate that Rapture Reef is likely a spawning aggregation site for giant trevally at French Frigate Shoals. Giant trevally tagged at Rapture Reef were detected there year round, suggesting that their core home range was located within the spawning habitat. These fish did not make long seasonal movements, as their core ranges were within the spawning area. The seasonal spawning behavior of giant trevally was characterized by daily runs to the spawning locations during the lunar spawning cycle. They did not shift their core home range to the spawning location, as they returned to their core range (e.g., La Perouse) after each spawning event.

At Pearl and Hermes Atoll, the greatest number of detections of tagged giant trevally (for each individual fish) occurred at the receiver closest to the location where the fish was originally tagged, providing evidence that they show strong site fidelity to core areas (Figure 9.12). Giant trevally were detected at receivers at other parts of the atoll, suggesting that these areas were on the periphery of the fish's home range. These were most likely areas visited during the diel habitat shifts exhibited by almost all individuals. Fish tagged at the Main Channel showed greater detections/day at large at the Main Channel receiver, compared to receivers close to fish tagged at other parts of the atoll (e.g., northwest corner). The Main Channel is shallow and experiences very strong, tidally-driven currents. These strong currents bring animals and materials in and out of the lagoons, which appears to make the Main Channel a desirable habitat for apex predators, as suggested by the large number of large sharks and teleosts seen at this location.

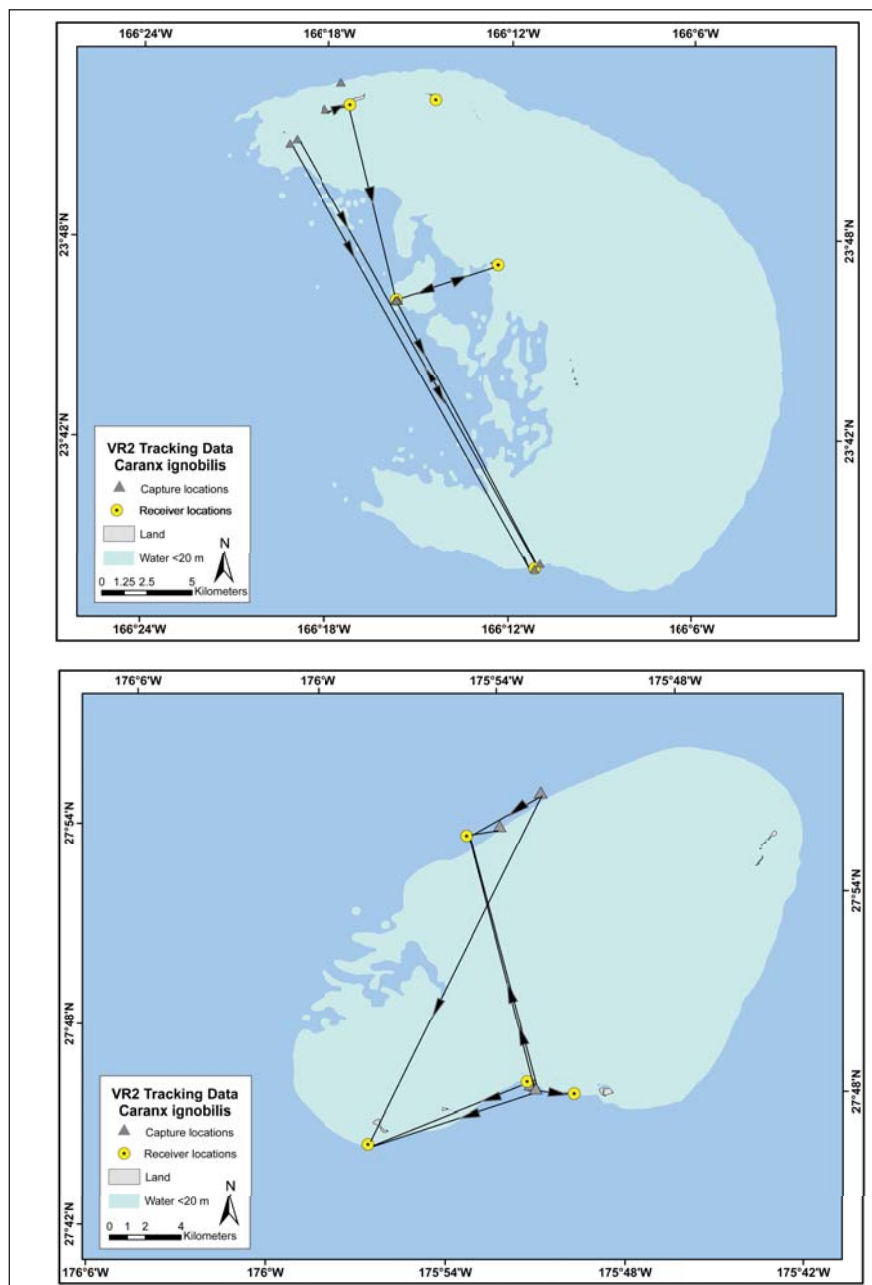


Figure 9.10. Trans-atoll movements of giant trevally at French Frigate Shoals (top) and Pearl and Hermes (bottom; Meyer et al., 2007a). Circles indicate locations of VR2 receivers, shaded squares indicate giant trevally capture sites (numbers within square symbols indicate sites where multiple individuals were tagged and released). Lines with arrows indicate most direct route between giant trevally release and detection locations.

Only a limited number of giant trevally were tagged at Midway and Kure Atolls, resulting in few detections and no evidence of movement (Figures 9.13 and 9.14). Shallow flats appear to be poor habitat for this species, as all receivers located in shallow flats at various atolls recorded very few detections.

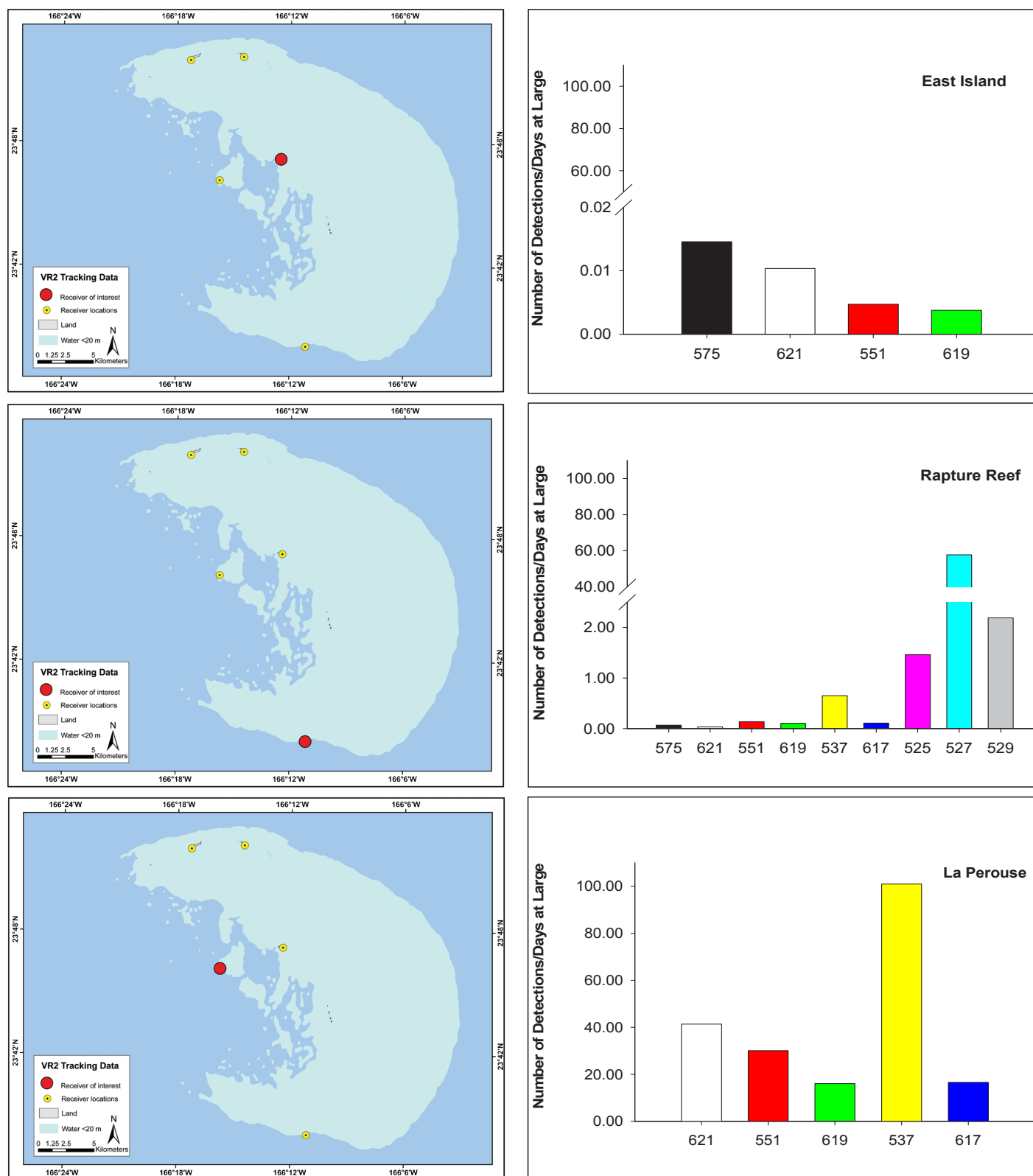


Figure 9.11. Number of tag detections/days at large for giant trevally tagged at French Frigate Shoals. Source: Friedlander, unpub. data; maps: L. Wedding.

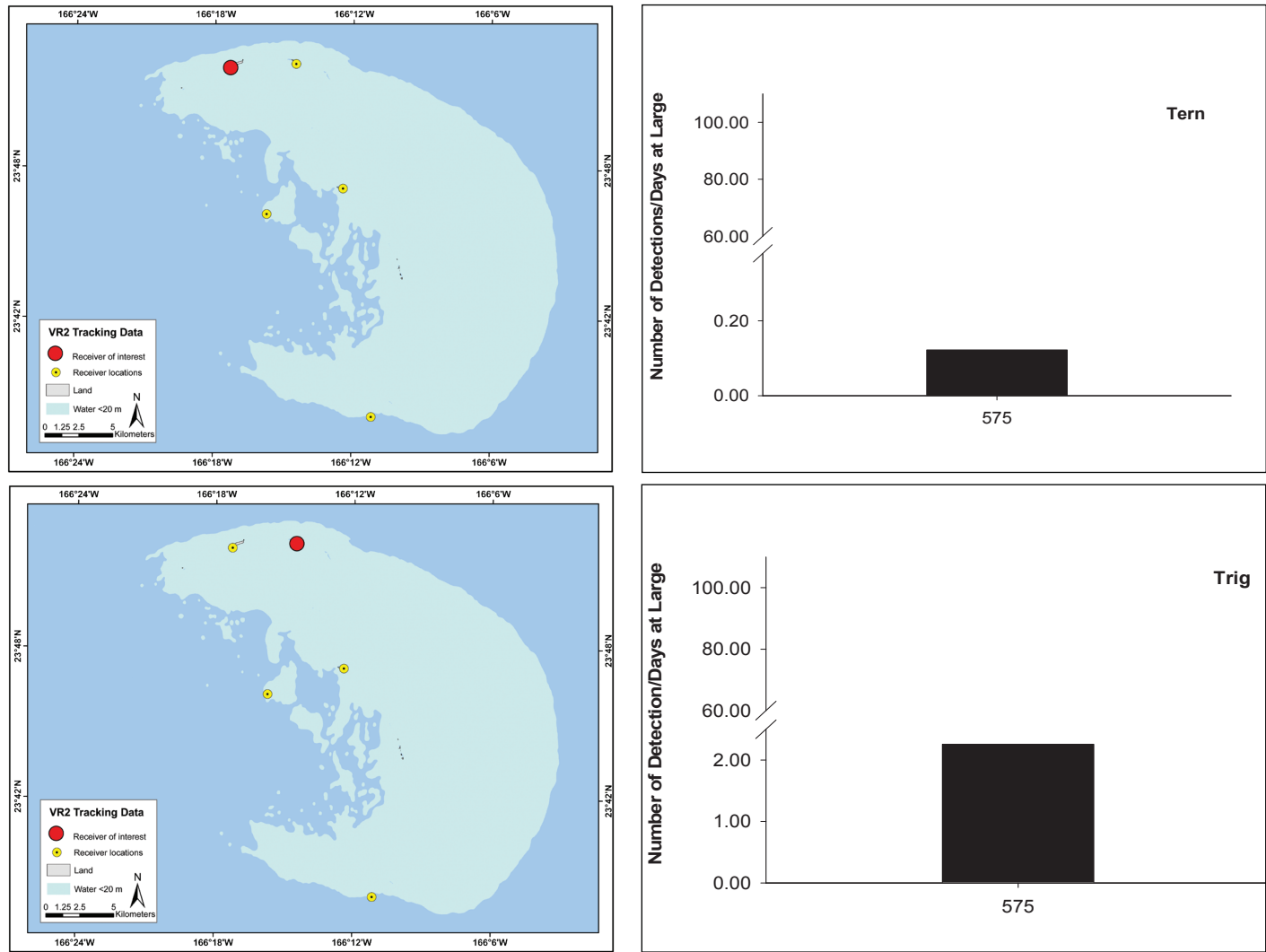


Figure 9.11 (continued). Number of tag detections/days at large for giant trevally tagged at French Frigate Shoals. Source: Friedlander, unpub. data; maps: L. Wedding.

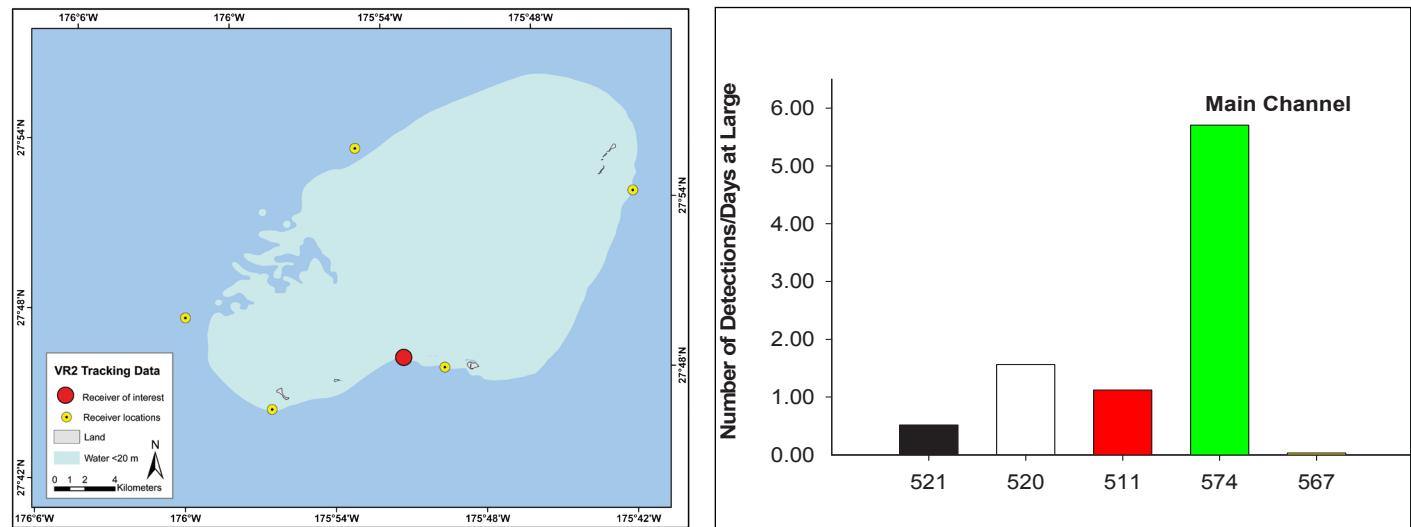


Figure 9.12. Number of tag detections/days at large for giant trevally tagged at Pearl and Hermes Atoll. Source: Friedlander, unpub. data; maps: L. Wedding.

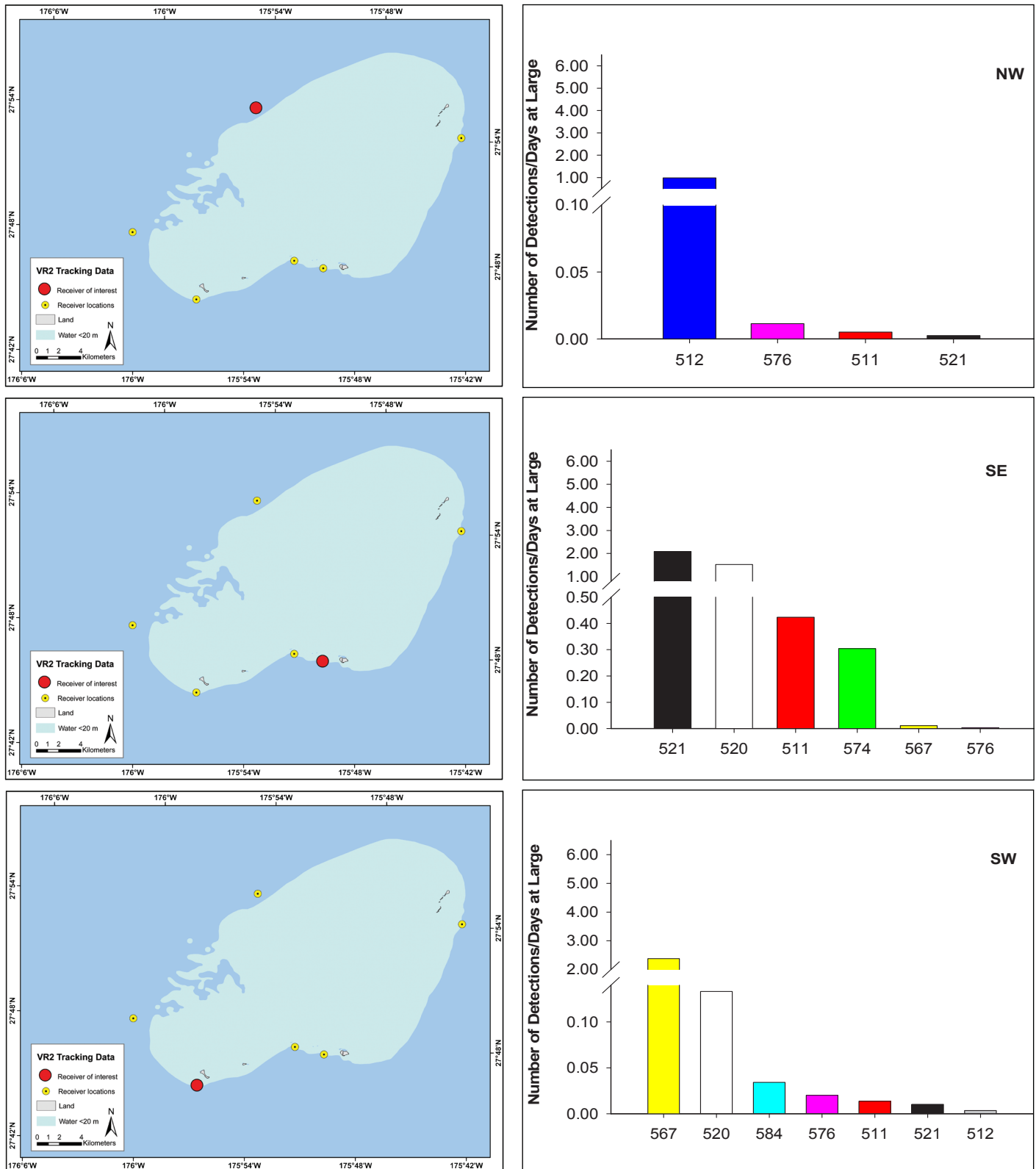


Figure 9.12 (continued). Number of tag detections/days at large for giant trevally tagged at Pearl and Hermes. Source: Friedlander, unpub. data; maps: L. Wedding.

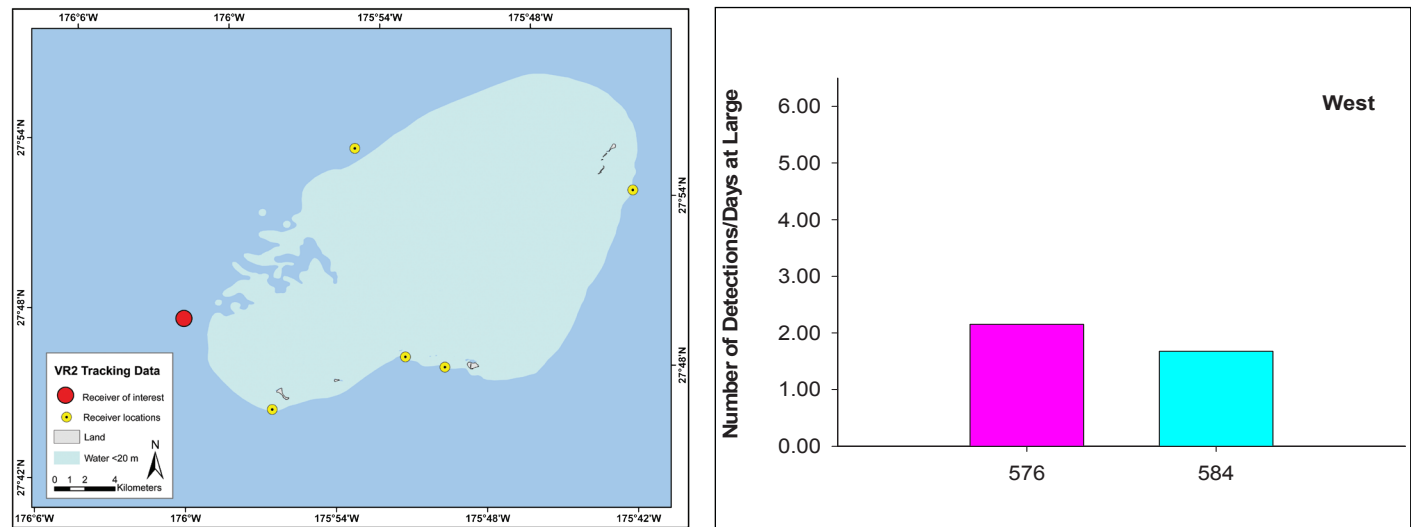


Figure 9.12 (continued). Number of tag detections/days at large for giant trevally tagged at Pearl and Hermes Atoll. Source: Friedlander, unpub. data; maps: L. Wedding.

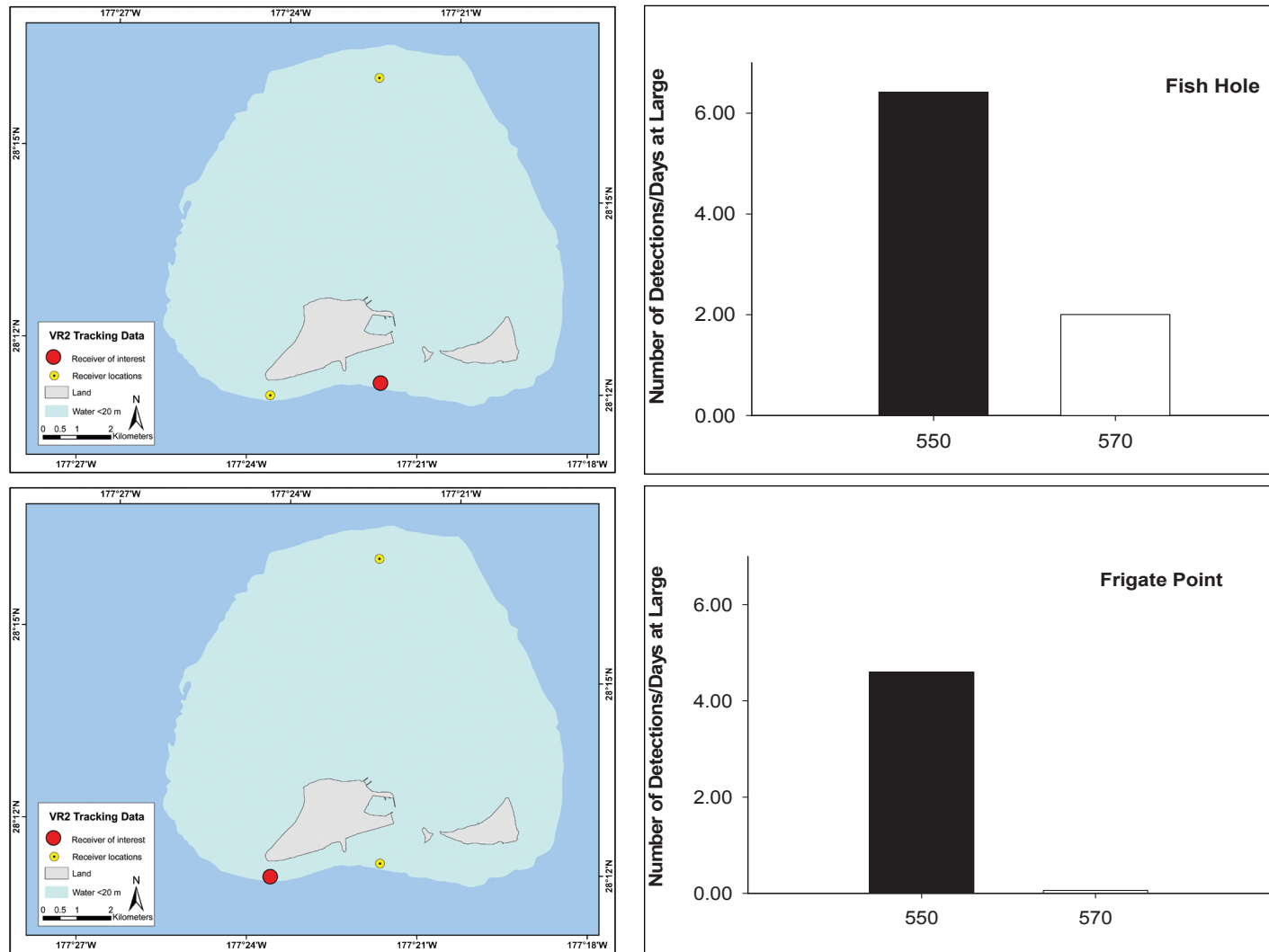


Figure 9.13. Number of tag detections/days at large for giant trevally tagged at Midway Atoll. Source: Friedlander, unpub. data; maps: L. Wedding.

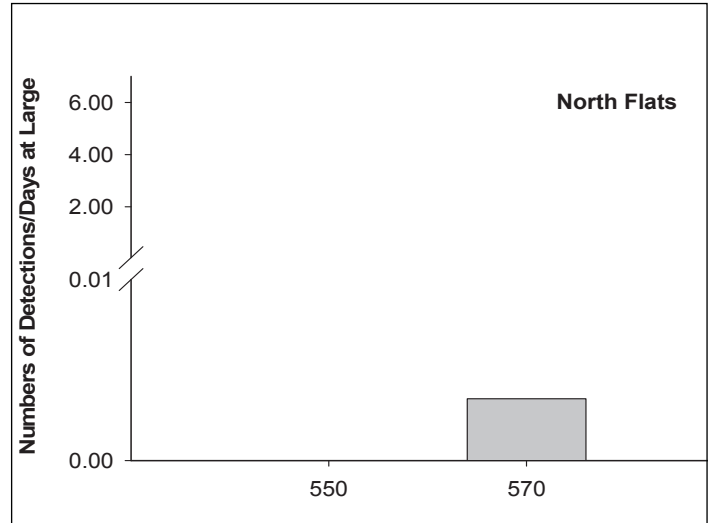
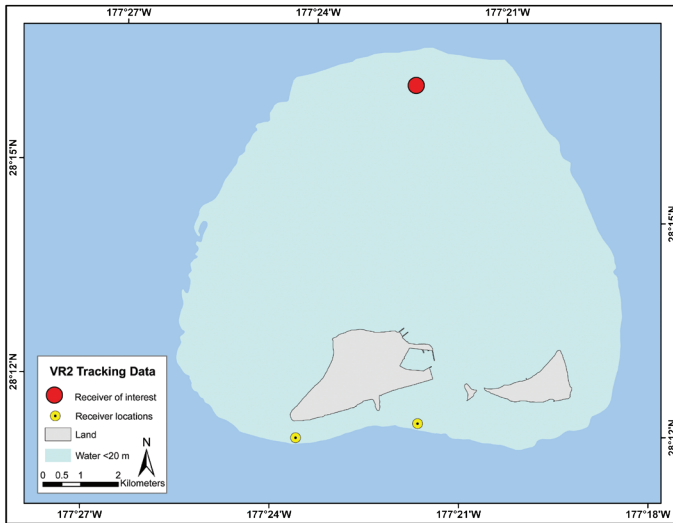


Figure 9.13(continued). Number of tag detections/days at large for giant trevally tagged at Midway Atoll. Friedlander, unpub. data; maps: L. Wedding.

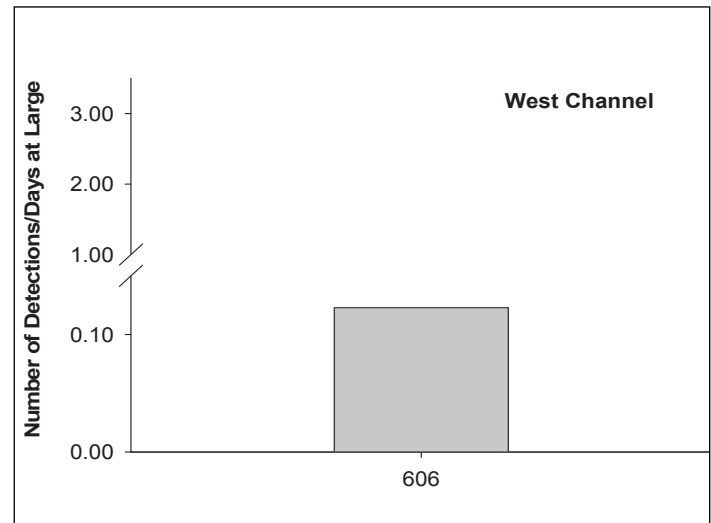
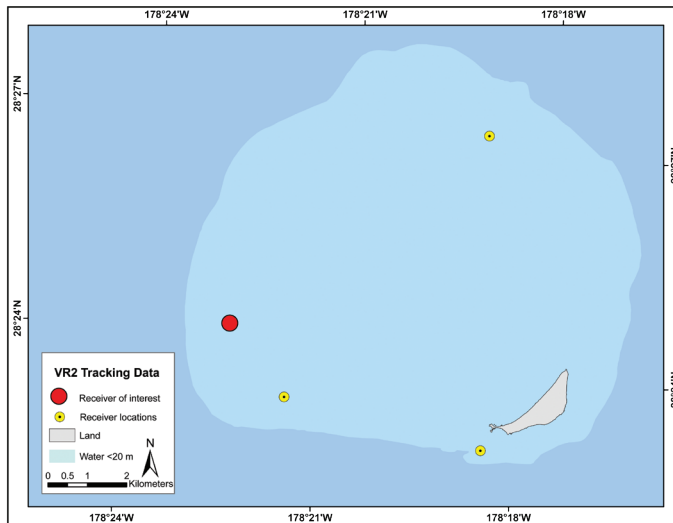
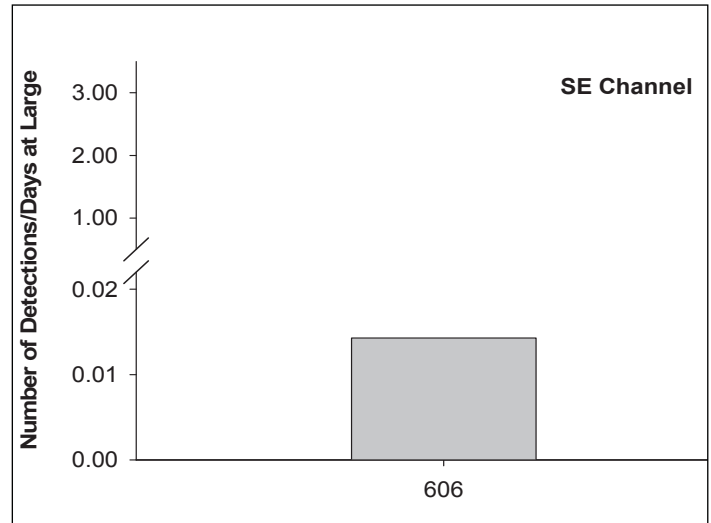
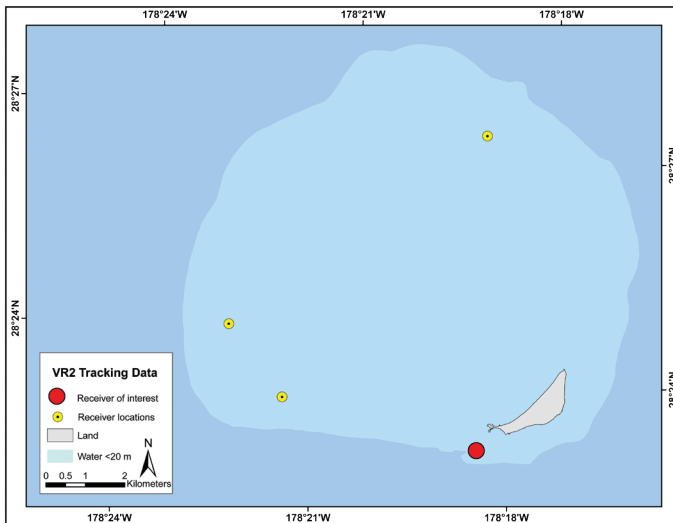


Figure 9.14. Number of tag detections/days at large for giant trevally tagged at Kure Atoll. Source: Friedlander, unpub. data; maps: L. Wedding.

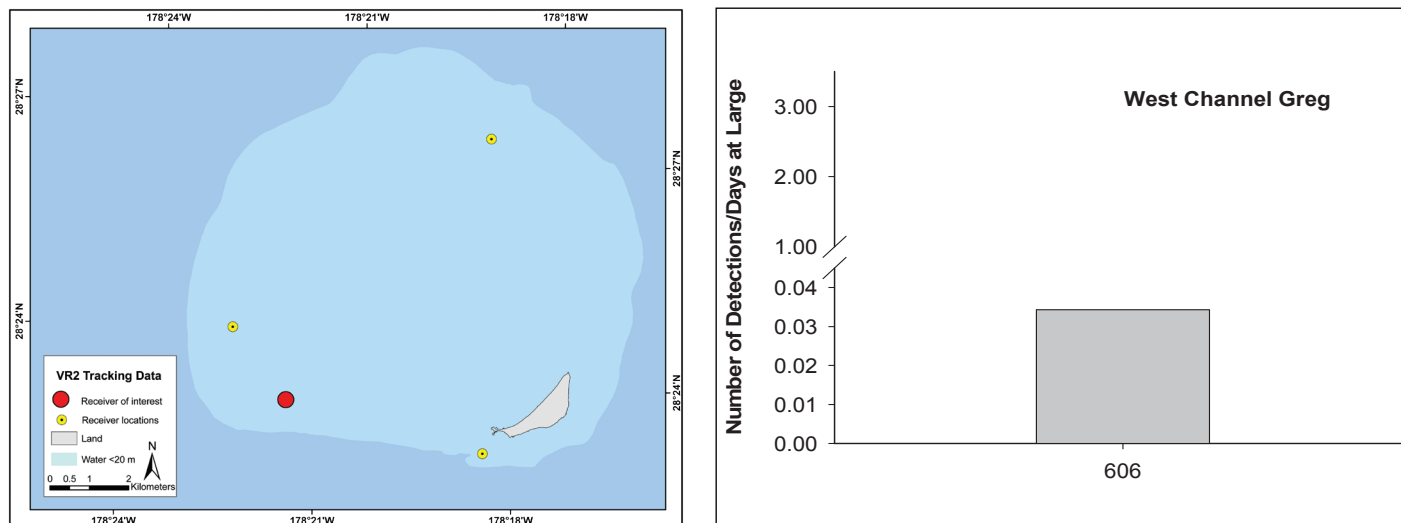


Figure 9.14 (continued). Number of tag detections/days at large for giant trevally tagged at Kure Atoll. Source: Friedlander, unpub. data; maps: L. Wedding.

Jobfish Movement

Movement patterns for jobfish were similar to those observed for giant trevally (Figures 9.15). For example, all fish detected at Rapture Reef were tagged at Disappearing Island, located close to Rapture Reef (Figure 9.16). However, there was no evidence that Rapture Reef is a spawning location for jobfish. Jobfish tagged along the south coast of Pearl and Hermes Atoll were detected by receivers on both the southwest and southeast tips (Figure 9.17). This suggests behavior associated with long, daily and tidal excursions.

Overall, jobfish had lower numbers of detections/day than giant trevally. This may be a function of a key difference in their spawning strategy, as well as a tendency for greater diel movement. Unlike giant trevally, jobfish perform complete seasonal shifts in their home range, occupying separate summer and winter core areas. These winter and summer locations do not overlap, which is why each receiver generally has fewer detections on an annual basis. However, jobfish were occasionally detected in their winter or summer location during the opposing season, suggesting that these seasonal core areas are relatively close to each other.

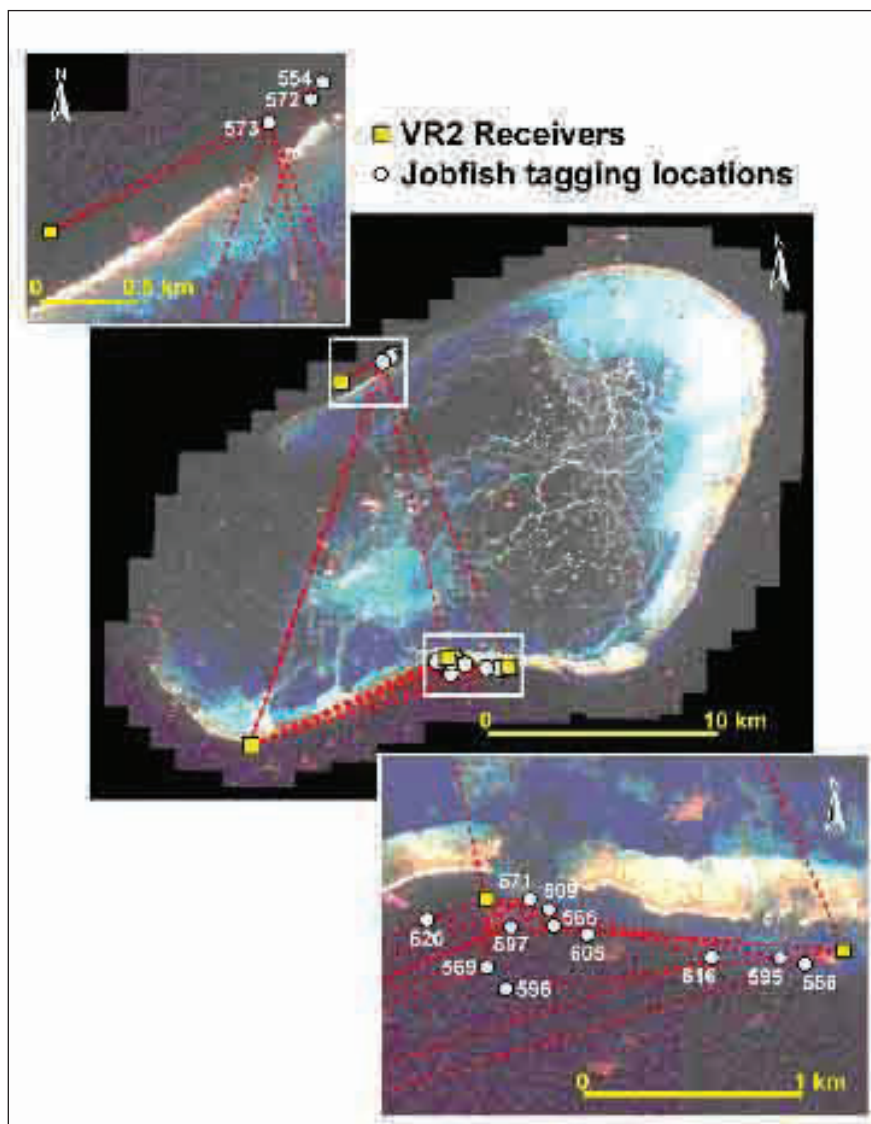


Figure 9.15. Trans-atoll movements of jobfish at Pearl and Hermes Reef with enlarged views of capture areas (insets) showing VR2 receiver locations (yellow squares), jobfish capture sites (white circles), jobfish transmitter codes (white numbers), most direct routes between jobfish release and detection locations (dashed red lines). Source: Meyer et al., 2007b.

Jobfish at Kure atoll also show strong site fidelity to core areas, and fish have been detected at one receiver for over three years. Again, however, diel and tidal movements result in jobfish moving over a large area, as exemplified by the different detection patterns for individual fish seen in Figures 9.18 and 9.19. These fish make complete seasonal shifts in habitat as can be seen by the absence of detections during either the summer or winter months. The fact that fish were detected, fish that were absent either during the summer or the winter months, suggests that the spawning habitats for this species were located at Kure, and that there is more than one spawning location at the atoll.

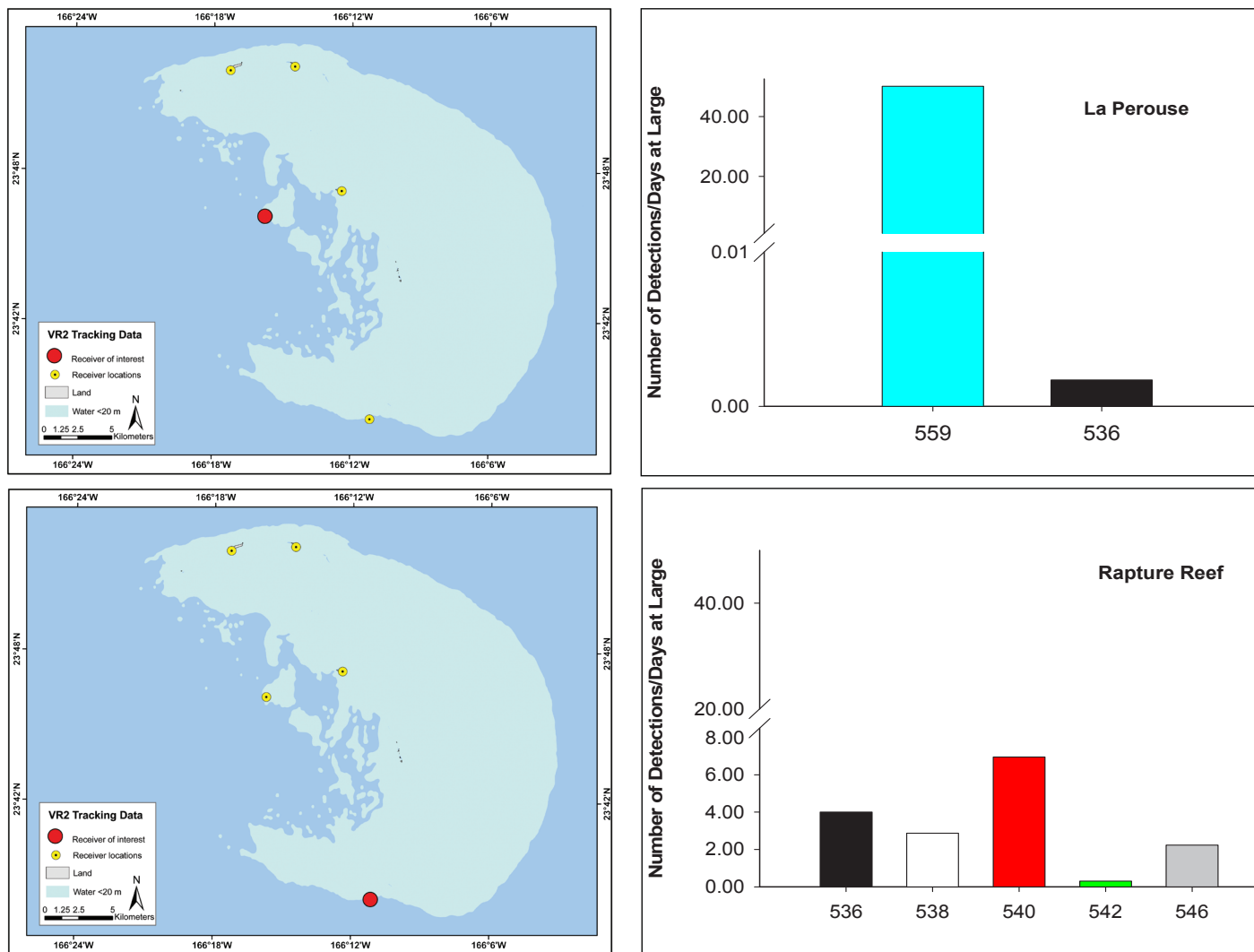


Figure 9.16. Number of tag detections/days at large for jobfish tagged at French Frigate Shoals. Source: Friedlander, unpub. data; maps: L. Wedding.

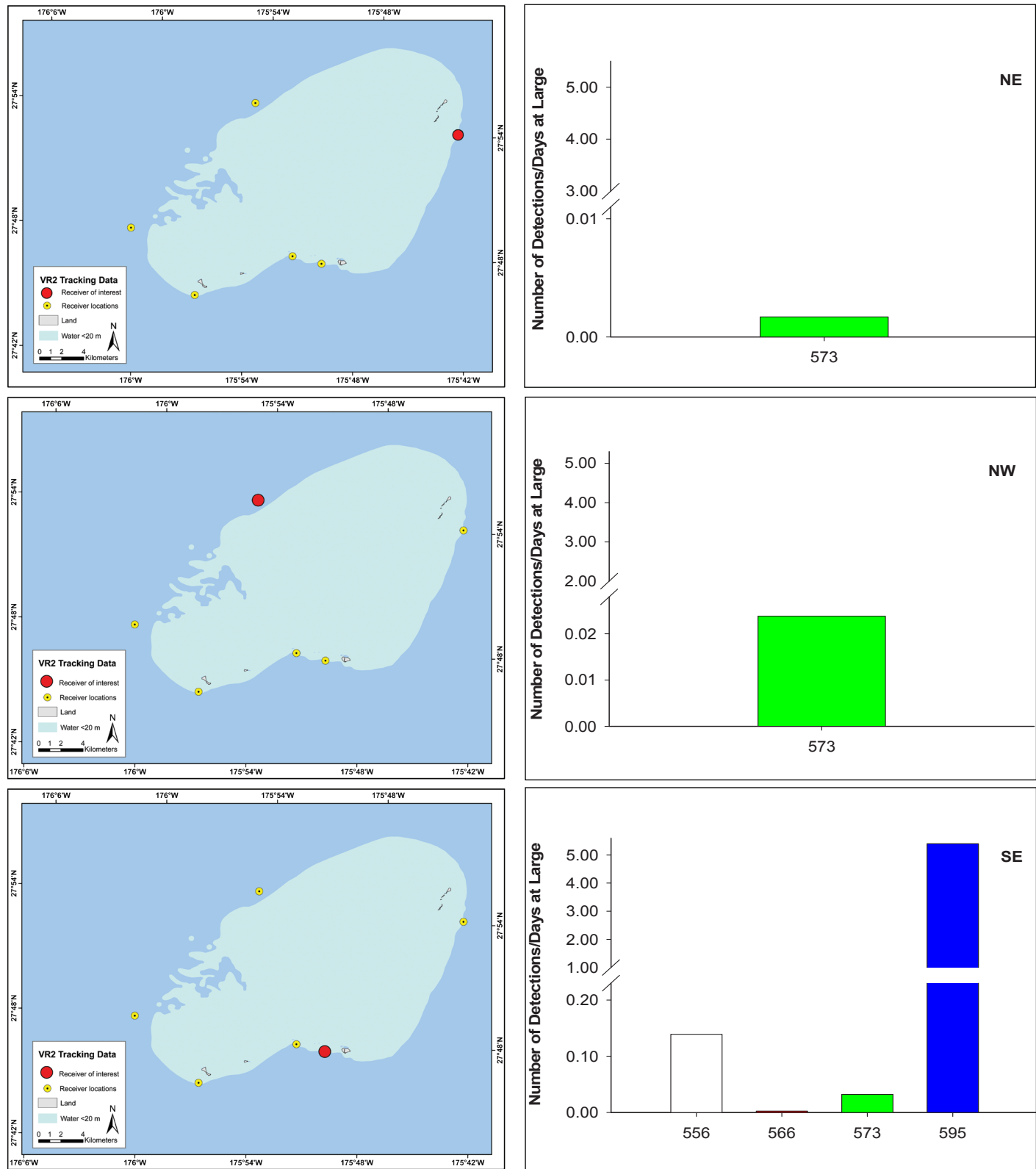


Figure 9.17. Number of tag detections/days at large for jobfish tagged at Pearl and Hermes Atoll. Source: Friedlander, unpub. data; maps: L. Wedding.

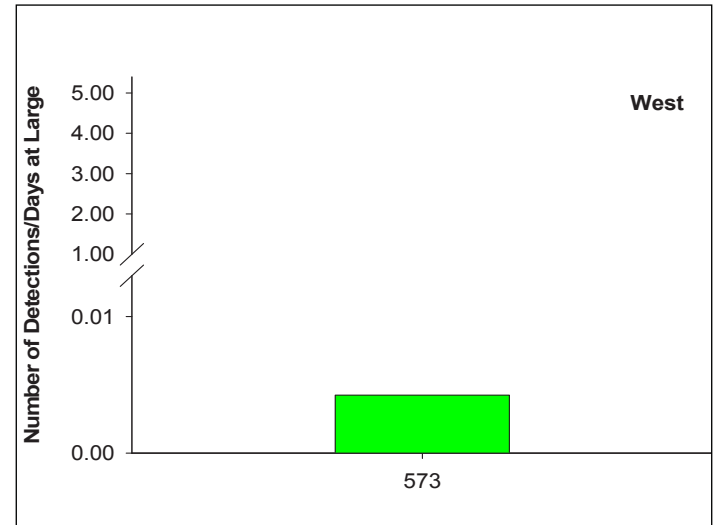
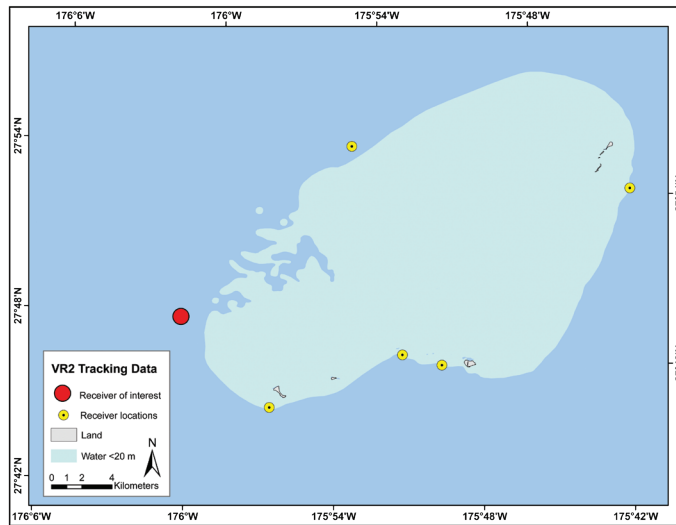
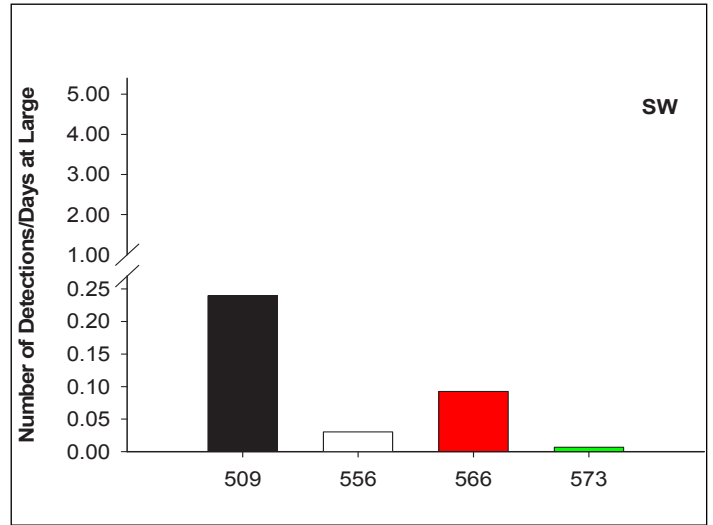
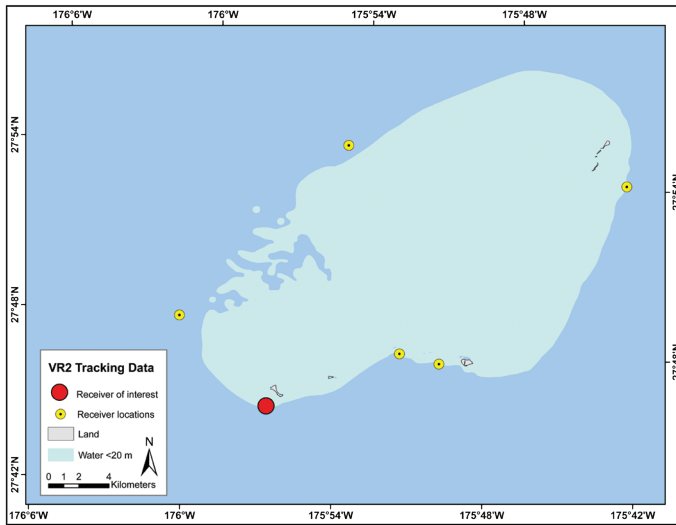


Figure 9.17 (continued). Number of tag detections/days at large for jobfish tagged at Pearl and Hermes Atoll. Source: Friedlander, unpub. data; maps: L. Wedding.

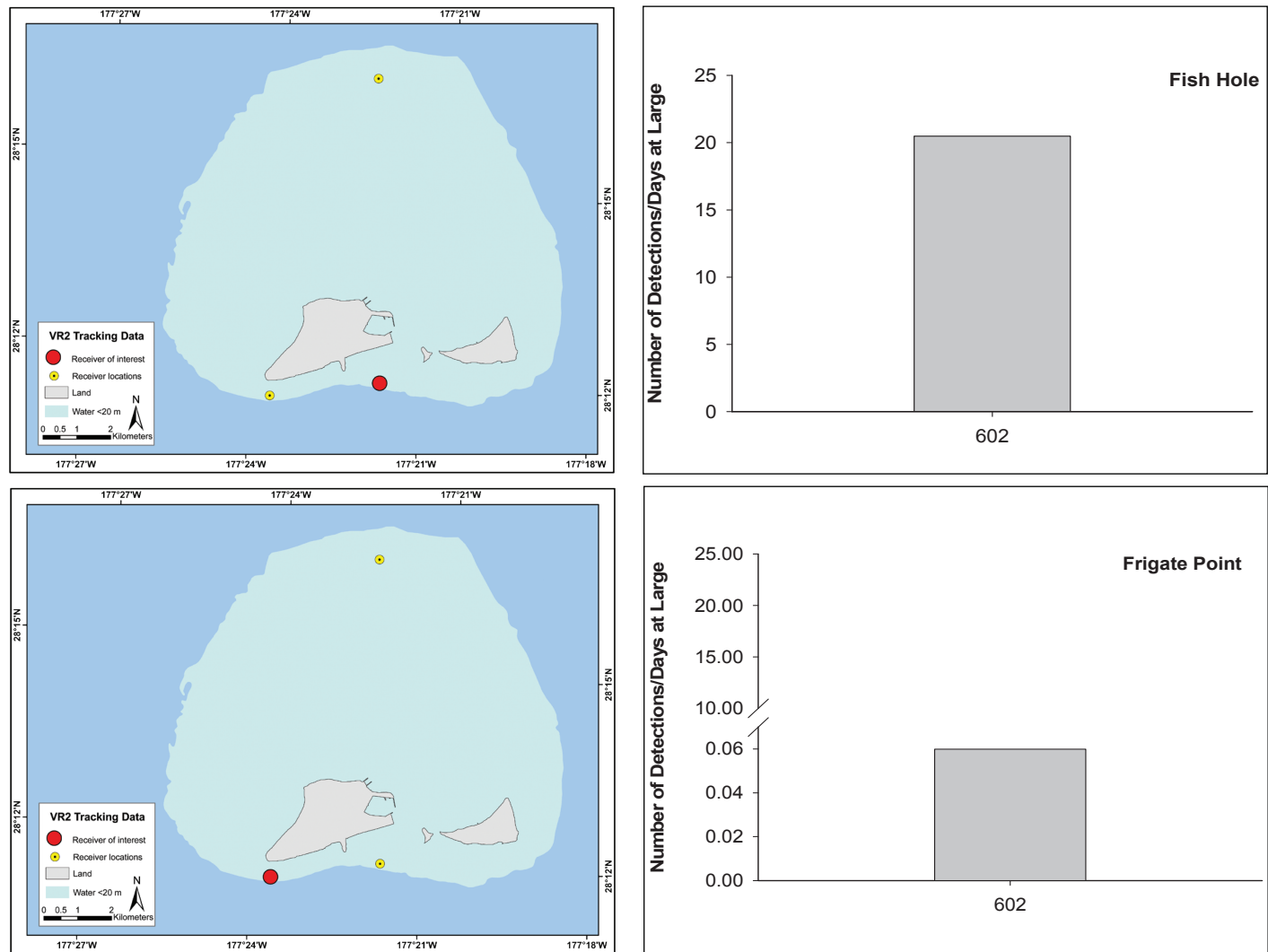


Figure 9.18. Number of tag detections/days at large for jobfish tagged at Midway Atoll. Source: Friedlander, unpub. data; maps: L. Wedding.

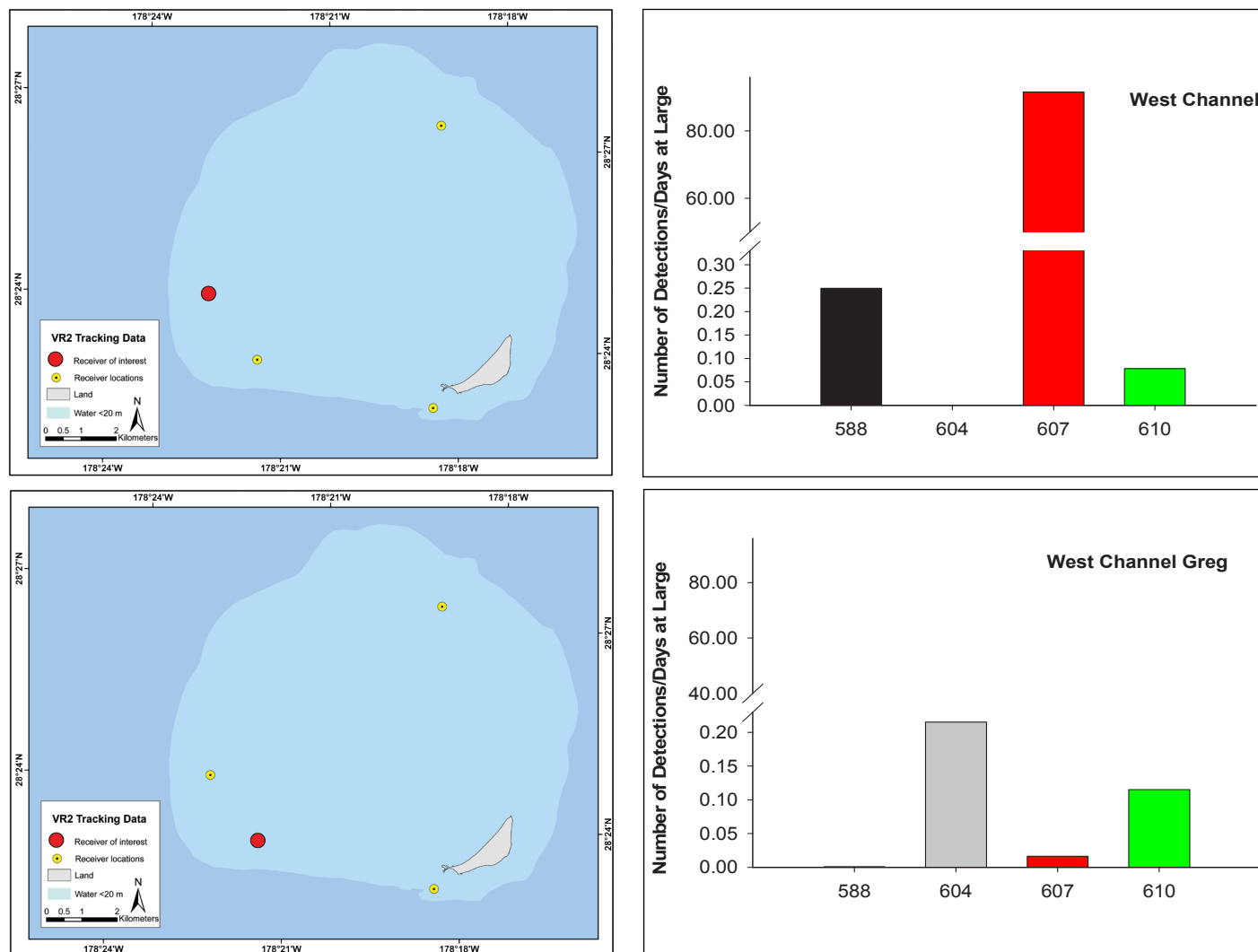


Figure 9.19. Number of tag detections/days at large for jobfish tagged at Kure Atoll. Source: Friedlander, unpub. data; maps: L. Wedding.

Inferring Dispersal and Movement by Tracking Introduced Species

Eleven species of shallow-water snappers (F. Lutjanidae) and groupers (F. Serranidae) were purposely introduced to one or more of the main (high) islands of the Hawaiian Archipelago in the late 1950s and early 1960s. Of these, three snapper species and one grouper have become established (Randall, 1987). One snapper, blueline snapper (Taape or *Lutjanus kasmira*), and one grouper, Peacock grouper (Roi or *Cephalopholis argus*), are well-established, and have histories of colonization along the island chain that are reasonably well-documented. Planktonic stage durations, although unknown for both species, are grossly estimable based on congeners elsewhere in the Indo-Pacific. These two species thus represent a unique opportunity to track the rate of colonization of introduced species within an oceanic insular ("stepping stone") environment.

Blueline snapper, if like several other Indo-Pacific congeners, has a planktonic stage duration approximating 25-47 days and a settlement size greater than 20-30 mm (Leis, 1987), but there is a great deal of geographic, seasonal, and other environmental variations in stage duration within and among closely related species (Leis, 1993; Victor, 1993). Given these same caveats, Peacock grouper, if a typical member of its genus in the subfamily Epinephelinae, settles at a size of about 18 mm (Leis, 1987) and is likely to have a shorter pelagic larval stage than blueline snapper.

A total of about 3,170 blueline snapper were introduced from the Marquesas Islands to Hawaii beginning in 1955, including 2,435 released in Kaneohe Bay, Oahu, in 1958 (Oda and Parrish, 1981; Randall, 1987; Figure 9.20). The species had colonized the Big Island of Hawaii, 140 nmi downchain of Oahu, by 1960 (Randall, 1987). Blueline snapper had spread upchain to French Frigate Shoals in the NWHI, 490 nmi from

Oahu, by sometime between 1977 and 1982 (Okamoto and Kanenaka, 1984). The species was sighted another 330 nmi farther upchain in the NWHI at Laysan Island (820 nmi from Oahu) in June 1979 (Parrish et al., 1980; Oda and Parrish, 1981). A few individuals were first observed at Midway Atoll, 240 nmi farther upchain from Laysan island (1,180 nmi from Oahu), in May-June 1992; the species had not been observed on similar surveys conducted at Midway in 1989 and 1991 (Randall et al., 1993). These records suggest rates of dispersal of about 18-70 nmi/year for blueline snapper subsequent to its introduction to Hawaiian waters. This is consistent with estimates of realized mean dispersal distance ranging from 33 to 130 km/year from Shanks et al. (2003).

The dispersal of Peacock grouper following its introduction to Hawaii is not as well documented. However it is clear that Peacock grouper has spread less extensively than blueline snapper over approximately the same time period (Figure 9.21). In 1956, a total of 571 *C. argus* were introduced from Moorea in French Polynesia to Oahu (n=171) and to the Kona coast of the Big Island (n=400; Randall, 1987). At present, it has been documented as far upchain as Niihau, 120 nmi from Oahu, where it was first observed in November 1978 (Hobson, 1980). No shallow reef fish surveys of the westernmost MHI were conducted prior to this time. Peacock grouper was absent at French Frigate Shoals in 1992 and has been mostly absent in annual surveys conducted there between 1995 and 2003 (E. DeMartini, unpubl. data). Based on this meager data, a dispersal rate of >5 nmi per year is suggested. Although pelagic duration estimates are approximate, Peacock grouper-- the species with a likely shorter-duration pelagic stage-- has spread much more slowly through the Hawaiian Archipelago than blueline snapper. Blueline snapper clearly belongs to the long-distance dispersal group (mode greater than 16 km/year); Peacock grouper probably belongs to this group as well, albeit closer to the lower bound.

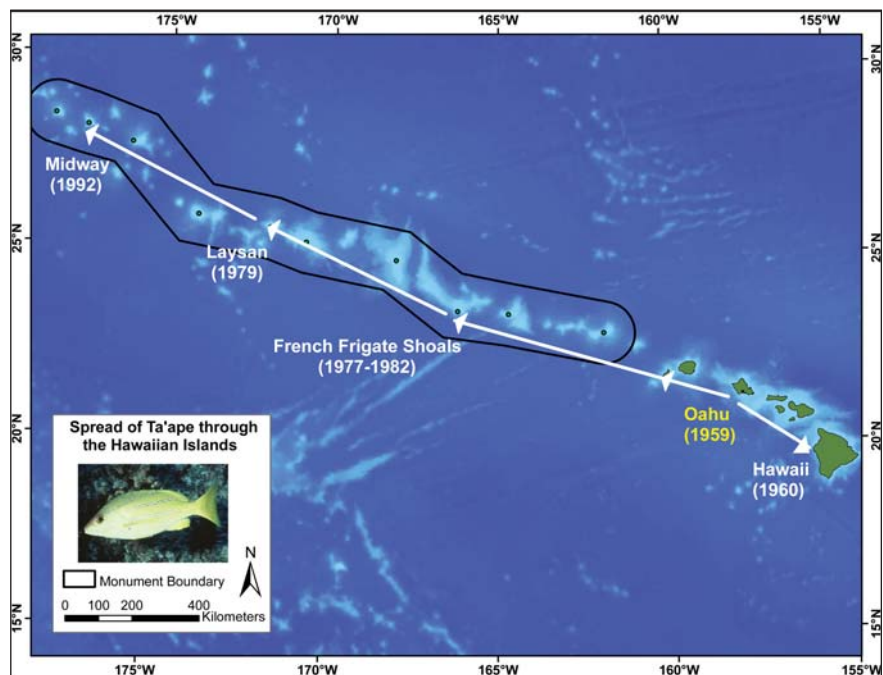


Figure 9.20. Spread of the introduced blueline snapper (*Taape*, *Lutjanus kasmira*) throughout the Hawaiian Islands. Source: Sladek Nowlis and Friedlander, 2004.

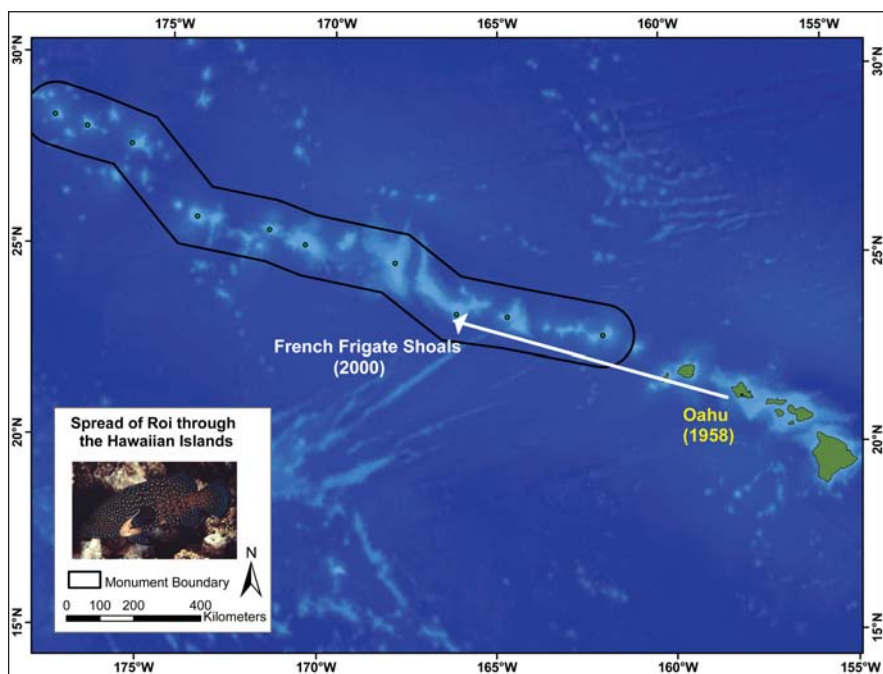


Figure 9.21. Spread of the introduced Peacock grouper (*Roi*, *Cephalopholis argus*) throughout the Hawaiian Islands. Source: Sladek Nowlis and Friedlander, 2004.

Genetic Connectivity Studies

Ongoing research will determine genetic dispersal among islands and atolls of the NWHI, including both invertebrates and reef fishes, using molecular genetic markers to resolve populations and evolutionary partitions. Preliminary results indicate large differences among taxa in their degree of connectivity throughout the archipelago. Some species appear to move around the archipelago with relative ease and show no significant population structure in the NWHI and MHI (e.g., reef fish; Schultz et al., 2007; Craig et al., 2007). Other species show modest but significant population structure, including the endemic grouper (Rivera et al., 2004), spinner dolphins (Andrews et al., 2006) and two damselfishes (Ramon et al., 2008).

Opihi, the Hawaiian endemic limpets (*Cellana exarata*; *C. sandwicensis*, Figure 9.22; and *C. talcosa*), show striking population differentiation between the MHI and NWHI (Bird et al., 2007). All three species of opihi show significant differentiation of populations across the Hawaiian Archipelago, but the spatial scales, patterns and magnitudes of partitioning differ by almost an order of magnitude among species. Preliminary data from hermit crabs (Baums et al., in prep) indicate variable connectivity in this group as well. There is significant population differentiation between the MHI and NWHI for all three species of opihi, and estimates of dispersal (migrants per generation ≤ 3) are so low that recruitment from the NWHI would likely have negligible impact on depleted MHI populations. Even within the MHI, the koele (*C. talcosa*) exhibits such strong population differentiation that if the Kauai population were depleted, it could not recover within our lifetime (Bird et al., 2007).

Kobayashi (2006) recently used a computer simulation to infer patterns of larval dispersal between Johnston Atoll and the Hawaiian Archipelago. Results indicate a “northern corridor” which connects Johnston Atoll and the central portion of the NWHI and a “southern corridor” which connects Johnston Atoll to the MHI. Sampling was conducted at Johnston Atoll in 2006 to assess connectivity between the NWHI and this isolated reef habitat. The sea cucumber *Holothuria atra* exhibited low connectivity between Oahu and French Frigate Shoals and between Oahu and Johnston (Skillings et al., in prep; Figure 9.23). In contrast, there was no significant difference between samples from French Frigate Shoals and Johnston, supporting the northern corridor for dispersal between Johnston and the Hawaiian Archipelago (Figure 9.23). This result



Figure 9.22. A yellowfoot opihi (*Cellana sandwicensis*) at Kauai. All Hawaiian *Cellana* spp. are endemic to the archipelago and exhibit a striking population differentiation between the main and northwestern islands. Photo: C.E. Bird.

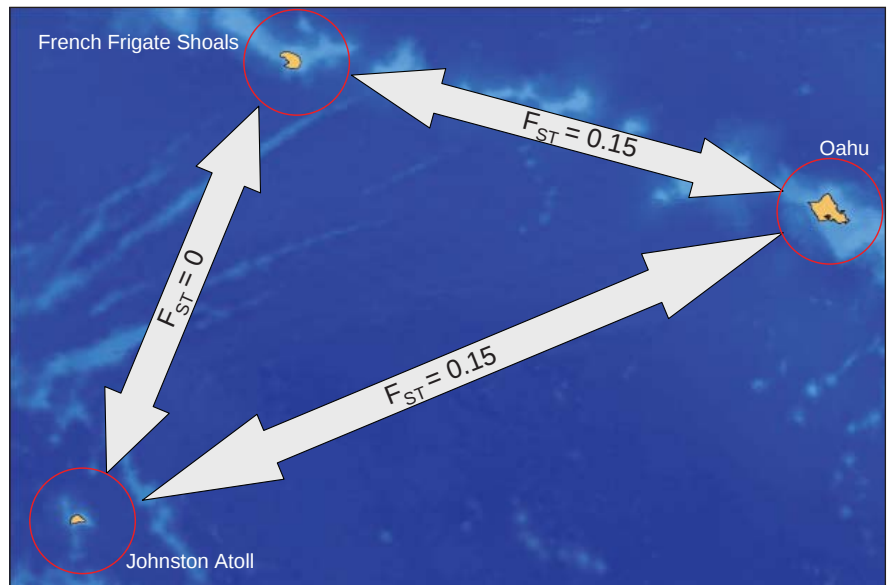


Figure 9.23. *F*-statistics demonstrate population genetic separations for the sea cucumber *Holothuria atra* between Oahu (MHI) and French Frigate Shoals (NWHI), and between the MHI and Johnston, but high connectivity between Johnston and French Frigate Shoals. Source: Skillings et al., in prep.

supports the hypothesis first advanced by Grigg (1981) and Maragos and Jokiel (1986) that Johnston is a potential gateway that enhances biodiversity in the NWHI. However the alternative hypothesis, that Johnston is an outpost of the Hawaiian fauna, remains a viable possibility pending further research.

Results thus far indicate that population structure across the Hawaiian archipelago does not fit a simple isolation-by-distance model, and generalizations based on average (geostrophic) oceanographic currents may not be warranted (Figures 9.24). Closely-related species with similar ecology and reproductive biology (including opihi, hermit crabs, and reef fishes) can have dramatically different patterns of connectivity (Bird et al., 2007; Rocha et al., 2007). Together, these results mandate that a suite of invertebrates and fish must be surveyed to resolve general trends, and to provide connectivity information pertinent to management of the PMNM.

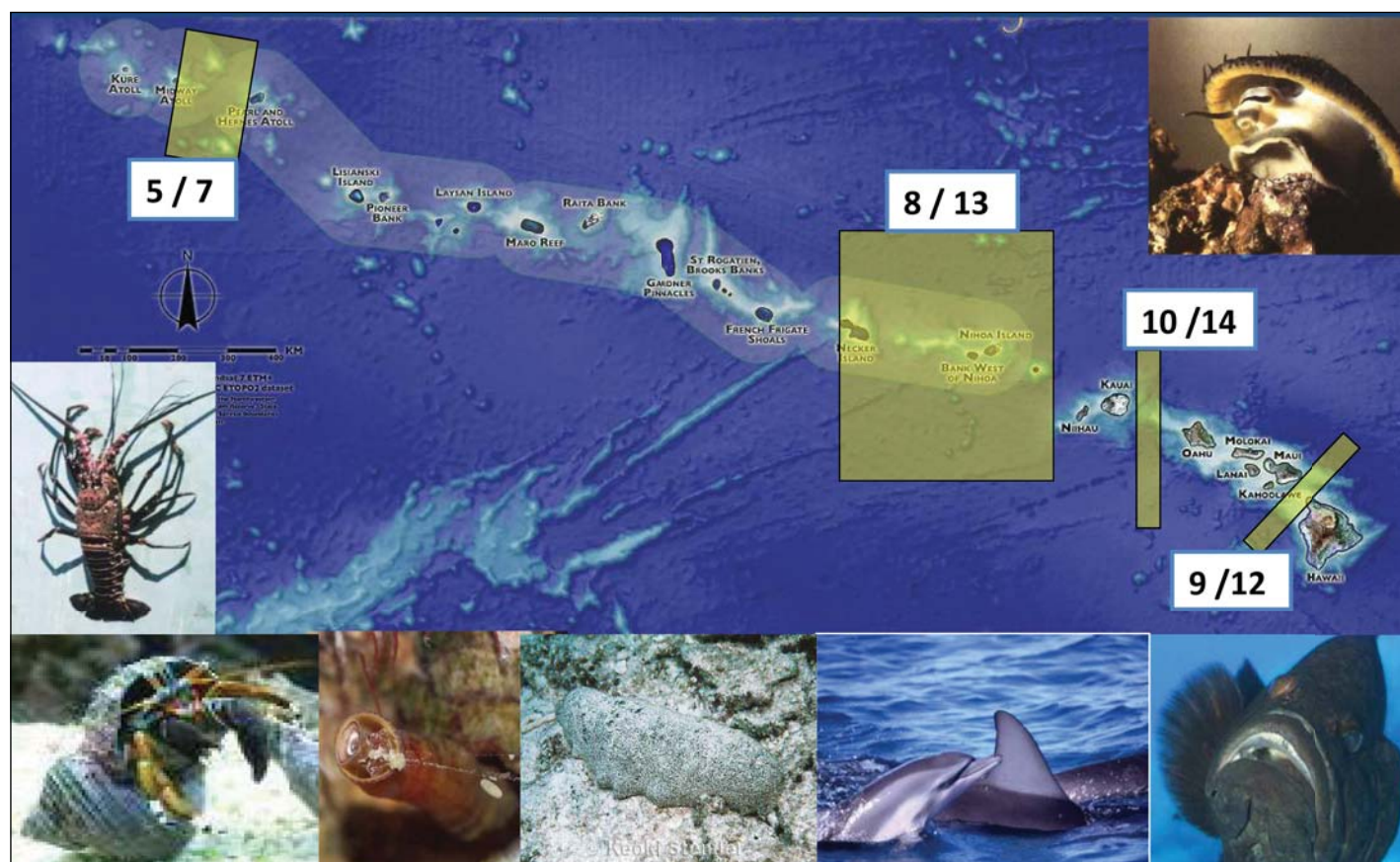


Figure 9.24. Apparent shared barrier to dispersal in the Hawaiian Archipelago. Consensus of significant genetic partitions among up to 14 marine species across the Hawaiian Archipelago. Locations of apparent restrictions to dispersal are marked with yellow bands, and the number of species that share that break out of the total number of species surveyed for each location are also given. These results are preliminary, but the shared genetic structure among highly divergent species thus far is striking.

Connectivity considerations are particularly important for Hawaiian endemic species. Conservation of Hawaiian endemic species should take into account the consequences of their restricted distribution, including reduced capacity for recovery following depletion. Recently, scientists at the Hawaii Institute of Marine Biology have begun to examine population structure in three species of endemic Hawaiian butterflyfishes: the milletseed butterflyfish (*Chaetodon miliaris*), the bluestripe butterflyfish (*C. fremblii*) and the pebbled butterflyfish (*C. multicinctus*). Thus far, they have collected and sequenced 170 individuals of bluestripe butterflyfish (Figure 9.25), 229 milletseed butterflyfish (Figure 9.26) and have made significant progress in collections of pebbled butterflyfish (Figure 9.27) throughout the Hawaiian Islands (M.T. Craig et al., pers comm.). These species perform distinct roles in the coral reef ecosystem and can provide examples of differential connectivity over meso-scale distances.

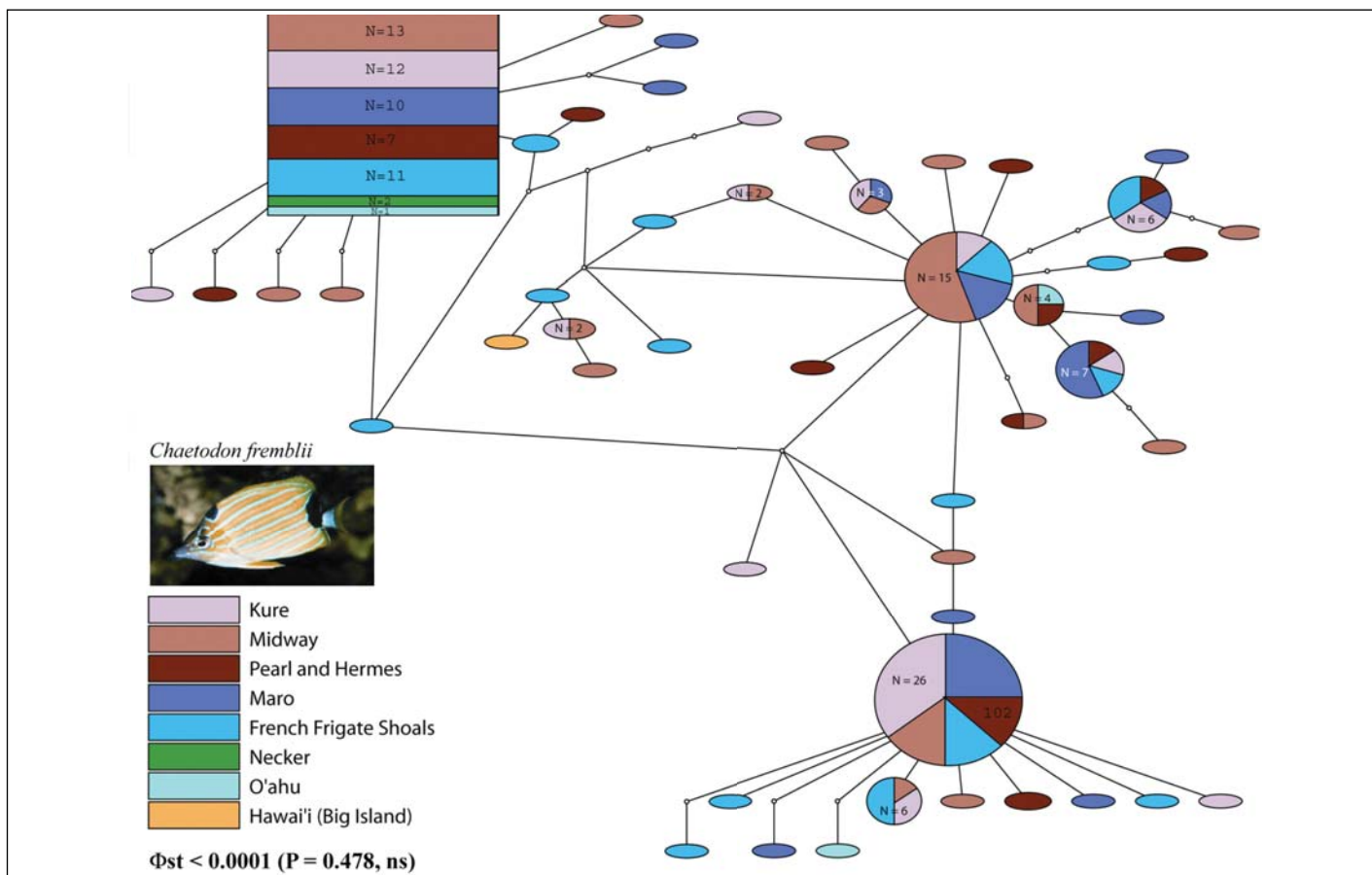


Figure 9.25. Haplotype network for the endemic bluesripe butterflyfish. Source: Craig et al., unpub. data.

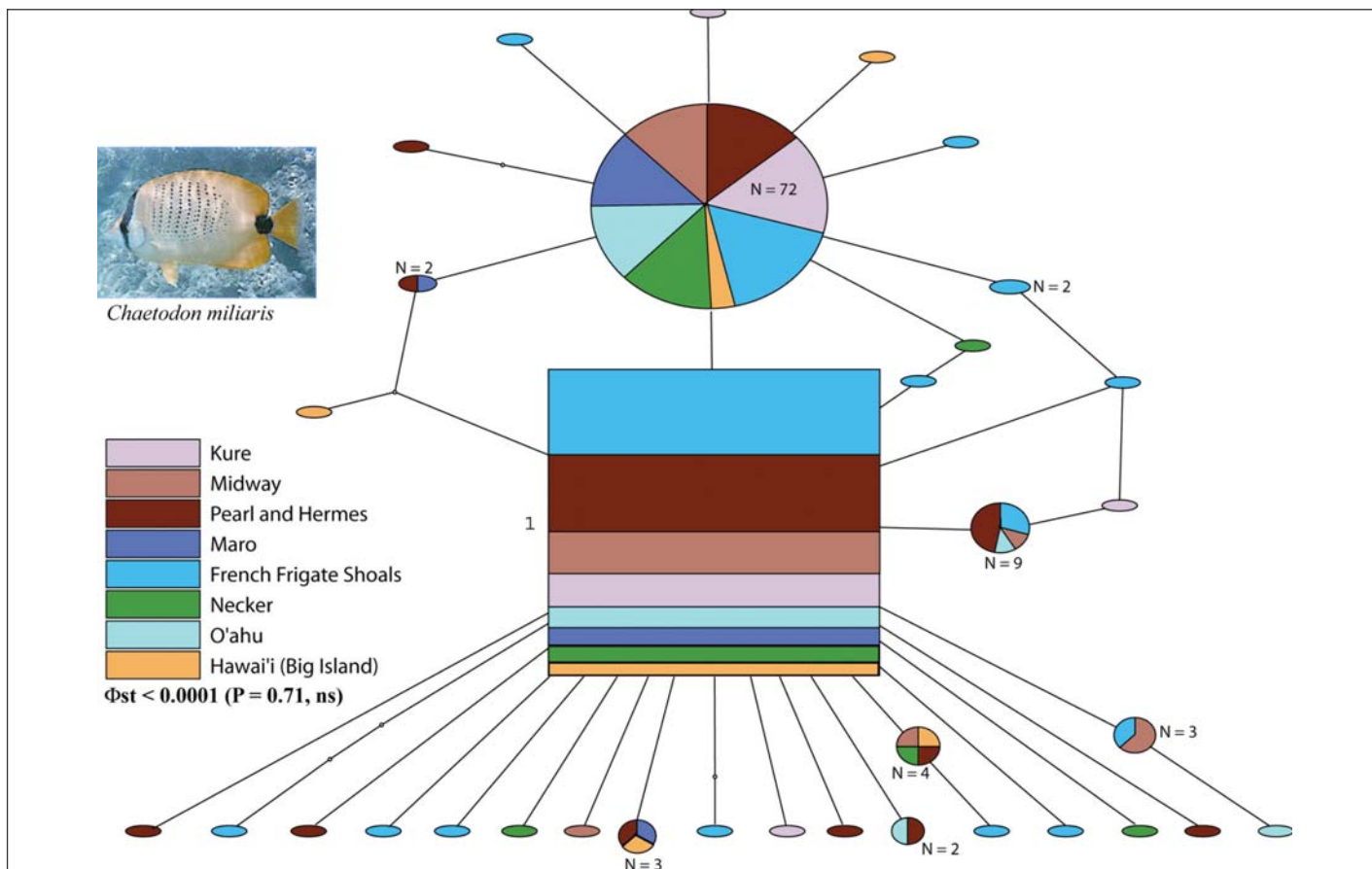


Figure 9.26. Haplotype network for of the endemic milletseed butterflyfish. Source: Craig et al., unpub. data.

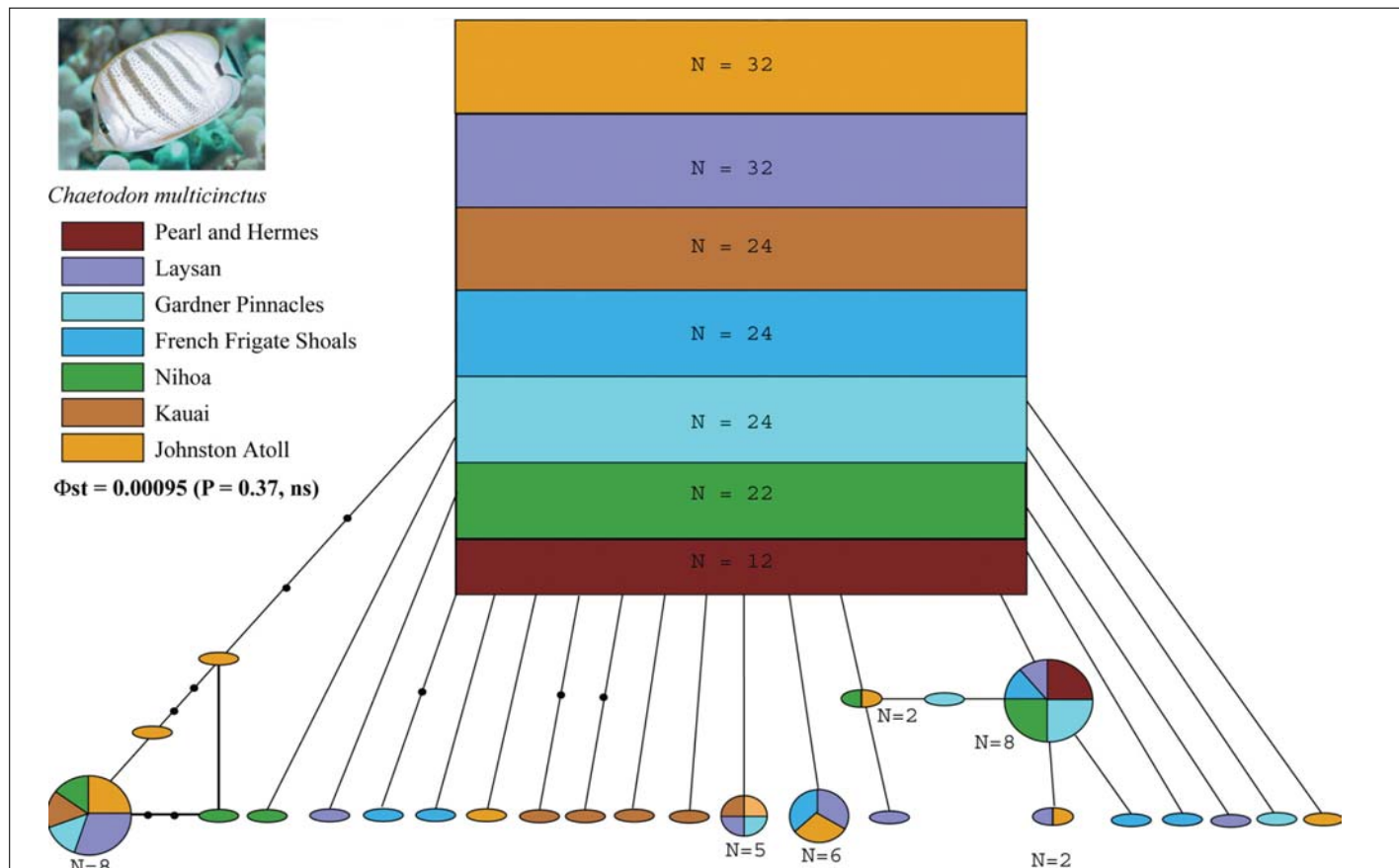


Figure 9.27. Haplotype network for of the endemic pebbled butterflyfish. Source: Craig et al., unpub. data.

ESSENTIAL FISH HABITAT

Fisheries-habitat links are an important consideration with respect to forms of spatial management such as marine protected areas. The composition of suitable habitat within an area can largely dictate fish distribution and abundance patterns. The formal concept of essential fish habitat (EFH) was defined with the reauthorization of the U.S. Magnuson-Stevens Fishery Conservation and Management Act in 1996, and refers to habitat that is recognized as ecologically important to fisheries resources. Critical fisheries habitats must be identified as valued ecosystem components in order to facilitate the formation of ecosystem-based management actions.

Congress defined EFH as “those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity” (16 U.S.C. 1802(10)). The EFH guidelines under 50 CFR 600.10 further interpret the EFH definition as follows: Waters include aquatic areas and their associated physical, chemical, and biological properties that are used by fish and may include aquatic areas historically used by fish where appropriate; substrate includes sediment, hard bottom, structures underlying the waters, and associated biological communities; necessary means the habitat required to support a sustainable fishery and the managed species’ contribution to a healthy ecosystem; and “spawning, breeding, feeding, or growth to maturity” covers a species’ full life cycle.

Analysis was conducted for NWHI bottomfish to determine EFH for these important resource species harvested by Hawaiian-based vessels. The bottomfish fishery has targeted about a half-dozen species of deep-slope (generally >75-100 fm) eteline snappers (family Lutjanidae) and one endemic species of epinepheline grouper (family Serranidae) out of a total of a dozen common Bottomfish Management Unit Species (WPFMC 2004; Table 9.1). These species typically inhabit depth ranges from 100 and 400 m and have been found to be associated with certain benthic features, such as high-relief hard-bottom slopes (Kelley, et al., 2006; Kelley and Ikehara, 2006; Kelley, 2000).

Table 9.1. Dominant species in NWHI bottomfish catch and research-based essential fish habitat boundaries (depth in meters). Illustrations by Les Hata from Hawaii Division of Aquatic Resources.

	LOCAL NAME	COMMON NAME	SCIENTIFIC NAME	DEPTH RANGE (m)
	Ehu	Red snapper	<i>Etelis carbunculus</i>	100-400
	Gindai	Flower snapper	<i>Pristipomoides zonatus</i>	100-350
	Hapuupuu	Hawaiian grouper	<i>Epinephelus quernus</i>	30-300
	Kalekale	Von Siebold's snapper	<i>Pristipomoides sieboldii</i>	50-350
	Lehi	Reddish snapperfish	<i>Apharues rutilans</i>	50-250
	Onaga	Scarlet snapper	<i>Etelis coruscans</i>	100-400
	Opakapaka	Pink snapper	<i>Pristipomoides filamentosus</i>	50-300

The NWHI fishery is divided into two management zones (Mau, Hoomalu), partly in order to distinguish between short- and long-duration fishing trips and short-duration trips to the closer (to the MHI) Mau and more distant (Hoomalu) zones, respectively (Figure 9.28). Between 1996 and 2004, the Mau zone bottomfish catch (Figure 9.29) was dominated by shallow-water species such as jobfish (39%) and thicklipped jack (butaguchi, *Pseudocaranx dentex*, 14%), with pink snapper (opakapaka, *Pristipomoides filamentosus*, 13%), Hawaiian grouper (hapuupuu, *Epinephelus quernus*, 13%), and red snapper (onaga, *Etelis coruscans*, 8%). In contrast, red snapper and pink snapper accounted for 28% and 25% of the Hoomalu catch, respectively, followed by Hawaiian grouper (15%).

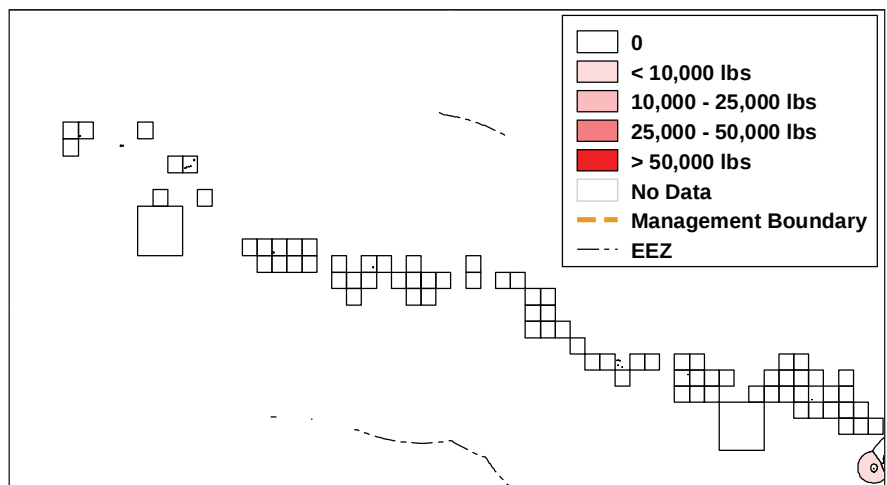


Figure 9.28. Total commercial bottomfish landings from 1996 to 2002. Data in several cells can not be shown due to confidentiality concerns. Data: DAR; Ehler, 2004.

The average annual reported landings of bottomfish in the NWHI between 1984 and 2003 were 336,000 lbs (SD $\pm$ 235,500; NOAA 2006). Of this, the Mau zone averaged 107,130 (SD $\pm$ 53,890) or 32% while the average catch in the Hoomalu zone averaged 228,730 lbs (SD $\pm$ 63,030) or 68% (Figure 9.29). In 2003, the gross

reported revenues for the Mau zone were \$611,000 and \$674,000 for the Mau and Hoomalu zones, respectively (Ehler, 2004).

In 2003, the number of vessels participating in the two zones remained the same from the previous year, but there were substantial changes in the number of fishing trips (NOAA, 2006). In 2003, Mau zone trips decreased by 51% resulting in a 29% drop in landings from the previous year. The number of trips in the Hoomalu zone increased by 50% in 2003, resulting in a 29% increase in landings.

With the initial designation of the NWHI Coral Reef Ecosystem Reserve and now PMNM, fishing activity in the NWHI has been on the decline. Proclamation 8031 allows commercial fishing by federally permitted bottomfish fishery participants that have valid permits until mid-2011 (FR 36443, June 26, 2006). This amounts to a maximum of eight permitted bottomfish vessels that fish within the Monument. Significant work was undertaken prior to the designation of the Monument in response to previously issued Executive Orders that created the Reserve in 2000. This fishery operates according to the management regime specified in the Fishery Management Plan for Bottomfish and Seamount Groundfish Fisheries in the Western Pacific Region. The management regime includes several precautionary measures that minimize potential effects of this fishery. The bottomfishery participants do not operate in the presence of the Hawaiian monk seals and the annual harvest limit for the eight vessels is 300,000 lbs.

The criteria used to delineate potential bottomfish habitat in the NWHI was based on previous analysis done in the MHI (Kelley, 2000; Parke, 2007). Multi-beam data sonar provided the GIS layers for bottom depth, slope and hardness. These factors were used as criteria to identify EFH and potential adult habitat for bottomfish (Table 9.2). The depth range found most appropriate for this analysis was 100-400 m based on EFH criteria. Areas with slopes greater than 20% were then selected in the GIS to further delimit the potential adult habitat areas. Lastly, areas designated as hard bottom based on backscatter values were selected for the final potential adult habitat delineation. The range of sonar backscatter values depended upon the instrument used to collect the data.

EFH and potential adult habitat analysis was completed for French Frigate Shoals, Kure, Maro, and Pearl and Hermes because these islands had sufficient multibeam data. These islands currently do not have complete coverage in the depth range designated for EFH, so the results of this analysis represent bottomfish EFH and potential

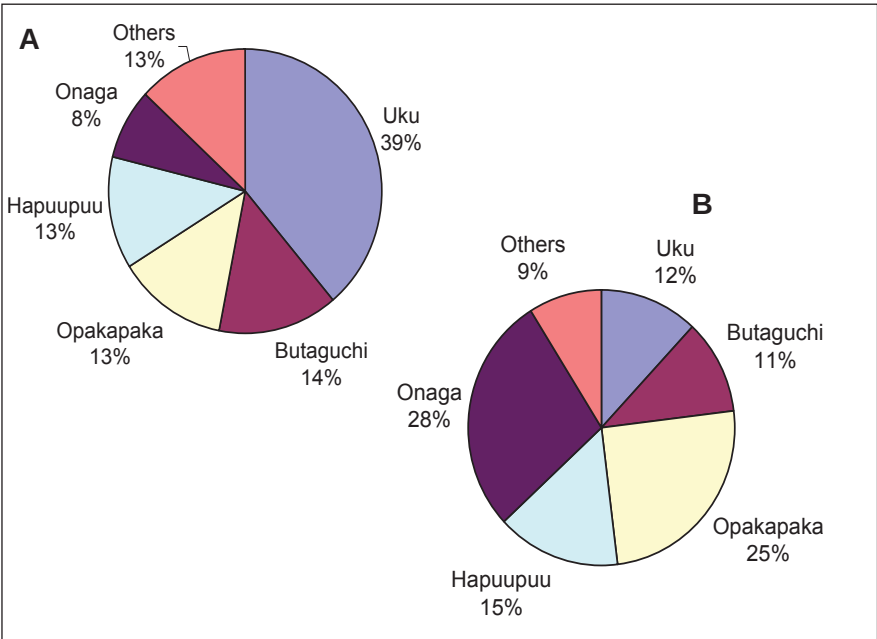


Figure 9.29. Average species composition (1996-2004) of bottomfish catches from the Mau (A) and Hoomalu (B) zones in the NWHI. See text for scientific and common names. Source: Kawamoto and Gonzales, 2005.

Table 9.2. Optimal bottomfish habitat criteria for NWHI. Source: PIBHMC.

GIS LAYER	SOURCE	RANGE
Depth	PIBHMC 20 m multibeam data	100-400 m
Slope	Derived from PIBHMC 20 m multibeam data	> 20 percent slope
Backscatter	R/V AHI	Hard (>120 m)
Backscatter	R/V Kilo Moana	Hard (> 1,000 m)

Table 9.3. Area (km²) of EFH based on available multibeam data detailing depth (100-400 m) within each island. Source: PIBHMC.

ISLAND AREA	EFH (km ²)	% OF TOTAL MAPPED AREA
French Frigate Shoals	243.93	23.51
Kure	138.79	31.19
Maro	407.97	30.32
Pearl and Hermes Atoll	54.12	10.98
Total km ²	844.81	24.00

adult habitat based on the data available to date. Maps for each island were created for areas that met each of the criteria. The areas in these map products that met all three criteria were considered to be “suitable” adult bottomfish habitat (Table 9.3; Figure 9.30).

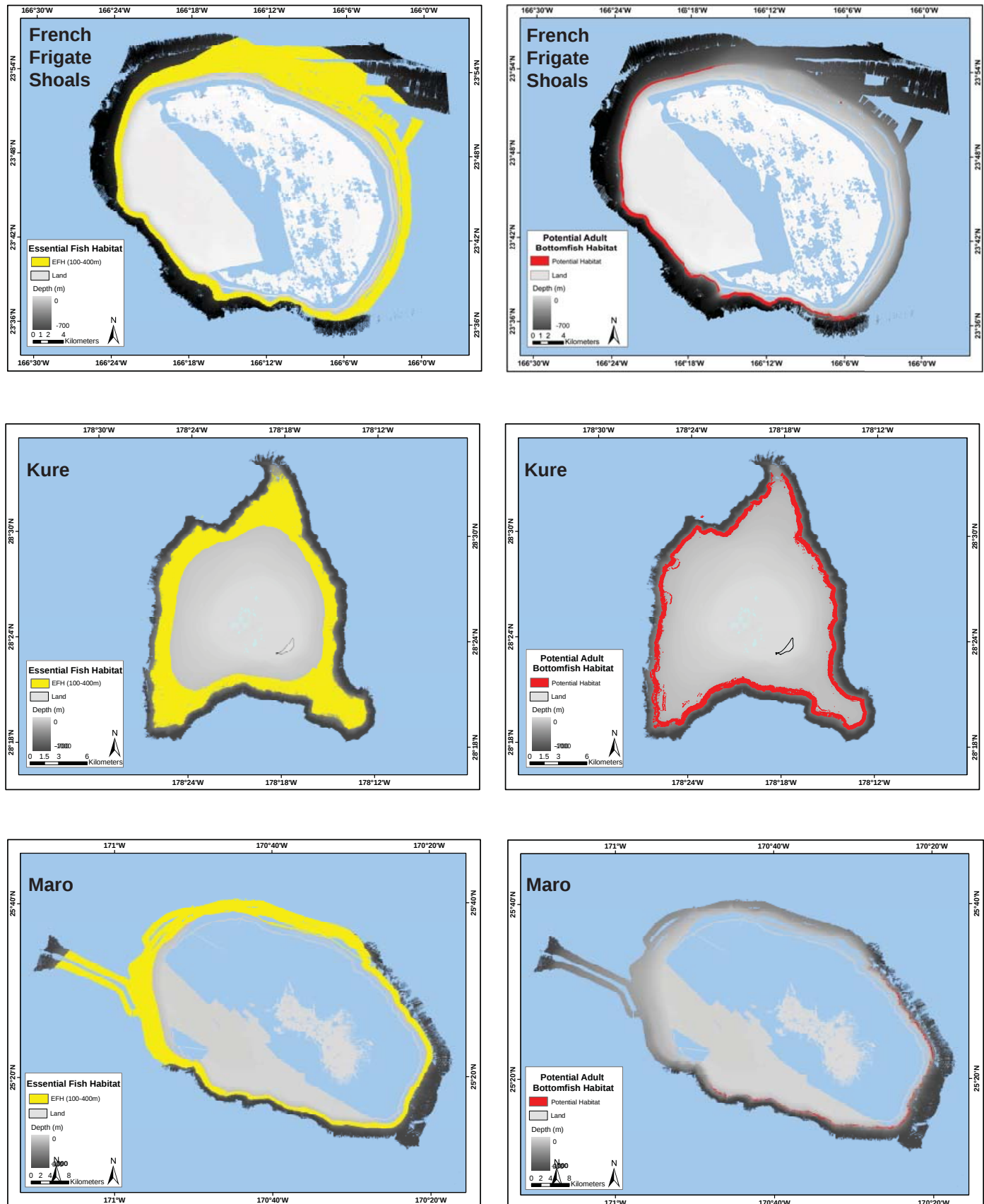


Figure 9.30. Essential fish habitat (yellow) and potential adult bottomfish habitat (red) based on GIS analysis of available multibeam data. Maps: L. Wedding.

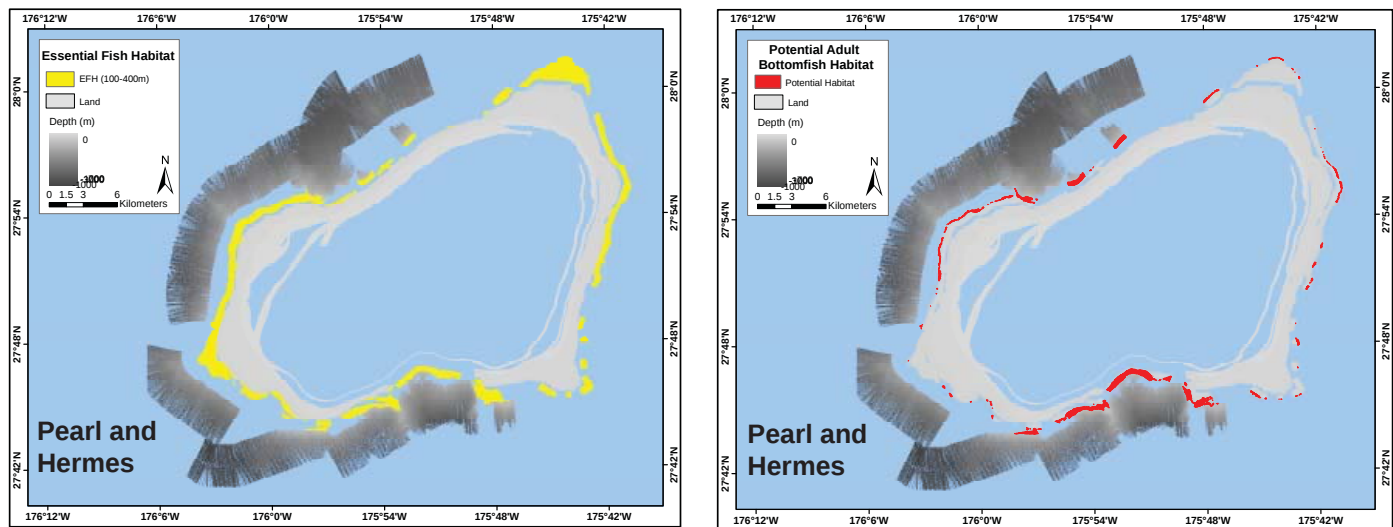


Figure 9.30 (continued). Essential fish habitat (yellow) and potential adult bottomfish habitat (red) based on GIS analysis of available multibeam data. Maps: L. Wedding

TROPHIC RELATIONSHIPS: STABLE ISOTOPE COMPOSITION OF PRIMARY PRODUCERS AND CONSUMER ORGANISMS

Analysis of the carbon (C) and nitrogen (N) stable isotope composition of primary producers, benthic invertebrates, bony (teleost) fishes and sharks was used to assess vertical trophic linkages between primary producers and consumer organisms in the NWHI, and horizontal trophic linkages between reef and pelagic ecosystems. Samples of fish, sharks, invertebrates, phytoplankton and benthic algae were obtained during a May 2005 cruise aboard the NOAA ship *Hiialakai* from six locations in the NWHI (Figure 9.31). Muscle tissue was removed from fish (dissection), sharks (plugs from tagged animals), and invertebrates (dissection). Animal tissue was rinsed in distilled water, dried and ground prior to stable isotope analysis. Seawater was prefiltered through a 200 micron mesh to remove zooplankton and retain phytoplankton on ashed glass fiber filters. Benthic macroalgae were collected by divers, cleaned and rinsed in distilled water, dried and ground. Benthic microalgae were collected by divers from surface sediments. Microalgae were separated from sediment either by vertical migration through nylon mesh (Currin et al., 2003) or by density centrifugation in colloidal silica (Moseman et al., 2004). Algal samples were fumed with concentrated hydrochloric acid to remove carbonates prior to stable isotope analysis. All samples were sent for analysis of ^{13}C and ^{15}N composition by mass spectrometry at the University of California-Davis.

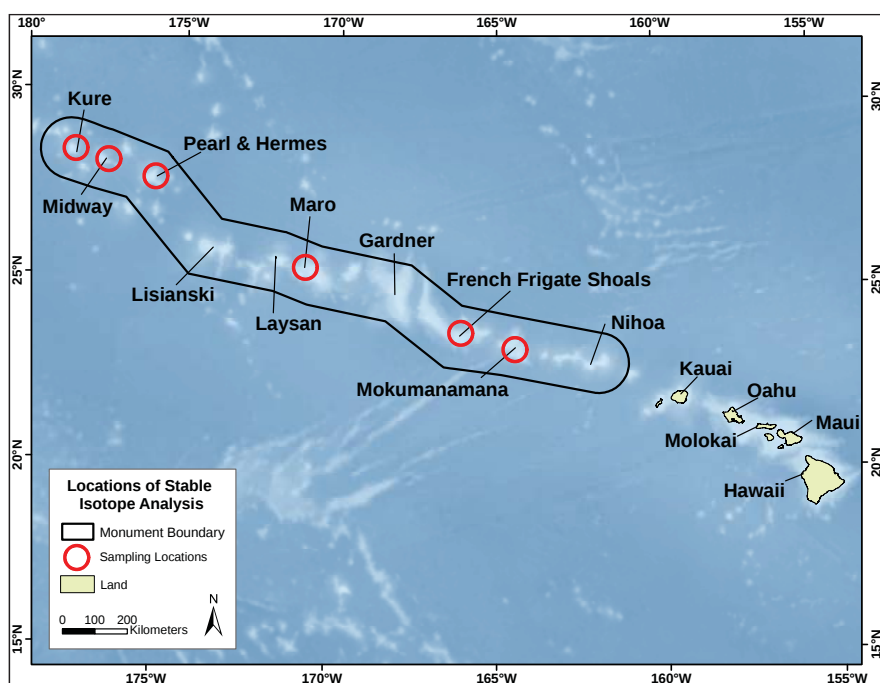


Figure 9.31. Locations for stable isotope analysis from cruises in April, May and September 2005. Map: L. Wedding.

The C and N stable isotope composition of algae is a function of ocean chemistry, photosynthesis and growth rates, and the specific nitrogen uptake mechanisms of the algae. Typically, phytoplankton have a C isotopic signature distinct from benthic algae, and this distinction can be followed through a food web, as animals are usually within 0.5‰ of the ^{13}C value of their food. In contrast, algae differ less in their ^{15}N values, and animals

usually have ^{15}N values that are 2.5 to 4 ‰ greater than their food, and so N isotopes provide a means to calculate the number of trophic steps between primary production and a higher level consumer.

Fish collected from the NWHI were assigned to one of seven trophic groups using diet information in Friedlander and DeMartini (2002) and Parrish and Borland (2004). Invertebrates, which consisted of Hawaiian spiny lobster and a single Hawaiian day octopus, were placed in a separate group. All sharks were classified as apex predators; see Table 9.4 for list of species collected, trophic group assignments and number of samples collected.

Table 9.4. Trophic group assignments for species collected for stable isotope analysis. Number of samples analyzed (n) and common names are also provided.

TROPHIC GROUP	GENUS SPECIES	COMMON NAME	n
Herbivores	<i>Acanthurus olivaceus</i>	orangeband surgeonfish	30
	<i>Acanthurus nigrofuscus</i>	brown surgeonfish	4
	<i>Acanthurus triostegus</i>	convict tang	35
	<i>Acanthurus nigroris</i>	bluelined surgeonfish	23
	<i>Stegastes fasciolatus</i>	Pacific gregory	5
	<i>Zebrasoma flavescens</i>	yellow tang	22
Corallivore	<i>Chaetodon lunulatus</i>	oval butterflyfish	15
Zooplanktivores	<i>Chaetodon milaris</i>	milletseed butterflyfish	54
	<i>Dascyllus albisella</i>	Hawaiian dascyllus	18
	<i>Myripristis berndti</i>	big-scale soldierfish	3
	<i>Myripristis amaena</i>	brick soldierfish	3
	<i>Priacanthus meeki</i>	Hawaiian bigeye	16
Invertebrates	<i>Octopus cyanea</i>	Hawaiian day octopus	1
	<i>Panulirus marginatus</i>	spiny lobster	42
Benthic predators	<i>Lutjanus kasmira</i>	bluestripe snapper	11
	<i>Parupeneus porphyreus</i>	whitesaddled goatfish	14
	<i>Parupeneus multifasciatus</i>	manybar goatfish	37
	<i>Pareupeneus cyclostomus</i>	yellowsaddle goatfish	2
	<i>Bodianus bilunulatus</i>	Hawaiian hogfish/wrasse	15
	<i>Chaetodon fremblii</i>	bluestripe butterflyfish	30
	<i>Thalassoma ballieui</i>	blacktail wrasse	29
Pelagic predators	<i>Euthynnus affinis</i>	wavy-backed tuna	5
Apex predators	<i>Caranx melampygus</i>	blue jack	19
	<i>Caranx ignobilis</i>	white jack	36
	<i>Aprion virescens</i>	green jobfish	6
	<i>Carcharhinus amblyrhynchos</i>	grey reef shark	6
	<i>Carcharhinus galapagensis</i>	Galapagos shark	28
	<i>Galeocerdo cuvier</i>	tiger shark	8
	<i>Epinephelus quernus</i>	Hawaiian grouper	2

There was a clear separation in the ^{13}C signatures of the primary producers in the NWHI system. Phytoplankton (Phyto) had an average ^{13}C value of -23.4‰, consistent with other published values for oceanic phytoplankton. Benthic macroalgae (BMA) and microalgae (BMI) were relatively enriched in ^{13}C , with average values of -18.2 and -9.5 ‰, respectively. There was less separation in the mean ^{13}N values of benthic algae, which ranged from 1.1 to 3.4 ‰ (Figure 9.32).

Fish which were a priori placed in the Herbivore category had lower ^{15}N values than other consumer organisms, as expected. However, the offset between the ^{15}N values of algae and several members of the Herbivore group was higher than the expected 2 to 4‰, suggesting that either some of the fish designated as herbivores are in fact omnivores, or that the algal N values obtained during the May 2005 cruise were more depleted than algal values earlier in the season. This latter point can reasonably explain the observed data, as the isotope composition of fish tissue turns over much more slowly than the isotopic composition of the faster growing algae. There was also a significant range in the C values within the Herbivore group, with yellow tang in particular

closest to the phytoplankton endmember, and the brown surgeonfish closest to the benthic microalgal endmember. Both yellow tang and brown surgeonfish are browsers of macroalgae but isotopic differences suggest there may be finer scale variations in diet (Jones, 1968).

Fish designated as Zooplanktivores and Corallivores, as well as lobster and octopus, had ^{15}N values of approximately 8.25‰, consistent with feeding at two trophic levels above primary producers with an average ^{15}N trophic fractionation value of 2‰. The Zooplanktivores had the lowest C isotope signature, suggesting a greater contribution of phytoplankton to their food web, although a significant portion of benthic production was also utilized by this group. In contrast, the Corallivore had a more enriched C isotope signature, consistent with a greater contribution of coral and benthic algae to its food web.

Fish designated as Benthic Predators exhibited approximately a 3‰ range in both C and N isotope signatures. Benthic Predators with ^{15}N values >10 (blacktail wrasse) may be feeding 2.5 to 3.0 trophic levels above the primary producers. The Benthic Predators with the most enriched ^{13}C values were the whitesaddle goatfish and the Hawaiian hogfish,

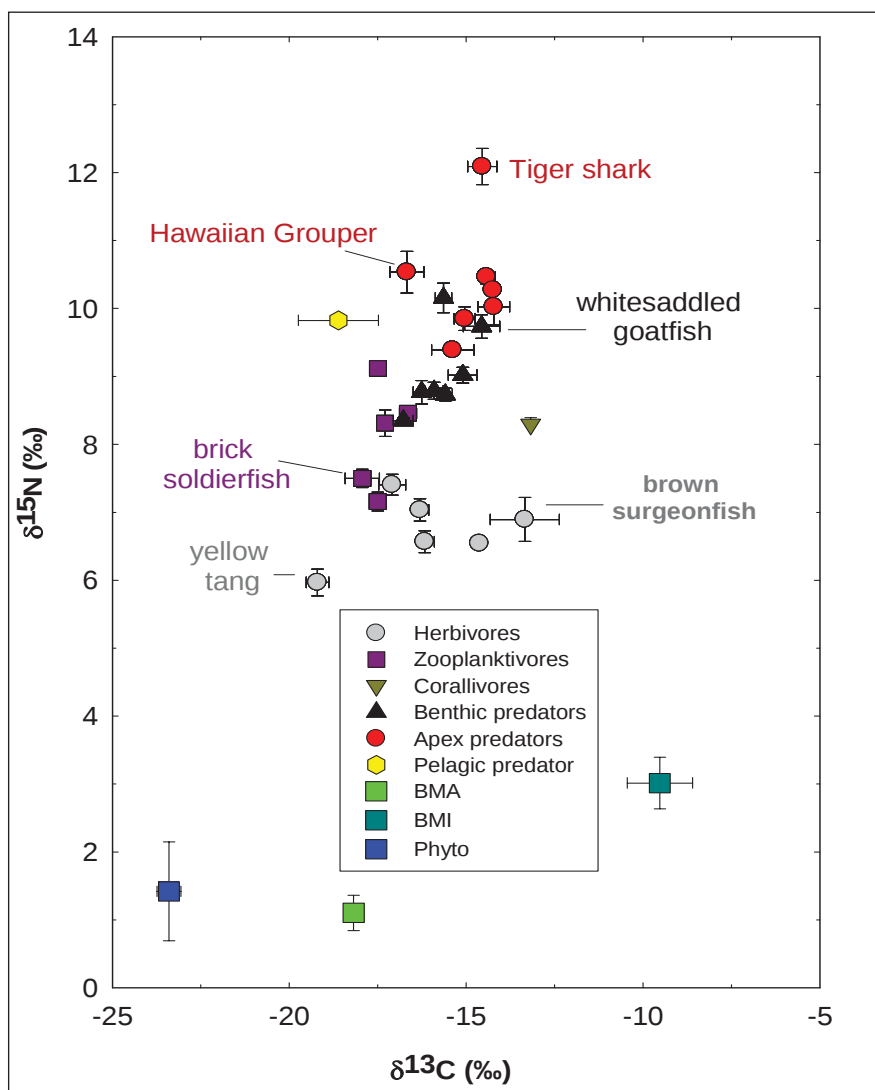


Figure 9.32. Dual isotope plot of consumer and producer groups from the NWHI. Each symbol represents the mean $\pm$ one standard error of the ^{15}N or ^{13}C value for a species of fish, shark or invertebrate. Species list, number of samples and trophic group designations are as in Table 9.4; arrows point to species referred to in the text.

The ^{13}C values of fish designated as Pelagic Predators were relatively depleted in ^{13}C , suggesting that phytoplankton did contribute substantially to the food webs supporting these fish. The ^{15}N values of Pelagic Predators averaged 9.3‰, which is very similar to the average trophic level of the Benthic Predator group, and consistent with an organism feeding two to three levels above the primary producers.

The ^{15}N values of fish and sharks designated as Apex Predators overlapped with the ^{15}N values of the Pelagic Predator (wavy-backed tuna) or Benthic Predator (blacktail wrasse). The exception is the enriched ^{15}N value of 12.1 for the tiger shark, which puts it nearly a full trophic level above other predators in the NWHI ecosystem. This is consistent with marine mammals, sharks, birds and other upper trophic level prey comprising a larger portion of the tiger shark diet than that of Galapagos and grey reef sharks (Papastamatiou et al., 2006). The ^{13}C values of several of the Apex Predator group were enriched in ^{13}C compared to other predators in the system. In particular, it appears that grey reef sharks, Galapagos sharks, giant trevally, and tiger sharks are obtaining the bulk of their C from a benthic-based food web.

The relative contribution of benthic primary production to the food webs supporting bony fish, shark and invertebrate production can be estimated by comparing the stable isotopic composition of these groups with values that would be expected from a prescribed food web. In Figure 9.33, the mean isotope values of each of the trophic groups described in Table 9.4 are displayed. The black dotted lines in the figure represent the

expected graphical position of a consumer group feeding at the first Trophic Level (1 TL) through the fourth Trophic Level (4 TL). The position of these black lines is based on the assumption that there is a 2 – 4‰ increase in ^{15}N values per trophic step, and a 0.5‰ increase in ^{13}C values per trophic step, and that the food web is based on equal parts phytoplankton, benthic microalgae, and benthic macroalgae. In terms of trophic level of the various groups, the figure clearly illustrates the discrepancy between the ^{15}N values of the primary producers as measured in May 2005 and the herbivores that are presumably grazing on them. As noted previously, this could be due to a short-term decrease in the ^{15}N values of the primary producers, and the longer-term average value of the primary producers may be closer to 3.5 – 4.5‰, which would result in the observed herbivore ^{15}N values. Alternatively, it may be that some members of the group designated as 'Herbivores' are in fact. Figure 9.33 also clearly illustrates that the groups designated as Zooplanktivores, Corallivores and Invertebrates (lobster) are feeding a full trophic level above the Herbivores, and that the Benthic and Pelagic Predator groups are feeding about one-half trophic level above that position. Apex Predators (sharks and jacks) are feeding nearly a full trophic level above the Invertebrate/Corallivore level, and about one-half trophic level above the Benthic and Pelagic Predators. As noted previously, and illustrated in Figure 9.32, tiger sharks are an exception and are feeding a full trophic level above the Benthic Predator group. The figure also reveals that all groups other than Pelagic Predators, Zooplanktivores and Corallivores fall roughly where they would be expected to fall if phytoplankton represented approximately 33% of the base of their food web, with the remaining portion deriving from equal parts benthic microalgae and benthic macroalgae. The position of the exceptions indicate that phytoplankton represent a greater proportion of the food web support for Pelagic Predators and Zooplanktivores, and that phytoplankton represent less than a third of the food web support for Corallivores. Taken together, these results from analysis of the stable isotope composition of primary producers and consumers from the NWHI are remarkably consistent with the Ecopath model estimates of the food web supporting fishery production in the NWHI (see next section). Both approaches indicate that benthic algae provide the majority of trophic support for apex predators, and that the entire system consists of a relatively short (three to four trophic levels above primary production) food chain.

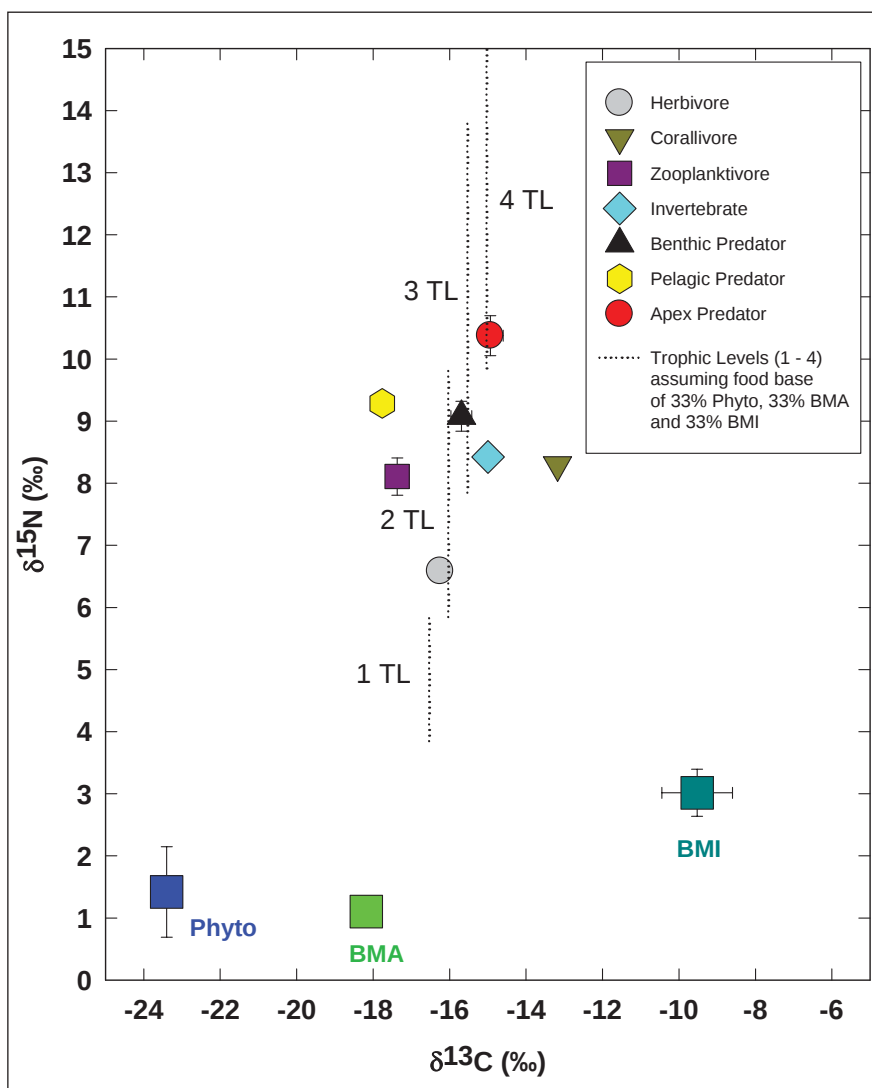


Figure 9.33. Dual isotope plot of mean isotope values of primary producers and each of the trophic groups described in Table 9.4. The black dotted lines in the figure represent the expected graphical positions of a consumer group feeding at the first Trophic Level (1 TL) through the fourth Trophic Level (4 TL), assuming a food web based on equal parts of each of the three primary producers (phytoplankton, benthic macroalgae, benthic microalgae). Further details on assumptions are in the text.

FOOD WEB MODELS

The coral reefs of the NWHI represent a diverse marine ecosystem that provides habitat to a number of organisms (Figure 9.34). In the mid to late 1970s, dozens of scientists participated in a large, multi-year field study program at French Frigate Shoals to describe and better understand this ecosystem (Grigg et al., 2008). These efforts yielded Ecopath, a simulation program designed to model the flow of energy throughout the system. Ecopath works by creating a snapshot of the ecosystem and the feeding relationships between species within that ecosystem. The trophically linked components consist of a single species, or a group of species representing ecological levels. For each species group, biomass, production/biomass ratio (or total mortality), consumption/biomass ratio and ecotrophic efficiency are measured (Polovina, 1984). Ecosim, a new dynamic modeling program based on the original Ecopath model, is now available at (<http://www.ecopath.org>).

Ecopath was first applied to data collected at French Frigate Shoals during the late 1970s (Figure 9.35). The ecosystem was divided into 12 species groups with sharks, jacks, monk seals, sea birds and tuna at the top trophic level, reef fishes at the center, and benthic algae, responsible for 90% of the productivity, at the bottom (Polovina, 1984). The large reef fishes group was further divided into four feeding guilds, resulting in an ecosystem spanning almost five trophic levels with sharks, jacks and piscivorous reef fish representing the top predators (Polovina, 1984). With the exception of limited handline fishing for snappers, the NWHI are not fished and experience relatively few, severe local anthropogenic threats (although sea level rise, acidification, and the warming/bleaching and loss of coral habitat will likely become a major human agent of change at basin and global scales later in this century). Because the NWHI presently has few severe local threats, the Ecopath model provides a picture of an increasingly rare coral reef ecosystem dominated by an abundance of apex predators.



Figure 9.34. The coral reefs of the NWHI are a very diverse and unique ecosystem, providing habitat for a wide range of marine life. Photo: J. Maragos.

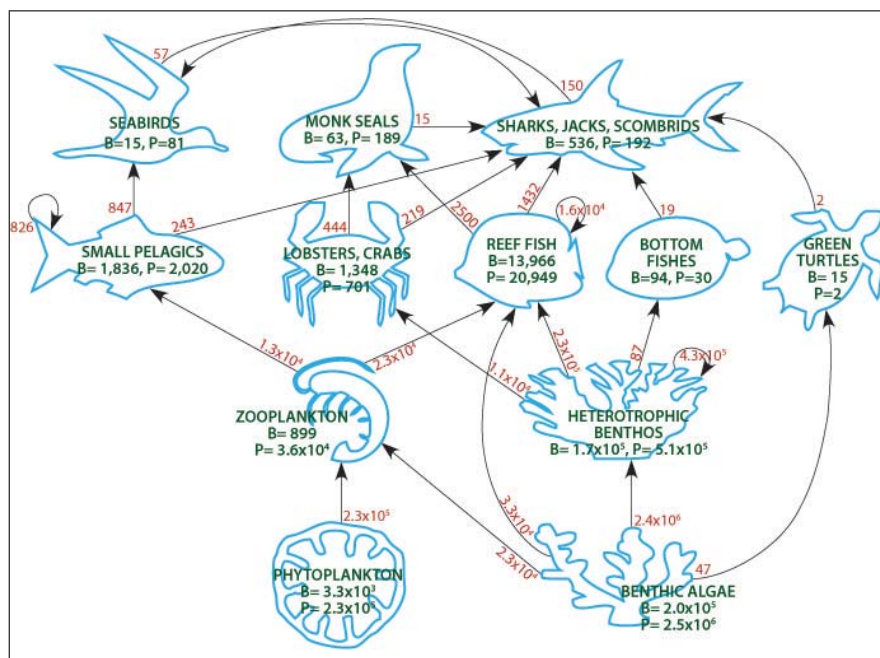


Figure 9.35. Illustration of the Ecopath Model for the food web at French Frigate Shoals. The trophic pathway, annual production (P), and mean annual biomass (B; kg/km²) is given for 12 species groups based on an area of 1,200 km². Source: Polovina, 1984.

The Ecosim was used to simulate changes in ecosystem dynamics over time in response to top-down or bottom-up forcing (Christensen and Walters, 2004) which was modelled by assuming 30 years of high benthic primary productivity, followed by 30 years of low benthic primary productivity (Grigg et al., 2008). Significant

temporal lags, varying by as much as a decade, were observed in the responses of the various trophic guilds both under an increase and a decrease in benthic productivity (Grigg et al., 2008). Planktivorous reef fish trended downward when benthic productivity was high due to the increase in predatory species (e.g., jacks). This was the case even when prey plankton was unchanged. When benthic productivity was changed from high to low there was an immediate sharp increase followed by a decline in benthic carnivorous reef fishes. The reef fishes quickly increased in abundance in response to higher prey availability, but five years later as their predators increased, their abundance declined (Grigg et al., 2008). Even with the more complex Ecosim model, it is important to note that ecosystem dynamics are more complicated than the model provides and are not always consistent with model forcing.

In the last 10 years the Ecosim model was revised using updated parameters and a reference biomass based on surveys of benthic/demersal fish taxa that exhibited habitat fidelity (Parrish, unpub data). Field surveys were spatially stratified by the region's primary habitat types in order to make the model more accurate (Grigg et al., 2008). The surveyed fish communities occupied the central portion of the ecosystem food web and were used to project a minimum biomass for the lower guilds, as well as a theoretical maximum value for the top level transient predators that preyed on the fish (Grigg et al., 2008). Work is now underway to validate the model with the best field estimates of population size, body size distributions, and size-specific food and feeding habits for the endangered Hawaiian monk seal, a top level predator in the NWHI. Numbers and body condition of the seals have been closely monitored for the last two decades and foraging studies indicate a diet of primarily benthic/demersal fish (Goodman-Lowe, 1998; Parrish et al., 2000, 2002 and 2005). Successful validation of the model using monk seals will depend on knowing the boundaries of the seal foraging activity and the relative composition of the diet (Grigg et al., 2008). Once initial validation efforts are complete, the dynamic simulation phase using Ecosim (Figure 9.36) will begin with the goal of forecasting and hindcasting situations to illustrate how the system might react to both natural and anthropogenic stressors.

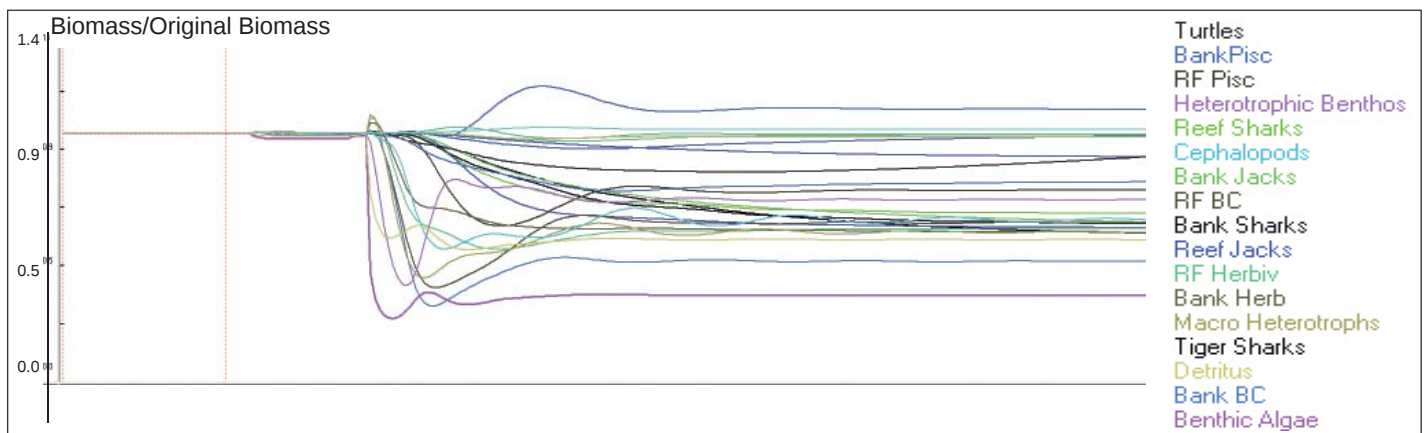


Figure 9.36. Capture of the Ecosim software output for the Ecopath model at French Frigate Shoals. Display shows the response of ecosystem component to a 50% reduction in benthic algae.

EXISTING DATA GAPS

To understand passive transport, there is a need for basic information on spatial and temporal patterns of water movement, quality and characteristics within the NWHI at a range of scales to determine the general patterns of passive transport for nutrients and living resources. Building on an understanding of oceanographic processes, specific research needs and opportunities include efforts to:

- Determine the transport pathways and patterns for the larvae of key organisms;
- Identify the sources and sinks of larval dispersal for key organisms;
- Define the sources and patterns of primary productivity resulting from upwelling sites and occurrences and nutrient input to the NWHI; and
- Undertake applied research into the design of protected areas in support of ecosystem resilience based on passive transports processes, patterns and pathways.

Overall there is a need for systematic information on the active transport and movement of biota into, out of and within the NWHI. This work can be extended to important applications such as stock identification, population dynamics and species interactions. All of these efforts should be undertaken in a way that contributes to the development of models that can predict movement patterns at multiple spatial scales to address questions of connectivity, including the linkages between the NWHI and the MHI.

Specific opportunities include research to improve the understanding of:

- What are the important species that have regular or episodic, active movements or migrations into and out of the NWHI and MHI?
- What life stages of these species are involved in the active movements?
- What are the important habitats for different life stages of these species that move among the reefs within the NWHI and between the NWHI and MHI?
- What are the effects of extreme events and anthropogenic stressors on movements and migrations?
- Which habitats are at risk from climate change and other forces (e.g., sea turtles and their nesting beach habitat)?

As the understanding of most of the species and populations in the NWHI is at the most basic level (e.g., identification of species and groups), genetic studies have the capability to enhance the understanding of the ecosystem, including distribution, dispersion rates, and connectivity or isolation among plant and animal populations in the NWHI. Specific research opportunities include:

- Characterizing the genetic structure of key species and populations;
- Determining genetically distinct subpopulations of flora or fauna between the MHI and the NWHI;
- Determining the value of selected species in the NWHI for repopulating MHI populations that are over exploited or subject to major impacts;
- Applying genetic techniques to key populations across the stress gradient of the archipelago to detect pools of individuals with a genetic makeup that keeps them from being filtered out by the environmental stressors;
- Studying individual species' response to natural and anthropogenic stress (determining the coral species that are more heat tolerant and can withstand coral bleaching);
- Identifying key species that may be at risk from the genetic influence of invasive species. Identifying pilot taxa to serve as proxies for ecosystem genetic connectivity; and

- Because management decision making will be improved by knowledge of many specific factors influencing ecosystem resilience, information is needed on resilience pathways, such as: acclimation to stress, adaptation to stress, the role of the environment and the role of the community. Specific examples of research opportunities include activities to determine:
 - The key aspects that affect ecosystem stability and resilience (e.g., rates of energy flow, oceanographic conditions, nutrient levels and recruitment);
 - The degree to which natural variability in an ecosystem may determine its capacity for resilience;
 - How ecosystem acclimation to change varies among taxa and in relation to survival and the ability to effectively reproduce;
 - How genetic makeup enhances the ability of taxa to recover from some kinds of stress;
 - Which environmental conditions, e.g., temperature, flow, geomorphology, have a mitigating influence on survival in a changed environment;
 - The extent to which the reduction or expansion of one or more species or functional groups results in top down predation or an increase in bottom up production;
 - How the rebound of an ecosystem depends on maintaining established pathways of energy flow which provide the system a stable means of recovery rather than risk a transition to a different state of equilibrium;
 - The extent to which reducing fish populations of the ecosystem undermine or realign energy flow and trophic stability; and
 - Whether self seeding systems are resilient.

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