Spatial connectivity of Pacific insular species: Insights from modeling and tagging

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Certificate of Authorship

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To all, *mahalo nui loa*

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Abstract

Animal movement was quantitatively investigated with computer simulation modeling and the analysis of animal-borne tagging data. Larval transport was simulated using advection-diffusion models driven by a variety of current fields. Seasonal, interannual, and spatial correlates of larval transport and retention were explored, as well as the effect of pelagic larval duration (PLD), using generalized additive modeling (GAM) analyses. Diel vertical migration (DVM) was simulated using layered current fields, and the effect on horizontal transport was examined over a range of PLDs, spawning locations, and spawning times. DVM was found to robustly facilitate natal retention in the simulations, using GAM analyses. Biogeographic transport routes linking Johnston Atoll and the Hawaiian Archipelago were elucidated using high-resolution current data and advection-diffusion models. The hypothesized transport routes were consistent with existing field survey data and genetic analyses. This connectivity has implications for both population maintenance and biogeographic affinities. Archipelagic connectivity was determined for all pairs of geographic strata in the region, and a simple metapopulation model was developed which was driven by the modeled linkages. Additionally, the flow fields used for the Johnston Atoll analysis and the archipelagic connectivity analysis were ground truthed with a drifter buoy database and found to be in good agreement. Conventional tags deployed on a deepwater snapper were examined to determine adult movement dynamics. Comparison to a simple model of swimming behavior suggested that biphasic swimming may be the characteristic swimming pattern for this species. Electronic tags deployed on sea turtles were used to characterize pelagic habitat in the North Pacific, using a suite of oceanographic and environmental data merged to the satellite tracks. Most of the analyses involved examination of a variety of remotely-sensed, modeled, or surveyed environmental data.

Chapter 1. Introduction

1.1 Dispersal of organisms: significance and difficulties

One fundamental determinant of an organism's role in populations, communities, and ecosystems is simply their physical placement in the environment (Andrewartha and Birch, 1954). The movement of organisms in this environment over a range of many spatial scales is often a critical aspect of their life history. For example, movement is a key element of gene exchange, disease transmission, and metapopulation connectivity; and is especially relevant to the effective management of harvested stocks since localized depletion of widely dispersing organisms is important to differentiate from overharvesting of organisms over their entire distribution. Population replenishment via connectivity of separated adult stocks (e.g., Roberts, 1997) or, alternatively, lack of such connectivity (e.g., Cowen et al., 2000; Jones et al., 2005; Almany et al., 2007) is vitally important to understand in the context of species inhabiting complex spatial mosaics in a dynamic environment (Sale and Kritzer, 2003). Over longer time scales, biogeographic dispersal and evolution in the marine environment is linked to the movement (both dispersal and retention) of different phases of the life-history. The geographic distribution of species has been contentiously debated for many years, with proponents of vicariance biogeography suggesting that habitat fragmentation and subsequent evolution of geographically isolated clades are more important towards understanding observed patterns of distribution and abundance (e.g., Carpenter and Springer, 2005), while proponents of dispersal biogeography suggest that dispersive events of an organism outside of its normal range and subsequent adaptive radiation are more important towards understanding observed patterns of distribution and abundance (e.g., Rosenblatt and Waples, 1986). Marine biogeographic patterns are likely a product of both vicariance and dispersal events (Paulay and Meyer, 2002), since these processes are merely endpoints of a continuum and not a dichotomy. Movement of individual organisms remains a vitally important aspect in the life-history of organisms in either framework of biogeographic study, especially for marine organisms considering such hypotheses as the ‘surface circulation vicariance’ mechanism put forth by Veron (1995) to explain biogeographic patterns in coral species. This hypothesis suggests that ocean currents underlie many observed patterns of distribution and abundance in the marine ecosystem, whereby this physical transport mechanism is thought to drive evolution (termed reticulated evolution) more so than biological mechanisms are thought to drive natural selection. This is a contentious point, but serves to underscore the importance of studying the movement, both passive and active, of marine organisms residing within a fluid environment.

The movement of organisms is often problematic for human study. The organisms in question may be too small to see or may inhabit areas that are difficult to visually assess by an observer, or the movements may be temporally episodic and therefore unpredictable and difficult to directly observe. For many marine organisms, nearly all of these constraints apply, hindering our understanding of movement dynamics. Small planktonic organisms inhabit the open water and are difficult to enumerate, capture, and even identify in many cases. Larger marine fauna may inhabit deeper water or the open ocean where direct observation is either difficult or interferes with the normal behavior of the organism. Similarly, movement pertaining to migration, reproduction, and foraging may be difficult to predict and observe until the temporal dynamics are well understood. This thesis presents the application of two very different yet complementary methodologies for understanding movement dynamics in marine organisms. Firstly, computer simulation modeling is shown to be a useful technique to address many movement questions involving pelagic, planktonic organisms. Secondly, utilization of tags, both conventional and electronic, is shown to be a useful technique to address many movement questions involving larger, mobile organisms in the marine environment. The rationale for using these techniques will be briefly developed.

Plankton and other small pelagic organisms in the marine environment are notoriously difficult to sample quantitatively. Most survey approaches, whether based on visual surveys, nets, traps, cameras, or acoustics are prone to various biases due to gear selectivity, visibility, organism behavior, and other factors which affect the rate of capture or ability to enumerate on a species-specific basis. Most planktonic organisms which are entirely planktonic throughout their life history, termed holoplankton, are relatively well-identified. However, the subset of planktonic organisms which are composed of the early life history stages of larger demersal or pelagic organisms, termed meroplankton, are very difficult to identify to species in most regions of the world, particularly in the tropics where there is relatively higher diversity. Many of these meroplanktonic larval forms are extremely rare due to temporally and spatially discrete spawning events, widespread dispersal/dilution, and generally lower abundance of individual species within a diverse ecosystem. This compounded effect of extreme rarity, difficulty of capture, and identification problem poses a unique challenge for researchers attempting to understand pelagic ecology of these meroplanktonic life history stages. For certain taxa (slow-moving, robust, abundant), plankton nets are an adequate sampling device, and rigorous field sampling programs built around these tools have yielded much useful ecological insights (Beaugrand et al., 2002; 2003; Hays et al., 2001; 2005). For other taxa (not slow-moving, not robust, or not abundant), impediments remain in their quantitative sampling.

For example, in Hawaii two widely-cited studies are Leis and Miller (1976), and Lobel and Robinson (1988). Both of these studies were attempting to document important oceanographic impacts on larval fish transport, yet were severely hampered by sampling difficulties as pointed out by Clarke (1991). Leis and Miller (1976) attempted to show how larvae were distributed horizontally from shore as a function of whether they originated from demersal or pelagic eggs. This was essentially a very early meta-analysis combining the results from several independent plankton surveys. There was a correspondingly heterogeneous mixture of survey locations (different sides of islands), years (1969, 1971-1973), seasons (poor monthly coverage), times (some day only, some night only, some both), sampling gear (mix of 1m, 3m plankton nets and midwater trawl), depths (some surface, some oblique), and sample sizes (few hundred cubic meters to few thousand cubic meters). Due to the unstandardized and inadequate sampling, the results were presented on a relative basis as percent of total larvae along a nearshore to offshore gradient. Lacking absolute abundance estimates, the initial conclusion that larvae of pelagic spawners are more abundant offshore while larvae of demersal spawners are more abundant nearshore is poorly supported, and the entire pattern is apparently driven by the distributional patterns of only a few abundant species of one spawning type (Clarke, 1991). Lobel and Robinson (1988) attempted to show how larval fish were more abundant in certain portions of mesoscale eddies. Despite the likely importance of eddies on larval transport, the inadequate survey gear and small sample sizes of this study preclude any type of conclusion (Clarke, 1991), especially when it is seen that over half of their larval density estimates presented are based on single captures of specimens per sampling station.

Physical sampling of pelagic larvae may be intractable in many situations. Typical towed plankton sampling gear is often inadequate for quantification of larval fish abundance. Notable attempts have been made, however. For example, in Hawaii it is worth mentioning two relatively recent, large-scale, field sampling programs which attempted to quantify spatial and temporal patterns of larval fish abundance around the archipelago, using state-of-the-art towed sampling gear in offshore regions. Both studies were driven by the need for scientific information on the meroplanktonic larval forms of demersal, insular species such as coral reef fishes and the commercially important bottomfish species complex (various snappers, jacks, and a grouper). The first study was a series of oblique (0-325m depths) Issacs-Kidd midwater trawl and bongo net samples taken around Oahu in 1977-1978 on 14 research vessel cruises (Clarke, 1991). This survey was targeted towards older larvae using larger gear with coarse-mesh nets. The second study was an extensive set of horizontally and vertically stratified (0-200m depths) samples with an opening-closing MOCNESS net system and a Manta neuston net in 1985-1986 around Oahu on 4 research vessel cruises (Boehlert and Mundy, 1996). This survey was targeted towards younger larvae using smaller gear and fine-mesh nets. The findings of these published studies are not widely known and are not readily available online or in most libraries, hence their mention and summary here (Table 1.1). Both studies, which required months of ship time and many years of sample processing, demonstrated that the extreme rarity of larvae of demersal, insular fish species, coupled with obvious problems in avoidance of the sampling gear by larger larvae and extrusion through the net meshes by smaller larvae, was an overall severe impediment to understanding their pelagic distributions. Only 14 species of nearshore fish were captured and identified to species by both studies, among the thousands of specimens and hundreds of types. Median densities of older and younger larvae of these 14 nearshore species were 0.0089 and 0.3125 per 1000 cubic meters, respectively, suggesting surveys on the order of 5.13X and 1.07X the original survey effort would have been required for quantifying a snapshot distribution of a typical species in this region (i.e., to capture ~100 individuals of the median abundance species at any one point in time and space). Expanding this to include some rudimentary seasonal and/or spatial coverage would tremendously magnify the requisite sampling effort. Given the present estimated species count at 451 “shore fish” species in the Hawaiian Archipelago (Mundy, 2006), it is apparent that many more surveys, and much improved larval identifications are needed to fully understand larval ecology in an ecosystem context, using traditional field sampling methods. This discourse is not intended to argue that field sampling is futile, but clearly other technologies must be developed to replace towed nets for the efficient quantification of larval distributions, preferably using non-lethal approaches. Light traps (Doherty, 1987) and crest nets (Dufour and Galzin, 1993) can be very effective for particular species/stages/regions of study, but both are primarily nearshore in application for the interception of late-stage larvae as they settle. A relatively new technology with much promise for efficient open ocean surveys is the use of a towed high-resolution imaging system such as the ISIIS (Cowen and Guigand, 2008).

Table 1.1 – Summary of Clarke (1991) and Boehlert and Mundy (1996) ichthyoplankton surveys around the Hawaiian Islands. Larval catch statistics are presented for species which were captured and identified in both surveys. Target sampling volumes are presented for a "typical" species using the median catch statistics. For perspective, volumes are also presented in OSSP[1] and Sydharb[2] units.

Description	Clarke (1991)	Boehlert & Mundy (1993)
Sampling gear used	3m Isaacs-Kidd midwater trawl, 125cm bongo nets, 70cm bongo nets	1m MOCNESS and 70cm Manta neuston net
Dates of survey	1977-1978	1985-1986
Location of survey	Leeward Oahu	Windward & Leeward Oahu
Number of cruises	14	4
Number of days	28	40
Number of tows	140	520
Depths sampled	0-325m	0-200m
Volume filtered (m^3)	2202324	299174
Volume equivalency in OSSP[1] units	881	120
Volume equivalency in Sydharb[2] units	1 / 227	1 / 1671

Species	Total number captured and number per 1000m^3 in Clarke (1991)	Total number captured and number per 1000m^3 in Boehlert & Mundy (1993)
Aprion virescens	9 (0.0041)	206 (0.6886)
Asterropteryx semipunctatus	3 (0.0014)	4710 (15.7433)
Brotula multibarbata	16 (0.0073)	2 (0.0067)
Crystallodytes cookei	4 (0.0018)	97 (0.3242)
Dendrochirus barberi	5 (0.0023)	2 (0.0067)
Eleotris sandwicensis	90 (0.0409)	90 (0.3008)
Eviota epiphanes	33 (0.0150)	54853 (183.3482)
Glossanodon struhsakeri	2 (0.0009)	2 (0.0067)
Gunnellichthys curiosus	29 (0.0132)	74 (0.2473)
Limnichthys donaldsoni	1 (0.0005)	337 (1.1264)
Luzonichthys earlei	260 (0.1181)	35 (0.1170)
Parapercis schauinslandi	521 (0.2366)	412 (1.3771)
Pseudojuloides cerasinus	149 (0.0677)	18 (0.0602)
Trachinocephalus myops	23 (0.0104)	629 (2.1025)

Metrics for sampling "typical" species	Clarke (1991)	Boehlert & Mundy (1993)
Median number per 1000m^3	0.0089	0.3125
Volume target for n=100 (m^3)	11293969	319972
Volume target equivalency in OSSP[1] units	4518	128
Volume target equivalency in Sydharb[2] units	1 / 44	1 / 1562
Volume target equivalency relative to entire original survey	5.13X original volume	1.07X original volume

[1] OSSP = volume of Olympic sized swimming pool ~2,500m^3

[2] Sydharb = volume of Sydney Harbour ~500,000,000m^3

Movement patterns of larger marine organisms also pose unique challenges to researchers. Direct observation is not always practical, and there may be unknown observer effects on normal behavior. Indirect methods to reconstruct movement are appealing since they do not interfere with the organism prior to sampling. This would include methodologies such as genetic fingerprinting (Raybould et al., 2002), examination of trace element/stable isotope deposition (Rubenstein and Hobson, 2004), and use of parasites to backtrack locations (Olson and Pratt, 1973). The drawbacks of these approaches are that they are costly, time-consuming, require sophisticated laboratory support and statistical analysis, and usually require an already dead specimen or the sacrifice of a live specimen. The latter concern is very relevant to the increasing number of species with some manner of conservation and/or protection status (e.g., collection of a large number of otoliths for elemental composition from an endangered species would be nearly impossible). In-situ video and passive listening devices may be useful to discern movement patterns; however, the requisite identification of individuals may be problematic. An array of passive listening devices coupled with acoustic tagging offers to yield much insight into movement patterns of large organisms (Klimley et al., 1998); however, this requires some prior knowledge of where the individuals will likely relocate. Passive listening devices for target species vocalizations may also assist in this regard if, for example, fish vocalizations could be identified to individuals as is possible in other taxa (Gilbert et al., 1994; Yin and McCowan, 2004). Computer simulation of adult movement is also a practical approach, but the models are difficult to parameterize without some actual data on movement. Active swimming is likely to be more important for larger organisms, in contrast to possibly more reliance on passive drifting with ocean currents for smaller organisms.

Despite being larger and seemingly easier to observe, the movement of large marine organisms is not easily quantified using simple, historical methodology.

Marine organisms which inhabit deep water and the open ocean present many of the above challenges to researchers studying their movement. For example, sea turtle hatchlings which leave the nesting beaches spend many years of their juvenile and subadult lives in the open ocean where there is virtually nothing known about them (Dodd, 1988). Coastal foraging and reproductive behavior near the nesting beaches are well understood; however, the logistics of surveying the offshore regions has hampered understanding of this portion of the life history. Deepwater demersal fishes which inhabit the deep slopes near islands or continents are often assumed to be relatively sedentary and unable or unwilling to cross deep channels separating areas of preferred habitat. This assumption has widespread implications for population dynamics, fisheries management, and conservation; yet this assumption is rarely confirmed because of the difficulty of monitoring individual fish which reside at depths beyond the reach of direct observation. The difficulties are only slightly moderated at shallower depths. Movement of individual fishes on and between coral reefs is also not well understood, but some data indicate that post-settlement movement between patch reefs can occur (Frederick, 1997; Johannes, 1981; Samoilys, 1997). This further emphasizes the need to study population-wide patterns of movement at all life-history stages. SCUBA, submersibles, and remote cameras are useful for casual observation but can be problematic for quantitative assessment of abundance or movement of individuals over large time and space scales.

1.2 Methodologies to study movement

Many types of computer simulation approaches are available for modeling organism movement. One particular approach based on individual trajectories is called Lagrangian modeling. This approach is very amenable to modeling individual organism movement because it is based on individual particle dynamics and not, for example, based on bulk, mass-transfer approaches which blur the distinction between individual behaviors and average, net fluxes across arbitrary boundaries. Lagrangian modeling principally arose as a tool to study drifter buoys deployed in the open ocean, but has since become a useful multidisciplinary methodology amenable to a variety of applications (Olson et al., 2001). Lagrangian modeling in marine biology has proven useful for reconstructing long-distance animal movements and migrations in the open ocean (e.g., Hays and Marsh, 1997; Kettle and Haines, 2006). Many applications of Lagrangian modeling will be explored in subsequent chapters of this thesis.

Models of larval dispersal may implicitly incorporate larval swimming behavior. Most of this thesis will focus on approaches examining passive transport of presumed eggs and larvae. This was done for several reasons. Firstly, the eggs and early stage (preflexion) fish larvae are almost assuredly passive, as are many invertebrate larvae for their entire duration. It is apparent from the literature that some, perhaps many, late stage fish larvae can be very good swimmers (Leis, 2007); however, it is unclear exactly how prevalent this is, as some late stage fish larvae do not swim as much and are more “floaters” and “drifters” (e.g., Hogan and Mora, 2005). Secondly, it is not clear which cues are generally being used by the swimming larvae and what the limits of sensory detection are, making parameterization very speculative. For example, the detection radius will be very differently shaped depending on whether an auditory, olfactory, visual, geomagnetic, etc. type of cue is assumed. While some older larvae can swim very well, it is not clear at all how much is random movement (hence, just another component of diffusivity) versus directional movement via some type of navigation, particularly in open ocean settings. Thirdly, there is also abundant literature on episodic settlement, interannual variability, and other important temporal variations. Much of this is clearly due to supply of larvae, i.e., a water mass with competent larvae is in the correct place at the correct time. At other times either the larvae were not physically in that water mass (advected elsewhere) or they have undergone mortality via starvation, predation, or some other process. It is conceivable that larvae may orient to and swim to the correct water mass, but without data to parameterize this process it can become very speculative and the results will be driven by the assumed behavior. I chose to concentrate on Lagrangian modeling of physical transport and habitat quality from an oceanographic perspective, and simply assume that behavioral processes of some type occur at the end of the larval duration if the propagules are within a certain symmetrical radius of the target site. The results presented in this thesis can be built upon as more becomes known about larval behavior (Leis, 2007), rather than be invalidated by the inadvertent choice of the wrong behavioral parameterizations.

The utilization of animal-borne tags is a very old methodology started in the 1800’s and continuing today with various evolutions in tagging technology. Conventional tags consisting of a simple external marker on the organism remains a useful technique, as well as more elaborate, electronic tags which have the ability to geo-locate from satellites or other listening stations, as well as monitor depth, time, temperature, and a suite of other environmental conditions. Some tags even monitor feeding events, swimming, orientation behavior, and physiology. Some of the most data-rich tags are animal-borne video cameras such as Crittercam™ (Marshall, 1998). In addition to the simple external markers, there are internal techniques as well such as, for example, microscopic coded wire tags, chemical marking, and dyes. Most of the external and internal techniques are simple enough to facilitate mass markings of individual organisms. With advents in tagging technology, and the lower costs of deployment and monitoring, many previously intractable problems in animal movement are now within reach of scientific study using a spectrum of low-technology to high-technology methodologies.

1.3 Conservation issues

Different methodologies to study movement require different input materials. Some of the more technologically advanced approaches may require samples of bones or fresh tissue necessitating the sacrifice of specimens. As mentioned earlier, in many instances this may be unacceptable due to conservation status, permit issues, or capture difficulties. Techniques which can use sloughings, natural carcasses, or biopsy samples may become more popular in elemental and genetic analyses. Sophisticated instrumentation attached to animals may also come under increased scrutiny as animal rights activism becomes more widespread. Inevitably, even seemingly innocuous activities such as plankton sampling, acoustic surveys, visual surveys, etc. may become excessively regulated. Extractive techniques, even when partnered with commercial harvesting activities, are problematic when dealing with regulated areas, seasons, or species. In many marine protected areas (MPAs) there are difficulties in acquiring scientific access to survey target species. The actual collection of specimens requires even more extraordinary measures, particularly with managed, protected, or endangered species. Nonextractive, nonintrusive, and nonlethal approaches are favored for future development and use. Additionally, methods which can forecast movement may facilitate targeted studies promoting more efficient use of scientific resources as well as minimize impact to the environment (e.g., temporally and spatially targeted larval surveys to minimize ship time needed, and to reduce associated environmental impacts). Data on organism movement can be used to parameterize easy-to-use tools to assist resource managers (e.g., Condie et al., 2005), particularly for the design and evaluation of MPAs (Botsford et al., 2003). Clearly, there is a need for improving and using methodologies to study organism movement which minimizes the impact to all aspects of the ecosystem. Two such approaches, computer simulation modeling and animal-borne tags will be the tools of choice in the applications presented in subsequent chapters of this thesis.

1.4 Statistical analyses and modeling

Generalized additive modeling (GAM) will be used throughout this study in addition to conventional statistics. GAM is a relatively new statistical technique which is particularly amenable to situations in which the underlying predictor variables are related to the response variable in patterns which may be complex and nonlinear (Hastie and Tibshirani, 1990). GAM is a nonparametric technique which offers much flexibility in handling a diverse suite of continuous and categorical variables for exploratory, explanatory, and predictive modeling. Chapter 7 also makes extensive use of another nonparametric technique called the Kolmogorov-Smirnov test.

Most of the simulation modeling performed in this study is written in the computer languages ***Xbasic*** or ***QuickBasic***. Both of these languages offer very straightforward syntax and structure, and run very efficiently on a desktop or laptop computer system within the Windows operating system environment. They also allow extensive graphical displays of real-time progress during execution of the simulations in GIS-type format. This feature is particularly useful for observing transitional stages of simulations, and as well as for debugging faulty code. Both languages also support very large multidimensional arrays, which are necessary when dealing with very large spatial grids in time-series fashion; for example, most of the variables examined in this study are in 3 dimensions (latitude X longitude X time). Depth could potentially add a fourth dimension to certain datasets, and these complex data structures are easily accommodated for instant indexing to desired values of the environmental data arrays stored within memory. In Chapter 6, the ***QuickBasic*** code was also used to perform a large number of nonlinear regression minimizations in batch mode.

1.5 Target species

Each of the chapters of this thesis pertains to different marine organisms found around the Hawaiian Archipelago. Chapters 2 and 5 relate to a general suite of insular organisms with pelagic larvae. Chapter 3 relates to insular organisms with vertically migrating pelagic larvae. It is presently unknown how prevalent this phenomenon is, but anecdotal evidence suggests that many species exhibit some aspect of vertical migration. Chapter 4 relates primarily to insular marine species which have colonized the Hawaiian Archipelago using Johnston Atoll as a biogeographic stepping stone, or to species which may rely on this linkage for present day population maintenance. Chapter 6 is focused upon the deepwater benthic snapper opakapaka, *Pristipomoides filamentosus*, and its movement dynamics around the lower portion of the Hawaiian Archipelago. Chapter 7 is focused upon the pelagic juvenile stage of the loggerhead sea turtle, *Caretta caretta*, and its movement dynamics across the entire North Pacific basin. These organisms and some brief description of their life history and other pertinent information are found in Table 1.2. It should be noted that PLDs in Hawaiian species are relatively poorly known, hence the presentation of familial proxies for reference.

Table 1.2 – Summary of target organisms addressed in this thesis, their relevant characteristics, challenges to researchers, and description of solutions explored in this thesis.

Taxa	Key life history characteristics	Challenges to researchers	Solutions explored in this thesis
Insular species of the Hawaiian Archipelago with pelagic larvae	Adult life history stages are geographically separated and primarily nondispersive. A larval form is spawned which resides in the oceanic environment during the pelagic larval duration (PLD) prior to settlement and recruitment. A wide range of PLDs occurs across taxa, some example familial PLDs (minimum-maximum, sample size, and references): PLD=13-35 days: damselfishes (n=100 species; Wellington and Victor, 1989) PLD=21-38 days: lutjanine snappers (n=5 species; Zapata and Herrón, 2002) PLD=26-39 days: butterflyfishes (n=3 species; Brothers et al., 1983) PLD=27-60 days: gobies (n=10 species; Brothers et al., 1983; Sponaugle and Cowen, 1994) PLD=17-104 days: wrasses (n=124 species; Victor, 1986a; Sponaugle and Cowen, 1997; Victor and Wellington, 2000) PLD=52-84 days: surgeonfishes (n=5 species; Randall, 1961; Brothers et al., 1983; Rocha et al., 2002) PLD=90 days: eteline snappers (n=1, Leis and Lee, 1994) PLD=36-274 days: slipper lobsters (n=17 species; Booth et al., 2005) PLD=152-548 days: spiny lobsters (n=11 species; Booth and Phillips, 1994; Polovina and Moffitt, 1995)	Unknown dispersive abilities of pelagic larvae, unknown spatial and temporal effects, unknown connectivity of geographically discrete areas, unknown importance of local retention, unknown importance of long distance transport.	Chapters 2 and 5 examine retention, transport, and connectivity for areas within the Hawaiian Archipelago using computer simulation modeling.
Insular species of the Hawaiian Archipelago with pelagic larvae	Insular species with pelagic larvae which migrate vertically; this is likely all taxa to varying extent.	Unknown effect of vertical migration on horizontal transport, unknown prevalence of vertical migration behavior.	Chapter 3 examines the effect of diel vertical migration on horizontal transport using computer simulation modeling and layered ocean current fields.
Insular species with pelagic larvae dispersing from Johnston Atoll to Hawaiian Archipelago	Various taxa in the archipelago appear to have biogeographic linkage to Johnston Atoll, including acroporid corals, coral pathogens, opihi, vermetid gastropods, bonefish, damselfish, and the Hawaiian grouper.	Unknown ability of pelagic, planktonic propagules to disperse from Johnston Atoll to the Hawaiian Archipelago since the prevailing winds and currents are in the opposite direction.	Chapter 4 examines possible routes of pelagic transport using computer simulation modeling with high resolution current fields.
***Pristipomoides filamentosus* in the Main Hawaiian Islands**	Opakapaka, a deepwater snapper found throughout the Pacific inhabiting patchily distributed pinnacles and deep slope habitats, is a commercially important species in the handline fishery, see eteline snappers above.	Unknown movement dynamics of the juvenile and adult opakapaka, despite being managed using a variety of spatial management measures.	Chapter 6 examines the movement dynamics of opakapaka using a database of conventional tags with comparison to a simple model of fish swimming behavior.
***Caretta caretta* in the North Pacific Ocean**	The North Pacific stock of loggerhead sea turtles nest in the Western Pacific, pelagic juveniles and adults range across the entire North Pacific Ocean.	Unknown movement behavior of life history stages in the open ocean.	Chapter 7 examines the movement dynamics of loggerhead sea turtles using a database of electronic tags coupled with remotely sensed environmental data.

1.6 Goals of this study

The goals of this thesis are to demonstrate the utility of computer simulation modeling and animal-borne tags towards understanding movement dynamics in a marine environment. Some technical aspects of the modeling are first presented, followed by some applications towards ecologically relevant questions. Chapter 2 reports a broad spatial and temporal scale set of simulations to examine seasonal, interannual, and spatial correlates of retention and transport. Chapter 3 incorporates an additional dimension of larval behavior to examine the effects of vertical migration on horizontal transport. These modeling results are then developed further into investigations bridging physical connectivity with ecological connectivity. Chapter 4 presents an application of transport modeling to address a historically intriguing question regarding physical linkages between 2 areas in Hawaiian region, followed by Chapter 5 which attempts a broader examination of physical linkages throughout the archipelago, with metapopulation consequences examined. Next, 2 types of tagging data (conventional and electronic) are presented for very different organisms, a deepwater demersal fish in Chapter 6 and the pelagic juvenile stage of a sea turtle in Chapter 7. In these two chapters it is shown how these types of data can be used to understand movement and habitat usage for species and areas which are very difficult to study by conventional means. Lastly, the results of this thesis are synthesized into an overlying theme related to ecological connectivity over many scales and dimensions of spatial patterning.

Chapter 2: Seasonal and interannual variability in larval transport and oceanography in the Northwestern Hawaiian Islands using satellite remotely sensed data and computer simulation

Kobayashi, D. R., and Polovina, J. J. 2006. Seasonal and interannual variability in larval transport and oceanography in the Northwestern Hawaiian Islands using satellite remotely sensed data and computer simulation. *Atoll Research Bulletin* **543**: 365-390.

2.1 Abstract

Larval transport and oceanographic conditions experienced by pelagic larvae in the Northwestern Hawaiian Islands were simulated using an individual-based approach to track daily movements in a Lagrangian modeling framework. These advection-diffusion models were configured with 1x1 degree resolution, monthly geostrophic currents estimated from satellite altimetry. Larval dispersal was simulated for each month of the year from 1993-2002 for 3, 6, and 12 month larval durations. Four release locations were evaluated, Midway Island, Maro Reef, Necker Island, and Oahu. Larval retention was evaluated by tabulating successful simulated settlement, which was scored based on larval proximity to release-sites after completion of the pelagic duration. Sea surface temperature and chlorophyll concentration at each daily larval location were tabulated utilizing similar resolution satellite remotely sensed data products (NOAA Pathfinder AVHRR SST and SeaWiFS ocean color), and these in situ values were integrated over the entire larval duration for each larval track. These oceanographic variables are of critical importance in the early life history because of their hypothesized relationships to larval growth and feeding success, both critical determinants of larval survival and successful recruitment. The sea surface temperature

and chlorophyll histories experienced by successfully settling larvae display strong seasonal and interannual patterns, which were decomposed using generalized additive models (GAMs). These patterns may be useful towards understanding episodic recruitment events, as well as for posing hypotheses towards understanding the mechanisms underlying spawning seasonality. These transport dynamics and oceanographic patterns have general implications for a variety of vertebrate and invertebrate meta-populations in the Northwestern Hawaiian Islands.

2.2 Introduction

Temporal patterns of reproduction are a widespread phenomenon in both plant and animal ecology. Organisms can attempt to maximize their fitness by propagating at times which are optimal for maximum reproductive output and/or enhanced survival of their young. It is commonly thought that the latter is of more importance for highly fecund aquatic species which broadcast their abundant young into the pelagic environment (Johannes, 1978; Thresher, 1984). Several scales of temporal variability may be of importance in the timing of reproduction. Diel patterns, such as spawning near dawn or dusk, may be important to minimize predation on both the spawning individuals and their pelagic propagules (e.g., Doherty, 1983). Lunar patterns, such as spawning near spring tides (full and new moon) may be related to key variables which change consistently on a monthly scale such as tidal currents and moonlight illumination (e.g., May et al., 1979). Seasonal patterns, such as spring or summer spawning, may be related to key variables which change consistently on an annual scale such as currents, plankton blooms, and temperature (Johannes, 1981). Seasonality in spawning has been well documented in a variety of Hawaiian fish and invertebrate species (e.g., Itano, 2000; Lobel, 1989; Randall, 1961; Reese, 1968; Walsh, 1987).

Various hypotheses have been put forth to explain such seasonality. Johannes (1978) has argued that predatory losses on pelagic propagules have been a driving selective force for spawning seasonality. More recent views of pelagic larval transport have emphasized retention issues and the concept of a closed population (Jones et al., 1999; Kingsford et al., 2002; Leis, 2002; Mora and Sale, 2002; Robertson, 2001; Sponaugle et al., 2002; Swearer et al., 1999). While predation and retention issues may be important, the predominately oligotrophic pelagic environment has led some to suggest that larval food supply is the single most important factor governing the numbers of marine fish (Cushing, 1972). Reese (1968) suggested that the different spawning seasons used by ecologically similar species of hermit crabs were a mechanism to reduce competition for pelagic larval food. Larval food supply involves spatial and temporal patchiness, and the species composition of the phytoplankton and microzooplankton is critically important (Lasker, 1975). In addition to starvation issues, variability in food supply has been shown to be a important determinant of larval growth and subsequent survival (e.g., Booth and Alquezar, 2002). Faster growth has been hypothesized to favor survival by reducing cumulative predatory mortality (e.g., Anderson, 1988). Leis and Carson-Ewart (1999) suggest that larger size is an important factor for evading predation during the settlement process, citing fin erection behavior and importance of speed when fleeing predators, based on field experiments with coral trout larvae. It is possible that small size may be an advantage for remaining undetected during settlement; however, the advantages of being larger in the plankton probably outweigh the disadvantages, considering the gauntlet of size-based pelagic predators (reviewed by Purcell and Arai, 2001; Zaret, 1980). Additionally, larvae which grow faster may retain a size and survivorship advantage during the critical first few weeks post-settlement on the reef (Bergenius et al., 2002; Booth and Hixon 1999; Sponaugle and

Pinkard, 2004). While size is most directly a function of age, both food and ambient temperature have been shown to have a strong positive effect on larval growth (e.g., Buckley et al., 2004). Clearly, in addition to physical retention, there are a suite of other considerations critical in the early life history survival of insular species.

Earlier works have used advection-diffusion models to examine larval transport and retention (e.g., Griffin et al., 2001; Hill, 1991a; Polovina et al., 1999; Siegel et al., 2003). Few such applications have integrated the oceanographic conditions experienced by individual larvae directly into the model. With the availability of remotely-sensed data products, it is logical to incorporate these environmental fields into the computer simulation framework, particularly with individual-based modeling approaches (e.g., Mullon et al., 2002). Sea surface temperature (SST) and chlorophyll-a concentration are widely available from a variety of satellite sensors, and both of these variables may have important linkages to the ecology of early life history stages, as described above for growth and mortality. The goals of this paper are to examine, via computer simulation and use of remotely-sensed environmental data, the seasonal and interannual components of larval retention, transport, growth, and survival in selected regions of the Hawaiian archipelago. The second author contributed some ideas towards this work in the early phases; all the modeling, analysis, and writing was performed by the first author.

2.3 Methods

Simulated larval releases were stratified by year (n=10: 1993-2002), month (n=12: January-December), locations spanning the Hawaiian archipelago (n=4: Midway, Maro, Necker, and Oahu, see Figure 2.1), and larval duration (n=3: 3, 6, and 12 months) to yield a total of 1440 model treatments. Five thousand simulated larvae were released for each model treatment for a total of 7.2 million individuals. Each individual was tracked daily for the entire larval duration in Lagrangian fashion using the following equations:

$$
\begin{aligned}
x_{t+\Delta t} &= x_t + \left[u_{(x_t, y_t, t)}\Delta t + \varepsilon\sqrt{D\Delta t}\right] / \cos(y_t) \\
y_{t+\Delta t} &= y_t + \left[v_{(x_t, y_t, t)}\Delta t + \varepsilon\sqrt{D\Delta t}\right]
\end{aligned}
$$

where x represents longitude, y represents latitude, t represents time in days, u represents the E/W component of the current speed, v represents the N/S component of the current speed, $\cos(y_t)$ adjusts distance by latitude to account for the spherical coordinate system, and D is the diffusivity coefficient (500 m^2/sec following Polovina et al., 1999). It is recognized that the diffusivity coefficient may be scale-dependent and not constant in the ocean; however, for the resolution of the circulation data utilized in this study the assumption of constant diffusivity may be adequate (Paris, pers. comm.). The currents utilized in this study were monthly 1° latitude/longitude resolution geostrophic flow fields calculated from satellite altimetry obtained from CNES/AVISO/SSALTO (CLS Space Oceanography Division, France). Integrated SST and chlorophyll-a histories encountered daily by individual larvae were tabulated daily using interpolations from monthly 1° latitude/longitude resolution data grids. SST data was obtained from the MCSST (NOAA Pathfinder AVHRR satellites) product from NASA/JPL. Chlorophyll-a data was obtained from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) instrument on board the Seastar satellite. Integration was performed by simply averaging the daily SST or chlorophyll-a interpolations over the entire pelagic duration. Additionally, only averages from the subset of larvae scored as successfully being retained by the source site following completion of the entire pelagic duration were tabulated to each treatment. A 140 km radius for scoring larval retention was used, similar to Polovina et al. (1999). This detection radius was chosen to allow adequate settlement for relative comparisons between sets of simulations. For each of the 1440 treatments, the following were tabulated: the number of larvae scored as retained, the number of larvae scored as settling at Oahu, the number of larvae scored as not settling at any of the 4 sites, the average SST encountered by this subset of retained larvae, and the average chlorophyll-a encountered by this subset of retained larvae. SST was available for the entire temporal duration of this analysis; however, chlorophyll-a data was only available from 1997 onwards. Mortality was not included in this modeling, aside from the predicted advective losses. The advection-diffusion model was written in the open-source software XBASIC (http://www.xbasic.org) and run on an Intel P4 Windows XP system. Generalized Additive Models (GAMs) were used to delineate relationships between a suite of response variables (retention, SST history, or chlorophyll-a history) and a suite of predictor variables (year, month, location, and larval duration). GAM is a relatively new analytical technique (Hastie and Tibshirani, 1990) which is useful when the predictor variables have unknown a priori and possibly nonlinear effects upon the response variable. GAM analysis was carried out using the analytical software package S-Plus v. 6.1.2r2 on an Intel P4 workstation using Redhat LINUX 7.3 OS. Six GAM analyses were performed as outlined in Table 2.1, with each utilizing a different suite of predictor variables as described. The graphical output in the form of smoothing splines and comparative categorical effects serve as the primary basis for interpretation after a satisfactory GAM is chosen.

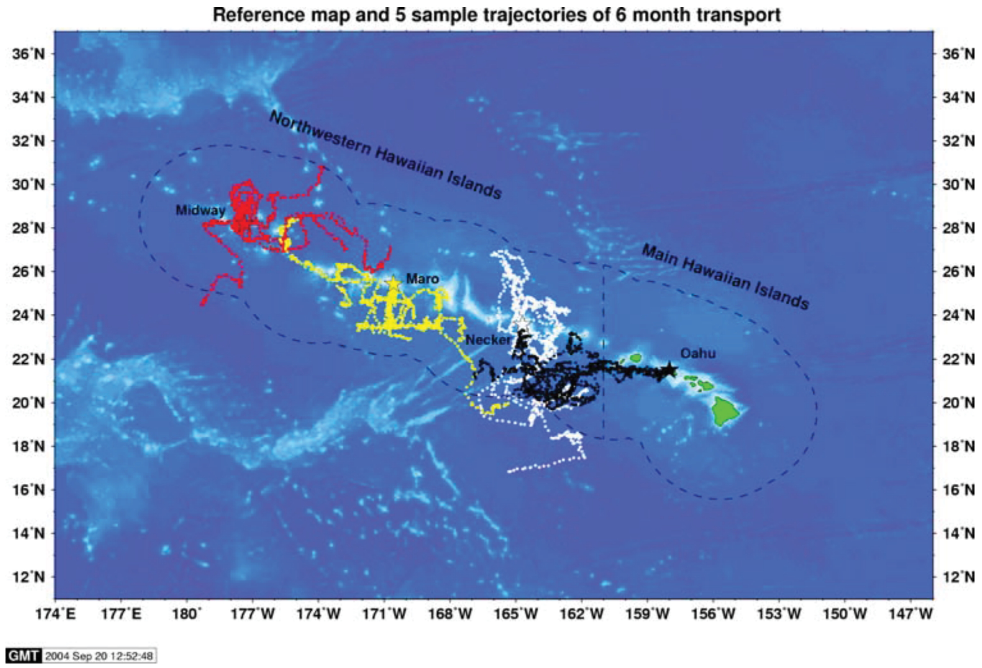


Figure 2.1 - Map of Hawaiian archipelago indicating larval release sites used in this analysis. Five sample releases from each site for a 6 month pelagic duration are shown.

Table 2.1 Summary variables used in generalized additive modeling (GAM) analyses.

Response variable	**Predictor variable(s)**
Larval retention (all data)	Year, Month, Site, and Duration
Larval settlement at Oahu (all data)	Site
Larval settlement at Oahu (separately by site)	Year, Month, and Duration
Larval non-settlement (all data)	Year, Month, Site, and Duration
Integrated SST history of retained larvae (separately by duration)	Year, Month, and Site
Integrated chlorophyll-a history of retained larvae (separately by duration)	Year, Month, and Site

2.4 Results and Discussion

Retention varied from a low of 0/5000 (scored for 39 different treatments) to a high of 3908/5000 (scored for October, 1993, Midway, 3 month release). Retention was strongly related to larval duration, and had weak relationships to year, month, and site (Figures 2.2A-2.2D). The negative relationship between retention and larval duration is intuitive, in that a longer larval duration implies a greater chance of long distance transport with subsequent loss to the system. This is similar to the hypothesis of Leis and Miller (1976) that larvae of demersal spawning reef fish (generally shorter pelagic duration) would be found closer to shore than larvae from pelagic spawning reef fishes (generally longer pelagic duration). Some of the proposed physical mechanisms which can transport reef fish larvae back to their spawning site operate on the time scale of 2-3 months (e.g., Lobel and Robinson, 1986), consistent with the relatively high retention found in this study for a 3 month larval duration. Late stage larvae of some reef fishes can occur at great distances from suitable adult habitat (e.g., Clarke, 1995; Victor, 1987), but are of unknown importance for local population persistence. This issue of long-distance dispersal may, however, be important for larval interchange in a metapopulation framework, which will be examined elsewhere for insular species in the Hawaiian archipelago (Kobayashi, in preparation).

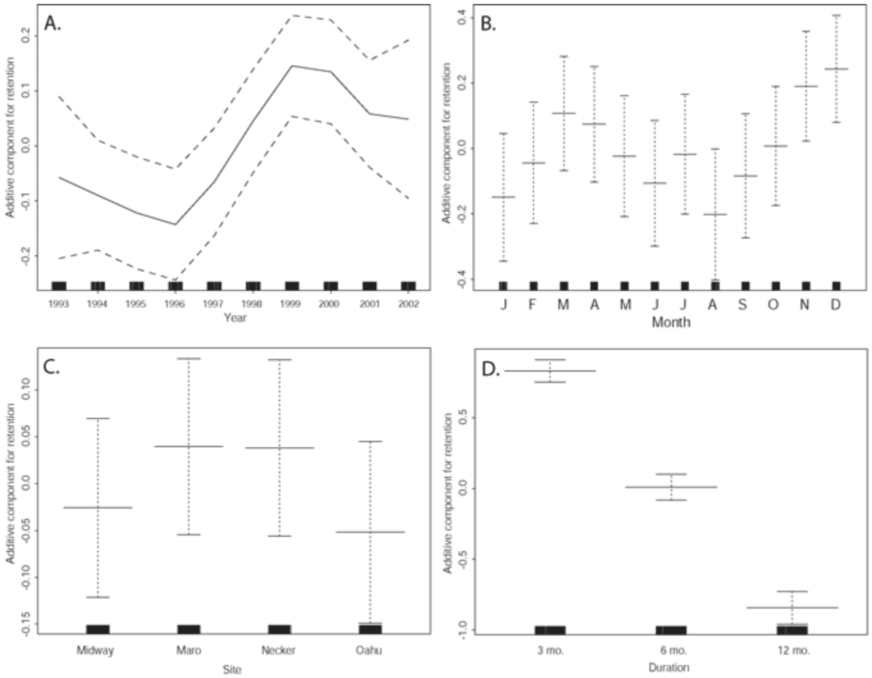


Figure 2.2 - Results of GAM application to larval retention. The predictor variables are year, month, spawning site, and larval duration. C.I. are ±2 standard errors.

Larval settlement at Oahu was strongly dependent on spawning site (Figure 2.3). This is an intuitive result, with Oahu settlement negatively correlated with distance from Oahu. The GAMs were run separately for the spatial effect and other variables due to the numerous zeros in the data for sites further from Oahu (e.g., 85% of the Midway runs yielded 0 larval settlement to Oahu). This lack of data contrast in other sites effectively weighted the GAM primarily towards the Oahu site, leading to difficult interpretation. Hence, the GAM was run separately for each site (Figures 2.4-2.7), with the last GAM being a simple retention analysis for Oahu only. Strong yearly effects were observed in all sites, with weak monthly effects, and duration only becoming important at Necker and Oahu. Oahu settlement was favored by a longer larval duration from Necker (Figure 2.6C, the closest site to Oahu), and by a shorter larval duration from Oahu itself (Figure 2.7C).

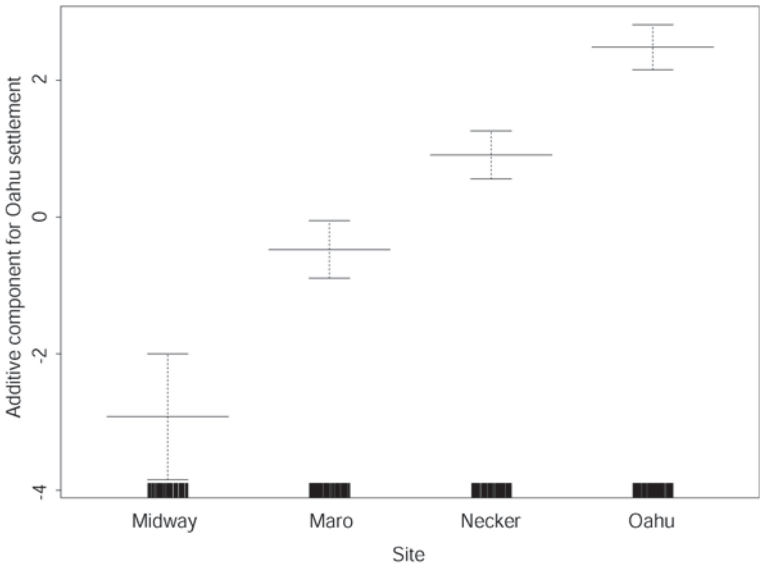


Figure 2-3 - Results of GAM application to larval settlement at Oahu. The predictor variable is spawning site. C.I. are ±2 standard errors.

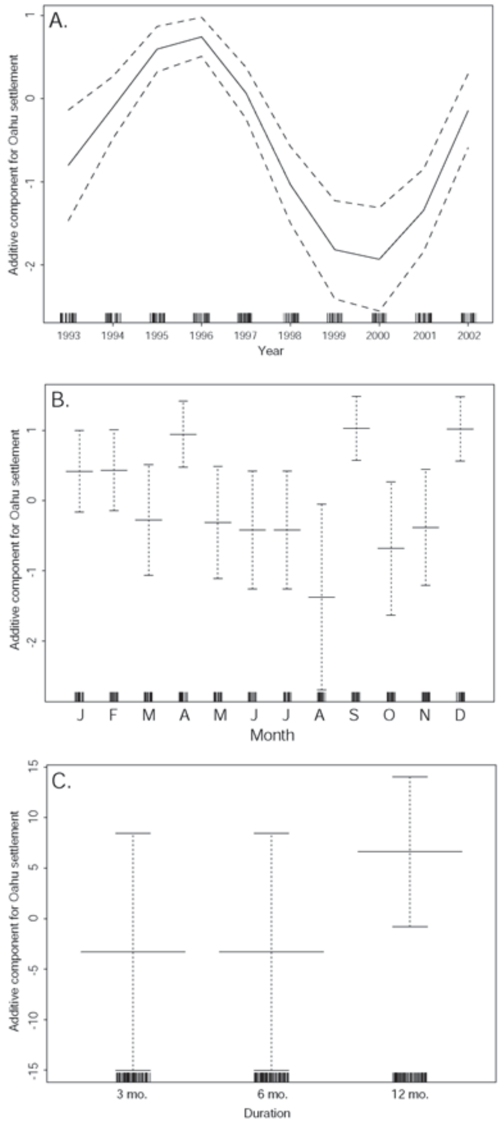


Figure 2-4 - Results of GAM application to larval settlement at Oahu from Midway spawning. The predictor variables are year, month, and larval duration. C.I. are ±2 standard errors.

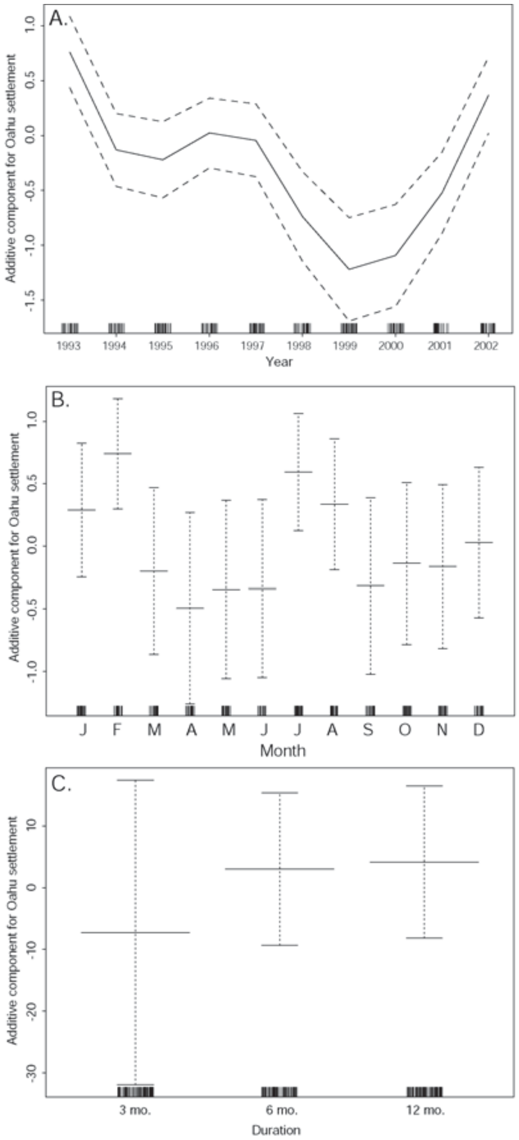


Figure 2-5 - Results of GAM application to larval settlement at Oahu from Maro spawning. The predictor variables are year, month, and larval duration. C.I. are ±2 standard errors.

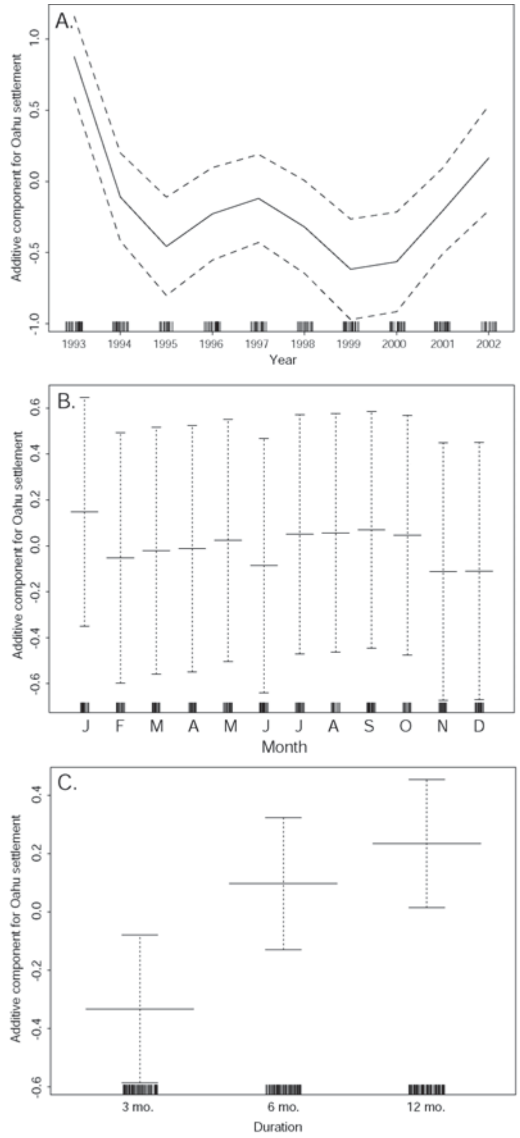


Figure 2-6 - Results of GAM application to larval settlement at Oahu from Necker spawning. The predictor variables are year, month, and larval duration. C.I. are ±2 standard errors.

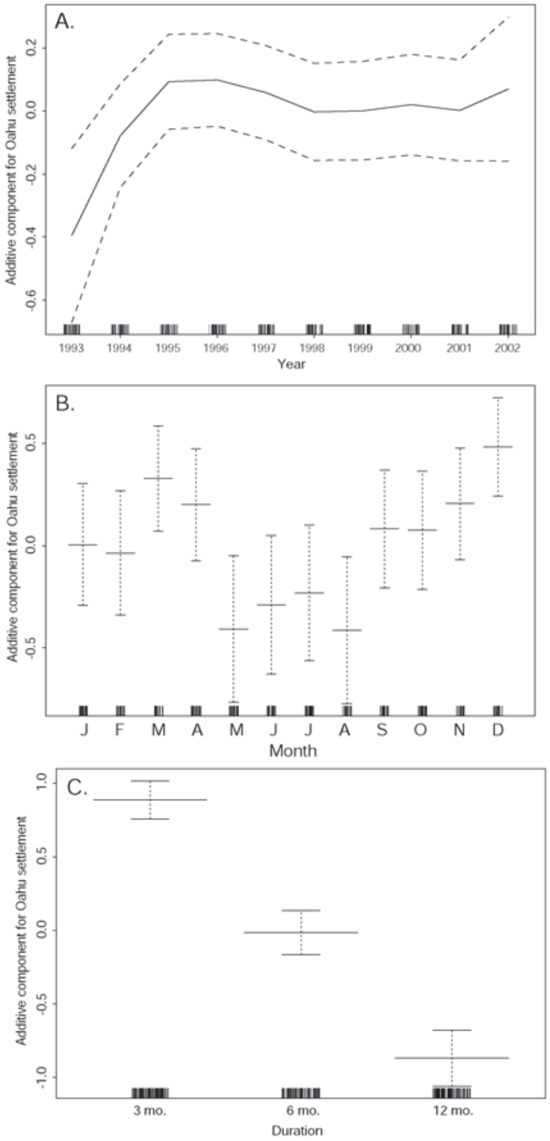


Figure 2-7 - Results of GAM application to larval settlement at Oahu from Oahu spawning. The predictor variables are year, month, and larval duration. C.I. are ±2 standard errors.

Larval non-settlement was cursorily examined in this analysis. Considering that there are abundant other sites available for larval settlement, this result should be treated with caution. However, by examining the larvae that did not settle at any of the 4 sites, some useful hypotheses can be posed for further analyses. The data suggest that yearly and monthly effects may be relatively weak and that perhaps there is a spatial component involved (Figure 2.8C). As expected, a longer larval duration is positively correlated to larval non-settlement (Figure 2.8D).

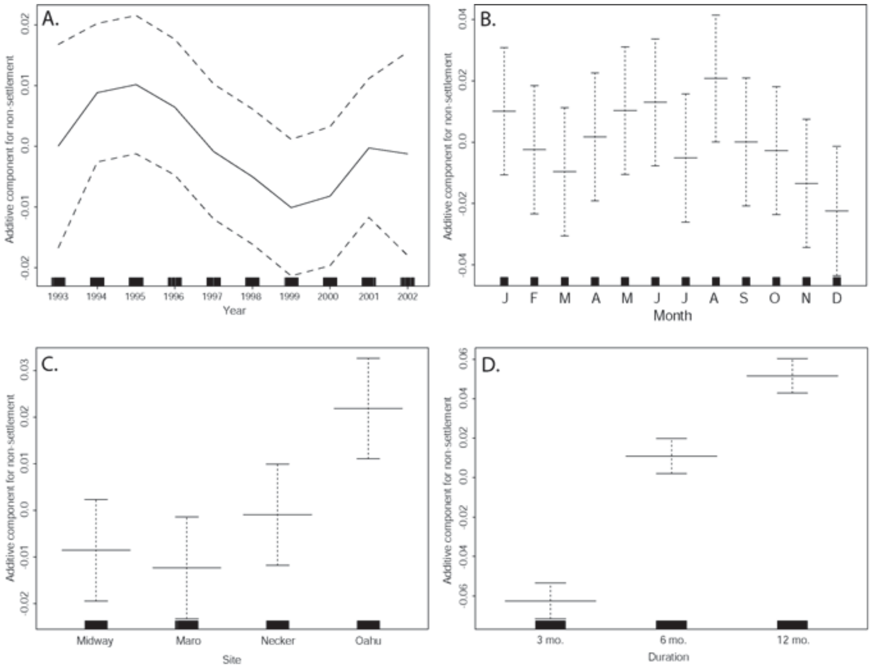


Figure 2-8 - Results of GAM application to larval non-settlement. The predictor variables are year, month, spawning site, and larval duration. C.I. are ±2 standard errors.

SST and chlorophyll-a histories had strong yearly, monthly, and site relationships (Figures 2.9-2.14), with the expected deterioration of a seasonal effect at a 12 month larval duration (Figures 2.11B, 2.14B). For a 3 month larval duration, SST history was optimized by a July-August spawning, peaking in late July/early August (Figure 2.9B). For a 6 month larval duration, the optimal spawning with respect to SST history is offset accordingly to May-July, peaking in June (Figure 2.10B). There appears to be an interesting tradeoff between SST and chlorophyll-a with respect to seasonal spawning (Figures 2.9B, 2.10B, 2.12B, 2.13B). Summer spawning is clearly conducive to placing the larvae into higher SST water masses; however, winter spawning clearly maximizes chlorophyll-a experienced by larvae. This dilemma does not appear to be mediated by seasonal retention (Figure 2.2B) or seasonal non-settlement (Figure 2.8B). Early summer and late summer may be satisfactory compromises to best optimize these factors. The 4 spawning sites examined in this study generally fall along a latitudinal transect, and the resulting site-related patterns in SST and chlorophyll-a are consistent with oceanographic work in this area (Polovina et al., 2001; Seki et al., 2002). The lowest SST and highest chlorophyll-a occurs at the northernmost release site of Midway, which is well within the TZCF (Transition Zone Chlorophyll Front). At lower latitudes there is a trend for higher SST values, as well as higher chlorophyll-a values. The latter may be due to increased nearshore processes (e.g., island effects) enhancing productivity around the larger islands in the archipelago (e.g., Seki et al. 2001).

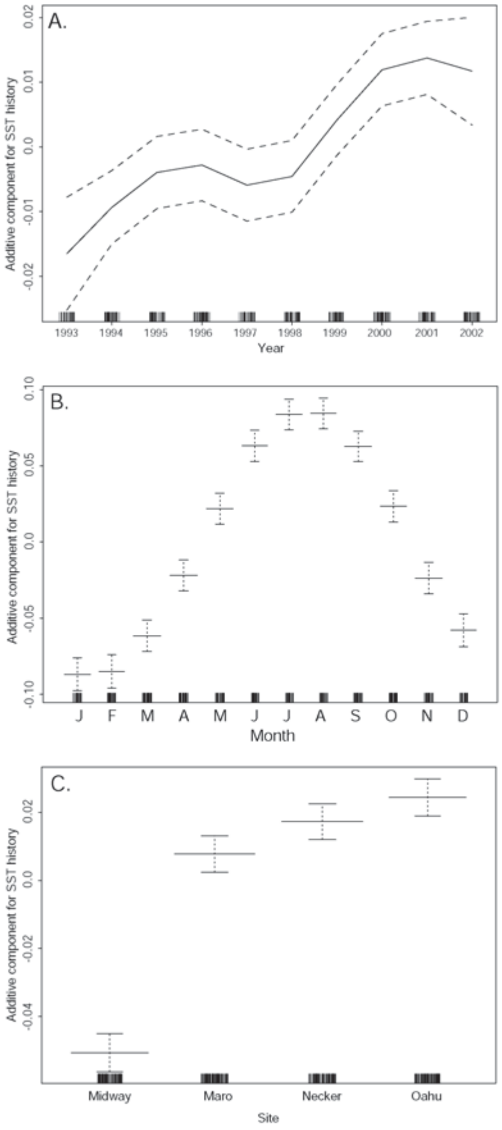


Figure 2.9 - Results of GAM application to SST history of retained larvae after 3 month pelagic duration. The predictor variables are year, month, and spawning site. C.I. are ±2 standard errors.

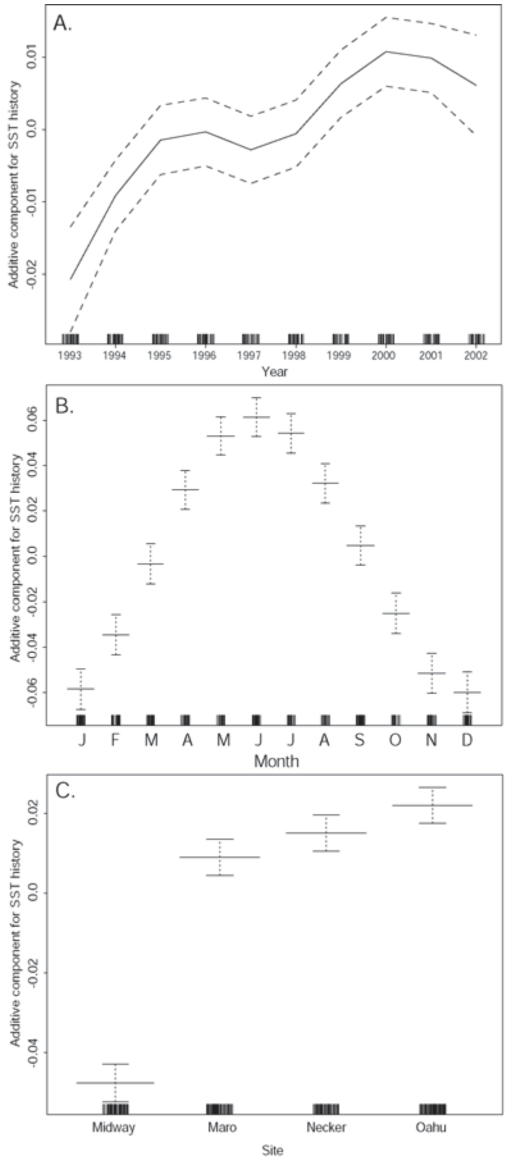


Figure 2.10 - Results of GAM application to SST history of retained larvae after 6 month pelagic duration. The predictor variables are year, month, and spawning site. C.I. are ±2 standard errors.

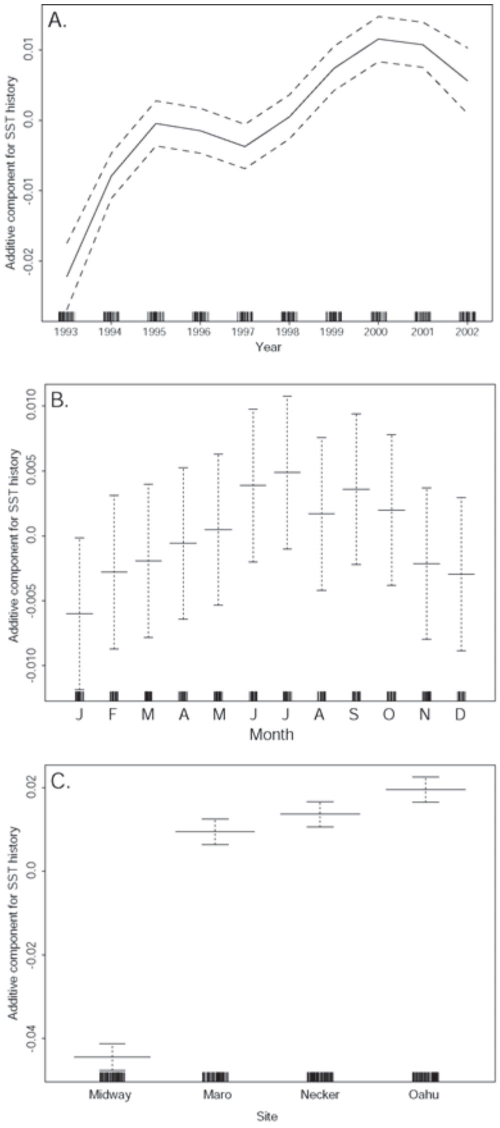


Figure 2.11 - Results of GAM application to SST history of retained larvae after 12 month pelagic duration. The predictor variables are year, month, and spawning site. C.I. are ±2 standard errors.

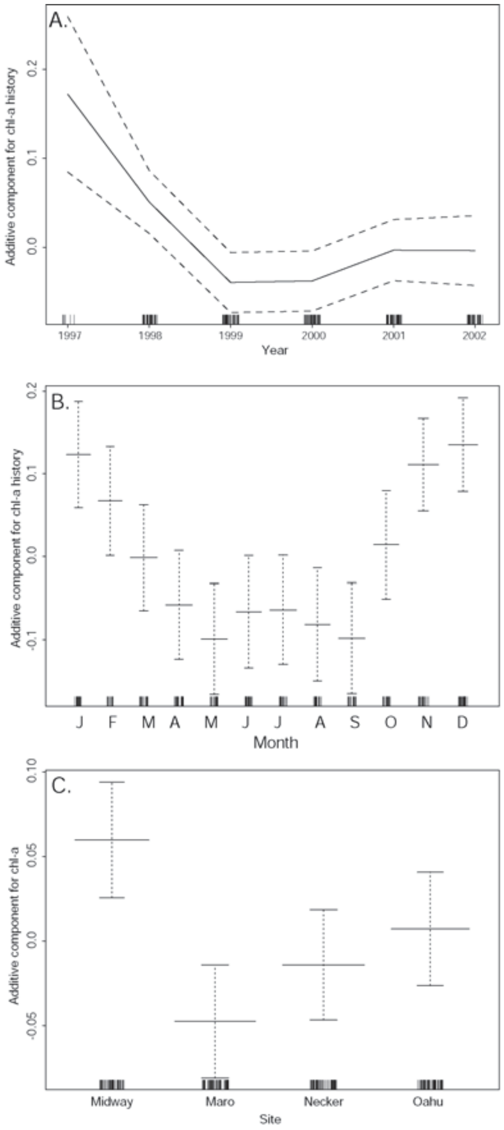


Figure 2.12 - Results of GAM application to chlorophyll-a history of retained larvae after 3 month pelagic duration. The predictor variables are year, month, and spawning site. C.I. are ±2 standard errors.

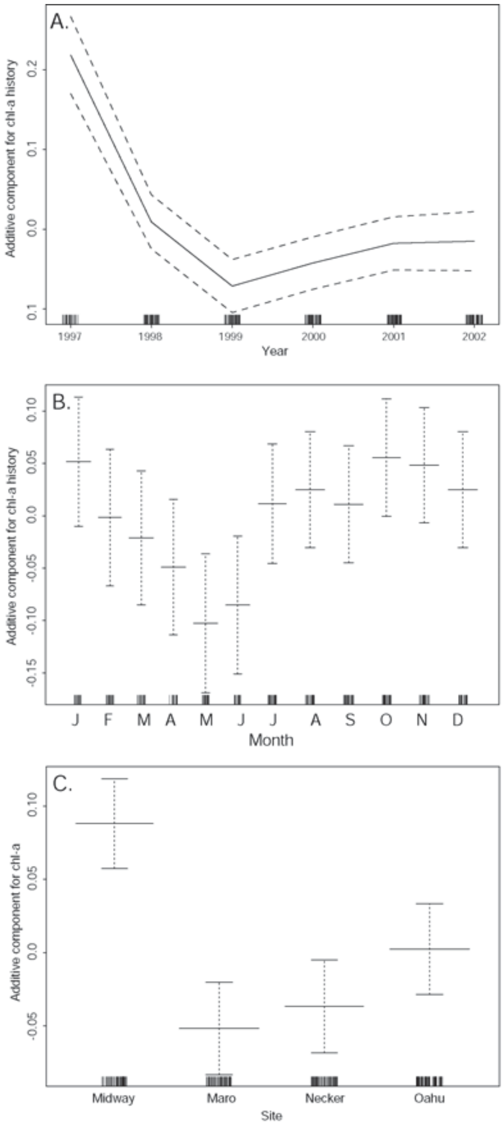


Figure 2.13 - Results of GAM application to chlorophyll-a history of retained larvae after 6 month pelagic duration. The predictor variables are year, month, and spawning site. C.I. are ±2 standard errors.

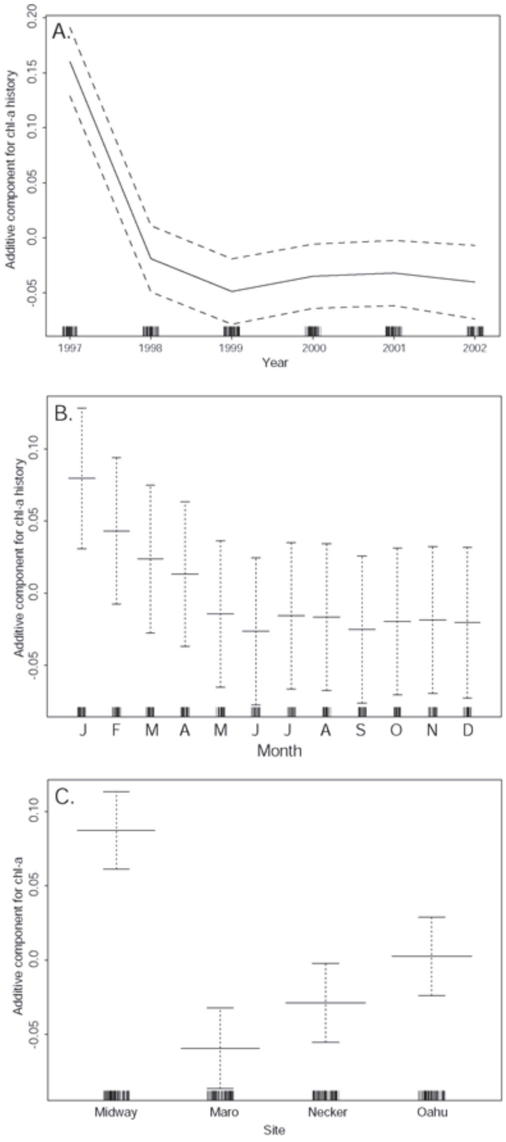


Figure 2.14 - Results of GAM application to chlorophyll-a history of retained larvae after 12 month pelagic duration. The predictor variables are year, month, and spawning site. C.I. are ±2 standard errors.

In summary, it has been shown that computer simulation may be a useful approach towards understanding important aspects of early life history and adult spawning ecology. Retention, transport, and environmental variables are shown to be expressed in complex spatial and temporal patterns. The utility of this approach depends critically on the passivity of larvae. Some late-stage fish larvae have been shown to be capable of directional orientation and active movement near the timing of settlement (e.g., Kingsford et al., 2002; Leis and Carson-Ewart, 1999; 2000; 2002; 2003; Leis et al., 2003; Tolimieri et al., 2004; Jeffs et al., 2003, Simpson et al., 2008); and future work needs to recognize the role of active swimming within a Lagrangian framework (e.g., Lohmann et al., 2008). However, it is quite likely that early life history stages (eggs and early-stage larvae) are passive drifters for a significant portion of the pelagic duration. The findings of this simulation study can be used to pose further hypotheses and corroborate existing empirical evidence. For example, there are observed biogeographic patterns in the Hawaiian archipelago which would benefit from a more quantitative mechanistic explanation, such as a higher rate of endemism being found at the northerly atolls (DeMartini and Friedlander, 2004) and the faunal similarity between Johnston Atoll and the main Hawaiian Islands (Kosaki et al, 1991). Additionally, the SST and chlorophyll-a histories provide a useful environmental perspective to recent findings emphasizing the importance of larval physiological fitness (e.g., Berkeley et al., 2004) towards population maintenance. The modeling efforts as described here can help understand and predict recruitment success, when coupled with empirical observations and field experiments.

Chapter 3: Limited horizontal dispersal mediated by vertical migration behavior: Larval transport modeling in the Hawaiian Archipelago with layered current fields

Kobayashi, D. R. Accepted with revision. Limited horizontal dispersal mediated by vertical migration behavior: Larval transport modeling in the Hawaiian Archipelago with layered current fields. *Pacific Science*.

3.1 Abstract

Lagrangian transport modeling was used to simulate the effects of diel vertical migration in selected areas of the Hawaiian Archipelago. Shallow and deep current fields were used in a factorial design to examine the effects of year, month, release site, pelagic larval duration, and a measure of diel vertical migration behavior. Generalized additive modeling was used to evaluate the effects of diel vertical migration on retention. The results showed that diel vertical migration, i.e. intermediate residency in both current strata, could restrict horizontal dispersal in pelagic larvae. This finding was robust over a range of conditions. This study provides quantitative evidence that diel vertical migration could be an adaptive mechanism to enhance natal retention and thereby minimize advective propagule losses in a patchily distributed metapopulation structure.

3.2 Introduction

The distributions of marine pelagic larvae are often found to be heterogeneous over time and space. Spatial distributions are manifested in both horizontal and vertical patterns (Ahlstrom, 1959; Leis and Miller, 1976). Vertical patterning in the water column is often related to diel vertical migration (henceforth DVM), whereby organisms change their vertical position in some repeatable pattern over a 24-hour time period. DVM is a phenomenon that is first observed in the deep scattering layers of the ocean and involves pelagic species such as euphausiids and myctophids (Johnson, 1948). Further studies have shown that meroplanktonic organisms display DVM as well (e.g., Rawlinson et al., 2004). DVM has been observed in both marine and freshwater ecosystems and is exhibited by a wide variety of taxa and life-history stages (Hays, 2003). The proximate mechanisms for DVM are relatively well understood, e.g., responses to light levels, sensory/orientation capability, swimming ability, and buoyancy regulation. In contrast, the ultimate, i.e., underlying selective advantages, are less understood, but are thought to be related to issues such as predator avoidance (Bollens and Frost, 1989), prey capture (Sims et al., 2005), metabolic advantages (Winder et al., 2003), and horizontal retention/transport (Smith et al., 2001).

Horizontal movement mediated by DVM is of particular interest to meroplanktonic larvae of coastal or insular species, because suitable habitat for settlement is geographically restricted (Roberts, 1997). The type of vertical current shear (differential movement of adjacent water layers) required for this to take place is frequently observed in the field (e.g., Firing, 1996) or predicted in ocean circulation models for a particular time and space, yet this alone does not ensure that DVM is robustly associated with retention since each larval propagule occupies portions of a moving window of time and space over the course of its trajectory. Larval connectivity and retention are key issues for species with patchy adult habitats, i.e., metapopulations (Sale and Kritzer, 2003).

There are a large number of geographically separated islands, coral atolls, seamounts, and banks throughout the Hawaiian Archipelago (Figure 3.1). Most of the benthic or island-associated species in this region do not routinely cross the large expanses of deep ocean between habitats as adults; however pelagic egg and larval stages can easily traverse these boundaries and even longer distances (Robertson et al., 2004). Despite the importance of these early life history stage towards understanding population dynamics and effectively managing these species or areas (e.g., Crowder et al., 2000; Valles et al., 2001), larval connectivity in this region is relatively unknown. Such information will also be extremely important towards understanding the impact of the Papahānaumokuākea Marine National Monument which was recently established in the archipelago. The purpose of this study is to examine the effect of DVM on pelagic larval natal retention in the Hawaiian Islands using computer simulation and ocean current data.

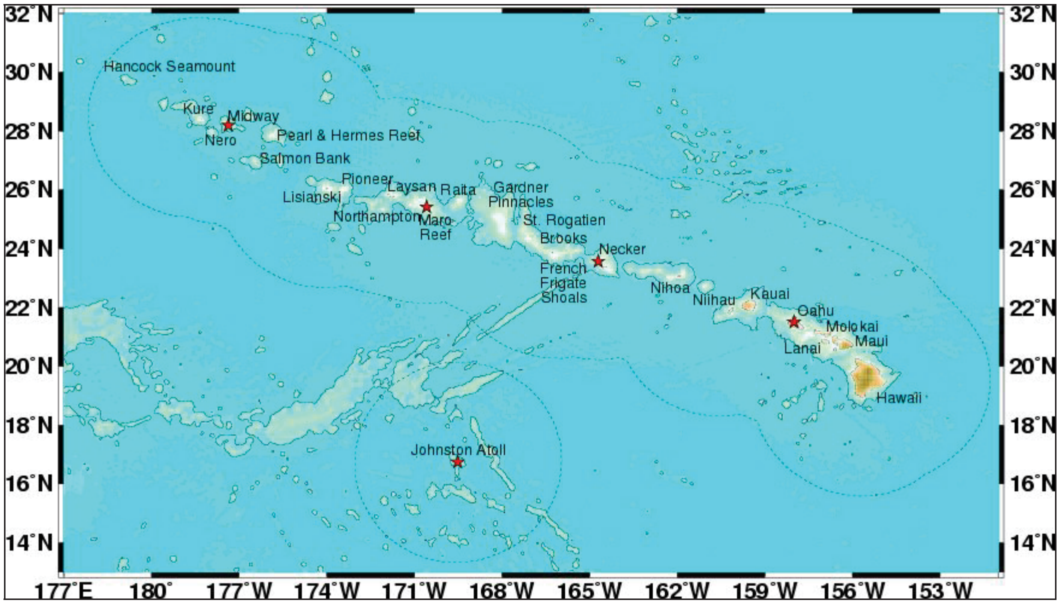


Figure 3.1 - Location of release sites in the Hawaiian Archipelago. Stars indicate positions of Midway Island, Maro Reef, Necker Island, Oahu, and Johnston Atoll, from North to South, respectively. Contours are shown at 2000 fathoms using the Smith and Sandwell (1997) bathymetric database.

3.3 Methods

Surface currents used in this study were monthly (January 1993 through December 2003) 0.5° x 0.5° latitude/longitude resolution gridded flow fields from the Ocean Surface Current Analyses—Real Time (OSCAR) project at NOAA Earth and Space Research, henceforth referred to as OSCAR currents. These surface flow fields are a composite of altimetry-derived geostrophic components and satellite-derived wind components, tuned to 15-m depth drogue trajectories; thusly capturing both the large-scale geostrophic motion as well as the surface, wind-driven, Ekman transport. This approach is documented in Lagerloef et al. (1999). Deep currents used in this study were monthly (January 1993 through December 2003) 0.5° x 0.5° latitude/longitude resolution gridded geostrophic flow fields calculated from satellite altimetry obtained from CNES/AVISO/SSALTO (CLS Space Oceanography Division, France), henceforth referred to as AVISO currents. The AVISO currents come from the next generation of satellite altimeters, such as JASON-1, which replaced the earlier TOPEX/Poseidon satellite altimeters. Geostrophic currents typically represent large-scale water movement throughout the mixed layer in the Hawaii region ranging from 30-m to 100-m depths depending on the season and location (Flament et al., 1998). While there is some undesired overlap in depths between these 2 current products (0-15m vs. 0-100m), the advantage of working with altimetry products was that it allowed examination of 11 years of a standardized and complete time series of oceanographic data. The OSCAR and AVISO currents were simultaneously applied in the larval transport simulation by allowing individual larvae to differentially access the two strata and mimic the consequences of DVM.

Larvae movement was simulated using the individual-based, lagrangian techniques outlined in Polovina et al. (1999). These techniques are also known as biased random-walk models. The modeling uses a daily time step while accessing the monthly current fields for the nearest pixel of data. A mixture of the 2 current fields was used in each daily time step, the coarseness of the data (e.g., monthly fields) did not warrant a higher resolution modeling time step (e.g., hours). Operationally, the location of individual larvae in Cartesian space was calculated with the following equations:

$$\begin{aligned} x_{t+\Delta t} &= x_t + \left[u_{(x_t, y_t, t)}\Delta t + \varepsilon\sqrt{D\Delta t}\right] / \cos(y_t) \\ y_{t+\Delta t} &= y_t + \left[v_{(x_t, y_t, t)}\Delta t + \varepsilon\sqrt{D\Delta t}\right] \end{aligned}$$

where x represents longitude, y represents latitude, t represents time in days, u represents the zonal East-West component of the current speed, v represents the meridional North-South component of the current speed, $\cos(y_t)$ adjusts distance by latitude to account for the spherical coordinate system, and *D* is the diffusivity coefficient (500 m^2 sec^{-1}). Simulated larvae at the end of their pelagic larval duration (PLD) and in the 140 km radius of a suitable habitat were scored as settled. Orientation and horizontal swimming were not part of the model structure, nor was the capability of early or delayed settlement. A factorial experimental design was applied (Table 3.1) to examine the results of the five following different categorical effects. (1) Interannual variability was examined by releasing larvae from 1993 to 2002, with releases in 2002 extending into 2003 depending on the PLD. (2) Uniform releases were conducted over the 12 months of each year to examine seasonal effects. (3) Release sites were chosen along the Hawaiian Archipelago, including Midway Island, Maro Reef, Necker Island, Oahu, and Johnston Atoll (Figure 3.1). (4) PLDs ranging from 1 month to 12 months were examined, which brackets most of the known PLDs of vertebrate and invertebrate species in the region., (5) The vertical occupancy index (VOI), a measure of DVM, was used to quantify the differential use of vertical current strata. The VOI is a simple linear measure of shallow vs. deep exposure to respective currents. Therefore, a VOI of 1 signifies exposure exclusively to shallow OSCAR currents, and a VOI of 5 signifies exposure exclusively to deep AVISO currents. The intermediate VOI levels of 2, 3, and 4 signify 75%:25%, 50%:50%, and 25%:75% of shallow:deep exposure, respectively. The intermediate VOI values were intended to simulate DVM, i.e., some manner of active swimming or buoyancy control to vertically navigate to a different current stratum. In all, there were 10 release years, 12 release months, 5 release sites, 4 PLDs, and 5 VOIs. For each combination of the five effects (12000 unique sets), 500 larvae were released and individually tracked. Natal retention was scored if the larva was within the 140-km radius around the release site at the end of the PLD. Average retention was tabulated for each suite of values within each potential effect.

Generalized additive models (GAMs, Hastie and Tibshirani, 1990) were used to further delineate relationships between retention and the examined variables. GAMs have been shown to be useful tools for understanding patterns in simulated larval retention and transport (Kobayashi and Polovina, 2006). Mapping of spatial distributions was performed using the software package called Generic Mapping Tools (Wessel and Smith, 1998).

Table 3.1 - Summary of factors examined in simulated spawning releases. For each unique combination of the five factors (total = 12000), 500 simulated larvae were released and tracked, and natal retention tabulated.

Year (*n* = 10)	Month (*n* = 12)	Site (*n* = 5)	PLD[1] (*n* = 4)	VOI[2] (*n* = 5)
1993	January	Midway	1 month	1 (100% shallow, 0% deep)
1994	February	Maro	3 months	2 (75% shallow, 25% deep)
1995	March	Necker	6 months	3 (50% shallow, 50% deep)
1996	April	Oahu	12 months	4 (25% shallow, 75% deep)
1997	May	Johnston		5 (0% shallow, 100% deep)
1998	June			
1999	July			
2000	August			
2001	September			
2002	October			
	November			
	December			

[1] Pelagic larval duration.

[2] Vertical occupancy index.

3.4 Results

Nonzero retention was observed in 75% of the strata examined (9016 out of 12000 total combinations). Retention varied from 0 to 500 (100% retention observed in 13 strata). Across all strata, retention averaged 17% (86.35 larvae retained out of 500 total). Retention appeared to be related to all experimental factors in the simulation. Interannual were apparent in the aggregated averages (Figure 3.2). There were indications of a time trend in retention over years, with more recent years exhibiting significantly higher retention than earlier years. Seasonal effects were less pronounced with no clear pattern or significant differences between months (Figure 3.3). Spawning site and PLD appeared to have stronger effects on retention. For example, Johnston Atoll appeared to have a substantially lower retention rate than the other release sites examined (Figure 3.4). The shorter pelagic durations, particularly 1 month, were clearly related to a higher probability of retention (Figure 3.5). An intermediate level of vertical occupancy was coincident with higher retention, with lower retention at both shallower and deeper strategies (Figure 3.6). Generalized additive modeling on subsets of data (Figure 3.7), as well as the aggregated data (Figure 3.8), indicated that this last finding was robust with respect to the other examined variables. An example spatial distribution for a set of 90-day PLD releases around Necker Island in the Northwestern Hawaiian Islands is shown in Figure 3.9, which suggests that strictly shallow and strictly deep strategies are associated with higher levels of horizontal advection in opposing directions, while the intermediate strategy mimicking DVM would minimize this effect.

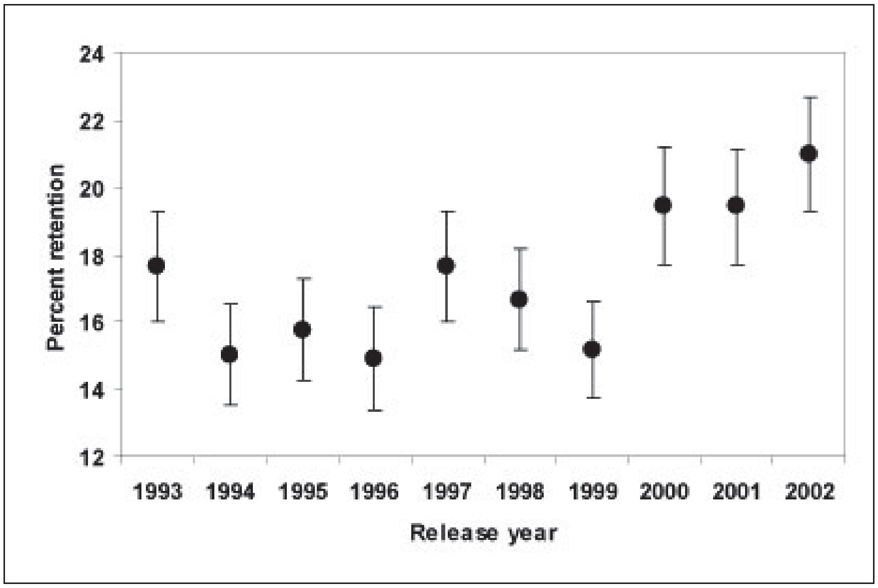


Figure 3.2 - Average larval retention rate as a function of larval release year across all simulation. Error bars indicate 95% parametric confidence bounds.

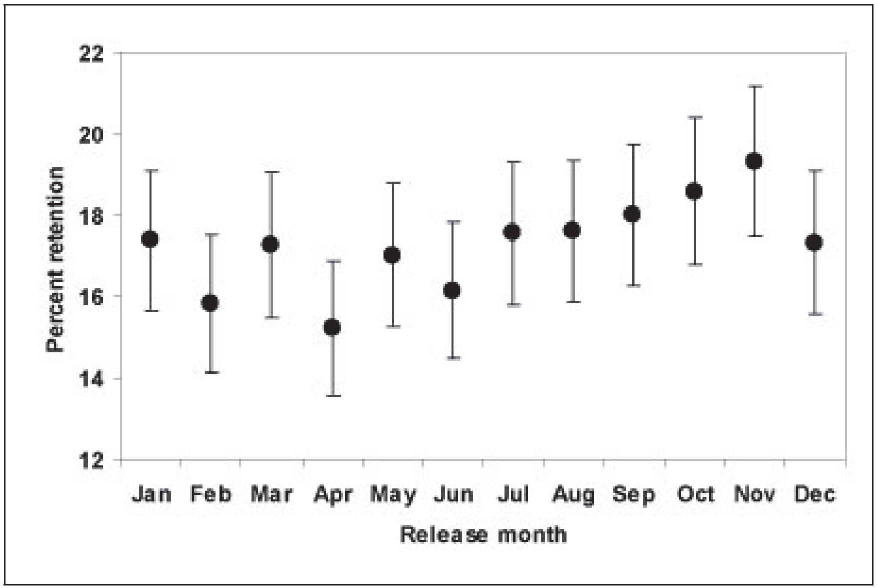


Figure 3.3 - Average larval retention rate as a function of larval release month across all simulation. Error bars indicate 95% parametric confidence bounds.

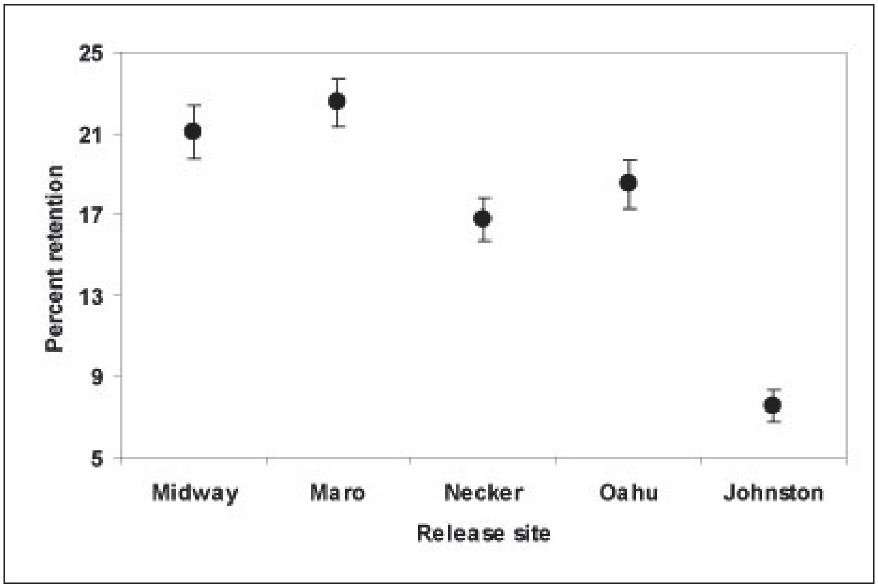


Figure 3.4 - Average larval retention rate as a function of larval release site across all simulation. Error bars indicate 95% parametric confidence bounds.

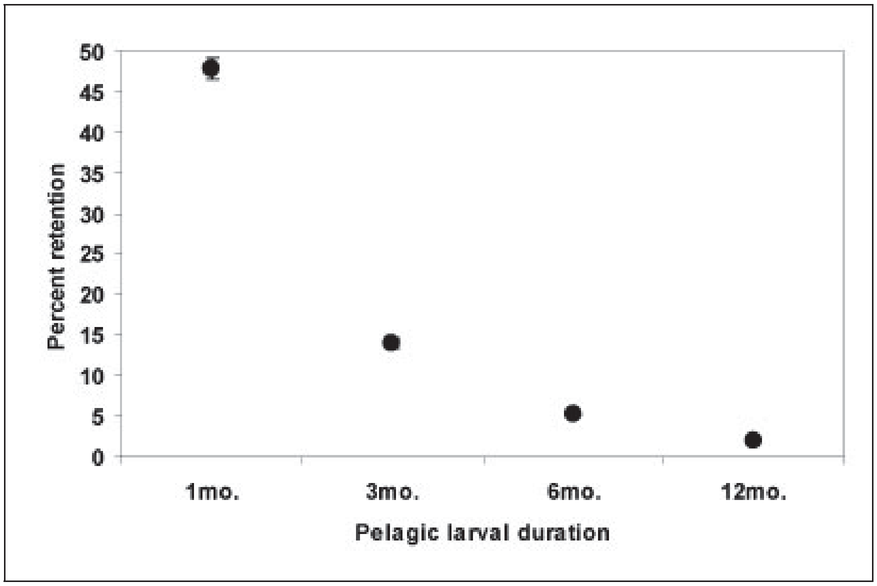


Figure 3.5 - Average larval retention rate as a function of pelagic larval duration across all simulation. Error bars indicate 95% parametric confidence bounds.

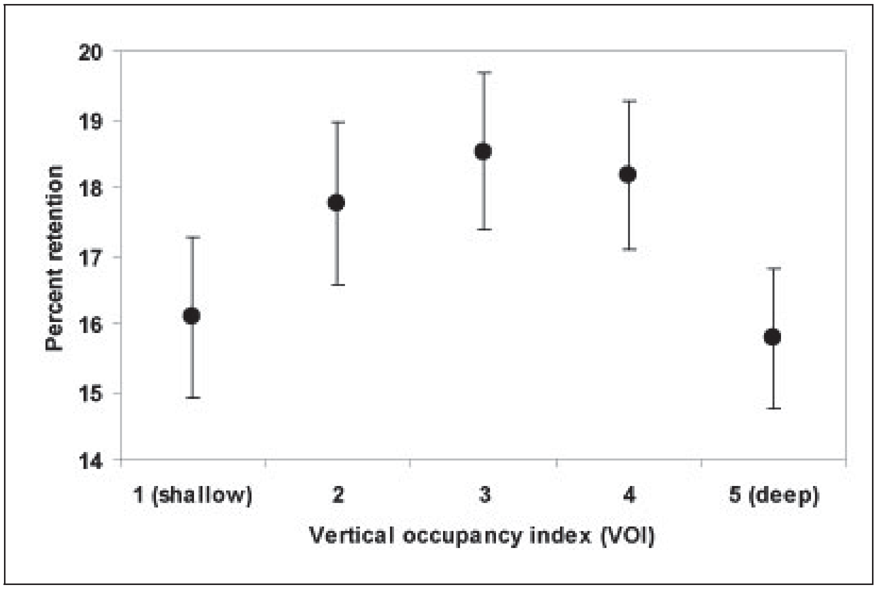


Figure 3.6 - Average larval retention rate as a function of larval vertical occupancy index across all simulation. Error bars indicate 95% parametric confidence bounds.

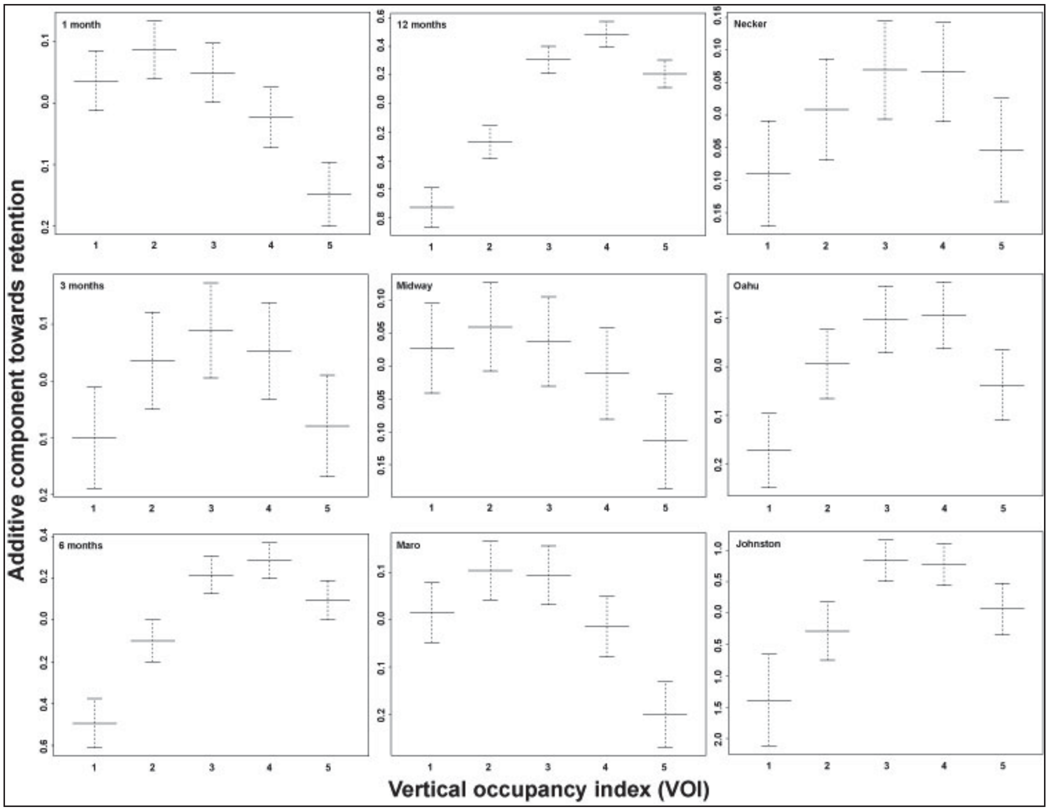


Figure 3.7 - Additive component of vertical occupancy index (VOI) towards retention using generalized additive models on subsets of data defined by common pelagic larval durations (PLDs) or release sites. Confidence bounds represent ± 2 standard errors.

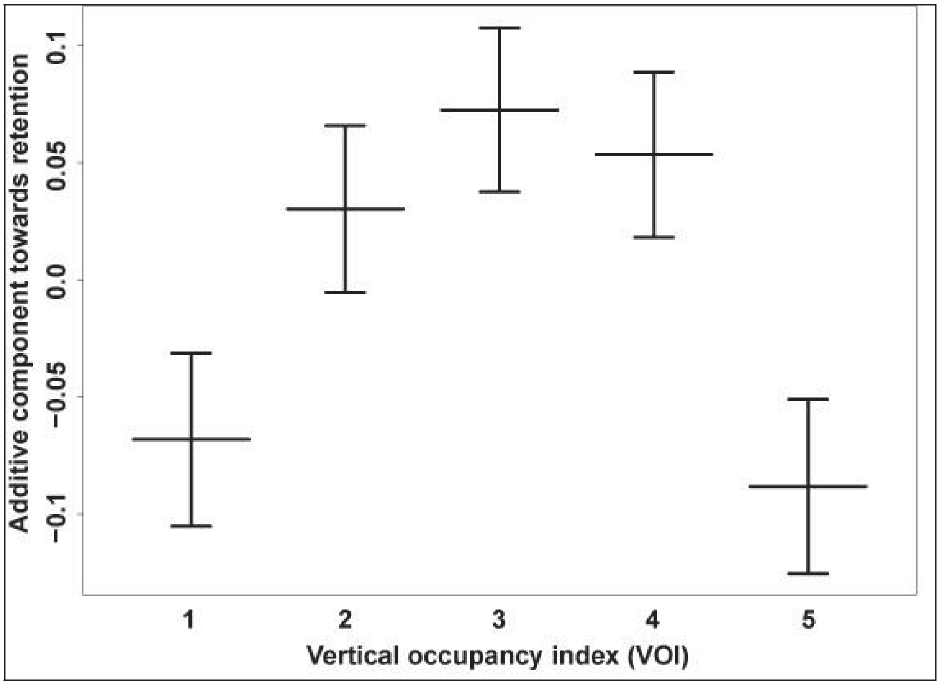


Figure 3.8 - Additive component of vertical occupancy index (VOI) towards retention using generalized additive models on all data pooled. Confidence bounds represent ± 2 standard errors.

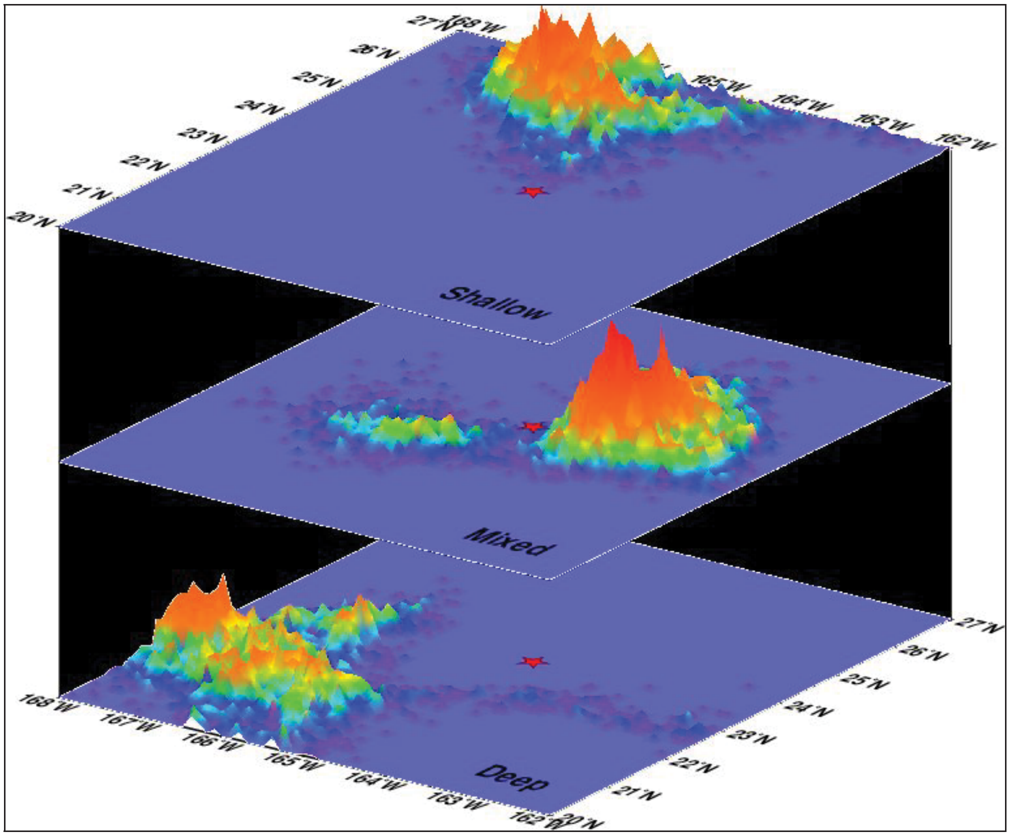


Figure 3.9 - Example larval spatial distributions after 90-day PLD from a June 1998 spawning at Necker Island for either a shallow (upper), mixed shallow and deep (middle), or deep (lower) configuration. The stars denote the location of the release site Necker Island.

3.5 Discussion

The findings of this analysis indicate that a relatively simple oceanographic mechanism can be related to retention, which could be utilized by the appropriate behavioral or physiological adaptations. Such adaptations would be more energy efficient than having to traverse great horizontal distances or swim against an unfavorable current. This notion of "efficient swimming" (Armsworth, 2001) to save energy, time, or any resource in limited supply is critically important towards understanding survival strategies and adaptations in the multi-dimensional pelagic environment. Even miniscule survival advantages can translate into a plausible mechanism for selective pressure to influence appropriate adaptations over evolutionary time. Vertical current shear has been observed in the Hawaiian Archipelago (Firing, 1996) and elsewhere (e.g., Tomczak et al., 2004).

Bartsch (1988), Hill (1991b), Armsworth (2001), Cowen (2002), and others have discussed or theoretically shown the possibility of larvae using different vertical strata to affect horizontal position. However, empirical evidence is scant. Smith et al. (2001) and Emsley et al. (2005) showed that DVM-mediated horizontal transport for zooplankton was a plausible mechanism to explain observed population abundance dynamics. Cowen et al. (2003) showed that adding active larval orientation in the vertical plane was necessary for their simulations to match field observations of fish recruitment dynamics. Roughan et al. (2005) suggested that crab larvae exhibiting DVM in the lee of a peninsula could be retained by current shear associated with wind-driven flow. Presently, DVM in insular fish species is poorly understood because of extreme rarity in samples and/or sampling difficulties. Some of the more extensive reef fish larval surveys using stratified sampling (e.g., Boehlert et al., 1992; Leis, 1991; 2004) showed much variability in depth distribution in both early-stage and late-stage reef fish larvae; in both stages, pronounced interspecific variability was shown, as well as changes over small geographic scales. However, because DVM has been well documented in a variety of zooplankton taxa, it is logical to assume that similar selective advantages would also apply to fish larvae. The slightly larger organisms in the island-associated scattering layer around Hawaii have been shown to be capable of up to 1.7 m min^{-1} active (swimming) or passive (flotation/sinking) movement, which would allow for a great range of vertical transport over a diel cycle (Benoit-Bird and Au, 2004). With the advent of better sampling devices and in-situ observations (e.g., De

Robertis and Ohman, 1999; Cowen and Guigand, 2008), it will be useful to explore DVM in a wider range of insular and pelagic fish species.

This study showed the apparent, low retention rates around Johnston Atoll, a region considered to be an important biogeographic stepping stone for colonization of the Hawaiian Archipelago (Gosline, 1955), as well as for reverse transport towards the Indo-West Pacific (Mundy, 2005). The generally lower retention rates around Johnston Atoll may be due to it's location within the bounds of the strong westward North Equatorial Current, and it's configuration tends to induce either turbulent or von Karman downstream patterns rather than the quasi-stationary eddies formed at lower Reynolds numbers (Barkley, 1972). Larval transport corridors between Johnston Atoll and the Hawaiian Archipelago have been documented using computer simulation (Kobayashi, 2006). While such corridors may be important for population maintenance at this remote location, it is plausible that DVM-mediated retention may be particularly important in such an isolated location for species unable to complete the long-distance transport.

The simulations in this study examined the potential role of DVM as it relates to horizontal retention. This requires active or passive depth control on hourly time scales. Another type of vertical migration may occur more slowly over the course of an organism's development, for example starting at a shallow depth when young then progressively moving deeper as the organism develops, or vice versa. This is similar to DVM but will have different consequences because of the spatial and temporal dynamics of the current fields. Stenevik et al. (2003) have shown that sardine larvae can enhance their retention by exhibiting stage-specific vertical distribution. Paris and

Cowen (2004) suggested that such ontogenetic vertical migration (OVM) manifested as a downward migration trend, coincident with development in damselfish larvae, could be a mechanism for enhanced retention in the Caribbean. More studies are needed, particularly on species with pelagic eggs, to document the locations of egg release, egg stage duration, and buoyancy profiles. These potential effects of OVM on horizontal transport in the Hawaiian region will be examined in a forthcoming study.

Chapter 4: Colonization of the Hawaiian Archipelago via Johnston Atoll: A characterization of oceanographic transport corridors for pelagic larvae using computer simulation

Kobayashi, D. R. 2006. Colonization of the Hawaiian Archipelago via Johnston Atoll: a characterization of oceanographic transport corridors for pelagic larvae using computer simulation. *Coral Reefs* **25**: 407-417.

4.1 Abstract

Larval transport between Johnston Atoll and the Hawaiian Archipelago was examined using computer simulation and high-resolution ocean current data. The effects of pelagic larval duration and spawning seasonality on long-distance transport and local retention were examined using a Lagrangian, individual-based approach. Retention around Johnston Atoll appeared to be low, and there appeared to be seasonal effects on both retention and dispersal. Potential larval transport corridors between Johnston Atoll and the Hawaiian Archipelago were charted. One corridor connects Johnston Atoll with the middle portion of the Hawaiian Archipelago in the vicinity of French Frigate Shoals. Another corridor connects Johnston Atoll with the lower inhabited islands in the vicinity of Kauai. Transport appears to be related to the Subtropical Countercurrent and the Hawaiian Lee Countercurrent, both located to the west of the archipelago and flowing to the east. A new analytical tool, termed CONREC-IRC is presented for the quantification of spatial patterns.

4.2 Introduction

Johnston Atoll is an extremely isolated coral atoll at 16° 45′ N, 169° 31′ W, approximately 1325 km southwest of the Hawaiian island of Oahu (Figure 4.1). The nearest island, French Frigate Shoals, in the middle of the Hawaiian Archipelago, is 865 km to the north-northeast, and Kingman Reef in the northernmost portion of the Line Islands is 1385 km to the southeast. The fauna of Johnston Atoll is relatively well documented (e.g., Gosline, 1955; Kosaki et al., 1991; Lobel, 2003), with biogeographic ties to both the Hawaiian Islands and the Line Islands (Springer, 1982; Robertson et al., 2004; Mundy, 2005), and has a relatively low rate of endemism.

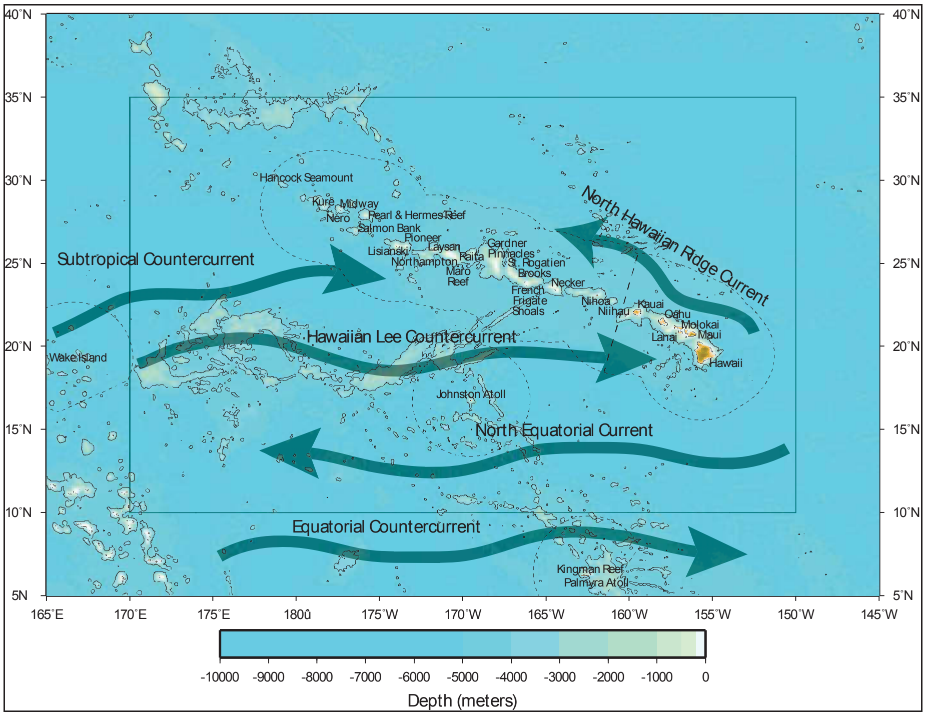


Figure 4.1 - Reference map of study area and general pattern of surface currents. Circular and oblong dashed lines represent US EEZ. Straight dashed line represents boundary between NWHI and MHI. Solid interior rectangle denotes data grid for NLOM ocean current data.

Several, recent scientific findings across a wide group of taxa have given rise to compelling evidence that Johnston Atoll is a stepping stone to species colonization in the Hawaiian Archipelago (Gosline, 1955). A genetics study of the Hawaiian grouper, *Epinephelus quernus*, has shown that the greatest genetic diversity of this species occurs in the middle of the Hawaiian Archipelago (Rivera et al., 2004). Based on this spatial pattern, it was hypothesized that ancestral *E. quernus* colonized the archipelago via Johnston Atoll and subsequently radiated to the north and south portions of the archipelago. Corals of the genus *Acropora* in and around the Hawaiian Archipelago have been the subjects of extensive biogeographic study (Grigg, 1981; Grigg et al., 1981). Despite the ability of *Acropora* to reproduce in the Hawaiian Archipelago (Kenyon, 1992), it is thought that *Acropora* initially arrived and may be primarily maintained by long-distance larval transport from Johnston Atoll. This is based on the distribution and abundance of adult colonies. These spatial patterns and likely colonization routes are also exhibited by other coral species, such as *Montipora tuberculosa* (Maragos et al., 2004). Recent genetics work on vermetid gastropods has also yielded evidence of a Johnston Atoll link for the colonization pathway of these species (Faucci, pers. comm.). These findings suggest that long-distance, pelagic larval transport from Johnston Atoll may be biogeographically significant and, at least for the corals mentioned above, may additionally be important for present-day population maintenance in the Hawaiian Archipelago.

Both the transporting of pelagic propagules and rafting of benthic organisms (Jokiel, 1989) may be important in dispersal, and these mechanisms depend critically on the spatial and temporal patterns in the local oceanography. The purpose of this analysis was to address the following two questions based on computer simulation and high-resolution ocean current data: (1) Can larvae reach the Hawaiian Archipelago from Johnston Atoll, and how is this related to larval duration and spawning season? (2) Are there identifiable larval pathways for such long-distance transport so that certain parts of the archipelago are more likely to receive Johnston Atoll propagules?

4.3 Methods

4.3.1 Ocean current data

The U. S. Naval Research Laboratory (NRL) operates a global, six-layered ocean model at a resolution of 1/16° (0.0625°) latitude by 45/512° (0.0879°) longitude (Rhodes et al., 2002; Wallcraft et al., 2003). This mesoscale model, henceforth termed NLOM, is eddy-resolving and thermodynamic; the density structure of the modeled ocean can be modified by physical processes. The NLOM is atmospherically forced using data from the Navy Operational Global Atmospheric Prediction System (NOGAPS). It also assimilates remotely-sensed, sea surface height data (GFO, JASON-1, and ERS-2 satellites) and sea surface temperature data (NRL/MODAS SST). Daily NLOM output is an operational product from NRL that is available from many cooperating data servers. One of these is the Asia-Pacific Data-Research Center (UH/SOEST/IPRC/APDRC — http://apdrc.soest.hawaii.edu/). One of the daily output layers routinely archived is the upper 100 m, henceforth termed surface layer. For this study, 365 days of daily surface layer data (31 January 2003 to 30 January 2004, these dates were not chosen but reflected availability at the time) spanning the region 170° E to 150° W longitude, 10° N to 35° N latitude were obtained from the APDRC. The daily surface-layer data included estimates of u (zonal East-West) component and v (meridional North-South) component for current vectors. The spatial grid (Figure 4.1) covered 457 x 401 pixels.

4.3.2 Modeling of transport

The movement of larvae was simulated using the individual-based, Lagrangian techniques outlined in Polovina et al. (1999). These are also known as biased random-walk models. The following modifications to the Polovina et al. (1999) approach were used. Firstly, the daily, higher-spatial-resolution NLOM data was used rather than the 10-day, 0.5° latitude/longitude resolution, TOPEX/Poseidon geostrophic current fields. Secondly, the detection radius for successful settlement was reduced from 140 km to 25 km. Thirdly, suitable settlement habitat was defined using a 2-minute, high-resolution bathymetric database (Smith and Sandwell, 1997) rather than the previously-used, four isolated locations along the archipelago. The bathymetric grid was screened to only include 2-minute pixels ranging in depth from 0 to 100 m. A latitudinal summary of habitat pixels is shown in Figure 4.2 using 0.1 degree bins. In all other respects, the modeling approach was identical to Polovina et al. (1999), using an eddy-diffusivity coefficient of 500 $m^2 s^{-1}$ and a daily time step. This value of eddy-diffusivity was qualitatively based upon drifter buoy observations (Polovina et al., 1999). The modeling refinements of this study primarily reflect better data availability for ocean currents and habitat definition, as well as further scientific research that is resolving the sensory and swimming capabilities of pre-settlement fish larvae (reviewed by Kingsford et al., 2002). For example, Fisher and Wilson (2004) found that sustainable swimming speeds were on the order of 30 cm s^{-1} for large, ready-to-settle larvae. The 25-km radius used in this study could be traversed in one day at these speeds, assuming continuous swimming and directional orientation. While the cues available on the high seas are poorly understood, the “Island Mass Effect” (Gilmartin and Revelante, 1974) can have significant, visually detectable effects out to this radius (e.g., Palacios, 2004) as well as significant downstream effects due to simple flow dynamics (Barkley, 1972). Elevated levels of chlorophyll-a, because of proximity to islands, banks, and seamounts, are also apparent at this spatial scale in the Hawaiian Archipelago (Kobayashi, unpublished data). Some larvae do not have well-developed swimming abilities, and appear to behave as passive drifters (corals, lobster, etc.). These larvae may require a more accurate "hit" on suitable substrate for successful settlement to occur. However, the 25-km radius was used in all simulations as a compromise to yield some settlement at a manageable level of larval release magnitude; i.e., the radius could be made smaller but would require more releases to attain non-zero settlement, requiring excessive computer time. By using these methodological improvements, 1000 simulated larvae were released on every calendar day of the year and tracked for varying pelagic larval durations (PLDs) ranging from 10 days to 6 months. The sample size of 1000 was chosen as a compromise because of computational speed and data storage concerns. This range of PLDs encompasses the known values for a wide variety of vertebrate and invertebrate species in the Hawaiian Archipelago, including commercially important species such as deepwater bottomfish and lobster, as well as coral reef inhabitants. Because the data spanned a discrete 365-day time block, data were allowed to "wrap around" for simulations initiated in the latter portions of the data. In other words, any larvae still at large on 30 January 2004 would next encounter currents from 31 January 2003, and carry on from that point forward. This would allow a symmetrical analysis of possible seasonal effects. One undesirable consequence of this approach is that it imposes a discrete "jump" in the data stream at the end of January; however, this approach was used to make best use of all available data for the widest range of PLDs possible. Operationally, the location of larvae in Cartesian space was calculated with the following equations:

$$x_{t+\Delta t} = x_t + \left[u_{(x_t, y_t, t)} \Delta t + \varepsilon \sqrt{D \Delta t}\right] / \cos(y_t)$$
$$y_{t+\Delta t} = y_t + \left[v_{(x_t, y_t, t)} \Delta t + \varepsilon \sqrt{D \Delta t}\right]$$

where *x* represents longitude in degrees, *y* represents latitude in degrees, *t* represents time in days, *u* represents the zonal East-West component of the current speed in degrees day 1, *v* represents the meridional North-South component of the current speed in degrees day 1, ε is a normal random variate (mean 0 and standard deviation 1), $\cos(y_t)$ adjusts longitudinal distance by latitude to account for the spherical coordinate system, and *D* is the diffusivity coefficient (500 m^2 s^{-1}, 0.0035 $degrees^2$ d^{-1}, Polovina et al., 1999). The full-resolution, daily 1/16° latitude by 45/512° longitude *u* and *v* arrays were sampled depending on the location in time and space of individual simulated larvae. Simulated larvae at the end of the PLD and in the 25 km radius of any habitat pixel were scored as settled. Orientation and swimming were not implicitly part of the model structure, nor was the capability of early or delayed settlement/metamorphosis. However, it was assumed that competent larvae were able to successfully navigate the last 25 km at the end of the pelagic duration. The tabulation of settled larvae includes a range of individuals from directly on the habitat pixel up to 25 km distant; therefore, the actual mean PLD within this grouping may slightly exceed the index value PLD due to variable final transit time among individuals.

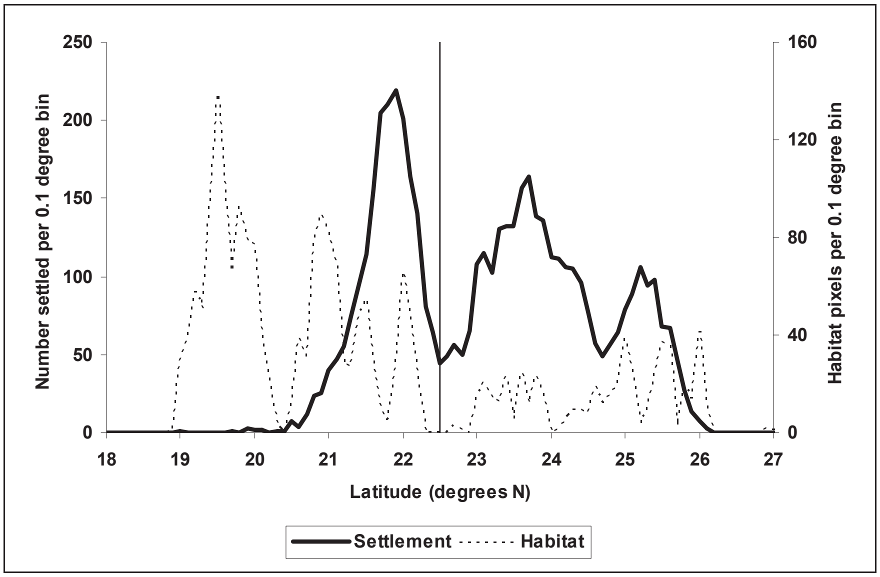


Figure 4.2 - Tabulation of successfully settling larvae at latitudinal bins of 0.1 degrees for a 90-day PLD from Johnston Atoll to the Hawaiian Archipelago (solid line). The vertical line represents the latitudinal breakpoint separating the NWHI and MHI. Habitat pixel counts (0-100m depth) at each 0.1 degree of latitude are also shown for reference (dashed line).

4.3.3 Experimental simulations

In the first set of releases, a range of PLDs was used to investigate the threshold of PLD for larvae to reach the Hawaiian Archipelago from Johnston Atoll. For each day of the year, 1000 larvae were released and tracked individually. Settlement was tabulated to either long-distance transport to the Hawaiian Archipelago or retention back to Johnston Atoll. PLDs ranging from 10 days to 180 days at 5-day intervals were examined. The percent of larvae settling in the two locations was evaluated as a function of PLD. The overall spatial pattern of larval abundance was examined for 1-, 3-, and 6-month PLDs.

In the second set of releases, a 3-month PLD was targeted for more detailed spatial analyses. This PLD was chosen based on evidence for coral and fish larvae. Harrison et al. (1984) found that planula larvae of *Acropora hyacinthus* could survive for up to 91 days prior to settling. Similarly, many of the insular deepwater snappers appear to have PLDs of this magnitude (Leis and Lee, 1994). Since the biogeographic evidence for the Johnston Atoll link is strongest for *Acropora* corals (Grigg, 1981; Kenyon, 1992; Maragos et al., 2004) and the deepwater, insular fish species *Epinephelus quernus* (Rivera et al., 2004), potential transport corridors for 3-month PLD larvae were investigated. For each day of the year, 1000 larvae were released and tracked individually. Successful settlement was tabulated into 0.1 degree latitudinal bins for spatial analysis (Figure 4.2). Larval settlement was tabulated to two arbitrary regions after a successful long-distance transport to the Hawaiian Archipelago. These regions were identified by coincident breakpoints in the latitudinal analysis and the geography of the archipelago (habitat pixel analysis). A northward region was defined as habitats north of 22°-30′ N latitude, and a southward region was defined as habitats south of 22°-30′ N latitude (Figure 4.1). This latitudinal breakpoint separates the populated Main Hawaiian Islands (henceforth MHI) from the more remote and uninhabited Northwestern Hawaiian Islands (henceforth NWHI). The overall spatial patterns of larval abundance were examined separately for these two subsets of larval trajectories. The seasonal effect was examined by tabulating successful settlement, either long-distance or retention, to the day of spawning. Daily data were binned into seasonal (3-month) strata for statistical comparison. Temporal patterns were examined as well as a general comparison between long-distance transport to the Hawaiian Archipelago and retention to Johnston Atoll.

4.3.4 Spatial analyses

One method of summarizing spatial data is by using data contours, which are lines representing a constant set of values in the data of interest (termed z-levels). For studies of larval retention, standard contouring techniques will not be informative because density contours by themselves do not necessarily answer the important question "Where are most of the larvae?" Contouring of simulated pelagic larval abundance in this study was accomplished using a new technique, CONREC-IRC. This is based on CONREC (Bourke, 1987), a standard contouring technique that uses a triangulation algorithm to recognize pixels that should be contoured. CONREC-IRC has the ability to iteratively refine the contouring z-level to encompass a user-defined percentage of the total data points, i.e., an "Iterative Region of Containment". This methodology is useful for situations in which the total sample sizes may differ from other simulations; hence, contouring at a constant z-level does not allow meaningful comparison of spatial patterns. In the simulated abundance data of this study, the data are aggregated at various levels, with different resultant sample sizes. Similarly, a variable such as PLD can effectively increase the sample size because there are more days per individual in the aggregated data. Such data can be binned into cells of latitude and longitude, and then standardized, yet the resultant contours are still not useful for describing a "region of containment" because standard contouring does not take into account the global distribution of data, only the very local scale of a few adjacent pixels of information. CONREC-IRC was used to define regions of 95% containment for selected simulation results. This approach may be generally useful in other applications such as mapping pollutants, invasive species, rare species, etc., in which it is desirable to know the location of most individuals.

4.4 Results

Based on transport by NLOM currents averaged over all seasons (Figure 4.3), there appeared to be a critical PLD of approximately 40-50 days for successful pelagic transport to the Hawaiian Archipelago from Johnston Atoll. Larvae with PLD less than 40 days did not reach the Hawaiian Archipelago. Shorter PLDs were conducive to local retention, however. Because of these offsetting patterns, mortality—as a result of loss from the system—peaks at the 40-50 day range (Figure 4.4). CONREC-IRC was used to identify the regions of 95% containment of all larvae for 1-, 3-, and 6-month PLDs (Figure 4.5). The containment regions are similar in shape but vary in size depending on the PLD. The oblong and diagonal features of the IRCs reflect prevailing zonal patterns of ocean currents. As an example, Figure 4.6 shows the July 2004 NLOM ocean currents averaged over 0.5° latitude and longitude for graphical presentation (temporal and spatial averaging). The latitudinal breakpoint of 22°-30′ N separating the MHI and NWHI also corresponded to a break in the tri-modal settlement data and in habitat pixels along the archipelago (Figure 4.2).

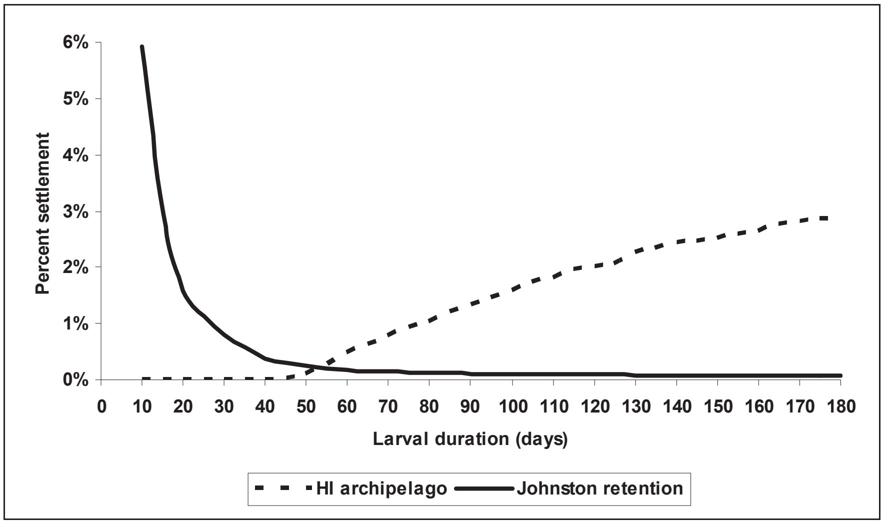


Figure 4.3 - Percent of total larvae retained at Johnston Atoll (solid) and transported to Hawaiian Archipelago (dashed) as a function of PLD using NLOM data. Data from all 365 calendar-day releases combined.

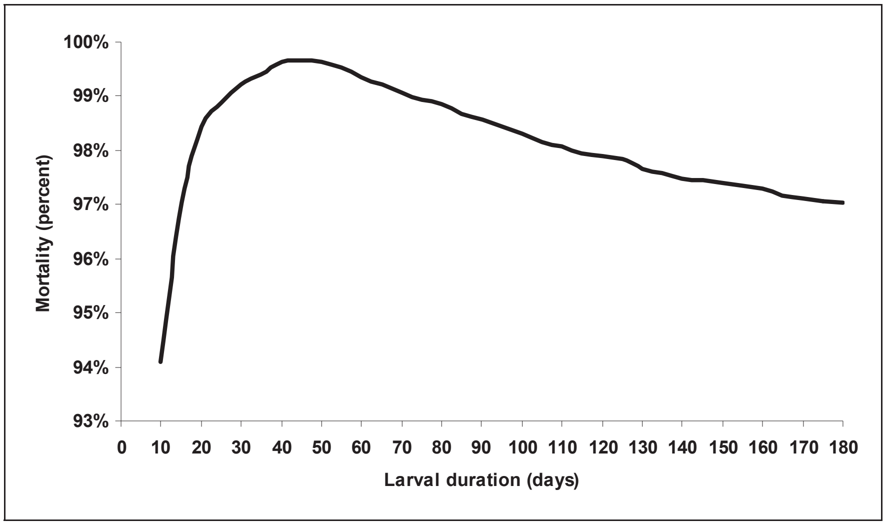


Figure 4.4 - Estimated larval mortality due to physical loss as a function of PLD, using NLOM data. Data from all 365 calendar-day releases combined. Larvae with PLD less than 40 days do not reach the Hawaiian Archipelago.

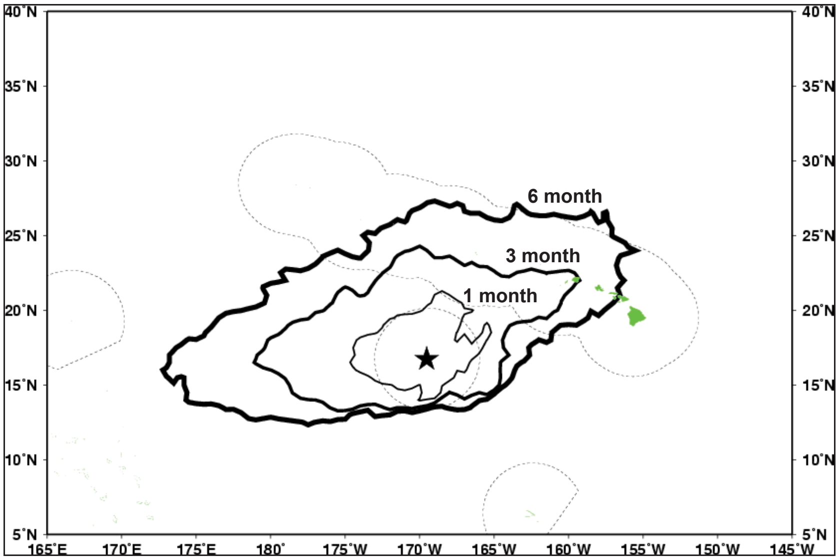


Figure 4.5 - Regions of 95% larval containment using CONREC-IRC for 1-month, 3-month, and 6-month PLDs, using NLOM ocean current data. Data from all 365 calendar-day releases combined.

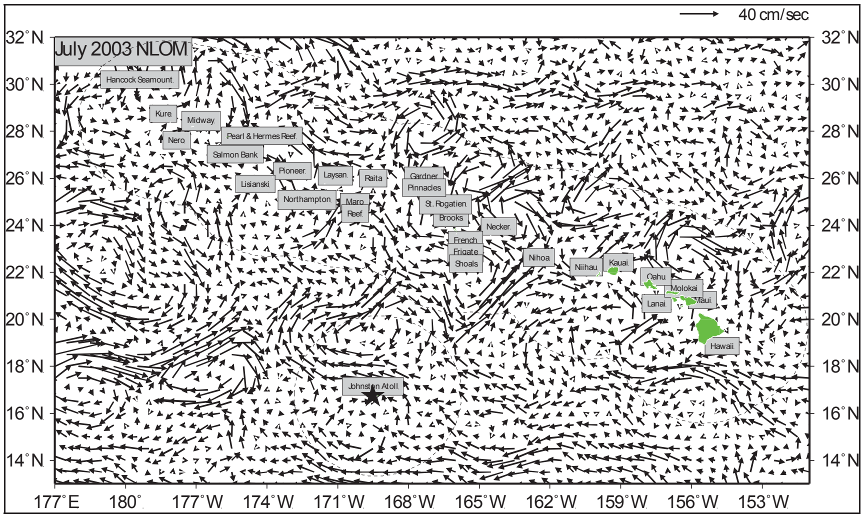


Figure 4.6 - Example plot of July 2004 NLOM ocean currents. All daily data of July 2004 were averaged into 0.5° bins of latitude and longitude for graphical presentation. The original NLOM data are at a resolution of approximately seven-fold spatial increase in data points as shown here and daily.

The 3-month PLD larvae were examined in more detail (Figures 4.7 and 4.8). These results suggest the possibility of larval transport corridors to both the mid-archipelago (e.g., French Frigate Shoals) and the northern portion of the main island group (e.g., Kauai). The seasonal timing of spawning was significant. For example, spawning earlier in the year appears to enhance both long-distance transport and local retention (Figure 4.9). The local minimum in transport at the end of January may be related to the data wrap around; however, there is no obvious reason why this discontinuity in the data stream would be associated with lower transport and/or retention. When examined in more statistical detail, seasonal differences are observed (Figure 4.10). As seen in the first set of simulations, long-distance transport exceeds local retention at the longer PLDs, such as the 3-months used in these simulations.

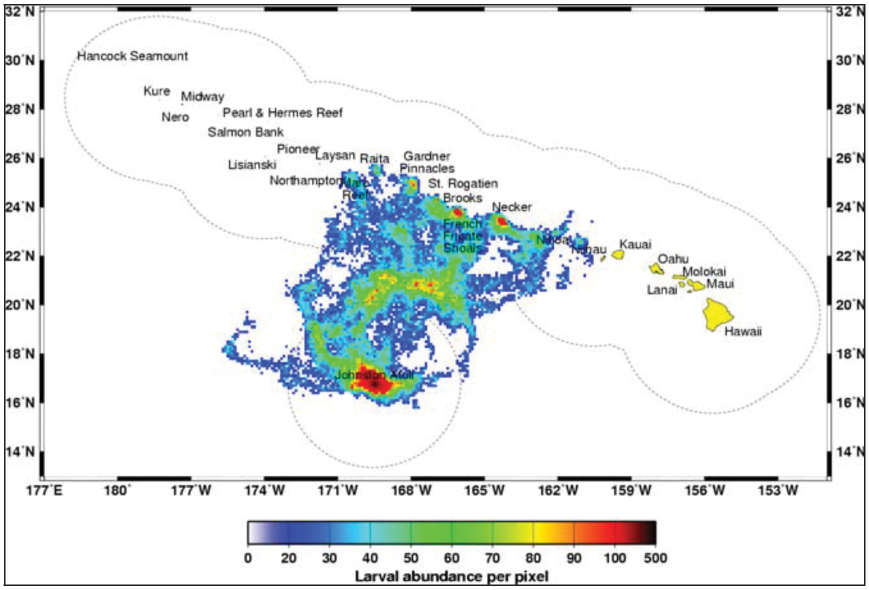


Figure 4.7 - Larval abundance from northern trajectories successfully reaching Hawaiian Archipelago from Johnston Atoll using NLOM currents and 3-month PLD. Data from all 365 calendar-day releases combined.

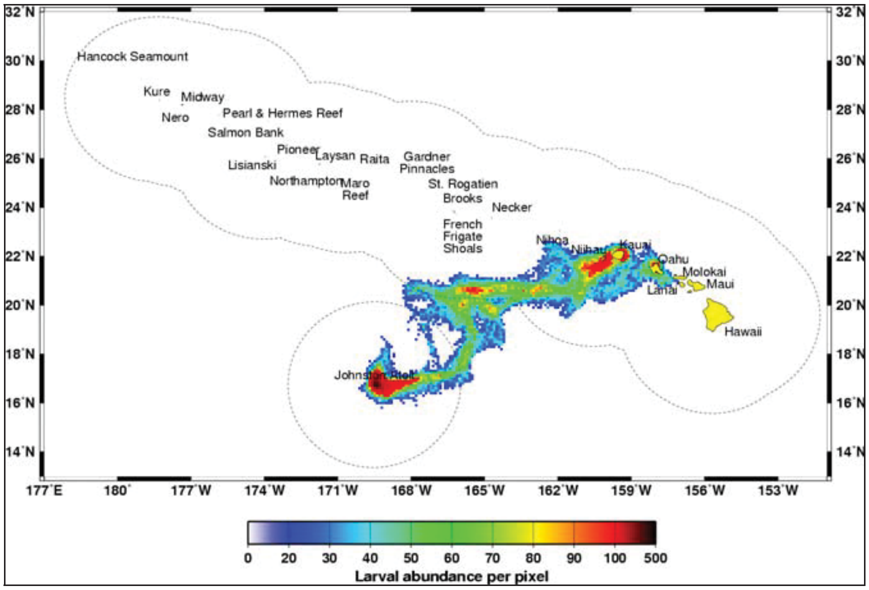


Figure 4.8 - Larval abundance from southern trajectories successfully reaching Hawaiian Archipelago from Johnston Atoll using NLOM currents and 3-month PLD. Data from all 365 calendar-day releases combined.

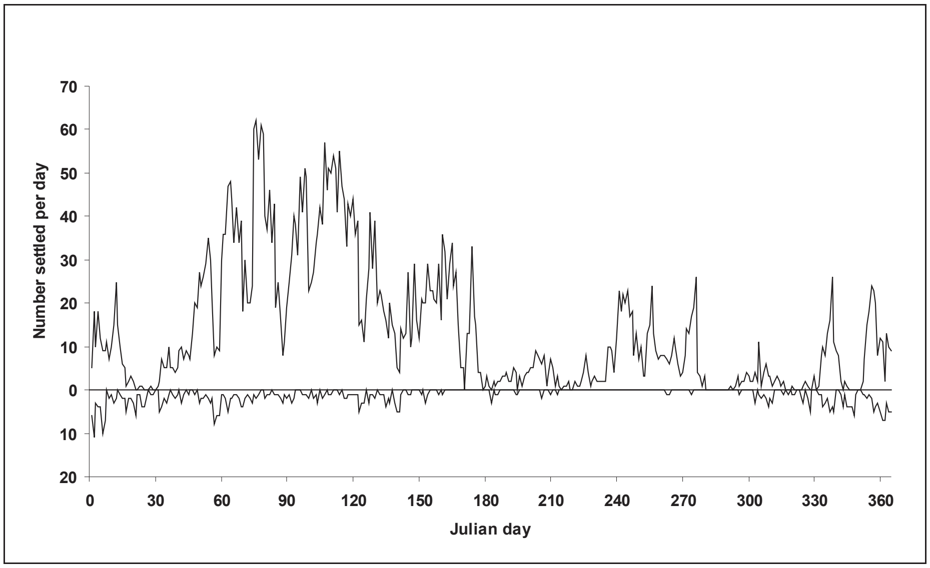


Figure 4.9 - Seasonal pattern of long-distance transport and local retention using NLOM currents and 3-month PLD. Number of successful settlers (out of 1000 released) tabulated to day of spawning.

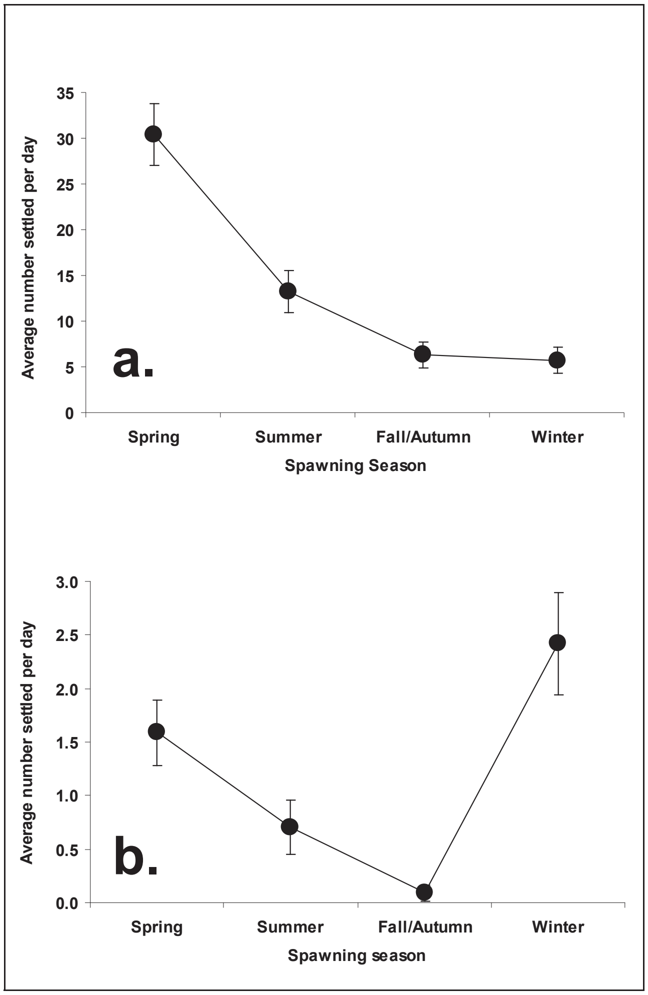


Figure 4.10 - Comparisons of long-distance transport (a) and local retention (b) segregated by spawning season using NLOM currents and 3-month PLD. Spring, summer, fall/autumn, and winter seasons are defined as February−April, May−July, August−October, and November−January, respectively. Means and 95% CIs from all daily data for each season are plotted.

4.5 Discussion

Ocean currents that could facilitate larval transport from Johnston Atoll to the Hawaiian Archipelago include the Subtropical Countercurrent (SCC; Yoshida and Kidokoro, 1967) and the Hawaiian Lee Countercurrent (HLCC; Qiu et al., 1997). Both the SCC and the HLCC generally flow in the eastward direction at latitudes between 19°-25° N. The dynamics of the SCC and the HLCC are not well understood, although it is thought that the HLCC is a result of a large-scale, island wake effect in the prevailing wind field (Xie et al., 2001). Dynamics of the SCC have been found to be important in the recruitment dynamics in other portions of the Hawaiian Archipelago (Polovina and Mitchum, 1992). Further study is necessary to understand the relationships of these important currents to pelagic larval ecology. Comparing other ocean current data will allow a better understanding and validation of the NLOM-driven simulations. As a start, the NLOM current fields (Figure 4.6) closely resembles the composite flow field presented by Qiu et al. (1997), which was estimated from a large dataset of surface drifter tracks. Both general features and overall magnitude of current speed match well for the region around the Hawaiian Archipelago and Johnston Atoll.

The 40−50-day PLD required to transit from Johnston Atoll to the Hawaiian Archipelago is consistent with the *Acropora* pattern, because their planula larvae can be competent for up to 91 days (Harrison et al., 1984). *Epinephelus quernus* larvae appear to have PLD exceeding this threshold as well (DeMartini, pers. comm.). In other species, PLD has been shown to be strongly related to genetic differentiation and, hence, biogeography. Riginos and Victor (2001) found that PLD for three blennioid species in the Gulf of California inversely correlated with the degree of genetic partitioning in the population. The spacing of biogeographic “stepping stones” will thusly serve to filter species colonization, depending on their reproductive strategy. Further simulations will examine this process in more detail for the Hawaiian Archipelago, using an approach similar to Dytham (2003). Taxa with relatively long PLDs or capable of delayed settlement/metamorphosis (e.g., Leis, 1983; Victor, 1986b) are more likely to complete the transit on a routine basis.

Lobel (1997) found that the PLD for the damselfish *Plectroglyphidodon imparipennis* was approximately 40 days, according to samples collected at Johnston Atoll and Hawaii. He concluded that this PLD was insufficient to successfully traverse the distance between the Hawaiian Archipelago and Johnston Atoll, hence populations were locally self-sustaining. Given the results of this study, it remains conceivable that this species could make the crossing. A follow-up study will examine the dynamics of the reverse path, from areas in the Hawaiian Archipelago to Johnston Atoll, as well as examine the very important role of larval retention for this oceanographically isolated region.

A larval fish survey around Johnston Atoll found indications of a retention zone on the leeward (Western) side of the atoll (Boehlert et al., 1992). This was primarily a result of the distribution of gobiid larvae with very short PLDs. Larvae of island-associated species were also most common in the upper 100 m, which supported the use of that particular NLOM layer of current data in the present study . The NLOM does not describe near-shore or near-bottom currents well and will not be useful for describing retention zones associated with sub-mesoscale oceanographic processes. Results from computer simulation are not intended to replace field sampling. However, the extreme scarcity of larvae of island-associated species in field samples has handicapped many such studies. With better knowledge of the oceanographic conditions, targeted sampling in both space and time could yield more meaningful scientific data, such as sampling areas that are significant to population maintenance and long-distance transport.

The findings of this study are relevant to any island-associated species with pelagic larval stages. Various vertebrate, invertebrate, and marine algal species all have pelagic stages with common processes affecting their distribution and survival (e.g., Bradbury and Snelgrove, 2001). Further study of this shared environment will be critical towards understanding biogeographic patterns and metapopulation structure. Other critical issues, such as invasive species colonization, could be addressed with these computer simulation tools.

Swimming behavior, especially for fish larvae, may be very important for the larger and older stages near the end of the PLD. Fisher and Wilson (2004), Fisher (2005), and others have shown that larval fish possess great mobility, and if the suitable orientation cues exist, they would be able to traverse many kilometers of ocean in the latter portions of the PLD. The 25-km detection radius used in this study could be traversed in a single day based on the findings of Fisher and Wilson (2004). Conveniently for modeling purposes, this region, where active swimming may take over, encompasses areas where oceanographic data usually lapse, because of the complexities of bottom topography, coastlines, tides, internal waves, etc. While swimming and orientation are undoubtedly important, the strongest visual, chemical, acoustic or other sensory cues appear to be localized to within a few kilometers of the target habitat (Leis, pers. comm.), and oceanographic processes remain significant in the transport of passive eggs and pre-flexion larvae as well as bringing older larger larvae close enough to the target habitat to orient and settle. The “Island Mass Effect” (Gilmartin and Revelante, 1974), as it relates to larval settlement cues, is an important area of future research.

The effect of spawning seasonality warrants further attention. The simulations indicate that the timing of spawning to be very important for subsequent larval survival, either via long-distance transport or local retention. Spawning seasonality in Hawaiian fishes is highly variable (Walsh, 1987), and further work is needed to understand the relationships between biogeography, adult reproductive strategies, and oceanographic variability.

The computer simulation results of this study serve to identify the PLD threshold needed to reach the Hawaiian Archipelago from Johnston Atoll. Additionally, potential oceanographic transport corridors have been charted and are consistent with the existing biogeographic theory for the region. Findings show that both long-distance transport and local retention are strongly dependent on spawning seasonality and pelagic larval duration. The high-resolution NLOM data appears to be a useful new tool for modeling larval transport in this region. A new analytical technique, CONREC-IRC, was introduced in this paper and its application in the quantification of spatial distributions was shown.

4.6 CONREC-IRC

CONREC-IRC (IRC refers to "Iterative Region of Containment") is an iterative program to objectively enclose a scatter of cartesian data points at a user-defined level of containment using a standard contouring algorithm to define the polygon. It was developed from CONREC, an open-source contouring subroutine originally written in FORTRAN-77 (Bourke, 1987). CONREC has been ported to many languages (see http://local.wasp.uwa.edu.au/~pbourke/papers/conrec/index.html), including the Visual Basic version (by James Craig), which was the precursor to CONREC-IRC. CONREC-IRC is written in QuickBasic 4.5 and takes advantage of the POINT command, which can query an individual pixel on the graphical output screen. This functionality was instrumental to CONREC-IRC by enabling tabulation of raw data points inside or outside of the contoured polygon. While mathematical algorithms exist to determine whether a point is within a polygon or not, the simplest method of plotting points, plotting the enclosing polygon, filling the enclosing polygon with color, then querying each data point's color was the most straightforward technique. The basic step-by-step methodology of CONREC-IRC is shown graphically in Figure 4.11. Because only a single value is being optimized, a simple, direct search algorithm (Hooke and Jeeves, 1961) was used to converge on the contouring level that would encompass the specified amount of data points. Proportional adjustments to the contour value were based on residuals from the percentage of data points encompassed. Testing with simulated data indicated that CONREC-IRC was able to quickly find the contouring solution within 10-15 iterations and was not sensitive to starting values. CONREC-IRC is suited for spatial data with a single center of mass with density tapers in all directions. More complex spatial patterns would yield multiple or nested contours and are not amenable to the CONREC-IRC approach since definition of a single mass is problematic. The source code for CONREC-IRC is available on request. An example application of CONREC-IRC example using Johnston Atoll retained larvae is shown in Figure 4.12.

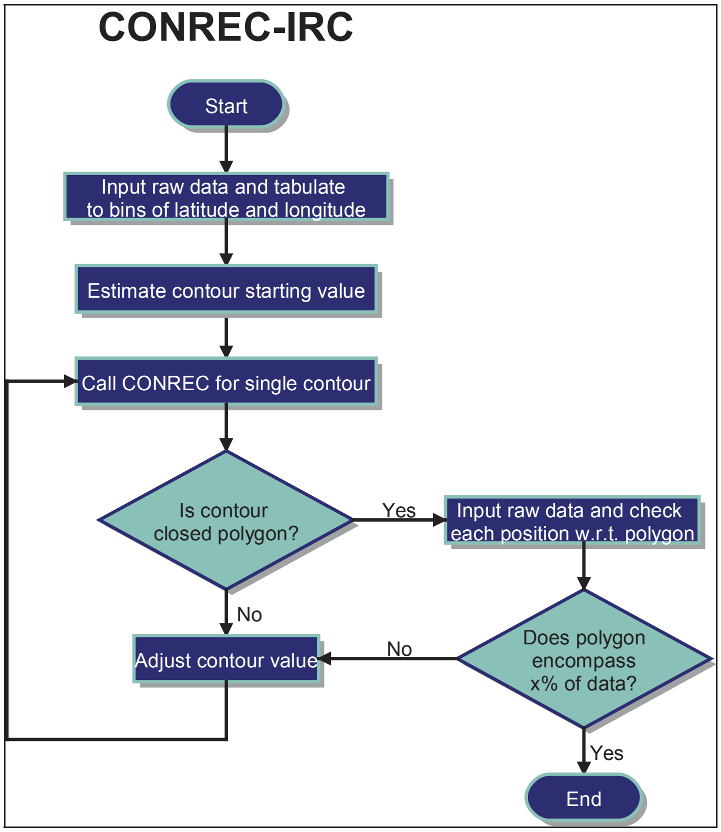


Figure 4.11 – Graphical representation of CONREC-IRC.

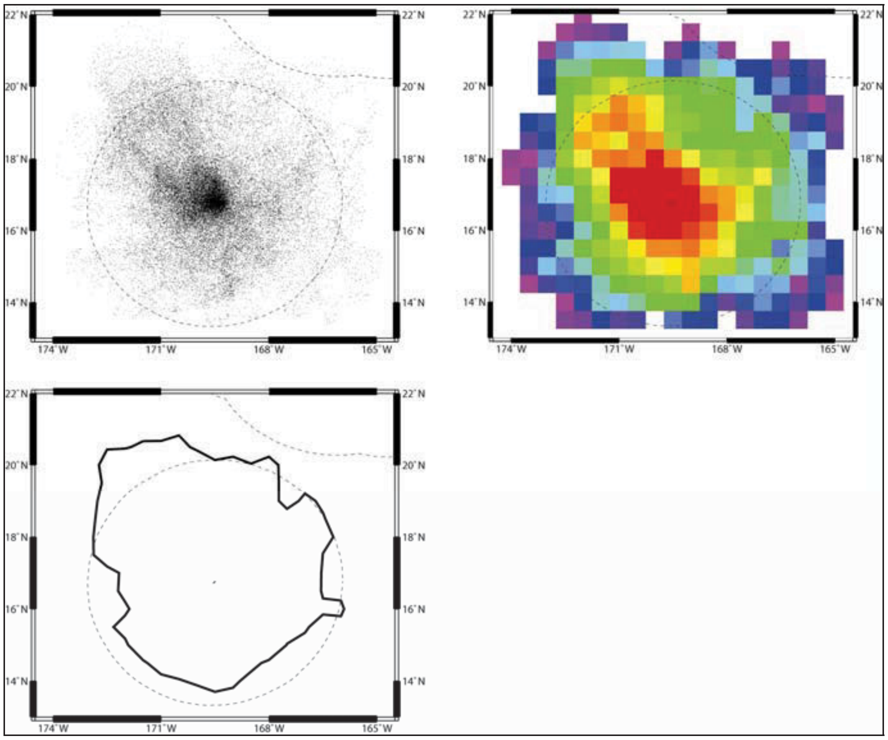


Figure 4.12 – Example application of CONREC-IRC to retained larval distribution around Johnston Atoll. Top left shows raw data, top right shows binned data, lower left shows CONREC-IRC 95% containment region.

Chapter 5: Larval retention versus larval subsidy: Marine connectivity patterns within and around the Hawaiian Archipelago

Kobayashi, D. R. Accepted with revision. Larval retention versus larval subsidy: Marine connectivity patterns within and around the Hawaiian Archipelago. *Marine Ecology Progress Series*.

5.1 Abstract

Metapopulation connectivity is poorly understood in the Hawaiian Archipelago, which hinders effective management and assessment of living marine resources in the region. This study addresses potential connectivity between geographically separated areas via the pelagic egg and larval life history phases assuming propagules are passive. Pelagic transport was investigated using high-resolution ocean current data and computer simulation. Connectivity measures between 25 geographic strata are presented for a suite of pelagic larval durations. Adjacent strata in the archipelago were well connected via pelagic larval transport regardless of larval duration, while connectivity of more distant strata was clearly mediated by larval duration. Retention, i.e., the return of natal propagules, is contrasted with subsidy, i.e., the influx of propagules from other sources. These 2 processes appear to be decoupled based on examination of archipelago-wide patterns. Single-generation and multi-generation effects of connectivity are considered using a simple population dynamics model driven by the dispersal kernel probability estimates. The Papahānaumokuākea Marine National Monument appears to be largely self-sustaining based on these results, with differential input to certain of the inhabited islands further southward in the archipelago depending on the pelagic larval duration.

5.2 Introduction

Many animal and plant populations are structured as relatively isolated geographic units due to patchy habitat distributions or other ecological constraints. This phenomenon was termed the metapopulation concept initially in a terrestrial arthropod system (Levins 1969), in which the original definition of a metapopulation required periodic extinctions and recolonization events. Following the approach of Hanski (1999) and others, Kritzer and Sale (2004) define marine metapopulations as a “system of discrete local populations, each of which determines its own internal dynamics to a large extent, but with a degree of identifiable and nontrivial demographic influence from other local populations through dispersal of individuals”. Many marine populations fall into this category due to relatively sessile adult life history stages and dispersive egg/larval propagules (Roberts, 1997). These propagules are pelagic for many species and are capable of long-distance transport due to both passive, planktonic drift in ocean currents (Hare et al., 2002) and active swimming and orientation of the older pelagic life history stages (Leis and Carson-Ewart, 2003; Fisher, 2005; Leis, 2007). These same mechanisms may also be important for natal retention (Cowen et al., 2000; Sponaugle et al., 2002; Jones et al., 2005; Almany et al., 2007). The degree of connection between metapopulations is often termed connectivity, and includes both the dispersal of early life history stages and the directed movements of adults, i.e., emigration/immigration and migration. For benthic marine species inhabiting island systems, connectivity during the early life history stages is thought to be most important with regard to population dynamics (Barlow, 1981).

There are a large number of geographically separated islands, coral atolls, seamounts, and banks throughout the Hawaiian Archipelago (Figure 5.1). Most of the benthic or island-associated species in this region do not routinely cross the large expanses of deep-ocean between habitats as adults; however pelagic egg and larval stages can easily traverse these boundaries and even longer distances (Robertson et al., 2004). Despite the importance of this issue towards understanding population dynamics and effectively managing these species or areas (e.g. Crowder et al., 2000; Valles et al., 2001; Sale and Kritzer, 2003), larval connectivity in this region 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 Northwestern Hawaiian Islands (DeMartini and Friedlander, 2004) make such information critically important for the Hawaiian Archipelago. Such information will also be extremely important towards understanding the ecological impact of the recently established Papahānaumokuākea Marine National Monument , as well as for understanding the source/sink dynamics of marine protected areas (MPAs) established for bottomfish, the Humpback Whale sanctuaries, the military-related closure around Kahoolawe, the Fish Replenishment Areas (FRAs) of west Hawaii, and various other areal closures in the state.

The purpose of this study is to examine patterns of larval connectivity between a large number of geographic strata in and around the Hawaiian Archipelago using high-resolution ocean current data and computer simulation. Ocean drifter data are compared to the ocean current data utilized in this study for ground-truthing the flow fields.

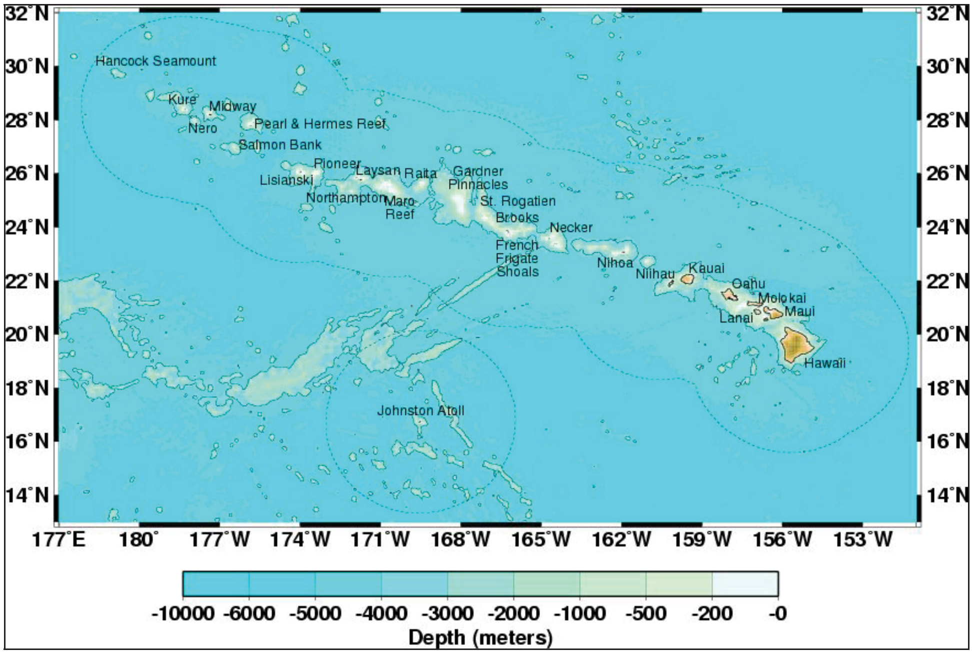


Figure 5.1 - Map of Hawaiian Archipelago study region showing location of primary habitat strata utilized in the larval transport simulations. Bathymetry is from the Smith and Sandwell (1997) 2-minute database.

5.3 Methods

5.3.1 Ocean current data

This study uses the same U. S. Naval Research Laboratory (NRL) ocean current data as used in Kobayashi (2006) for a study on Johnston Atoll connectivity. The NRL operates a global, six-layered ocean circulation model called NLOM for NRL Layered Ocean Model. The NLOM operates at a resolution of 1/16° (0.0625°) latitude by 45/512° (0.0879°) longitude (Rhodes et al., 2002; Wallcraft et al., 2003). This mesoscale model is eddy-resolving and thermodynamic, meaning that the density structure of the modeled ocean can be modified by physical processes. The NLOM is atmospherically forced using data from the Navy Operational Global Atmospheric Prediction System (NOGAPS). It also assimilates remotely-sensed, sea surface height data (GFO, JASON-1, and ERS-2 satellites) and sea surface temperature data

(NRL/MODAS SST). Daily NLOM output is an operational product from NRL that is available from many cooperating data servers. One of these is the Asia-Pacific Data-Research Center (UH/SOEST/IPRC/APDRC — http://apdrc.soest.hawaii.edu/). One of the daily output layers routinely archived is the upper 100 m, henceforth termed surface layer. For this study, 365 days of daily surface layer data (31 January 2003 to 30 January 2004, these exact dates were not chosen but reflected data availability at the time) spanning the region 170° E to 150° W longitude, 10° N to 35° N latitude were obtained from the APDRC. The daily surface-layer data included estimates of u (zonal East-West) component and v (meridional North-South) component for current vectors. The spatial grid (Figure 5.1) covered 457 x 401 pixels.

5.3.2 Geographic location

The Hawaiian archipelago spans from SE Hancock Seamount in the northwest to the island of Hawaii in the southeast. Locations and sizes of the 25 primary geographic features utilized in this study are presented in Table 5.1. Several sub-regions of the archipelago are recognized. The Main Hawaiian Islands (MHI) are mostly larger populated islands in the southern portion of the chain, but also include some submerged and/or uninhabited islands. The Northwestern Hawaiian Islands (NWHI) includes all areas recently designated as a Papahānaumokuākea Marine National Monument1, but is also further divided for some fishery management purposes. The lower portion of the NWHI is referred to as the Mau Zone (Necker and Nihoa Islands), and the larger region further north as the Hoomalu Zone (French Frigate Shoals and northward), in the Bottomfish and Seamount Groundfish Fishery Management Plan (FMP) implemented by the Western Pacific Regional Fishery Management Council (WPRFMC). The commercial NWHI spiny lobster fishery is currently closed but this fishery was managed on a bank-specific basis since 1998, with primary fishing grounds located at Maro Reef and Necker Island. Aside from a short-lived black coral fishery north of Midway there are no other extractive activities of nearshore resources in the NWHI. Conversely, the nearshore resources of the MHI are relatively heavily fished by recreational, subsistence, and commercial activities; hence connectivity to more pristine areas is of extreme concern. Although geographically separated from the archipelago, Johnston Atoll was examined as part of the spatial matrix utilized in this study considering its proximity to the archipelago and its ability to provide larval exchange (Kobayashi, 2006). Understanding connectivity between these larger strata as well as the individual islands, banks, seamounts, and coral atolls is important towards effective management and scientific understanding of population dynamics in a metapopulation context.

Table 5.1 - Listing of geographic strata utilized in connectivity simulations. Inclusion criteria was presence of at least one 2' pixel in the Smith and Sandwell bathymetric database. Also presented are locations, sizes, and summary of releases/retentions/subsidies per strata aggregated over all simulations performed.

Index #	Location	Longitude E	Latitude N	2' pixels 0-100m	Total releases	Total retention	Retention per release	Total subsidy	Total settlement	Settlement per pixel
1	Kure	181.66	28.41	11	2409000	30747	1.28%	38426	69173	6288
2	Midway	182.62	28.21	9	1971000	38579	1.96%	89336	127915	14213
3	Pearl & Hermes	184.17	27.86	24	5256000	176189	3.35%	131800	307989	12833
4	Salmon	183.57	26.93	2	438000	3072	0.70%	92505	95577	47789
5	Lisianski	186.07	26.05	24	5256000	258803	4.92%	217695	476498	19854
6	Pioneer	186.57	26.00	29	6351000	91598	1.44%	288039	379637	13091
7	Laysan	188.26	25.82	27	5913000	189576	3.21%	556023	745599	27615
8	Northampton	187.85	25.38	4	876000	24289	2.77%	572478	596767	149192
9	Maro	189.30	25.48	91	19929000	1335332	6.70%	400380	1735712	19074
10	Raita	190.57	25.64	14	3066000	88058	2.87%	414671	502729	35909
11	Gardner	191.96	24.88	143	31317000	1822490	5.82%	363624	2186114	15288
12	St. Rogatien	192.86	24.33	19	4161000	26880	0.65%	375485	402365	21177
13	Brooks	193.10	24.16	5	1095000	10549	0.96%	308981	319530	63906
14	French Frigate Shoals	193.80	23.79	51	11169000	319006	2.86%	343052	662058	12982
15	Necker	195.50	23.44	66	14454000	1176951	8.14%	399529	1576480	23886
16	Nihoa	197.89	23.11	37	8103000	277273	3.42%	377511	654784	17697
17	Middle	198.93	22.73	3	657000	2593	0.39%	137013	139606	46535
18	Niihau	199.84	21.91	21	4599000	67025	1.46%	220240	287265	13679
19	Kauai	200.45	22.09	36	7884000	628720	7.97%	504455	1133175	31477
20	Oahu	202.21	21.28	92	20148000	2125237	10.55%	1373999	3499236	38035
21	Molokai	202.95	21.01	84	18396000	2759697	15.00%	2521814	5281511	62875
22	Lanai	203.28	20.57	4	876000	3399	0.39%	178743	182142	45536
23	Maui	203.58	20.76	63	13797000	2378704	17.24%	2601584	4980288	79052
24	Hawaii	204.32	19.64	99	21681000	3490738	16.10%	1628482	5119220	51709
25	Johnston	190.45	16.75	1	219000	1241	0.57%	7850	9091	9091

5.3.3 The spawning event

The spatio-temporal pattern of propagule release is a key part of this study. For the spatial component, spawning output was assumed to be proportional to the amount of shallow-water habitat identified through the 2-minute pixel analysis of the Smith and Sandwell (1997) bathymetric database, as described below. This does not take into consideration substratum composition, habitat type, habitat quality, population size, spawning biomass, fecundity, or propagule viability. This approach further assumes that the shallow-water habitat is either fully saturated or equally so across strata. For the purposes of this study, the target organism (whether plant, invertebrate, or fish) is assumed to be an insular species residing uniformly from 0-100m depth throughout the archipelago. Forthcoming analyses will be tailored toward particular species using specific release locations as available. Spawning output was assumed to be uniform throughout the year for the temporal component. While many marine species in Hawaii are known to display seasonal spawning patterns (e.g., Walsh, 1987), these patterns are not clearly unimodal nor are they likely to be similar even across ecologically similar species (Reese, 1968). The target organisms (whether plant, invertebrate, or fish) are assumed to spawn continually throughout the year or with sufficient variability which dampens pronounced seasonality for the purposes of this study. Clearly, no one species meets these stringent assumptions, and the results presented here apply to a hypothetical species. This analysis is intended as a proof of concept rather than documenting a specific result for a particular species of interest.

5.3.4 Modeling of transport

The movement of larvae was simulated using the individual-based, Lagrangian modeling techniques identical to that used in Kobayashi (2006). These are also known as biased random-walk models. The daily NLOM data was used to advect larvae horizontally. A detection radius of 25 km from suitable settlement habitat at the end of the pelagic larval duration (PLD) was used as an indicator of settlement. Suitable settlement habitat was defined from a 2-minute resolution bathymetric database (Smith and Sandwell, 1997), by screening to only include 2-minute pixels ranging in depth from 0 to 100 m. A summary of these habitat pixels is presented in Table 5.1. An eddy-diffusivity coefficient of 500 $m^2 s^{-1}$ was utilized, which was qualitatively based upon drifter buoy observations (Polovina et al., 1999).

Fisher and Wilson (2004) found that sustainable swimming speeds were on the order of 30 cm s^{-1} for large, ready-to-settle fish larvae. The 25-km radius used in this study could be traversed in one day at these speeds, assuming continuous swimming and directional orientation. Invertebrate larval swimming speeds of this magnitude have also been observed in the late larval stage of spiny lobster called the peurulus (Philips and Olsen, 1975), and in the late larval stage of crabs called the megalops (Fernandez et al., 1994). While the cues available on the high seas are poorly understood, the "Island Mass Effect" (Gilmartin and Revelante 1974) can have significant, visually detectable effects out to this radius (e.g. Palacios, 2004). Elevated levels of chlorophyll a, because of proximity to islands, banks, and seamounts, are also apparent at this spatial scale in the Hawaiian Archipelago (Kobayashi, unpublished data). Olfactory and auditory cues may also be functional many km from shore (Atema et al., 2002; Leis and Lockett, 2005; Wright et al., 2005, Leis, 2007; Simpson et al., 2008). Some larvae do not have well-developed swimming abilities and appear to behave as passive drifters (coral planula, lobster phyllosomes, etc.), or may exhibit "behavioural drifting" despite being able to swim capably (Hogan and Mora, 2005). These larvae may require a more accurate "hit" on suitable substrate for successful settlement to occur. However, the 25-km radius was used in all simulations as a compromise to yield some settlement at a manageable level of larval release magnitude; i.e., the radius could be made smaller but would require more releases to attain non-zero settlement.

For each of the 2238 pixels of shallow-water habitat, 100 simulated larvae were released on each of the 365 calendar days in the NLOM current data and tracked for pelagic larval durations (PLDs) of 15, 30, 60, 90, 180, and 365 days. The sample size of 100 was chosen as a compromise because of computational speed and data storage concerns. Given 27 habitat units, this works out to approximately 8289 larvae released per habitat unit per 365 days per 6 PLDs. The range of PLDs encompasses the known values for a wide variety of vertebrate and invertebrate species in the Hawaiian

Archipelago, including commercially important species such as deepwater bottomfish and lobster, as well as coral reef inhabitants. Among some of the more commercially important or conspicuous fauna, the spiny lobster has approximately 12 month PLD (Kittaka and Kimura, 1989), the various slipper lobsters range from 2-9 month PLD (Booth et al., 2005); the deepwater snappers and grouper are approximately 1-3 month PLD (Leis, 1987); and most coral reef fishes are typically 0.5-3 month PLD (Victor and Wellington, 2000). Because the data spanned a discrete 365-day time block, data were allowed to "wrap around" for simulations initiated in the latter portions of the data. In other words, any larvae still at large during their PLD on 30 January 2004 would next encounter currents from 31 January 2003, and carry on from that point forward. This would allow a symmetrical analysis of possible seasonal effects. One undesirable consequence of this approach is that it imposes a discrete "jump" in the data stream at the end of January; however, this approach was used to make best use of all available data for the widest range of PLDs possible. Operationally, the location of larvae in Cartesian space was calculated with the following equations:

$$\begin{aligned} x_{t+\Delta t} &= x_t + \left[u_{(x_t,y_t,t)}\Delta t + \varepsilon\sqrt{D\Delta t}\right] / \cos(y_t) \\ y_{t+\Delta t} &= y_t + \left[v_{(x_t,y_t,t)}\Delta t + \varepsilon\sqrt{D\Delta t}\right] \end{aligned}$$

where x represents longitude in degrees, y represents latitude in degrees, t represents time in days, u represents the zonal East-West component of the current speed in degrees day^{-1}, v represents the meridional North-South component of the current speed in degrees day^{-1}, ε is a normal random variate (mean 0 and standard deviation 1), $\cos(y_t)$ adjusts longitudinal distance by latitude to account for the spherical coordinate system, and D is the diffusivity coefficient (500 m^2 s^{-1}, 0.0035 degrees^2 d^{-1}, Polovina et al., 1999). The full-resolution, daily 1/16° latitude by 45/512° longitude u and v arrays were sampled depending on the location in time and space of individual simulated larvae. Simulated larvae at the end of the PLD and in the 25 km radius of any habitat pixel were scored as settled. Orientation and swimming were not implicitly part of the model structure, nor was the capability of early or delayed settlement and/or metamorphosis. However, it was assumed that competent larvae were able to successfully navigate the last 25 km at the end of the pelagic duration. The tabulation of settled larvae includes a range of individuals from directly upon the habitat pixel up to 25 km distant; therefore, the actual mean PLD within this grouping may slightly exceed the index value PLD due to variable final transit time among individuals.

5.3.5 Evaluating connectivity

Successful settlement was cross-tabulated into matrices defined by source site (larval release site) and receiving site (larval settlement site). Data for individual pixels were collapsed into the 25 strata presented in Table 5.1. Since the raw counts of settlement are a function of release sample size it is desirable to standardize the counts into meaningful indices. Settlement was standardized by source site across all receiving sites, in other words calculating what proportion of a batch of larvae released from a particular source site settled at a particular receiving site; when summed across all receiving sites this would add up to 1. These data are presented in tabular form and graphically for particular subsets of the data such as examining retention as a function of PLD or geography. Retention, i.e., the return of natal propagules, is contrasted with subsidy, i.e., the influx of propagules from other sources, realizing that both processes are important towards population dynamics. All settlement data were pooled across 365 days for a coarse examination of retention and subsidy geographic patterns.

5.3.6 Multi-generation dynamics

A simple metapopulation simulator was parameterized with the connectivity measures and forecast for many generations to account for the cumulative effects of the linkages (e.g., Hastings and Botsford, 2006). An initial baseline condition was defined by the spatial distribution of habitat and propagule releases. The baseline condition started with 100% natal composition; i.e., all residents were considered to be derived from retention. The total initial number of propagules released per habitat stratum was used as a cap in subsequent generations as a simple means of density-dependence. In other words after each generation was tabulated with respect to retention and subsidy from all sources, the overall population at each geographic strata was trimmed until it was equivalent to the starting population size at that strata while preserving the relative metapopulation structure contained therein. This stabilized the overall archipelagic population to a constant level for the purposes of examining the source composition within each habitat strata over time. For each generation, the connectivity measures were used to drive retention and subsidy at each of the strata, followed by a leveling-down process to achieve the initial metapopulation size. This was repeated for 1000 generations for each of the 6 PLDs, keeping careful track of lineages of all propagules. This number of generations was observed to be adequate for achieving source composition stability. Quasi-equilibrium was quickly achieved within 30-40 generations depending on the PLD. It is realized that the number of propagules released will determine this time to equilibrium, but this exercise was undertaken to examine the resulting equilibrium structure, not the absolute time trajectory to reach said equilibrium. A technique called nonmetric multidimensional scaling (NMDS) was used to examine spatial affinities among equilibrium metapopulation structure across all geographic strata and PLDs. NMDS is an iterative ordination approach that is also useful to assess dimensionality in a dataset. It is considered the method of choice for ordination of most ecological data (McCune and Grace, 2002). NMDS of the metapopulation structure across all geographic strata and PLDs was accomplished using the commercial software package PC-ORD. The NMDS output is a 2-D scatterplot of points, each representing a particular combination of geographic strata and PLD. Similarity or dissimilarity is assessed from visual examination of the relative location of points in Cartesian space.

5.3.7 Ground-truthing flow fields with drifter buoys

Drifter buoy data are publicly available from the NOAA Global Drifter Program (http://www.aoml.noaa.gov/phod/dac/gdp.html). These drifters are deployed from NOAA research platforms and vessels of opportunity, have their drogues at 15m depth, and communicate daily with Argos, an American-French satellite data network (Lumpkin and Pazos, 2006). For the spatial and temporal window of NLOM data utilized in this study there were 64 individual drifters with some level of intersection representing a total of 29750 records at 6-hour kriged (smoothed) data resolution (Table 5.2). This represents an average of approximately 116 days of information per drifter buoy in this area at this time. The aggregated tracks are shown in Figure 5.2. Each drifter buoy data record was matched to a corresponding NLOM daily current at its location and the differences were tabulated for statistical analyses. Four components were examined separately: the u-component, v-component, magnitude, and direction. NLOM observations were binned at 1 cm sec-1 or 1° intervals of drifter values. Simple linear regressions were used to characterize the relationships between modeled and observed current components, applying the regression to the portion of the data range where sample size was high (n>=100 per 1 cm sec-1 binned mean).

Table 5.2 - Listing of NOAA drifter buoys intersecting the NLOM region over the studied time interval. Number of datapoints used represents the number of 6 hour resolution data available.

Drifter ID	Start-end dates	Number of datapoints used
13519	5/21/2001-10/17/2003	1033
13575	7/3/2001-4/19/2003	310
17956	4/24/2001-4/18/2003	96
18288	4/4/2001-2/4/2003	15
19241	7/7/2001-7/11/2003	21
20098	6/20/2001-8/29/2003	302
21532	7/1/2001-9/2/2003	155
22936	3/21/2001-10/10/2005	1092
23122	12/12/2001-8/7/2003	159
23173	6/30/2001-3/16/2003	175
24014	6/6/2001-7/28/2003	711
24097	7/1/2001-5/11/2003	254
24443	1/13/1996-4/6/2003	255
25764	1/1/1996-11/27/2004	869
25770	3/15/2001-6/24/2003	575
25929	3/15/2001-3/14/2004	246
26035	3/11/2001-12/31/2004	1391
27465	9/6/2001-12/24/2003	364
33862	5/17/2002-1/12/2005	403
33866	6/22/2002-8/31/2003	525
33867	6/23/2002-11/11/2003	212
33920	10/5/2001-11/25/2004	469
33922	10/6/2001-10/30/2005	152
33997	2/26/2002-5/4/2004	81
34000	6/6/2002-4/13/2004	236
34009	12/19/2001-10/20/2003	1047
34021	7/4/2002-2/16/2004	756
34026	7/17/2002-11/4/2003	147
34042	7/24/2002-2/10/2004	401
34051	8/14/2002-9/27/2004	1460
34052	8/15/2002-3/1/2003	113
34061	7/1/2002-7/19/2003	642
34071	6/20/2002-7/7/2004	701
34102	1/29/2002-8/12/2003	596
34108	2/10/2002-7/22/2004	588
34131	11/4/2002-11/2/2004	157
34319	11/16/2002-6/17/2003	124
34320	6/30/2003-1/10/2005	255
34325	11/17/2002-3/31/2004	1448
34332	5/31/2002-4/15/2003	292
34333	6/6/2002-9/29/2003	213
34334	6/22/2002-7/22/2004	1453
36009	9/9/2002-6/8/2004	224
36907	11/11/2002-11/8/2004	440
36909	9/29/2002-1/28/2004	471
36911	9/17/2002-1/23/2005	999
36914	10/17/2002-11/5/2004	487
36919	9/15/2002-2/1/2006	1140
36920	9/16/2002-2/1/2006	716
36924	9/10/2002-1/2/2006	1197
36925	9/28/2002-4/1/2004	93
36948	1/18/2003-4/1/2004	94
36956	2/1/2003-1/31/2006	324
36957	2/3/2003-6/23/2004	389
36958	2/3/2003-1/13/2006	218
36960	1/17/2003-1/15/2005	466
36961	1/16/2003-2/1/2006	1111
39092	1/12/2003-2/28/2004	107
39099	2/15/2003-6/24/2004	138
39109	1/15/2003-1/13/2004	24
39155	4/30/2003-8/11/2004	262
39167	7/25/2003-3/14/2004	151
39602	6/24/2003-2/1/2006	187
39631	8/1/2003-2/1/2006	18

29750 total

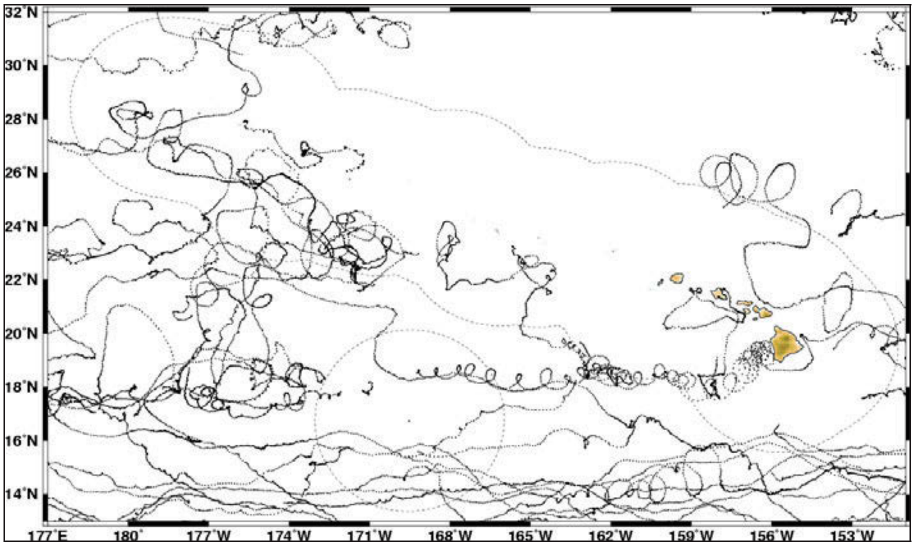


Figure 5.2 - NOAA drifter buoy trajectories in the Hawaiian Archipelago region over the time interval 31 January 2003 – 30 January 2004.

5.3.8 How representative is 2003-2004 data?

The results presented here reflect modeled processes during the 2003-2004 calendar years. Temporal variability in the oceanographic processes clearly exists, including interannual variability, decadal variability, regime shifts, climate change, global warming, etc. Such changes in oceanography and resulting current patterns are principally driven by large-scale climate events. Two commonly used indices of temporal variability in the Hawaiian Archipelago climate and oceanography are the Southern Oscillation Index (SOI) and the Pacific Decadal Oscillation (PDO). The former is thought to capture interannual variability around the equatorial regions related to El Nino and La Nina, while the latter is thought to capture dynamics related to decadal variability in the higher latitudes north of 20°N. Monthly time series of these two oceanographic indices were obtained from NOAA Physical Sciences Division of the Earth System Research Laboratory (http://www.cdc.noaa.gov/ClimateIndices/) over the time period 1980-2007. Monthly values from the 2003-2004 time period were compared to monthly values from this larger 28 year span of data using a Student's t-test. The results of this test are used to judge the applicability of the findings of this study to other time periods.

5.4 Results

The overall geographic patterns of retention and subsidy are tabulated in Table 5.1. This aggregated all settlement data for the 365 daily releases. Retention rate (as a fraction of propagules released) ranged from a low of 0.39% at Middle Bank and Lanai, to a high of 17.24% for the island of Maui. This is not an artifact of stratum size since this measure is scaled by the amount of propagules released, which is directly proportional to shallow-water habitat area; therefore the retention rate is “per area”. When retention and subsidy were pooled to estimate total settlement per unit of habitat, settlement ranged from a low of 6288 settlers per pixel at Kure Atoll, to a high of 149192 settlers per pixel at Northampton. The high settlement rate at the relatively small Northampton is attributed mostly to subsidy (Table 5.1).

The connectivity results were converted to probabilities and tabulated into transition matrices; these are also often referred to as dispersal kernels. This standardized settlement by source site across all receiving sites for each PLD. The dispersal kernel probabilities are presented in Tables 5.3-5.8.

Table 5.3 - Dispersal kernel matrix for 15 day PLD. Each cell represents probability of a larva leaving source site and arriving at receiving site using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

	Source sites																								
Receiving sites	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.043	0.019	0.001	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.033	0.078	0.011	0.026	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.003	0.011	0.128	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salmon	0.000	0.006	0.024	0.022	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.000	0.000	0.000	0.004	0.201	0.046	0.001	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pioneer	0.000	0.000	0.000	0.001	0.095	0.051	0.013	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Laysan	0.000	0.000	0.000	0.000	0.002	0.024	0.118	0.073	0.048	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northampton	0.000	0.000	0.000	0.000	0.009	0.040	0.057	0.104	0.030	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maro	0.000	0.000	0.000	0.000	0.000	0.006	0.032	0.034	0.250	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Raita	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.001	0.011	0.122	0.012	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Gardner	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.018	0.224	0.018	0.012	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
St Rogatien	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.021	0.025	0.024	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Brooks	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.010	0.036	0.043	0.011	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
French Frigate Shoals	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.029	0.045	0.131	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Necker	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.005	0.033	0.326	0.017	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nihoa	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.132	0.035	0.010	0.003	0.000	0.000	0.000	0.000	0.000	0.000
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.011	0.014	0.004	0.000	0.000	0.000	0.000	0.000	0.000
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.018	0.061	0.034	0.001	0.000	0.000	0.000	0.000	0.000
Kauai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023	0.102	0.306	0.007	0.000	0.000	0.000	0.000	0.000
Oahu	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.015	0.344	0.084	0.028	0.008	0.002	0.000
Molokai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.147	0.463	0.136	0.128	0.005	0.000
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.009	0.013	0.010	0.002	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.152	0.240	0.502	0.044	0.000
Hawaii	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.024	0.146	0.064	0.384	0.000
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.024
Lost	0.921	0.886	0.836	0.925	0.691	0.833	0.777	0.762	0.660	0.826	0.727	0.888	0.871	0.818	0.657	0.833	0.910	0.810	0.638	0.468	0.268	0.436	0.288	0.563	0.976

Table 5.4 - Dispersal kernel matrix for 30 day PLD. Each cell represents probability of a larva leaving source site and arriving at receiving site using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

	Source sites																								
Receiving sites	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.020	0.014	0.003	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.017	0.023	0.014	0.019	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.012	0.016	0.042	0.017	0.006	0.002	0.003	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salmon	0.003	0.007	0.014	0.008	0.004	0.001	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.000	0.001	0.005	0.006	0.063	0.020	0.008	0.013	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pioneer	0.000	0.000	0.003	0.005	0.040	0.018	0.016	0.012	0.006	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Laysan	0.000	0.000	0.000	0.000	0.009	0.024	0.046	0.039	0.034	0.007	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northampton	0.000	0.000	0.001	0.000	0.016	0.023	0.033	0.037	0.025	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maro	0.000	0.000	0.000	0.000	0.003	0.018	0.037	0.041	0.098	0.031	0.005	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Raita	0.000	0.000	0.000	0.000	0.000	0.002	0.004	0.005	0.017	0.033	0.013	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Gardner	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.003	0.010	0.028	0.084	0.011	0.009	0.005	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
St Rogatien	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.003	0.006	0.013	0.006	0.005	0.003	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Brooks	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.004	0.008	0.007	0.008	0.005	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
French Frigate Shoals	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.005	0.006	0.013	0.017	0.028	0.012	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Necker	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.008	0.012	0.031	0.119	0.015	0.008	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000
Nihoa	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.003	0.010	0.038	0.025	0.019	0.010	0.002	0.000	0.000	0.000	0.000	0.000
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.006	0.006	0.006	0.004	0.001	0.000	0.000	0.000	0.000	0.000
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.013	0.016	0.016	0.003	0.000	0.001	0.000	0.000	0.000
Kauai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.026	0.051	0.127	0.012	0.002	0.005	0.001	0.000	0.000
Oahu	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.012	0.026	0.181	0.077	0.033	0.017	0.007	0.000
Molokai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.004	0.004	0.118	0.264	0.102	0.116	0.012	0.000
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.003	0.006	0.005	0.006	0.002	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.004	0.002	0.033	0.146	0.167	0.314	0.038	0.000
Hawaii	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.009	0.001	0.018	0.035	0.111	0.067	0.264	0.000
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007
Lost	0.948	0.938	0.919	0.937	0.856	0.892	0.852	0.846	0.803	0.876	0.870	0.950	0.947	0.925	0.852	0.922	0.913	0.874	0.808	0.631	0.469	0.577	0.478	0.676	0.993

Table 5.5 - Dispersal kernel matrix for 60 day PLD. Each cell represents probability of a larva leaving source site and arriving at receiving site using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

	Source sites																								
Receiving sites	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.007	0.008	0.004	0.007	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.008	0.010	0.007	0.008	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.013	0.010	0.016	0.012	0.009	0.004	0.003	0.004	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salmon	0.003	0.004	0.006	0.006	0.003	0.002	0.001	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.001	0.002	0.005	0.005	0.017	0.010	0.006	0.006	0.005	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pioneer	0.001	0.002	0.004	0.003	0.013	0.008	0.006	0.006	0.005	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Laysan	0.000	0.000	0.002	0.001	0.010	0.013	0.016	0.014	0.015	0.008	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northampton	0.000	0.000	0.003	0.002	0.011	0.011	0.013	0.012	0.012	0.007	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maro	0.000	0.000	0.001	0.000	0.009	0.016	0.024	0.022	0.030	0.020	0.006	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Raita	0.000	0.000	0.000	0.000	0.002	0.005	0.007	0.006	0.011	0.009	0.006	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Gardner	0.000	0.000	0.000	0.000	0.001	0.004	0.007	0.009	0.015	0.018	0.025	0.008	0.007	0.005	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
St Rogatien	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.003	0.004	0.005	0.007	0.004	0.003	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Brooks	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.003	0.004	0.006	0.004	0.003	0.002	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
French Frigate Shoals	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.004	0.006	0.008	0.007	0.006	0.007	0.002	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Necker	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.003	0.009	0.012	0.017	0.027	0.009	0.008	0.004	0.003	0.000	0.000	0.000	0.000	0.000	0.001
Nihoa	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.005	0.006	0.008	0.016	0.020	0.015	0.010	0.009	0.002	0.001	0.000	0.000	0.000	0.000
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.004	0.003	0.003	0.003	0.001	0.000	0.000	0.000	0.000	0.000
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.006	0.005	0.005	0.006	0.003	0.001	0.001	0.001	0.000	0.001
Kauai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.011	0.014	0.017	0.030	0.010	0.005	0.005	0.002	0.001	0.001
Oahu	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.007	0.013	0.018	0.025	0.067	0.049	0.025	0.022	0.009	0.000
Molokai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.007	0.012	0.012	0.065	0.108	0.059	0.073	0.014	0.000
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.002	0.003	0.003	0.003	0.001	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.004	0.011	0.008	0.039	0.098	0.088	0.136	0.029	0.000
Hawaii	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.004	0.013	0.007	0.024	0.038	0.076	0.058	0.164	0.000
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
Lost	0.967	0.964	0.952	0.957	0.919	0.922	0.912	0.913	0.895	0.917	0.935	0.958	0.959	0.956	0.933	0.934	0.924	0.906	0.897	0.786	0.697	0.742	0.704	0.781	0.994

Table 5.6 - Dispersal kernel matrix for 90 day PLD. Each cell represents probability of a larva leaving source site and arriving at receiving site using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

	Source sites																								
Receiving sites	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.004	0.004	0.004	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.004	0.005	0.006	0.006	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.007	0.006	0.009	0.010	0.006	0.004	0.004	0.005	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salmon	0.002	0.003	0.004	0.004	0.002	0.002	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.002	0.003	0.005	0.005	0.010	0.007	0.004	0.005	0.003	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pioneer	0.002	0.002	0.003	0.003	0.007	0.006	0.004	0.004	0.003	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Laysan	0.001	0.002	0.003	0.002	0.008	0.008	0.008	0.008	0.008	0.006	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northampton	0.001	0.001	0.003	0.002	0.009	0.008	0.008	0.008	0.007	0.005	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maro	0.001	0.001	0.002	0.002	0.009	0.012	0.014	0.013	0.016	0.012	0.005	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Raita	0.000	0.000	0.001	0.000	0.003	0.005	0.005	0.005	0.007	0.005	0.003	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Gardner	0.000	0.000	0.000	0.000	0.003	0.006	0.008	0.009	0.012	0.012	0.011	0.006	0.005	0.004	0.003	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
St Rogatien	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.003	0.004	0.003	0.004	0.003	0.003	0.002	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Brooks	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.002	0.003	0.003	0.004	0.003	0.003	0.002	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
French Frigate Shoals	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.002	0.003	0.006	0.006	0.005	0.004	0.004	0.002	0.003	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.001
Necker	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.004	0.007	0.008	0.009	0.011	0.006	0.006	0.004	0.003	0.001	0.000	0.000	0.000	0.000	0.001
Nihoa	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.003	0.004	0.006	0.007	0.011	0.010	0.009	0.007	0.006	0.002	0.001	0.001	0.000	0.000	0.001
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.002	0.002	0.003	0.002	0.002	0.002	0.001	0.001	0.000	0.000	0.000	0.000
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.002	0.004	0.003	0.004	0.003	0.002	0.001	0.001	0.001	0.001	0.001
Kauai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.002	0.005	0.009	0.009	0.010	0.011	0.007	0.005	0.004	0.003	0.002	0.002
Oahu	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.004	0.009	0.011	0.014	0.017	0.031	0.029	0.020	0.018	0.010	0.001
Molokai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.005	0.008	0.011	0.013	0.036	0.052	0.035	0.042	0.013	0.000
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.002	0.002	0.001	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.003	0.004	0.010	0.009	0.031	0.057	0.048	0.066	0.022	0.000
Hawaii	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.004	0.012	0.009	0.025	0.035	0.058	0.047	0.107	0.000
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Lost	0.975	0.973	0.961	0.962	0.935	0.935	0.938	0.933	0.929	0.939	0.953	0.965	0.964	0.964	0.950	0.944	0.938	0.923	0.924	0.863	0.817	0.831	0.821	0.843	0.988

Table 5.7 - Dispersal kernel matrix for 180 day PLD. Each cell represents probability of a larva leaving source site and arriving at receiving site using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

Receiving sites	Source sites																								
	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.002	0.002	0.002	0.002	0.001	0.001	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.004	0.005	0.004	0.005	0.003	0.003	0.002	0.003	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salmon	0.001	0.002	0.001	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.003	0.003	0.003	0.003	0.004	0.003	0.003	0.003	0.002	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Pioneer	0.002	0.002	0.002	0.003	0.003	0.003	0.002	0.002	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Laysan	0.002	0.002	0.003	0.003	0.004	0.004	0.003	0.003	0.004	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Northampton	0.002	0.002	0.003	0.002	0.004	0.004	0.003	0.004	0.003	0.003	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Maro	0.003	0.003	0.004	0.004	0.006	0.006	0.006	0.006	0.006	0.004	0.003	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
Raita	0.001	0.001	0.002	0.001	0.002	0.003	0.002	0.003	0.003	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Gardner	0.002	0.003	0.003	0.003	0.005	0.005	0.005	0.006	0.006	0.005	0.004	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.003
St Rogatien	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Brooks	0.000	0.000	0.001	0.001	0.001	0.002	0.001	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
French Frigate Shoals	0.000	0.000	0.001	0.000	0.001	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.001
Necker	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.002	0.003	0.003	0.003	0.003	0.003	0.002	0.002	0.002	0.002	0.001	0.001	0.000	0.000	0.000	0.002
Nihoa	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.003	0.003	0.003	0.004	0.004	0.004	0.003	0.003	0.002	0.001	0.001	0.001	0.001	0.003
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.001
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Kauai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.002	0.002	0.003	0.004	0.004	0.004	0.003	0.003	0.003	0.003	0.003	0.003	0.002
Oahu	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.001	0.001	0.001	0.002	0.003	0.003	0.004	0.005	0.007	0.006	0.006	0.006	0.008	0.009	0.008	0.008	0.007	0.003
Molokai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.002	0.004	0.005	0.005	0.006	0.006	0.009	0.011	0.011	0.011	0.008	0.002
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.003	0.004	0.005	0.006	0.006	0.011	0.014	0.013	0.014	0.011	0.001
Hawaii	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.002	0.002	0.003	0.005	0.006	0.009	0.008	0.016	0.020	0.027	0.024	0.039	0.001
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lost	0.973	0.971	0.970	0.968	0.958	0.958	0.962	0.959	0.959	0.967	0.971	0.972	0.971	0.971	0.965	0.962	0.962	0.960	0.962	0.948	0.939	0.933	0.938	0.928	0.971

Table 5.8 - Dispersal kernel matrix for 365 day PLD. Each cell represents probability of a larva leaving source site and arriving at receiving site using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

Source sites

Receiving sites	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.002	0.003	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Salmon	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.002	0.002	0.001	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Pioneer	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Laysan	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Northampton	0.001	0.001	0.001	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Maro	0.002	0.002	0.002	0.003	0.002	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
Raita	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Gardner	0.002	0.002	0.002	0.002	0.003	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
St Rogatien	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Brooks	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
French Frigate Shoals	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Necker	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002
Nihoa	0.001	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.001	0.000	0.000	0.000	0.001	0.000	0.001	0.001
Kauai	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002
Oahu	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.003	0.002	0.003	0.003
Molokai	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.003	0.002	0.003	0.002
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.002	0.002	0.002	0.003	0.003	0.003	0.004	0.002
Hawaii	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.003	0.003	0.003	0.004	0.004	0.005	0.006	0.007	0.006	0.008	0.003
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lost	0.981	0.980	0.980	0.979	0.978	0.978	0.981	0.979	0.980	0.983	0.984	0.984	0.984	0.984	0.983	0.984	0.984	0.984	0.985	0.983	0.982	0.979	0.982	0.976	0.971

The metapopulation simulation was performed for each of the PLDs for 1000 generations. Starting from a purely natal population, the composition at each habitat strata was allowed to change over time as determined by the dispersal kernel probabilities. An example time trajectory of this process is shown in Figure 5.3 for Maro Reef. Predictably, at longer PLDs, the equilibrium condition consisted of fewer of natal origin, corresponding to more mixing between metapopulations. At shorter PLDs the equilibrium condition was primarily composed of individuals of natal origin. The NMDS ordination graphically shows the strong impact of PLD on metapopulation structure (Figure 5.4). As PLD increases the NMDS coalesces into a nearly uniform pattern of metapopulation structure. Three such examples are graphically presented for comparison, with PLDs of 15 days (Figure 5.5A), 90 days (Figure 5.5B), and 365 days (Figure 5.5C). A breakdown of habitat size by area is shown in Figure 5.6, which is proportional to the amount of propagules released in the simulations. The standardized retention per pixel and subsidy per pixel are shown in Figure 5.7.

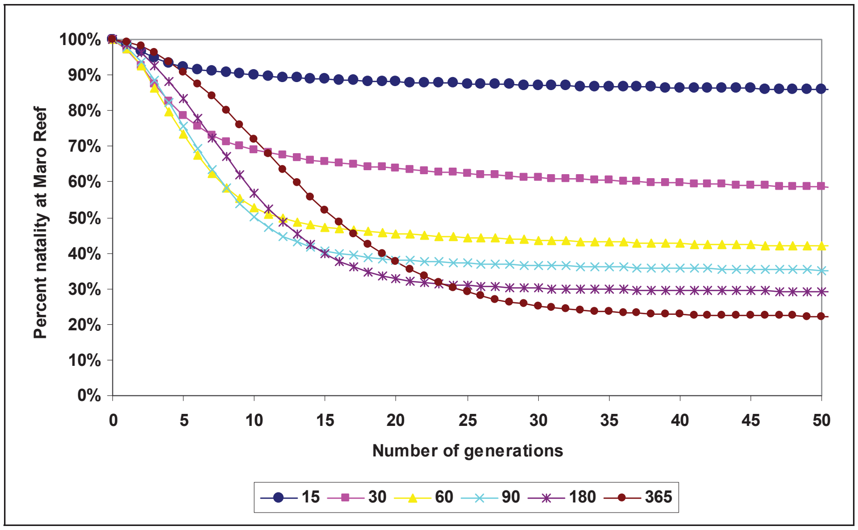


Figure 5.3 - Trajectories of Maro Reef percent natality using metapopulation simulation driven by NLOM derived dispersal kernels. Different lines correspond to different PLDs. Generations beyond 50 were not appreciably different from simulation endpoints at generation 1000.

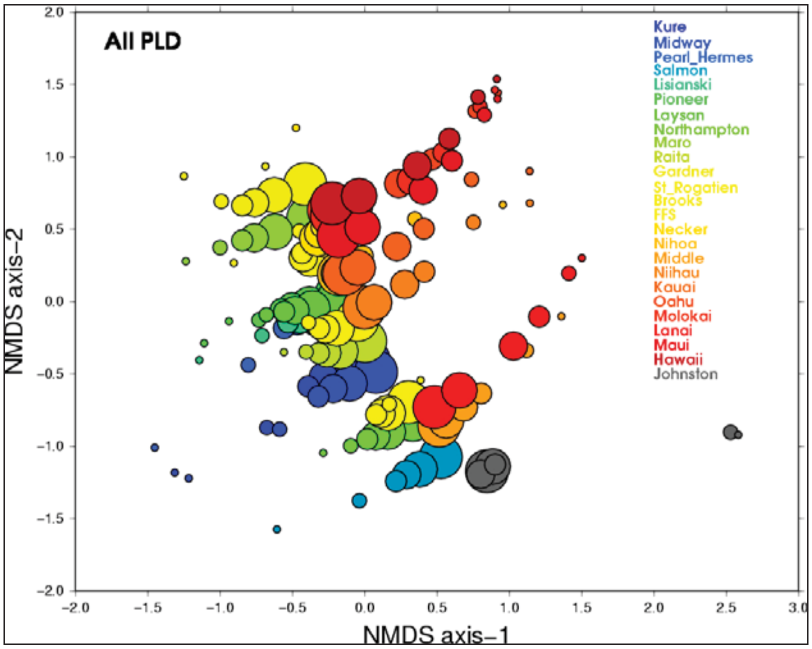


Figure 5.4 - NMDS ordination of metapopulation structure. Circle size is scaled linearly as a function of PLD, smallest circle representing 15 day PLD and largest circle representing 365 day PLD. Each geographic strata is color-coded in a gradient which approximately follows the geographic layout of the archipelago (Northwest to Southeast and lastly Johnston Atoll).

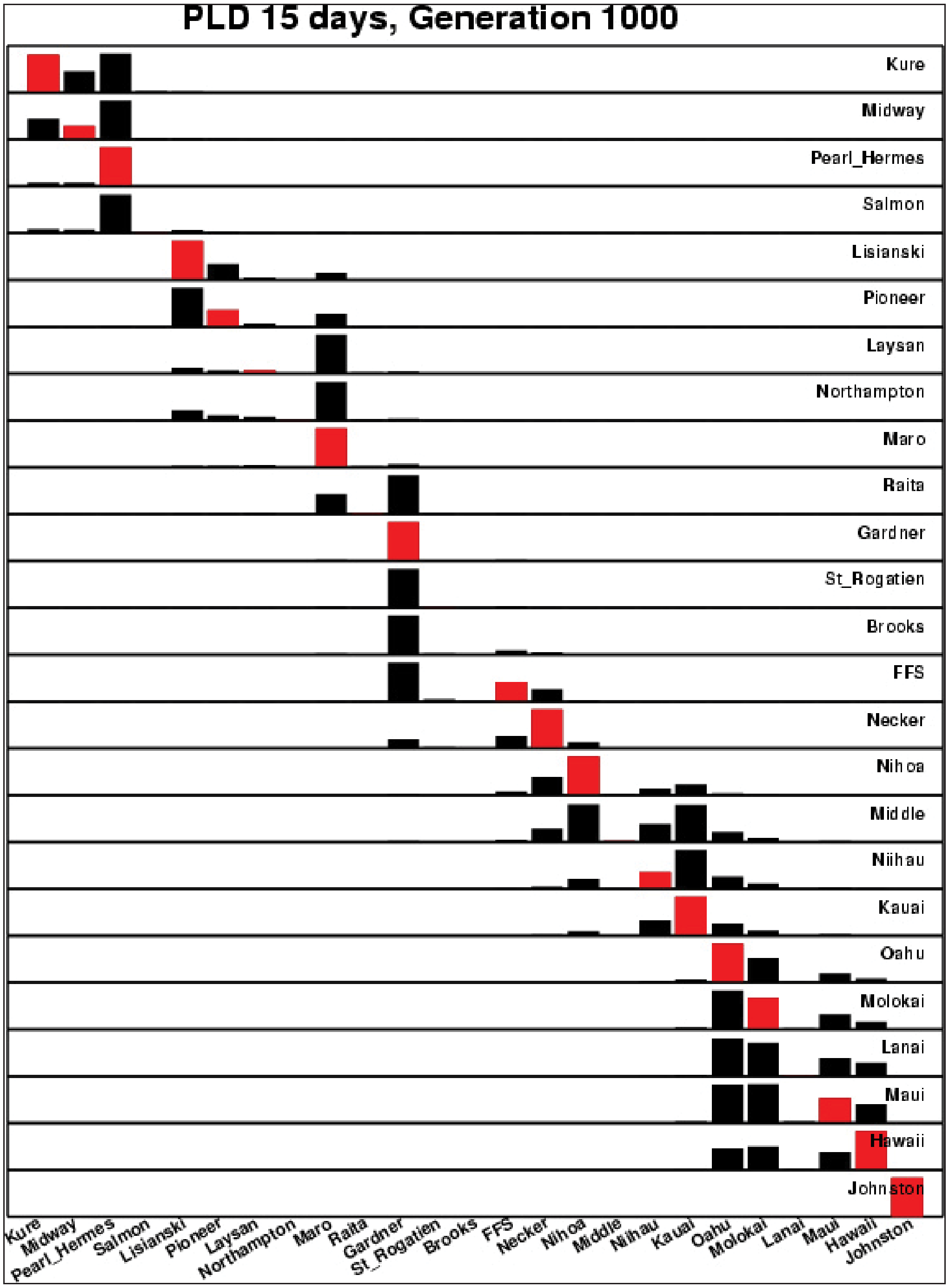


Figure 5.5A - Equilibrium metapopulation composition for 15 day PLD after 1000 generations of simulation using NLOM dispersal kernel probabilities. Red bars indicate natal origin. Each subplot y-axis is scaled independently to maximize data display.

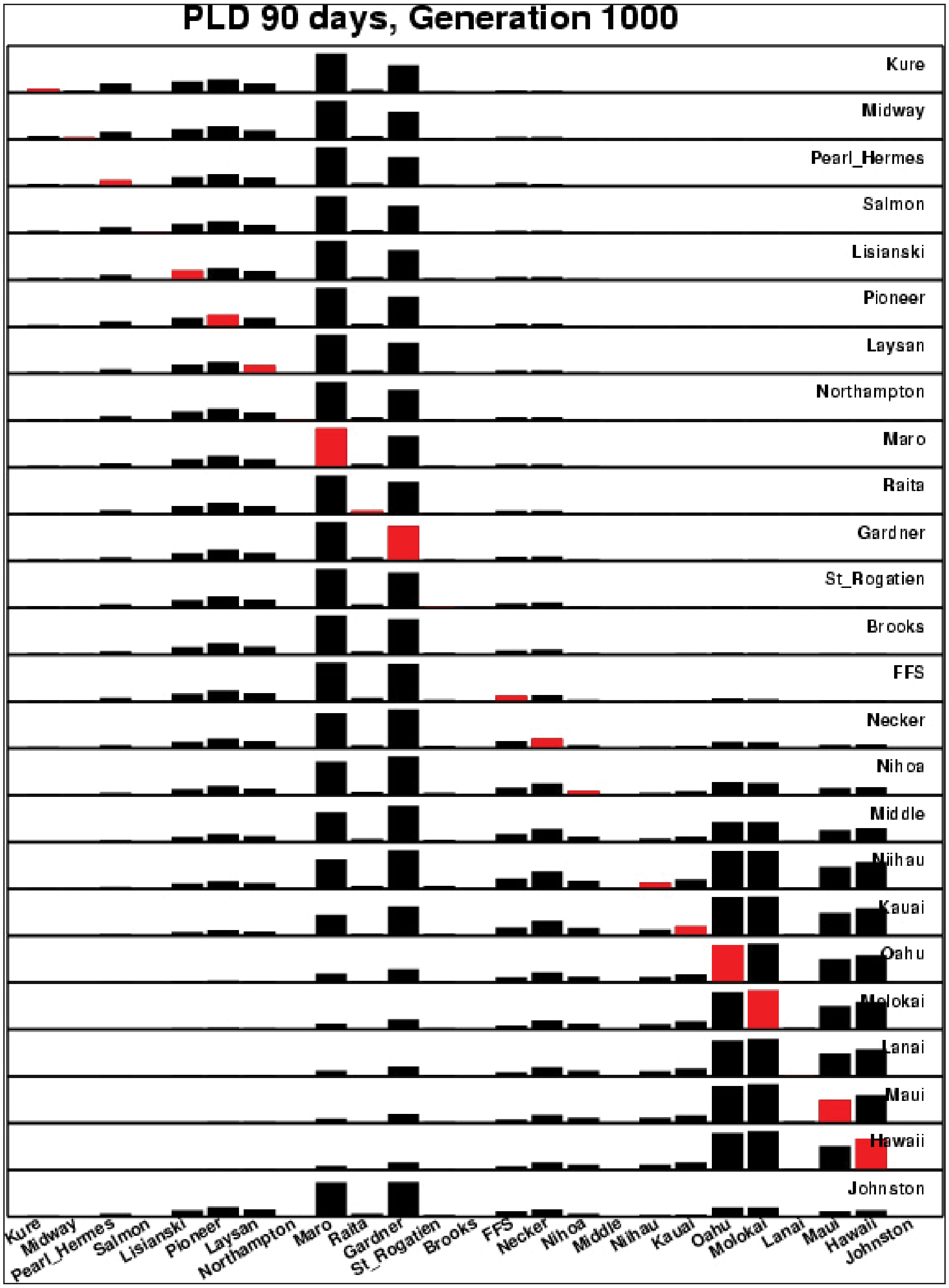


Figure 5.5B - Equilibrium metapopulation composition for 90 day PLD after 1000 generations of simulation using NLOM dispersal kernel probabilities. Red bars indicate natal origin. Each subplot y-axis is scaled independently to maximize data display.

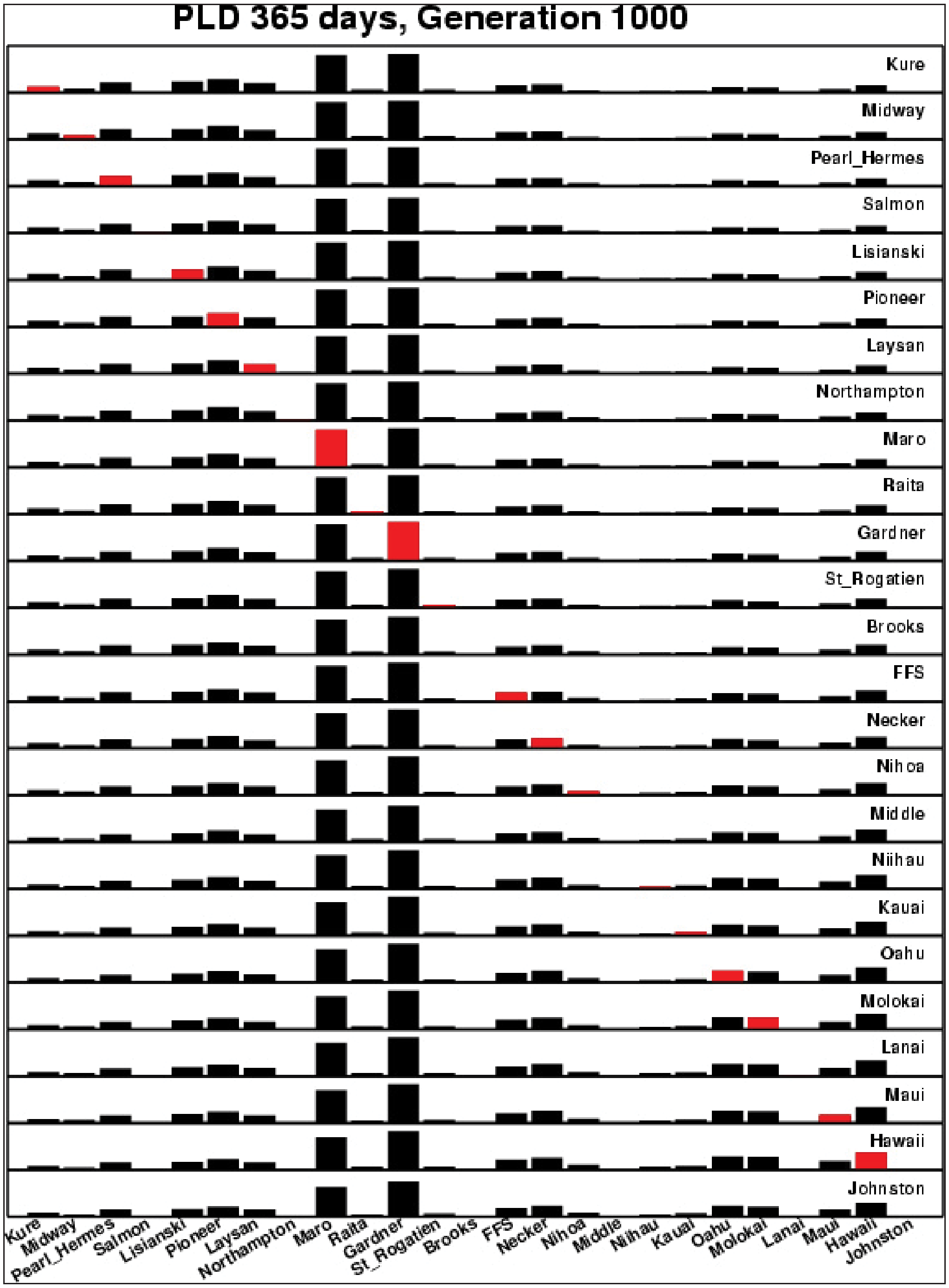


Figure 5.5C - Equilibrium metapopulation composition for 365 day PLD after 1000 generations of simulation using NLOM dispersal kernel probabilities. Red bars indicate natal origin. Each subplot y-axis is scaled independently to maximize data display.

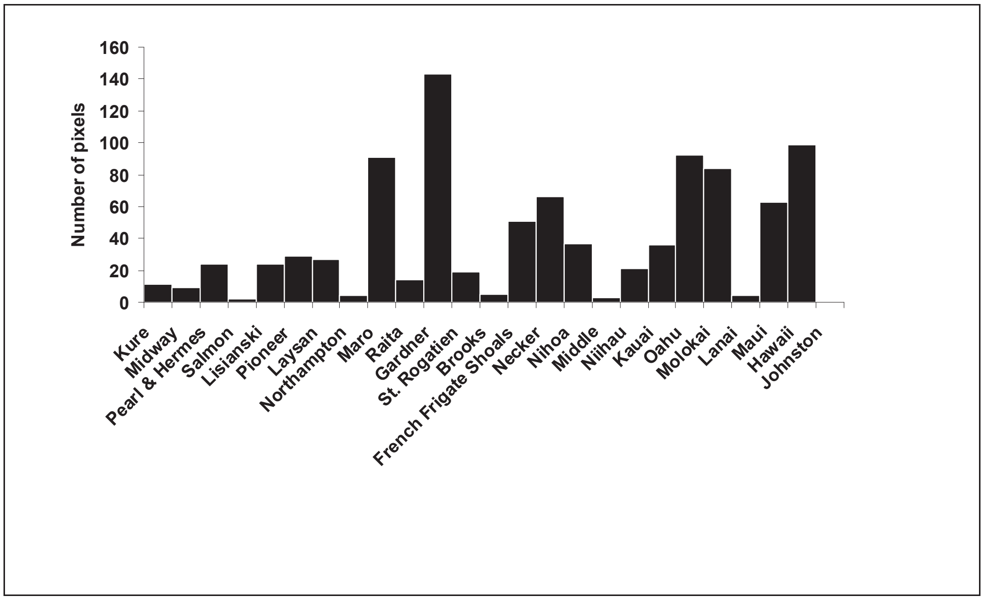


Figure 5.6 - Pixel counts of 0-100m habitat from Smith and Sandwell (1997) bathymetric database. Spawning output in simulations was proportional to these counts. Johnston Atoll has a pixel count of 1.

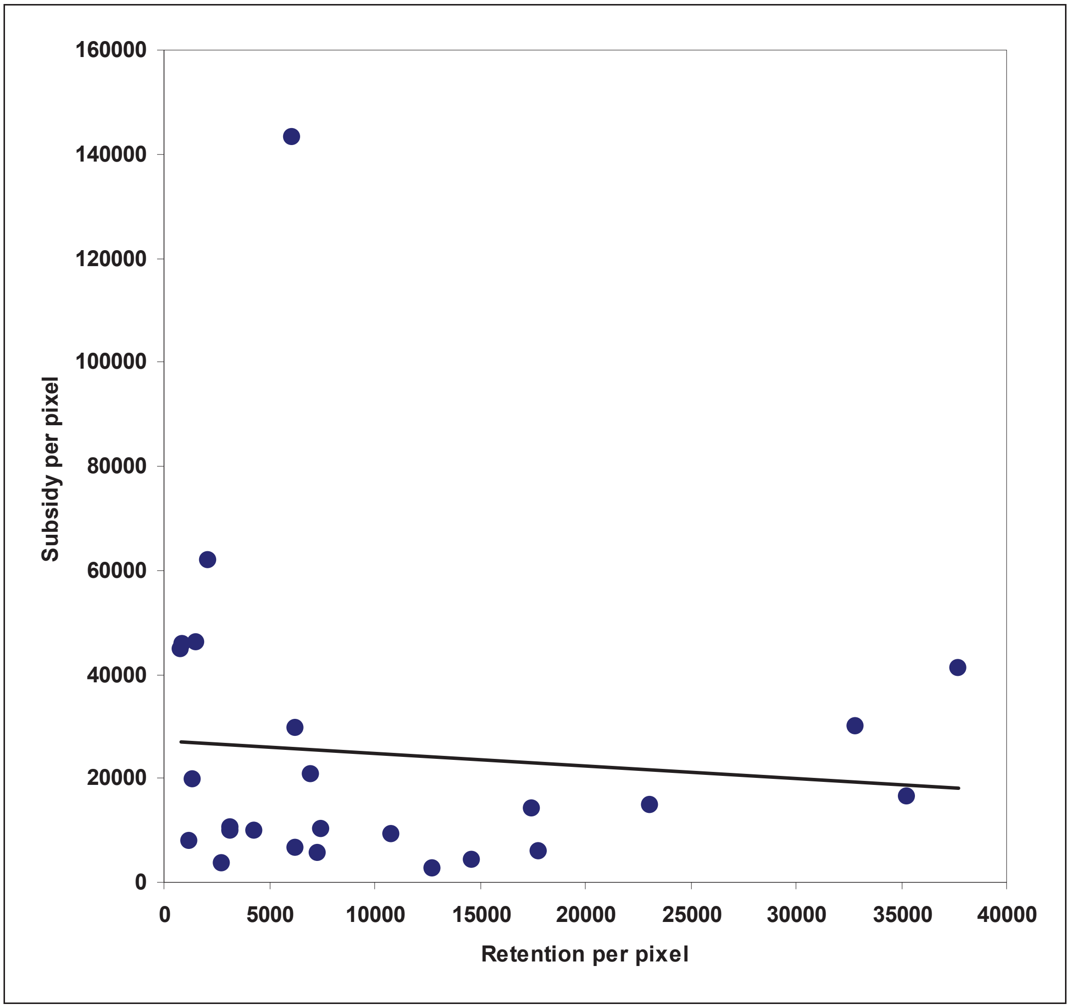


Figure 5.7 - Scatterplot of retention per pixel of habitat (x-axis) versus subsidy per pixel of habitat (y-axis). Each point represents 1 of the 25 habitat strata listed in Table 5.1. Solid line is non-significant linear regression.

NLOM currents were found to be in good correspondence to drifter data over the time interval and location studied (Figure 5.8). The three regression slopes clearly depart from the 1:1 relationship which might be expected if the currents were exactly synchronized. The u-component, v-component, and resultant magnitude of the NLOM currents were consistently lower in value than the corresponding drifter data. There was also a slight rightward deflection in direction when comparing NLOM currents to drifter data. The NLOM currents reflect an average water flow over the 0-100m layer, loosely termed the “mixed layer”, while the drifters are measuring water movement at a drogued 15m depth. These two measurements of water movement are theoretically expected to be different due to the Coriolis Effect and resulting Ekman Spiral pattern of circulation where successive vertical layers of water move at a lesser velocity and at a slight offset to each other. The magnitude of dampening and the overall deflection qualitatively match what would be predicted with Ekman Spiral dynamics in the Northern hemisphere (rightward deflection).

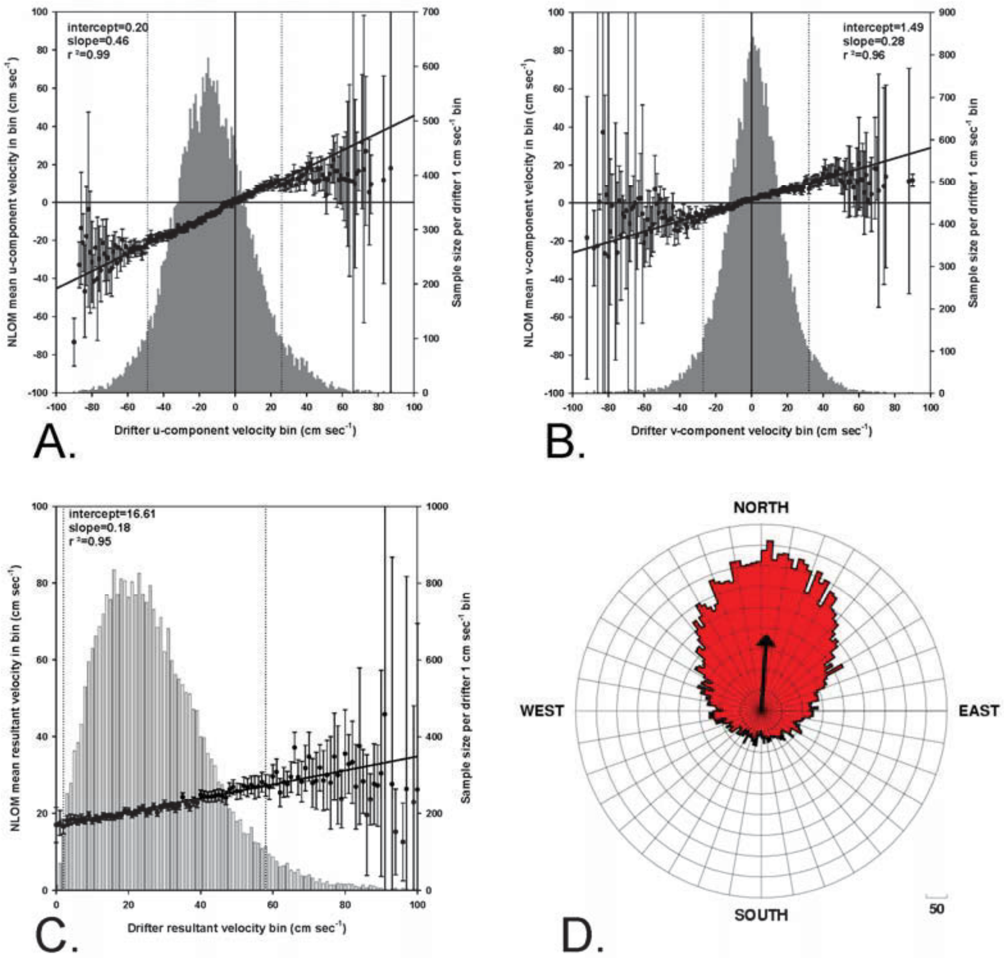


Figure 5.8 - Comparison of NLOM currents and NOAA drifter data, for u-component (A), v-component (B), resultant speed (C), and direction (D). Histogram bars in panels A-C indicate sample size of drifter observations at each 1 cm sec-1 bin, error bars are 95% parametric confidence intervals about each mean (points). Dotted vertical lines represent limits of data span used in regression where n>=100 per bin. The fitted regression line is shown as a solid

line. The angular displacement is tabulated in panel D as a polar histogram showing the departure of NLOM from drifter observations. Northward represents complete agreement between NLOM and drifter observations, with other directions indicating the offset of NLOM from drifter observations.

Examination of the SOI and PDO monthly time series (Figure 5.9) indicated that the 2003-2004 time period was non-anomalous, both for short term interannual events and longer term events. The majority of this time interval has been classified as neither "warm" nor "cool" by the NOAA National Weather Service Climate Prediction Center. The SOI and PDO values for the months of NLOM data used in this study were not significantly different when compared to all other months spanning 1980-2007 using a Student's t-test (SOI t-value = 0.37, df= 329, p=0.71; PDO t-value = -1.33, df= 324, p=0.18), suggesting that the connectivity findings presented here may be of general applicability.

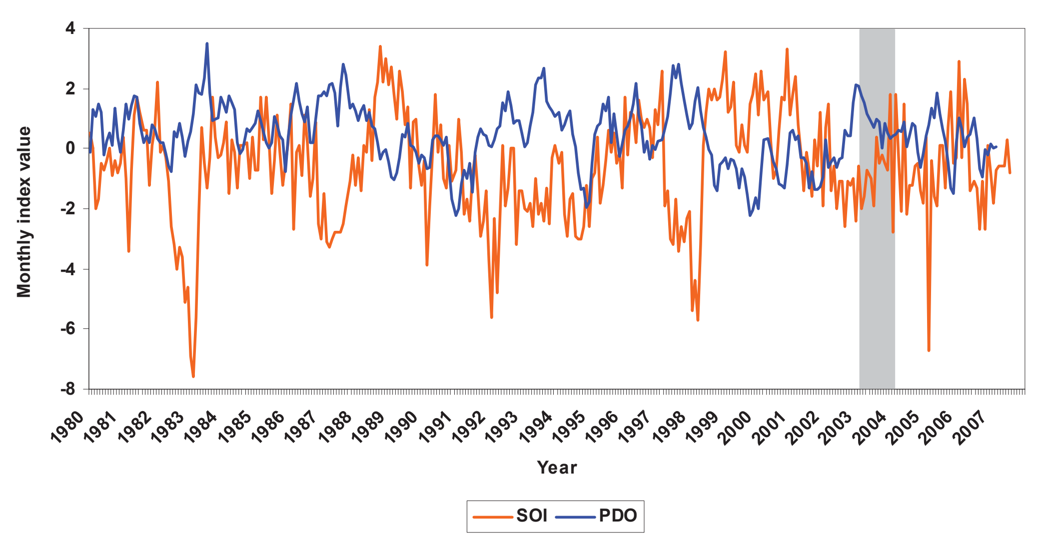


Figure 5.9 - Monthly time series of SOI and PDO climate indices over the time interval 1980-2007. Shaded region delineates the 2003-2004 time interval of NLOM data used in this study.

5.5 Discussion

This paper presents the first complete series of connectivity measures for the Hawaiian Archipelago. These measures are used in a metapopulation simulation to provide insight into population structure and between-stratum dependencies. The distinction between larval retention and larval subsidy is put forth here, since this critical difference in larval source is often overlooked. Field studies of settlement and recruitment often lump these 2 distinctly different processes together due to the inherent difficulty in sourcing incoming propagules. The findings presented here advance our understanding of population dynamics in this region and will assist in posing useful hypotheses for future research, both for purely scientific questions as well as applied issues such as spatial closures and other fishery management and conservation tools. Dispersal kernels such as those estimated here are important inputs towards optimizing these types of protective measures (Cowen et al., 2006; Aiken et al., 2007).

The biological significance of the Papahānaumokuākea Marine National Monument to the entire Hawaiian Archipelago can be examined from the connectivity probabilities and the metapopulation analysis. The equilibrium metapopulation composition predicted after many generations can be useful to understand the importance of adjacent or even non-adjacent geographic strata. The importance of retention for the shorter PLD is apparent. A relatively narrow transitional region including Nihoa, Middle Bank, Niihau, and Kauai are composed of settlers from both the Papahānaumokuākea Marine National Monument and MHI regions. Areas further north and south have negligible crossover. However, at longer PLD, nearly all regions throughout the MHI have some component of Papahānaumokuākea Marine National Monument derived settlers, whereas most of the Papahānaumokuākea Marine National Monument is self-seeding until approximately Necker is reached. For extremely long PLDs, the entire archipelago is connected nearly uniformly after many generations. This process is easily visualized in the NMDS ordination. Shorter PLDs are scattered widely over the 2-D ordination space, but coalescence of the pattern is seen as the PLD increases. At 365 day PLD the patterns are most clustered, yet still not entirely identical. The abrupt shift in Johnston Atoll position from 30 day PLD to 60 day PLD is consistent with the results of Kobayashi (2006) suggesting a threshold PLD of 50 days for significant colonization from Johnston Atoll to the Hawaiian Archipelago. A similar threshold PLD likely operates in the reverse direction based on the NMDS results of Johnston Atoll metapopulation structure. The equilibrium composition is somewhat driven by the spatial pattern in spawning magnitude, which is a function of habitat size in this analysis. 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 consequence of dispersal kernel probabilities operating over many generations. When the effect of habitat size is removed by scaling total retention and subsidy by habitat pixel counts, this yields evidence of a decoupling of retention and subsidy 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 subsidy. 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).

It should be noted that the raw connectivity measures presented in this study (Tables 5.3-5.8) are a product of examining the single-generation effects of connectivity, i.e., a “snapshot” of pair-wise connectivity values rather than the cumulative effects of many generations. Clearly since the connectivity measures are high for adjacent habitats, over evolutionary time the genetic connectivity will be more pronounced than inferred here (e.g., Hastings and Botsford, 2006). This could be particularly important at the southern boundary of the Papahānaumokuākea Marine National Monument, 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. Previous studies which have relied upon the “snapshot” approach should be revisited with a multi-generational approach to better understand metapopulation dynamics. The simple metapopulation model utilized in this study is a useful start; however there is much more that can be accomplished with a better understanding of habitat, target species density, and reproductive output patterns. A demographic model linked to an ocean circulation model is an ambitious undertaking but will be necessary to understand population dynamics in a complex source/sink marine environment.

Clearly, these results can be improved for specific target organisms with a better understanding of their spatial and temporal reproductive output patterns, their pelagic larval ecology, and their settlement behavior when competent. This approach can be tailored to model dispersal of invasive or introduced species, and can be a useful tool towards establishing effective closed areas for population recovery and conservation.

Chapter 6: Adult movement of the deepwater snapper opakapaka, *Pristipomoides filamentosus,* in Hawaii: Insights from a large-scale tagging program and computer simulation

Kobayashi, D. R., H. Y. Okamoto, F. G. Oishi. Manuscript. Adult movement of the deepwater snapper opakapaka, *Pristipomoides filamentosus,* in Hawaii: Insights from a large-scale tagging program and computer simulation.

6.1 Abstract

Results from a long-term tagging program by the State of Hawaii on the deepwater snapper opakapaka, *Pristipomoides filamentosus*, in the Hawaiian Archipelago are summarized. A total of 4179 adult and juveniles were captured by hook-and-line, and tagged with surgically implanted, conventional streamer tags. Most tagging took place around the main inhabited islands in the southeastern portion of the archipelago. There was a high 12% rate of recapture of tagged fish over the following 15 years by scientific, recreational, and commercial fishers. Some individual fish appeared to remain in the general vicinity of their initial capture, while others exhibited remarkable trajectories crossing deep channels between major island groups. Tag recoveries were standardized to fishing effort in an attempt to remove biases due to spatial effort allocation, yielding an index of tag recaptures per unit of fishing effort (TPUE). A simple computer simulation was constructed which attempted to mimic individual movement using a wide range of swimming behaviors, and compared to the observed tag recovery pattern. There was no one single swimming behavior that was parsimonious with the observed pattern from these simulation results, and there were indications of biphasic swimming behavior involving 2 distinct modes of swimming.

Potential mechanisms of these alternate swimming behavior modes for opakapaka are discussed.

6.2 Introduction

Deepwater bottomfishes in the Hawaiian Archipelago are the target of an important commercial and recreational fishery (Haight et al., 1993). One of the principal species in this complex is the pink snapper (*Pristipomoides filamentosus*), locally and henceforth called opakapaka. Opakapaka primarily reside in the 100-400m depth range in hard bottom areas of high vertical relief, making direct observations of behavior very difficult (Ralston et al., 1986). Certain aspects of opakapaka biology have been gleaned from hook-and-line captured specimens such as general distribution, diet, growth, reproduction, mortality, fishery, and population dynamics (Humphreys, 1986; Polovina and Ralston, 1987). However, there is very little known about opakapaka movement pertaining to metapopulation connectivity in the Hawaiian Archipelago.

Connectivity during the egg and larval phases is difficult to address due to the rarity and difficulty of identification of these early life history stages (Leis and Lee, 1994). Modeling approaches have been shown to be a useful nonextractive and nonlethal technique to explore movement of these pelagic stages. The juvenile and adult benthic stages of opakapaka are thought to be relatively sessile, and this was partially the basis for a large series of fishing area closures in the Main Hawaiian Islands (henceforth MHI), which are the inhabited southeastern portion of the Hawaiian Archipelago. These area closures, initiated by the State of Hawaii (Figure 6.1), were prompted by concerns of overfishing in the MHI (Hawaii Administrative Rules 13-94; effective June 1, 1998). The utility of these closures critically depends on the movement patterns of opakapaka, both during the pelagic stages and more importantly during their benthic juvenile and adult stages since the protection of spawning stock is one of the primary goals of area closures.

The maintenance of adequate spawning stock is a common objective of fisheries management as a deterrent to recruitment overfishing, which is reached at some high level of harvest at which point there is no longer enough reproductive output remaining to replenish the population. Stocks which reach the stage of recruitment overfishing can continue to decline even in the absence of fishery removals, with ensuing stock crash and high risk of extinction. The deepwater bottomfishes in Hawaii are thought to be particularly susceptible to recruitment overfishing due to their slow growth, large size at maturity, and heavy fishing pressure (Haight et al., 1993). Anecdotal evidence has suggested that adult opakapaka can, on occasion, move long distances, sometimes even over deep channels separating suitable habitat. This pattern of adult movement has not previously been characterized with scientific data. It is also not known how frequent this behavior might be.

Comparison to shallow water fishes might be useful to determine the prevalency of long-distance movement in adult opakapaka, since these assemblages are more accessible and have received more scientific study. However, there is no clear pattern, some adults are found to be very site attached, and others widely ranging. For example, many shallow water reef fishes in Tasmania were found to be very site attached (Edgar et al, 2004). Similarly, small coral reef associated fishes in Barbados appeared to be relatively sedentary as adults, with few individuals crossing barriers of >20 m of sand/rubble between habitats (Chapman and Kramer, 2000); although the same study found that some of the larger jacks were highly mobile and not site attached. Wetherbee et al. (2004) and Meyer et al. (2007a) found that jacks in Hawaii could cover long distances despite having well-defined home ranges. Some species of grunts in the Caribbean are known to make very predictable short migrations yet show very good site fidelity (Verweij and Nagelkerken, 2007). Among the serranids, coral trout on the Great Barrier Reef typically move several kilometers while maintaining a large home site (Samoilys, 1997), some species such as Nassau grouper undertake extensive spawning migrations (Smith, 1972), and the greasy grouper has been shown to have a large home range with excellent homing ability (Kaunda-Arara and Rose, 2004). The galjoen (a coastal sportfish) in South Africa is hypothesized to have a dual behavior with regard to movement, with 95% very site specific and 5% widely roaming (Attwood and Cowley, 2005). It remains unclear whether the behavioral combination is structured within or between individual galjoen. Clearly, a wide range of adult movement patterns are plausible for opakapaka based on comparison to the shallow water fish fauna.

The purpose of this study was to evaluate an untapped dataset of conventional tags deployed on juvenile and adult opakapaka in the MHI of the Hawaiian Archipelago to determine general patterns of movement. The raw data from this field study conducted by DAR staff from 1989-2003 was made available to the first author for quantitative analysis of growth, mortality, and movement. The first author performed all of the data parsing, modeling, analysis, and writing. This manuscript presents an analysis of opakapaka movement using the DAR tagging data.

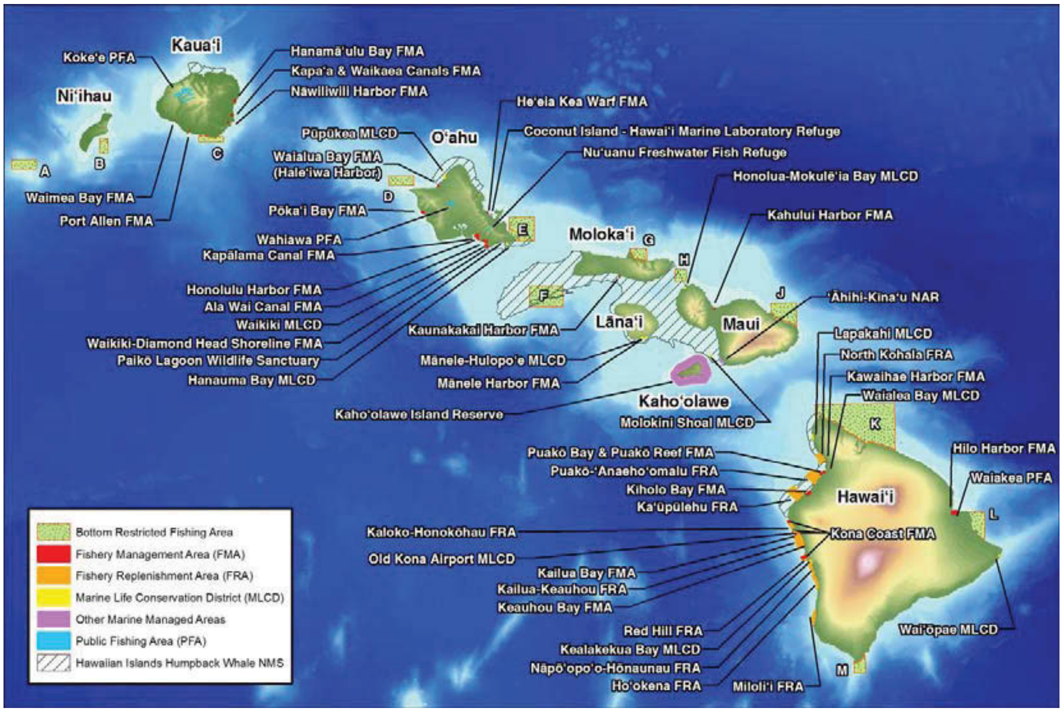


Figure 6.1 – Summary of marine managed areas in the MHI portion of the Hawaiian Archipelago. Figure courtesy of State of Hawaii DAR.

6.3 Methods

6.3.1 DAR tagging data

The State of Hawaii Division of Aquatic Resources (DAR) Opakapaka Tagging Program, administered by Aquatic Biologist Henry Y. Okamoto, tagged 4179 juvenile and adult opakapaka ranging in size from 23-76 cm fork length ($\bar{x}$ =41.17 cm, std. dev.=9.00 cm) over a 5 year time period (1989-1995) in the main Hawaiian Islands. Opakapaka were captured by hook-and-line fishing gear, measured, tagged with internally anchored nylon streamer tags, surgically degassed if necessary, and released. Occasional immediate mortality was observed; however, due to the resulting high rate of recapture and longevity of tagged fish, tagging mortality was apparently not a serious issue in this project (Kobayashi et al., manuscript in prep.). Announcements to fishers and a reward program were used to encourage data recovery in the commercial and recreational fisheries. Research fishing also continued, and was responsible for much of the recoveries. Date, location, and fish size upon release and recapture were recorded in the data. Due to the concern of confidential fishing locations being compromised, the DAR tagging program agreed with fishers to record their locations using the State of Hawaii statistical fishing grids (Figure 6.2). These grids have been used to track all of Hawaii's fisheries monitored by the DAR commercial catch reporting program since 1948 in a standardized database. Centroids for each of the DAR statistical area polygons were calculated using GIS software and used as a proxy for tag location. Distance moved was compared to time at liberty, and also binned for tabulation of average values and construction of frequency histograms. Net movement patterns were compared to bottomfishing effort and simulation results, as described below.

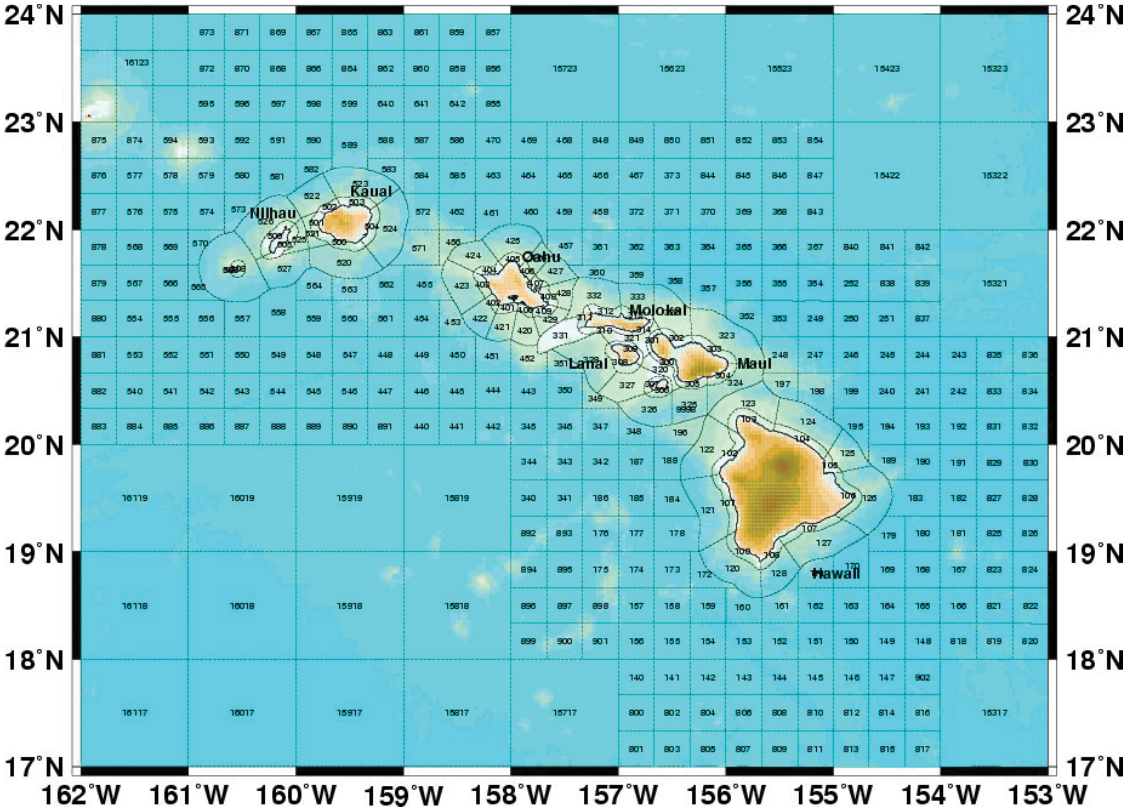


Figure 6.2 – State of Hawaii DAR commercial fishing statistical areas used for geographic reference in this analysis.

6.3.2 Bottomfishing effort

The spatial pattern of opakapaka tag recaptures is likely to be influenced by the spatial pattern of bottomfishing effort. If fishing effort is higher in the vicinity of the tag release locations, then there would be more tag recoveries that show very little movement. Conversely, if fishing effort is higher at more distant areas than the tag release locations, then there is an opposite bias towards recovering tags which traveled a long distance. Removing these types of sampling bias from the recovery pattern would yield a better understanding of the natural, underlying movement patterns, in the same manner that raw fish catches in a fishery are scaled by fishing effort to produce an informative index of abundance called CPUE (catch per unit of fishing effort).

However, fishing effort in this application is not uniformly, randomly, or predictably spaced from tagging locations, and therefore a spatial analysis of actual bottomfishing effort is needed as a function of distance from tagging locations. Fortunately, bottomfishing effort data in the Hawaiian Archipelago are available. These data are gathered by the State of Hawaii DAR to track fishery economics and stock health, using a mandatory reporting program for any fisher who sells a portion of his catch. This reporting system is thought to capture most of the commercial and recreational fishers who target bottomfish since most bottomfishers sell their catch to dealers, markets, or at the centralized auction in Honolulu. Bottomfishing effort was extracted from the commercial catch reports by accumulating fish catch records into unique combinations of commercial license number and date of fishing. Most bottomfishing trips in the MHI occur on a single day, and are recorded on that single day basis regardless of when the fish were offloaded and/or sold. Day trips which utilized the deepwater handline gear and caught at least 90% by weight of the deepwater bottomfish species assemblage were tabulated as a unit of bottomfishing effort for a particular DAR statistical area. For multiarea trips, a single area code that was most prevalent in the catch data was used to assign the fishing effort. Centroids for each of the DAR statistical areas were calculated using GIS software and used as a proxy for fishing effort location. For each DAR opakapaka tag, this daily bottomfishing effort was tabulated into bins of distance from point of release using all corresponding commercial catch report data in that time interval for the duration of the time that particular tag was at liberty. Since movement into the Northwestern Hawaiian Islands (NWHI) appeared unlikely, and fishing effort in the NWHI is much less than in the MHI, only MHI fishing effort was tabulated for each tag. This approach seems reasonable since most of the tags were released in the middle portion of the MHI, and no NWHI recaptures of these tags have been documented to date. Tag recaptures per unit of fishing effort (TPUE) was calculated using the binned data.

6.3.3 Simulation

A stochastic computer simulation was constructed to mimic the movement of opakapaka, with a flexible, horizontal step-size parameter intended to represent a variable amount of regular, exploratory swimming behavior. The simulation incorporated a grid of potential habitat using the 2-minute resolution bathymetric database of Smith and Sandwell (1997). Pixels within the depth range 100-400 meters (Figure 6.3) were used as a definition of opakapaka habitat (Haight et al., 1993). Three sets of simulations were attempted, with incremental stages of complexity. Firstly, a set of simulations with a fixed starting point to facilitate graphical visualization of how movement was related to the swimming parameter were accomplished. Secondly, a set of simulations with random starting points to better estimate the entire population were accomplished. Thirdly, a version which attempted to best mimic the DAR tagging data using the observed release locations and times at liberty was accomplished.

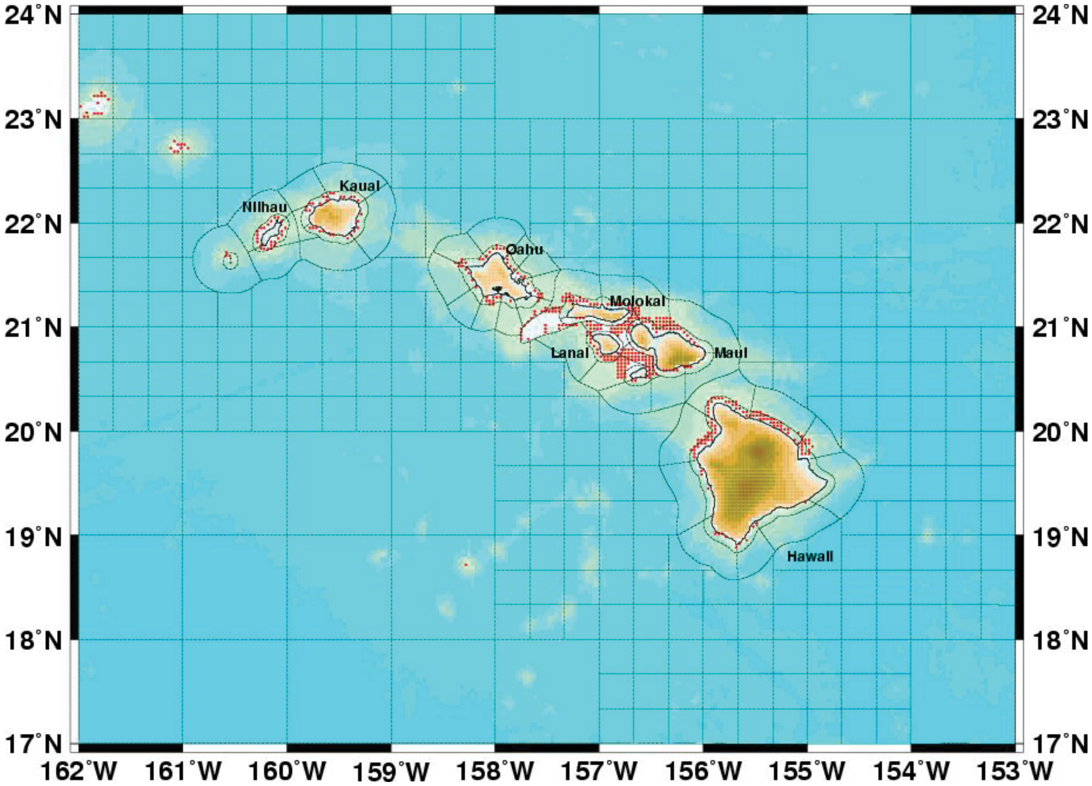


Figure 6.3 – Habitat grid for movement simulation from the Smith and Sandwell (1997) bathymetric database of 2-minute pixels ranging from 100-400 m depth. DAR statistical areas are also shown for reference.

For the first simulations, the starting point of the simulation was centered on the popular fishing grounds called Penguin Bank, located off the southeast corner of Oahu and west of Molokai (Figure 6.2). The majority of the bottomfish catch in the MHI is caught on or around Penguin Bank, and it is conveniently located in the center of the MHI for the visualization purposes of this first simulation. A simulated opakapaka was tracked for 5-years of its life, during which time it would embark on daily exploratory excursions horizontally in the water column, independent of prevailing currents and bottom depth between endpoints. The upper bound of this horizontal excursion was allowed to vary in the simulation for separate fish, representing the variable amount of swimming behavior. Swimming speed was allowed to vary randomly as a uniform variate bounded by a parameter *X*, where *X* varied systematically over 24 levels ranging from 1.2 to 120 cm/sec swimming speed spanning a 12 hour diurnal period. For the average sized fish tagged in this study (41.17 cm), this corresponds to approximately 0.06 to 6.0 body lengths per second. Most studies of fish swimming speeds have found maximum sustained swimming speeds on the order of 3-5 body lengths per second (Alexander, 1978); therefore, the range of swimming values used in this simulation is arbitrary but thought to bracket the hypothesized value for opakapaka directed swimming behavior. The first 5 swimming values were relatively finely spaced at slow swimming speeds; the subsequent 19 were at a larger increment. The direction of the exploratory excursion was allowed to randomly vary, but the fish was assumed to know that a suitable habitat was located within the chosen exploratory excursion. In other words, unsuccessful trips were ignored for the purposes of this study. Fish were also not allowed to cross emergent features in a single step, but could circumnavigate such features with a series of steps. Upon reaching a new suitable habitat the movement excursion process was repeated on successive days, until an elapsed time of 5-years (1825 daily excursions) was achieved. No serial correlation in movement was built into the simulation; in other words, long-distance movement was not forced but allowed to occur as a diffusive process in the manner of a “random walk” (e.g., Johnson et al., 1992). Excursions were repeated for 1000 fish, for each of the 24 values of the *X* parameter. The distances from the Penguin Bank release point were tabulated into frequency histograms, and compared to the observed spatial pattern of recaptured opakapaka.

In the second set of simulations, a random starting point was chosen from among all MHI pixels of suitable habitat. The simulations were run in the same manner as the first simulations except that the tabulation of distance took into account the different starting points.

In the third set of simulations, the starting points were chosen based on the distribution of tagged opakapaka releases. The actual time at liberty was also mimicked for each simulated fish. Since the third simulation was attempting to reconstruct the observed data, the results were scaled using the commercial catch distributions as described above, whereby the observed tag recaptures were scaled by fishing effort in the corresponding distance bin to produce a TPUE (tag recaptures per unit of fishing effort) as an operational counterpart to CPUE. Nonlinear regression was used in a quantitative attempt to tune the simulation to the observed tag data pattern, and the resultant mean square error was used as a measure of fit for each of the values of the *X* parameter. This approach would yield a predicted opakapaka swimming behavior from the value of the *X* parameter best describing the observed tag data pattern. Potential biphasic swimming behaviors was investigated by examining weighted averages of pairwise dispersal results, also using nonlinear regression. All possible pairwise combinations of swimming were combined using a differential mixing parameter, and fit to the observed pattern. The mixing parameter and a scaling parameter were solved for each combination of pairs using the Marquardt-Levenberg minimization algorithm in the ZXSSQ subroutine of the IMSL library (IMSL, 1979). This parameter ranges from 0-1 where the endpoints represent pure swimming behaviors of one or the other in the pairwise behaviors. Intermediate values of this mixing parameter represent a combination of the swimming behaviors.

6.4 Results

A timeline summary of all opakapaka releases and recaptures is shown in Figure 6.4. Releases occurred primarily from 1989-1995. A tabulation of all releases and recaptures with valid location data (*n*=4671) are shown in Table 6.1. The spatial distribution of tagged opakapaka releases is shown in Figure 6.5. There was a resultant 12% recapture rate over the next 15 years (1989-2003), with 500 fish recaptured once, 40 fish recaptured twice, 4 fish recaptured 3 times, and 2 fish recaptured 4 times. Most captured fish were retagged and released, so that some tagging was still occurring beyond the primary tagging interval of 1989-1995. The spatial distribution of tagged opakapaka recoveries is shown in Figure 6.6. The time elapsed to recapture ranged from 1-3748 days, averaging 549 days. A total of 523 data ensembles for the movement analysis were used, each comprising a matched set of: release location, time-at-liberty, and recapture location. Examination of the raw data revealed a weak relationship between net displacement and time-at-liberty (Figure 6.7). Several of the individual fish travelled remarkable distances including deep channel crossings over water depths greatly exceeding known habitat preferences of opakapaka.

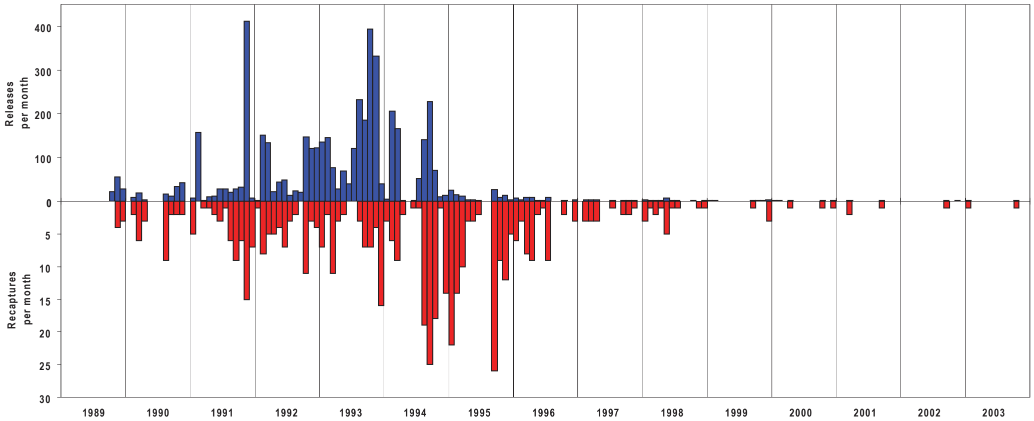


Figure 6.4 – Timeline of releases and recaptures in the DAR opakapaka tagging program, 1989-2003, used in the movement analysis. Note that y-axis scaling is different for releases and recaptures to display temporal patterns. Total number of releases numbered 4697 and total number of recaptures numbered 523.

Table 6.1 - Summary of opakapaka tagged fish releases, recaptures, and non-recoveries over the time period 1989-2003 in the DAR statistical areas. Shaded diagonal region indicates tag recoveries at initial tag release locations.

Recovery location	Release location																															
	127	304	306	307	308	309	311	312	313	320	321	327	331	332	351	401	402	403	404	405	407	408	409	421	423	424	428	429	452	505	528	Total
127							1																									1
304				1						2																						3
306			1							1																						2
307				5								1																				6
308			1		2						5																					8
309											2																					2
311							25	1					4																			30
312							1	1																								2
313				1				1					3																			5
320			1	3						24		1																				29
321											31																					31
327				3						2		2																				7
331							46	2					128			4																180
332													1																			1
351													1																			1
401																131																131
403																1																1
404																1																1
405							1															1										2
407													1									1										2
408													1									12										13
409																4																4
421																14								1								15
423											1					14						1										16
424					1								4			3						1										9
428							2	1					2									3										8
429							2				1		1			1																5
452											1		1																			2
505										1																						1
528							2																									2
No recovery	1	3	44	278	35	2	582	168	5	333	429	84	875	1	1	937	7	1	1	2	2	293	4	20	16	9	8	5	2	1	2	4151
Total	1	3	47	291	38	2	662	174	5	363	470	88	1022	1	1	1110	7	1	1	2	2	312	4	21	16	9	8	5	2	1	2	4671

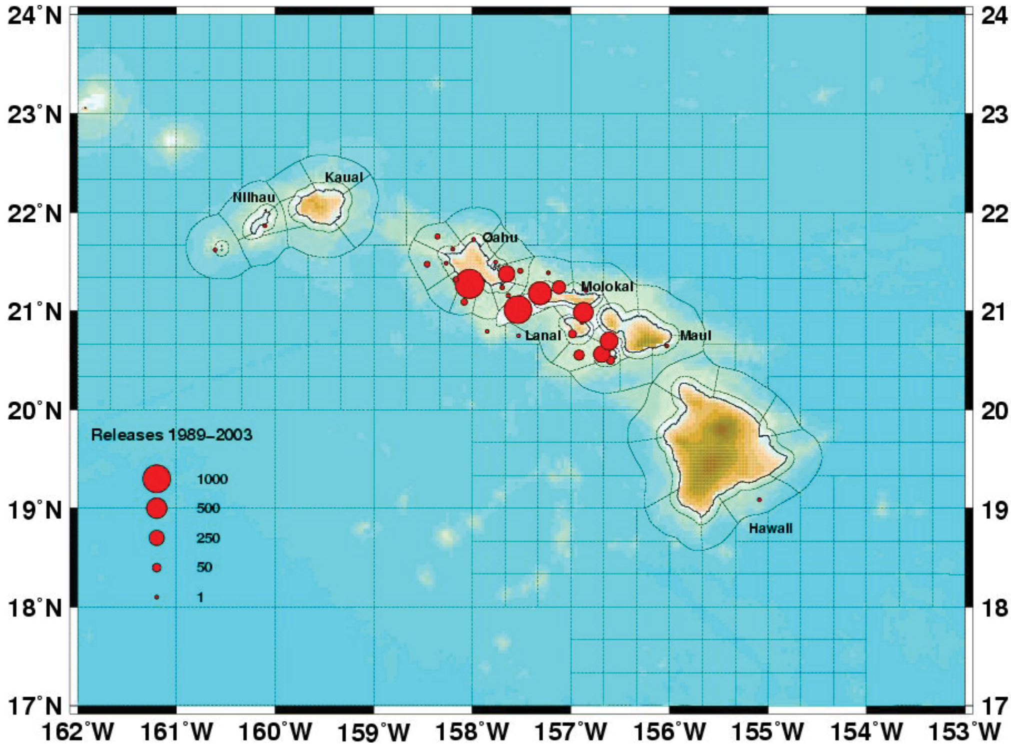


Figure 6.5 – Spatial tabulation of tagged opakapaka releases for DAR statistical areas, 1989-2003.

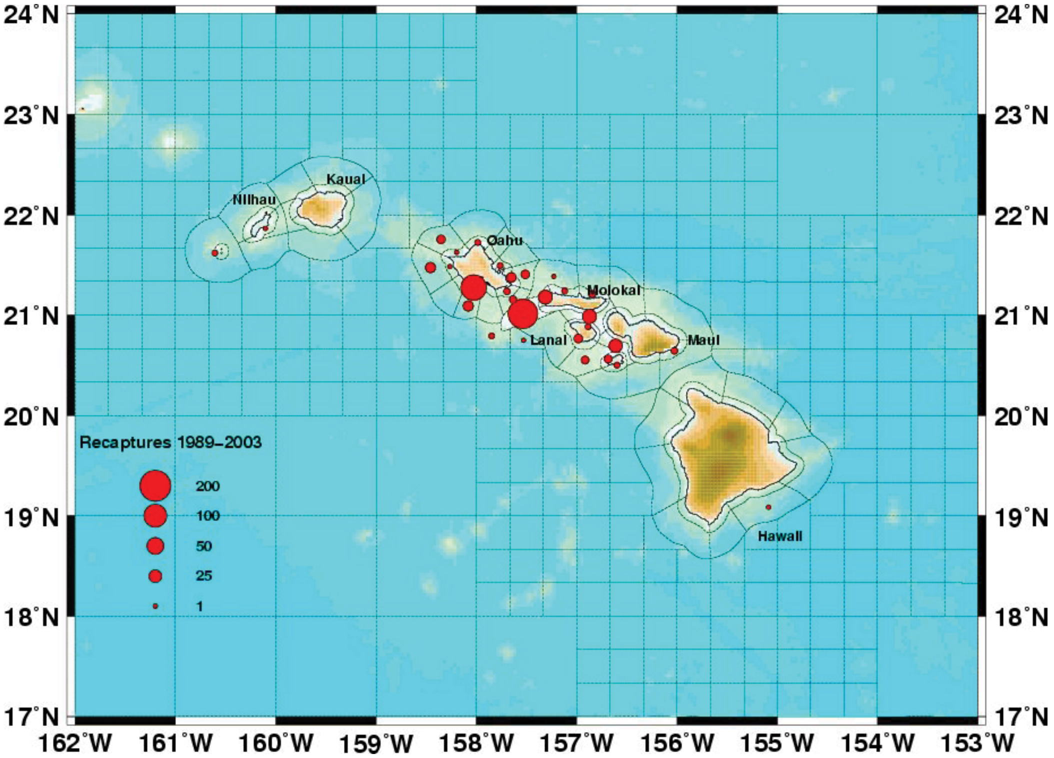


Figure 6.6 – Spatial tabulation of tagged opakapaka recaptures for DAR statistical areas, 1989-2003.

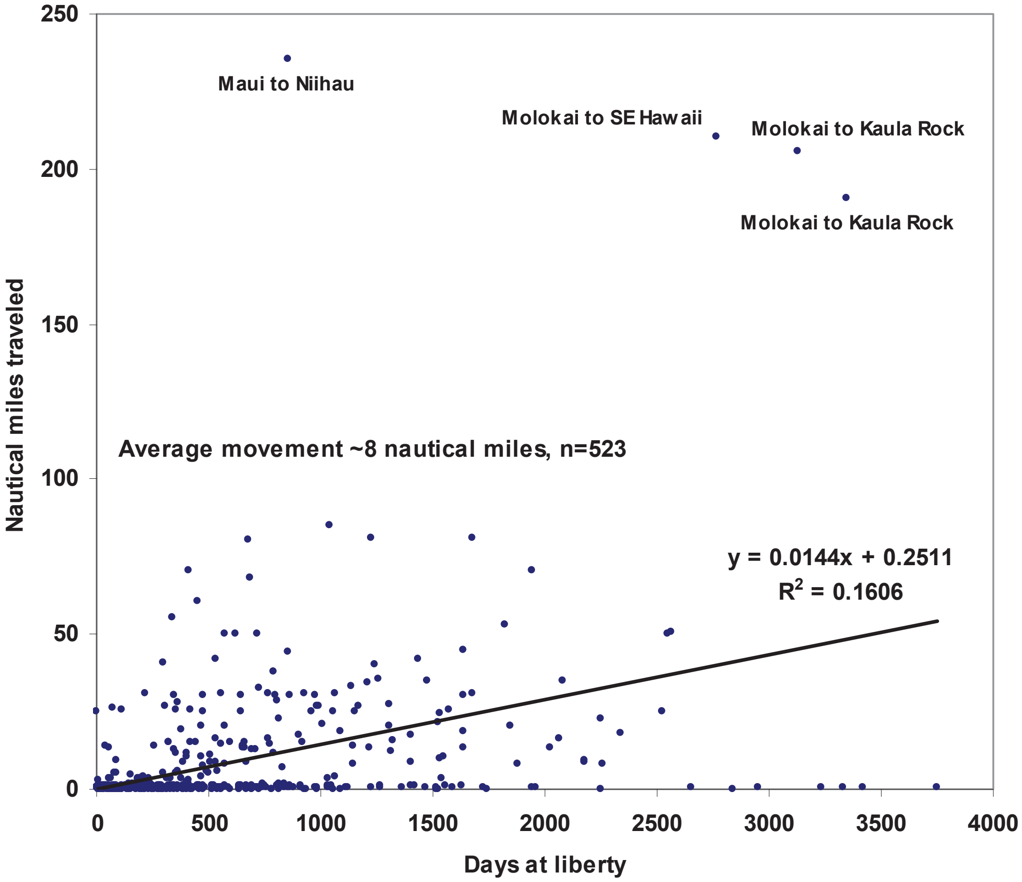


Figure 6.7 – Summary of displacement and days at liberty for tagged opakapaka. Four tagged fish displaying maximum displacement are highlighted in the plot. The fitted regression is significant.

Overall bottomfishing effort over the time period 1989-2003 is shown in Figure 6.8. The primary bottomfishing areas are around the central MHI near Maui, Lanai, and Molokai. The Penguin Bank area received the most effort of all the DAR statistical areas with 816,782 bottomfishing days of effort over this 15 year time period. Tag recaptures and fishing effort as a function of distance from initial tag release sites is shown in Figure 6.9. The majority of tagged fish (80%) were recaptured within 0-12 nm from the initial release location (Figure 6.9A). Fishing effort peaked in the range of 24-60 nm from initial release locations (Figure 6.9B). Tag recaptures per unit of fishing effort (TPUE) as calculated from the recaptures and fishing effort is shown in

Figure 6.9C. When standardized to the pattern of fishing effort, the prevalence of long-distance movement becomes more apparent.

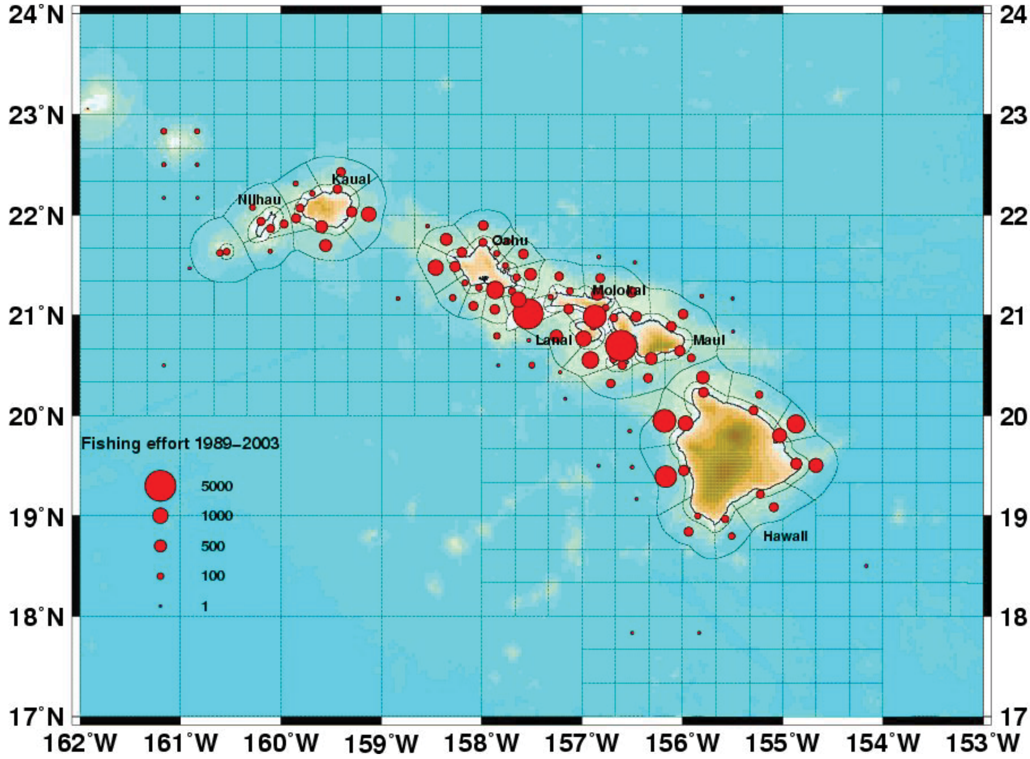


Figure 6.8 – Spatial tabulation of bottomfish commercial fishing effort in units of days fished for DAR statistical areas, 1989-2003, using State of Hawaii commercial catch reports.

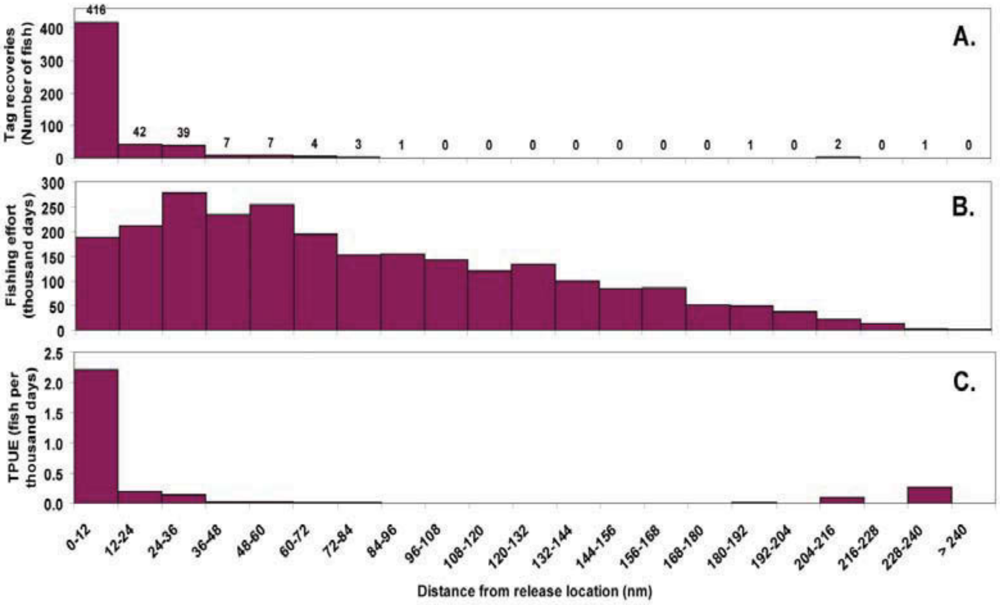


Figure 6.9 – Tabulation of net distance traveled by tagged opakapaka (A.), tabulation of bottomfish commercial fishing effort distance from tagged opakapaka release sites, 1989-2003, using State of Hawaii commercial catch reports (B.), and standardized TPUE (tag recaptures per unit of fishing effort) (C.).

The spatial distribution of 5000 simulated opakapaka after 5 years from an origin at Penguin Bank is shown in Figure 6.10, for each of the 24 *X* values of swimming magnitude. Some notable events in Figure 6.10 are as follows: at ~8 cm/sec the Kalohi Channel (separating Molokai and Lanai), Pailolo Channel (separating Molokai and Maui), and Auau Channel (separating Lanai and Maui) are traversed successfully; at ~ 10 cm/sec the Kaiwi Channel (separating Penguin Bank and Oahu) is traversed successfully; at ~ 70 cm/sec the Alenuihaha Channel (separating Maui and Hawaii) is traversed successfully; and at ~ 230 cm/sec the Kauai Channel (separating Oahu and Kauai) is traversed successfully.

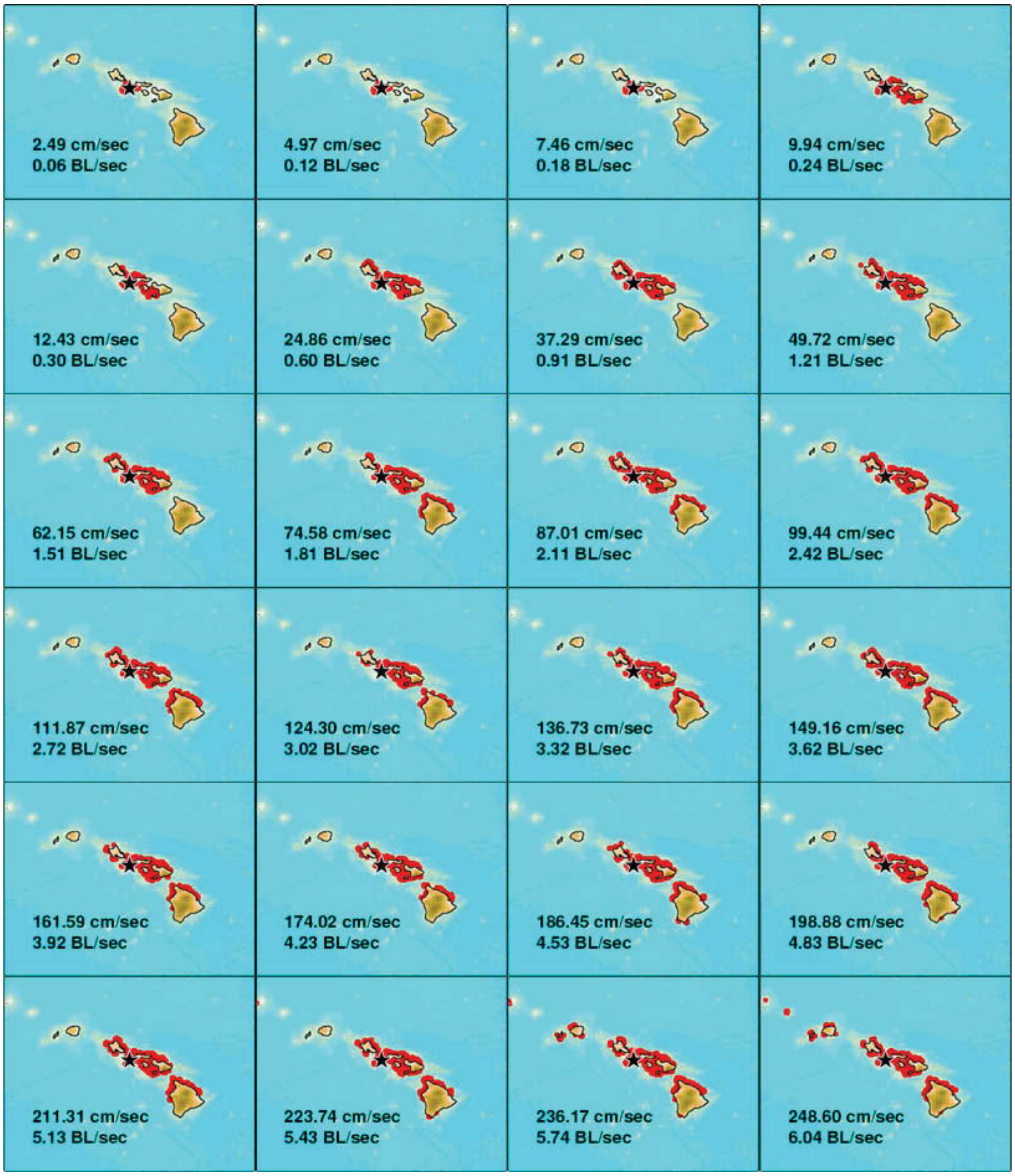


Figure 6.10 – Spatial distribution of 5000 simulated opakapaka with variable, daily swimming excursions with origin at Penguin Bank (denoted by star symbol) using a stochastic computer simulation model. The magnitude of swimming is expressed both as cm/sec and BL/sec (body lengths per second, assuming 41.17 cm FL average body size). Red symbols denote locations in a "snapshot" taken at exactly 5 years after release for 24 levels of swimming behavior.

The tabulations of distance traveled for releases throughout the MHI is shown in Figure 6.11. At the lowest levels of swimming speed there were no fish traveling long distances in the MHI. At the highest levels of swimming speed examined, most fish were no longer near the release site and had diffused far away.

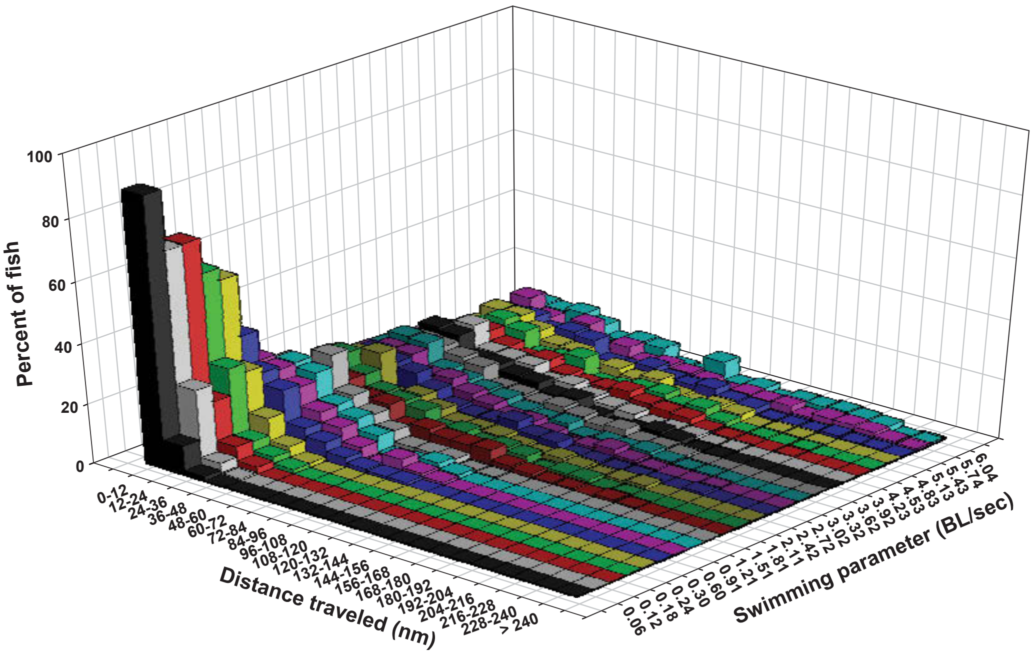


Figure 6.11 – Tabulation of net distance traveled for simulated opakapaka as a function of swimming parameter in the second set of simulations using random starting locations throughout MHI. Distances were tabulated after 5 years at liberty.

The simulations tuned to the observed tag release locations and times at liberty yielded patterns of distance traveled as shown in Figure 6.12. These results were fit to the observed patterns, in both single and in biphasic modes with fits summarized in Table 6.2. Operationally, the mixing parameter was constrained to range over the interval 0.1-0.9 to force some level of biphasic swimming for each pairwise combination. A large number of biphasic results yielded improved fits over single swimming behavior fits. The best fits were biphasic modes with some combination of slow swimming (#2-#5) coupled with fast swimming (#24). Slow swimming (#1-#5) coupled with faster swimming (#7-#24) yielded generally similar results based on mean square error. The biphasic fits indicated that a combination of 54%-90% slow swimming and 10%-46%

fast swimming was most parsimonious with the observed data, suggesting that slow swimming is the predominant swimming mode. Additionally, the best fitting single mode swimming behaviors were at the slowest swimming (#1, #2).

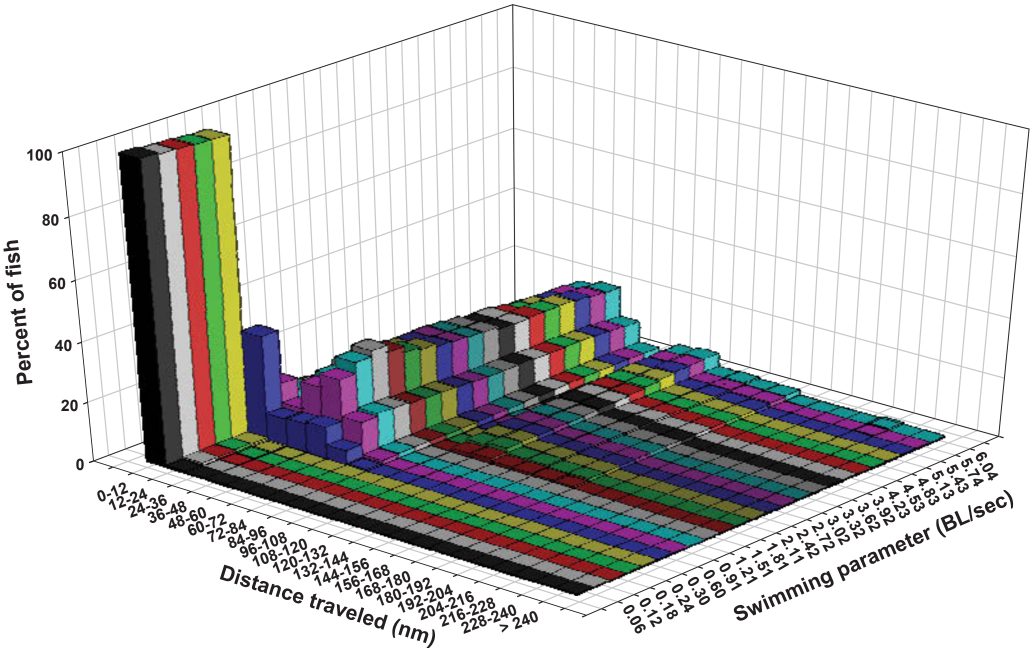


Figure 6.12 – Tabulation of net distance traveled for simulated opakapaka as a function of swimming parameter in the third set of simulations using starting locations and times at liberty observed in DAR tagging database.

Table 6.2. Summary of fits of simulated swimming results to observed tagging recovery pattern of numbers at distance. Values above solid line represent a measure of fit from 0-100 where 0 is the worst fit and 100 is the best fit (as scaled to the mean square error from the nonlinear regression). Highlighted diagonal represents the fits of single swimming behavior simulation results. Other values in upper right half of table represent fits of biphasic swimming behavior results. Matching values in lower left half of table represent the mixing parameter for swimming behavior 1 in the nonlinear regression solutions. The multiplier for swimming behavior 2 in the biphasic results is simply (1 - 'mixing parameter for swimming behavior 1'). Values of 0.1 and 0.9 in lower left half of table denote biphasic combinations where the nonlinear regression terminated at the constrained 0.1-0.9 bounds of the mixing parameter (i.e., a biphasic solution within the bound was not optimal for this combination). Grey shaded regions denote biphasic parameter space where fits were high (within 90% of maximum observed).

Swimming behavior 2*

Swimming behavior 1*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	45.0	45.1	45.2	45.4	45.4	74.3	99.6	99.5	99.6	99.6	99.6	99.6	99.7	99.8	99.8	99.8	99.7	99.7	99.5	99.4	99.3	99.3	99.7	99.9
2	0.10	45.0	45.1	45.3	45.3	74.2	99.6	99.5	99.6	99.6	99.6	99.6	99.7	99.8	99.8	99.8	99.7	99.7	99.5	99.4	99.3	99.3	99.7	100.0
3	0.10	0.10	44.9	45.1	45.2	73.9	99.6	99.5	99.6	99.6	99.6	99.6	99.7	99.8	99.8	99.8	99.7	99.7	99.6	99.4	99.3	99.3	99.7	100.0
4	0.10	0.10	0.10	44.8	44.9	73.7	99.7	99.5	99.6	99.6	99.7	99.6	99.7	99.8	99.8	99.8	99.7	99.7	99.6	99.5	99.3	99.4	99.7	100.0
5	0.10	0.10	0.10	0.10	44.8	73.5	99.7	99.6	99.6	99.7	99.7	99.6	99.7	99.8	99.8	99.8	99.7	99.7	99.6	99.5	99.3	99.4	99.7	100.0
6	0.10	0.10	0.10	0.10	0.10	31.0	53.6	56.1	59.8	56.9	57.0	57.0	57.1	57.2	57.1	57.1	56.8	56.8	56.9	56.9	98.5	57.3	58.2	58.6
7	0.45	0.45	0.45	0.45	0.44	0.10	11.0	11.8	12.2	12.0	12.2	12.3	12.5	12.6	12.7	12.8	13.0	13.1	13.2	13.4	13.6	13.9	14.3	14.8
8	0.41	0.41	0.41	0.41	0.41	0.10	0.10	6.9	7.2	7.3	7.8	8.1	8.3	8.6	8.8	8.9	9.6	9.8	9.8	10.1	10.2	10.7	10.8	11.8
9	0.40	0.40	0.40	0.39	0.39	0.10	0.10	0.10	4.9	5.7	6.4	6.7	7.1	7.3	7.8	8.0	9.7	10.0	9.8	10.2	9.9	11.0	10.8	12.5
10	0.41	0.41	0.41	0.41	0.40	0.10	0.10	0.10	0.10	3.0	3.6	4.0	4.5	4.8	5.3	5.6	8.9	9.5	8.1	8.4	7.3	9.0	7.9	9.7
11	0.42	0.42	0.42	0.41	0.41	0.10	0.10	0.10	0.10	0.10	1.8	2.2	3.1	3.7	5.5	5.8	12.3	14.6	12.3	16.7	6.8	10.9	6.1	8.6
12	0.42	0.42	0.42	0.42	0.42	0.10	0.10	0.10	0.10	0.10	0.10	1.6	3.0	3.7	22.0	20.2	6.0	7.3	20.8	28.1	6.4	10.9	5.5	8.0
13	0.42	0.42	0.42	0.42	0.42	0.10	0.10	0.10	0.10	0.10	0.10	0.10	1.5	2.2	19.3	19.5	3.6	4.2	13.4	25.4	6.2	11.1	4.9	7.2
14	0.42	0.42	0.42	0.42	0.42	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	1.4	1.9	3.7	3.0	3.3	8.7	17.7	7.4	27.5	4.9	7.8
15	0.43	0.43	0.43	0.42	0.42	0.10	0.10	0.10	0.10	0.10	0.10	0.90	0.90	0.90	1.4	19.0	2.7	2.9	10.4	25.6	5.4	8.3	4.2	6.4
16	0.43	0.43	0.43	0.43	0.43	0.10	0.10	0.10	0.10	0.10	0.10	0.90	0.90	0.90	0.90	1.4	2.2	2.4	7.5	21.7	4.4	6.8	3.7	5.6
17	0.44	0.44	0.44	0.43	0.43	0.10	0.10	0.10	0.10	0.10	0.90	0.90	0.90	0.90	0.90	0.90	1.9	2.5	2.3	3.0	2.8	3.3	3.0	3.9
18	0.44	0.44	0.44	0.43	0.43	0.10	0.10	0.10	0.10	0.10	0.90	0.90	0.90	0.90	0.90	0.90	0.10	1.8	2.3	3.0	2.7	3.2	2.9	3.8
19	0.44	0.44	0.44	0.43	0.43	0.10	0.10	0.10	0.10	0.10	0.90	0.90	0.90	0.90	0.90	0.90	0.10	0.10	1.5	2.3	2.0	2.4	2.3	3.2
20	0.44	0.44	0.44	0.44	0.43	0.10	0.10	0.10	0.10	0.10	0.90	0.90	0.90	0.90	0.90	0.90	0.10	0.10	0.10	1.3	1.5	1.8	1.9	2.8
21	0.44	0.44	0.43	0.43	0.43	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.7	1.7	1.4	2.9
22	0.44	0.44	0.44	0.44	0.44	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.90	0.10	0.10	0.10	0.10	0.10	0.10	0.90	0.8	1.2	2.1
23	0.45	0.45	0.45	0.44	0.44	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.0	0.0
24	0.46	0.46	0.46	0.46	0.46	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.50	0.0

***Swimming behaviors are coded 1-24 which represent 0.06, 0.12, 0.18, 0.24, 0.30, 0.60, 0.91, 1.21, 1.51, 1.81, 2.11, 2.42, 2.72, 3.02, 3.32, 3.62, 3.92, 4.23, 4.53, 4.83, 5.13, 5.43, 5.74, and 6.04 body lengths per second, respectively.**

6.5 Discussion

The DAR Opakapaka Tagging Program was very successful in tagging large numbers of opakapaka using a methodology with high survivorship, and there was an ensuing high recapture rate over many years following the initial tagging effort. The pattern of tag returns indicates that opakapaka are not entirely site-dependent throughout their lifespan. Many individuals remain in the general vicinity of their initial capture, but others are capable of long-distance movement. Opakapaka may have territories or home ranges but appear to possess more mobility than conventional thought would suggest. Opakapaka is considered a benthic or demersal fish, and usually only occurs near the bottom in the 100-400m bottom depth range. Most of the major island groups in the MHI are separated by much deeper channels which would present a natural barrier to fish unaccustomed to either swimming at great depths or for long distances in the water column. Standardization of the tag returns by the spatial pattern of fishing effort suggests that long-distance movement may be more pronounced than the raw data by itself would indicate (Figure 6.9C). The small number of long-distance tag returns is made more notable by the pattern of rapidly declining fishing effort at these further distances. Preliminary genetic analysis of opakapaka in the Hawaiian Archipelago discovered weak genetic differentiation and a likely panmictic population (Shaklee and Samollow, 1984). This is consistent with genetic work on other deepwater bottomfish species in Hawaii (Bagley and Geller, 1998), suggesting that either larval dispersal or adult movement allows significant mixing within the population. This is not always the case for deepwater bottomfish, however. The Hawaiian grouper hapu`upu`u (*Epinephelus quernus*) was also found to have significant genetic differentiation in the Hawaiian Archipelago (Rivera et al., 2004). Conventional and electronic tagging of shallow water fishes in the MHI (Meyer et al., 2007a; 2007b; Tagawa and Tam, 2006;

Wetherbee et al., 2004; Ziemann, 2004) found that these relatively large, mobile species (the jacks *Caranx ignobilis* and *C. melampygus*, a snapper *Aprion virescens*, and the Pacific threadfin *Polydactylus sexfilis*) displayed limited movement throughout the archipelago, with well delineated home ranges or limits of dispersal. A congener of opakapaka, *Pristipomoides multidens*, was shown to have pronounced genetic population structure in other areas of the Pacific Ocean, particularly off of Northern Australia. While limited dispersal of eggs and larvae are thought to be one factor, another hypothesis is that there is very limited movement of adult fish (Ovenden et al., 2002; 2004).

Clearly, the movement of opakapaka as inferred from tag returns is not a simple or necessarily single strategy of swimming behavior. Biphasic swimming with both a slow swimming mode and a faster swimming mode was found to be most parsimonious with the observed data. This dual movement behavior is consistent with quantitative research on the movement of other animals; for example, dolphins (Bailey and Thompson, 2006), elk (Morales et al., 2004), and sea turtles (Jonsen et al., 2007). The earlier mentioned goljoen from South Africa may be the most analogous since this fish species also had a predominant low dispersive behavior combined with a small amount of high dispersive behavior (Attwood and Cowley, 2005). Biphasic movement could be manifested in several very different ways, involving different ecological mechanisms and aspects of their life history.

Opakapaka could undergo an ontogenetic change in swimming behavior, whereby certain phases of the life history swim relatively more or less. This developmental behavior could be related to migration, spawning, foraging, habitat changes, or simply a dispersive evolutionary adaptation. However, opakapaka swimming does not appear to be a simple correlate of age or body size since most of the fish tagged in this study were approximately the same size, and presumably close in age. Ontogenetic changes do not have to be linear though; for example, swimming behavior could peak at a certain age and subsequently decline. Most of the opakapaka tagged in this study (23-76 cm FL) are larger than the juveniles (7-25 cm FL) which are known to migrate from a shallow soft-bottom habitat to the deeper adult habitats (Parrish, 1989; Moffitt and Parrish, 1996). However, a closer evaluation of fish size as it relates to adult movement is probably warranted in future work. Alternatively, the biphasic swimming behavior could be something that every individual fish possesses and utilizes in response to some extrinsic environmental cue or some intrinsic cue.

Forage may be an important extrinsic factor. For example, if food supply is reduced, this may prompt a long-distance excursion. The individual movement patterns aggregated over a long time interval may then appear biphasic. Such prey-mediated migration has been documented in other fish species (Polovina, 1996). The biphasic behavior identified here may also be indicative of a stop-and-go foraging tactic more formally termed the saltatory search strategy (O'Brien et al., 1989). Opakapaka may also be simply following a dynamic, transient food source which could lead to biphasic swimming pattern. Large zooplankton is the dominant prey of opakapaka (Haight et al., 1993), and more study is needed on the spatial and temporal dynamics of this forage base.

A similar extrinsic cue could occur if thermal habitat requirements are impinged upon by diel, seasonal, or interannual changes in water temperature (Norris, 1963). The exact thermal habitat of opakapaka is not well understood but is an area of needed research considering the recent incorporation of Essential Fish Habitat requirements into the existing Fishery Management Plans (FMPs) nationwide (NOAA, 1997), including the Bottomfish and Seamount Groundfish Fisheries of the Western Pacific Region FMP which has management jurisdiction over opakapaka in the Hawaiian Archipelago. Temperature, currents, tides, waves, light levels, water clarity, and moon phase are just some of the key variables which could be related to periodic patterns of swimming behavior. Such variables could relate to intrinsic or extrinsic circadian rhythms (Katz, 1978) or other periodicities.

Biphasic swimming behavior could also be related to reproduction. Long-distance movement could be tied to temporally discrete reproductive events such as travel to spawning aggregations or spawning grounds (Domeier and Colin, 1997). It is also possible that the biphasic behavior is linked to gender, with one sex being more resident and the other sex being more migratory (Jonsson and Jonsson, 1993).

From a biomechanical point of view, biphasic swimming could be related to some aspect of hydrodynamics or physiological processes. For example, different modes of swimming could involve differential utilization of body and caudal/medial/paired fins (Blake, 2004), red muscle vs. white muscle (Brill and Dizon, 1979), or due to other physical body constraints. Most studies of energetics have shown that swimming efficiency nearly always peaks at some intermediate speed (e.g., Lee et al., 2003); therefore, energy conservation is an unlikely explanation for opakapaka swimming behavior. *In-situ* observations via submersible or remote camera will be useful to further examine some of these possibilities, as well as computer simulation.

Another likely scenario is that a certain fraction of the opakapaka population is genetically predisposed or programmed at an early stage to swim more than the remaining fraction. Such divergent movement patterns have been documented in other taxa (e.g., Helbig, 1996). Divergent patterns of swimming behavior linked to early life history experience and/or decisions has been suggested for other fish species (Secor, 1999), where the different groups are termed ‘contingents’ within a particular stock. The maintenance of retentive and exploratory contingents can involve complex responses to evolutionary pressure, perhaps best displayed by ayu in Japan which possess alternating retentive and exploratory cohorts in successive generations (Tsukamoto et al., 1987). The maintenance of insular fish stocks in a mosaic of patchy adult habitats could easily lead to adaptive dispersive/nondispersive behaviors.

Finally, it is plausible that different swimming behaviors occur randomly at any portion of the life history. Examples of chaotic swimming behavior have been documented in other taxa. It is likely, however, that some intermediate level of stochasticity and deterministic processes underlie actual fish movement (e.g., Kim, 2003), which will become easier to understand with better tracking and tagging methodologies amenable to deepwater fish species.

Future work with opakapaka will examine many of the above possibilities, by data-mining existing databases such as submersible and remote-camera video, ongoing genetic analyses, and electronic tagging. Any remaining biases due to the reward system, areal closures, or patterns of fishing effort will be removed. Further analyses of the DAR tagging data are also planned, with evaluation of opakapaka growth, mortality, and follow-up work on movement using recently available, higher resolution habitat data for deepwater bottomfish (Parke, 2007).

Chapter 7: Pelagic habitat characterization of loggerhead sea turtles, *Caretta caretta,* in the North Pacific Ocean (1997-2006): Insights from satellite tag tracking and remotely-sensed data

Kobayashi, D. R., J. J. Polovina, D. M. Parker, N. Kamezaki, I-J. Cheng, I. Uchida, P. H. Dutton, G. H. Balazs. In press. Pelagic habitat characterization of loggerhead sea turtles, *Caretta caretta*, in the North Pacific Ocean (1997-2006): Insights from satellite tag tracking and remotely-sensed data. *Journal of Experimental Marine Biology and Ecology*.

7.1 Abstract

We analyzed satellite track data for 186 loggerhead sea turtles in the North Pacific Ocean using remotely-sensed environmental data to characterize pelagic habitat. A large number of candidate habitat variables were merged to the satellite track data and statistically compared to background values over a large spatiotemporal grid which bounded overall occupancy. Five statistically significant variables were identified out of the 16 environmental variables examined. Two of these variables have strong seasonal, interannual, and spatial patterns (sea surface temperature and chlorophyll a concentration), while three others were primarily spatial (earth magnetic force, earth magnetic declination, and earth magnetic inclination). Habitat selectivity for these variables was quantified using preference curve methodology established in the foraging literature, which gave predicted ranges of preferred values for each of the variables deemed significant using a Kolmogorov-Smirnov test. The output from the selectivity curves was used to predict a pixel-by-pixel multivariate loggerhead sea turtle

habitat index across the pelagic North Pacific. This predicted habitat was ground-truthed with newly available satellite track data.

7.2 Introduction

The spatial distribution of pelagic organisms is determined by physical forcing mechanisms (winds, waves, currents, tides, etc.) coupled with active movement by the organisms. Large pelagic macrofauna such as nekton (by definition) possess good swimming ability and can regulate their location actively. Despite the apparent homogeneity of the open ocean habitat, many scales of structure in the physical environment can be used by nektonic organisms to locate and maintain position in preferred habitat (Longhurst, 2006). The distribution and abundance of most studied nekton exhibit this type of patterned occupancy, i.e., they are not simply distributed randomly or uniformly throughout the open ocean.

Sea turtles are one such group of nekton which displays structured pelagic distributions (Carr, 1987; Luschi et al., 2003; Polovina et al., 2000, 2006), presumably via some component of active orientation since even hatchling sea turtles possess good swimming ability (O'Hara, 1980; Davenport and Clough, 1986). Some species, such as leatherback sea turtles, have been shown to have complex patterns of pelagic habitat utilization, not always related to forage or biological "hot spots" (Hays et al., 2006). Loggerhead sea turtles (*Caretta caretta*), a threatened species under the US Endangered Species Act, are capable of traversing both major ocean basins during their ontogenetic migrations (Bowen et al., 1995; Bolten et al., 1998; Alfaro-Shigueto et al., 2004). Many of these long-distance migrations are between nesting grounds and foraging grounds. Juvenile, subadult, and adult loggerhead sea turtles in the North Pacific Ocean have been shown to occupy specific areas of the pelagic environment, possibly related to sea surface temperature and/or ocean productivity (Polovina et al., 2000, 2004, 2006). Based on these and previous studies (e.g., Zug et al., 1995), it is clear that loggerhead sea turtles use some portion of the open ocean for a large fraction of their life history, yet their particular habitat requirements are largely unknown.

Habitat characterization for broad-ranging pelagic organisms has historically been hampered by a lack of complete positional data as well as a lack of biologically pertinent and synoptic environmental data. With recent advances in satellite-mediated tagging technology and accessibility to many remotely sensed environmental data products, much more information is now available on location and movement of individuals and their exposure to a wide variety of environmental variables. We have been tagging loggerhead sea turtles in the North Pacific with Argos-linked satellite tags since 1997 via the collaborative efforts of a large, multinational group of marine turtle researchers (Table 7.1). Both captive-reared and wild-caught individuals have been tagged and tracked. Subsets of this satellite tag dataset have been used elsewhere to examine relationships to fronts (Polovina et al., 2000), diving behavior (Polovina et al., 2003), foraging behavior (Polovina et al., 2004), and characterization of geographic “hot spots” of distribution (Polovina et al., 2006). In this paper, we use the satellite tag data coupled with remotely sensed environmental data to characterize loggerhead sea turtle pelagic habitat across the North Pacific Ocean using quantitative approaches. The tagging work for this study was conducted by the junior authors and their research teams; the raw tag data was made available to the first author who did all of the data-merging, modeling, analysis, and writing. This manuscript presents an analysis of loggerhead sea turtle pelagic habitat using this multinational tagging data.

Table 7.1 - Summary of loggerhead sea turtle satellite tag deployments by major dataset grouping. Summary includes latitude ranges (south to north), longitude ranges (east to west), date ranges, SCL size ranges (cm straight carapace length), number of high-quality satellite data hits, percent of track data in pelagic habitat, and number of tags deployed (not counting dual tagged individuals). Latitude, longitude, and date ranges refer to the range of values throughout the satellite tracks, from deployment through to the time of this summary (July 2006). SCL ranges refer to the size upon release and does not account for growth. A description of the data is included in the bottom row.

	Nagoya Aquarium	Hawaii by-catch	Japan by-catch	Taiwan by-catch	Baja by-catch
Latitude$_{min}$	22.54°N	20.94°N	23.77°N	3.99°N	15.69°N
Latitude$_{max}$	45.42°N	41.46°N	39.48°N	37.75°N	35.05°N
Longitude$_{min}$	136.60°E	162.30°E	125.15°E	108.88°E	168.03°E
Longitude$_{max}$	144.23°W	131.03°W	164.15°E	162.31°E	108.95°W
Date$_{min}$	23-Apr-2003	26-Jan-1997	9-Dec-2002	10-May-2002	10-Oct-1998
Date$_{max}$	30-Jun-2006	23-Oct-2001	12-Jun-2006	1-Jul-2006	14-Dec-2002
SCL$_{min}$	25.60	41.00	66.50	64.00	54.50
SCL$_{max}$	64.80	83.00	89.10	83.00	77.10
Datapoints	41509	5392	2170	1459	725
Tags	110	30	15	18	13
"Pelagic"	90.23%	97.50%	26.87%	10.08%	13.10%
Description	Refers to tag and release conducted upon reared turtles by Dr. Itaru Uchida, Masanori Kurita, Tomomi Saito, and other Port of Nagoya Public Aquarium staff.	Refers to tag and release conducted upon by-catch in the Hawaii-based longline fishery by Pacific Islands Fisheries Science Center, National Marine Fisheries Service staff and fishery observers.	Refers to tag and release conducted upon nesting individuals and by-catch in the Japanese pond net fishery by Dr. Naoki Kamezaki and colleagues.	Refers to tag and release conducted upon by-catch in the Taiwanese pond net fishery by Dr. I-Jiunn Cheng and colleagues.	Refers to tag and release conducted upon by-catch in the Baja California Sur, Mexico coastal gillnet fishery by Dr. Peter Dutton, Wallace J. Nichols, Hoyt Peckham and The Grupo Tortuguero of Baja California.

7.3 Methods

7.3.1 Satellite tracking

All wild-caught (fishery bycatch or nesting individuals) and captive-reared loggerhead sea turtles tagged in this analysis are summarized in Table 7.1, and the track data are shown graphically in Figure 7.1. Turtles were outfitted with satellite transmitters attached to the dorsal carapace using the procedures outlined in Balazs et al. (1996). Turtles were equipped with Telonics (Mesa, AZ, USA) model ST-18, ST-19, ST-24, and Wildlife Computers (Redmond, WA, USA) model SDR-T10, SDR-T16, or SPOT 3/4/5 Argos-linked satellite transmitters. Only the highest quality position data (Argos codes 0-3) were kept initially, and only one dataset from a tag was used for twelve dual-tagged turtles. A subsequent screening removed satellite fixes which predicted unlikely sustained swimming velocities, similar to the methodology of McMahon and Hays (2006), although we used a slightly larger arbitrary cutoff of 5 m/sec instead of 2.5 m/sec since some of the surface current speeds in this area can be ~2.5 m/sec.

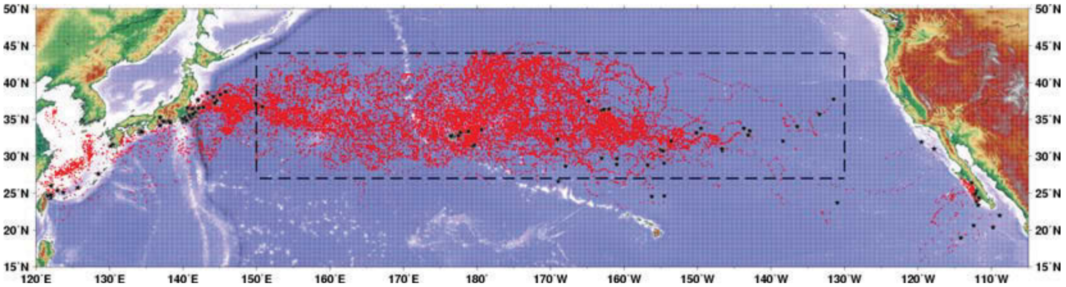


Figure 7.1. Map of North Pacific Ocean and 186 satellite tagged loggerhead sea turtle locations (red) covering the time span 26 January, 1997 – 1 July, 2006. Dashed line delineates grid used for pelagic habitat study, 150°E – 130°W longitude, 27°N - 44°N latitude. Stars indicate release points for individual tracks.

Environmental data grids were merged to the satellite track data using the software package Generic Mapping Tools (GMT), extending the approach of Ellis and Balazs (1998). A GMT subroutine called *grdtrack* was used to extract trackline values from the weekly or monthly gridded data fields with a spatial bicubic interpolation. Monthly data fields were used when weekly resolution resulted in excessive missing values as a result of cloud cover, sensor malfunction or missing files. The GMT software package (Wessel and Smith, 1991) is available from http://gmt.soest.hawaii.edu/ and was used for most of the gridding, mapping, and analysis of this study. Missing values affected 11.30% of the total records in the satellite track data, primarily because of missing coverage in SST and Sea-viewing Wide Field-of-view Sensor (SeaWiFS) data.

7.3.2 Environmental data products

Satellite-derived chlorophyll a pigment concentrations were taken from the SeaWiFS instrument aboard the Seastar earth-orbiting satellite (http://oceancolor.gsfc.nasa.gov/SeaWiFS/). The data used in this paper is chlorophyll a data derived from the raw measured wavelength bands (9 km, 8-day resolution) available from NASA using the SeaWiFS algorithm (SeaWiFS L3 CHLO Version 5). Regridded monthly data at 0.1° latitude/longitude data were merged to the satellite track data. Chlorophyll a is a likely key variable for pelagic habitat since it may be indicative of forage availability for loggerhead sea turtles (Polovina et al., 2001).

Sea surface temperature (SST) from Advanced Very High Resolution Radiometer (AVHRR) sensors aboard earth-orbiting NOAA satellites was merged to the satellite track data. The 4 km resolution Pathfinder v5.0 SST (http://www.nodc.noaa.gov/sog/pathfinder4km) is a new reanalysis of the AVHRR data stream, developed and administered by the University of Miami Rosenstiel School of Marine and Atmospheric Science, the NOAA National Oceanographic Data Center, and NASA Physical Oceanography Distributed Active Archive Center. This was regridded to 8-day 0.1° latitude/longitude data product covering 1997–2003 for this study. For SST subsequent to 2003, NOAA Global Area Coverage SST was used in place of Pathfinder SST at an identical resolution. Correspondence between these two SST datasets is very high (Evan A. Howell, pers. comm.), and for simplicity SST is henceforth referred to as Pathfinder SST. Ocean surface temperature was chosen as a candidate variable because it is known to be a strong orientation cue for sea turtles (e.g., McMahon and Hays, 2006).

An SST-related index of thermal fronts was also merged to the satellite track data. This was a weekly 0.1° latitude/longitude Pathfinder SST-gradient index, a combined N/S, E/W gradient of SST used as an indicator of thermal discontinuities. Such features may be important for pelagic habitat, since previous work has shown relationships of loggerhead sea turtles to thermal fronts (Polovina et al., 2003; 2004).

Sea surface height (SSH) and geostrophic flow fields derived from the sea surface topography were obtained from NOAA OceanWatch, Central Pacific regional node, at the Pacific Islands Fisheries Science Center (PIFSC) National Marine Fisheries Service (NMFS) (http://oceanwatch.pifsc.noaa.gov/). SSH is measured by microwave radar altimeters aboard earth-orbiting satellites Topex/POSEIDON and Jason-1. Geostrophic currents were calculated using the methodology of Polovina et al. (1999). Changes in sea surface topography are related to large-scale water mass dynamics, geostrophic flow; and, for example, 170 cm SSH is used as a marker for the Kuroshio Extension axis (Qiu and Chen, 2005), a biologically important region for loggerheads (Polovina et al., 2006).

Wind data was obtained from microwave scatterometer sensors aboard earth-orbiting satellites ERS-1, ERS-2, and QuickSCAT. Monthly data grids at a resolution of 0.1° latitude/longitude were accessed from NOAA OceanWatch, Central Pacific regional node at the PIFSC, NMFS. Wind stress components in the east-west and north-south directions were evaluated separately, as well as the total resultant wind stress vector magnitude. Wind stress is a potentially important variable for sea turtles since they are air-breathing and, therefore, epipelagic for a significant portion of their time. There may be strong wind-driven circulation in that section of the water column, and possible wind effects on the sea turtle carapace or even on the satellite transmitter unit (e.g., Watson and Granger, 1998).

Global magnetic data were calculated using the software GeoMag 6.0 available from the NOAA National Geophysical Data Center (http://www.ngdc.noaa.gov/seg/geom_util/geomutil.shtml). This software is driven by the International Geomagnetic Reference Field 10th generation (henceforth IGRF-10) coefficients. These coefficients are updated every 2–6 years by the International Association of Geomagnetism and Aeronomy and were last updated in 2005. Four magnetic variables were examined in this study: declination, inclination, total force, and orthogonality of the inclination and total force gradients. Declination is the departure between true north and magnetic north (degrees), which is biologically relevant for the many organisms possessing simple compass-like abilities (Lohmann and Lohmann, 2006). Inclination is a measure of the direction of the total force field into the earth (degrees) and has been shown to be detectible by sea turtles (Light et al., 1993). Both declination and inclination characterize the direction of the earth's magnetic field and may be significant for pelagic orientation. Total force is a measure of the intensity of the earth's magnetic field in nanoteslas and has also been shown to be detectible by sea turtles (Lohmann and Lohmann, 1996). These three variables were output from the GeoMag 6.0 software at a monthly resolution of 0.1° latitude/longitude. The index of orthogonality was constructed to measure the degree of perpendicularity of inclination and total force axes. If these two variables have gradients at 90° or 270° of one another, this may serve as an effective Cartesian coordinate system for pelagic navigation, analogous to an *x*–*y* coordinate system such as longitude and latitude. Orthogonality was calculated pixel-by-pixel using the

Generic Mapping Tools (GMT) subroutines *grdgradient* to calculate the directional gradient in a grid at a particular pixel location, and *grdmath* to perform calculations on the two grids. The linear index created ranged from 0 (gradients in identical or exactly opposite directions) to 1 (gradients at 90° or 270° of one another), using simple geometric functions.

Bathymetric data, both depth and two depth gradients (N/S, E/W), were incorporated into the satellite track data. The Smith and Sandwell (1997) 2-minute resolution global database was accessed for this step of the analysis. Since sea turtles nest on land, and are neritic for some portion of their life history, it is conceivable that water depth or water depth gradients could be important habitat descriptors.

7.3.3 Data analyses

The satellite track data were first examined with a nonmetric multidimensional scaling (NMDS) analysis. NMDS is an ordination approach that is also useful in assessing dimensionality in a dataset (McCune and Grace, 2002). Potential groupings of the satellite tag data were investigated since this data covers a wide geographic area, different seasons of the year, and different sizes of individuals, among many other variables. Since it is known that loggerhead sea turtles occupy a relatively narrow latitudinal range in certain instances (Polovina et al., 2000), frequency distributions of this variable (latitude) were examined in the NMDS across aggregations defined by four seasons (Winter = November–January, Spring = February–April, Summer = May–July, and Autumn = August–October), six uniformly sized longitudinal bins (breakpoints at 140°E, 160°E, 180°, 160°W, and 140°W), and two size classes of individuals defined by their straight carapace lengths (SCL) on release (small ≤40 cm

SCL, and large >40 cm SCL). The 40 cm SCL size cutoff corresponds ecologically to the transition between the “juvenile” and subsequent “subadult” stage, whereby swimming is thought to be more important than passive rafting (Dodd, 1988), and occurs at 8–9 years of age (Zug et al., 1995). Most of the tags and track data are from juveniles, with a small number of subadults and very few adults >70 cm SCL (Figure 7.2). NMDS was chosen as the ordination technique since most of the latitudinal frequency distributions were nonsymmetrical, and such distributions are not easily characterized by a single measure such as a mean or median. NMDS is an iterative, nonparametric technique and is considered the method of choice for ordination of most ecological data (McCune and Grace, 2002). The NMDS of these 48 aggregations was accomplished using the commercial software package PC-ORD. The NMDS indicated a possible “coastal” component of the data which will be analyzed in a separate study; this study will focus on the “pelagic” aggregation of track data (Figure 7.3), spanning the bounds of 150°E–130°W longitude.

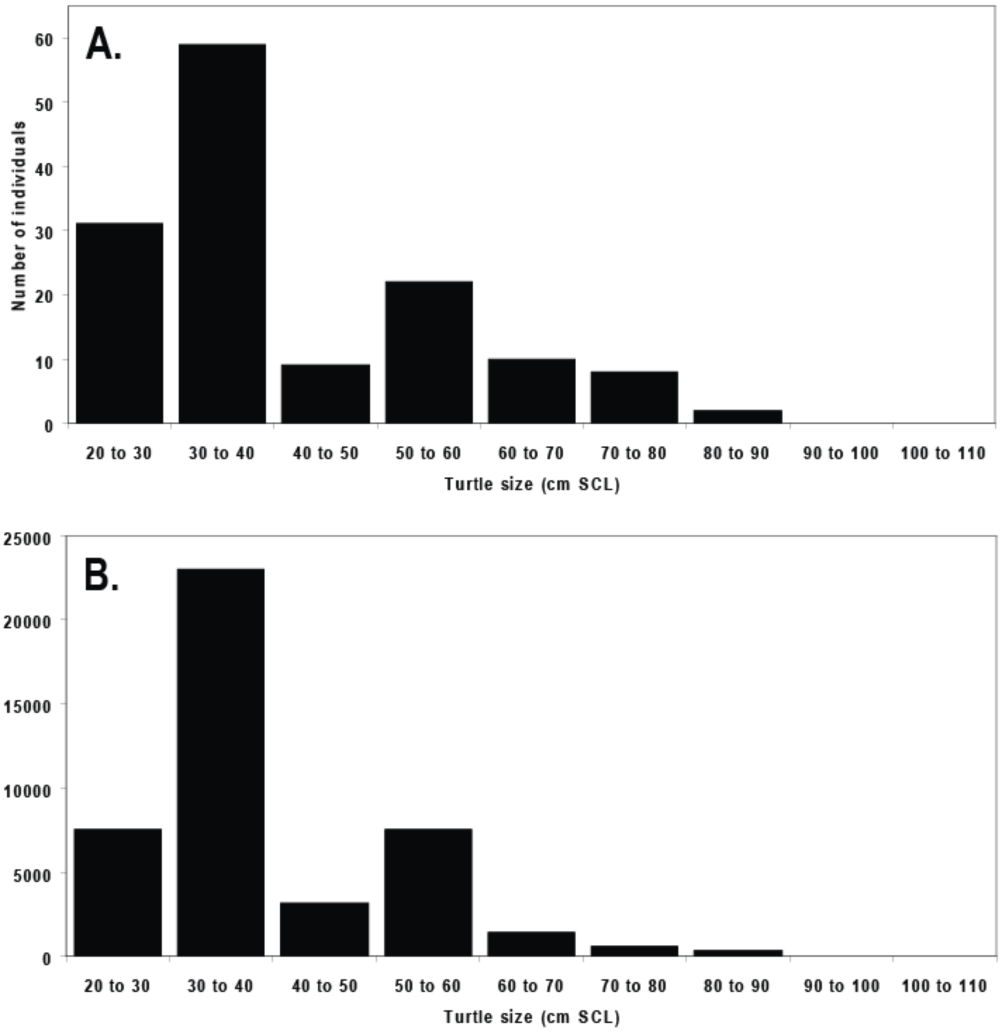


Figure 7.2. Size frequency histograms of tagged loggerhead sea turtles (A.) and track data (B.) used in the analysis. Each bar represents the frequency of data in a 10 cm SCL bin.

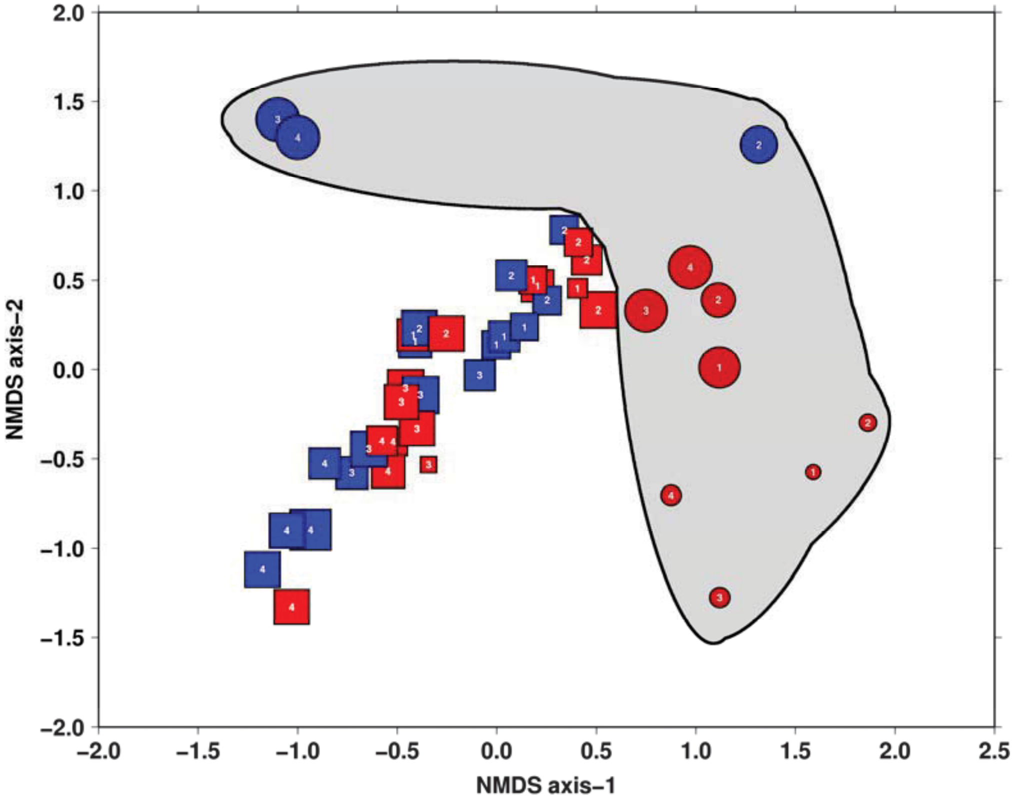


Figure 7.3. Ordination results from nonmetric multidimensional scaling (NMDS) analysis of latitudinal frequency distributions in the loggerhead sea turtle satellite track data. Data were aggregated into 48 data ensembles defined by unique combinations of 6 longitudinal bins, 4 seasonal bins, and 2 size-based bins. Circles represent data ensembles from the farthest east and west strata, squares represent all non-coastal data ensembles. Symbol size is proportional to mean latitude of that data ensemble (small–large symbols reflect the data range 18.5–42.8 degrees North latitude). Blue denotes juvenile (≤ 40 cm SCL), red denotes subadult and adult (> 40 cm SCL). The number located within each symbol represents the season of that particular data ensemble (1 = winter, 2 = spring, 3 = summer, 4 = autumn). Shaded polygon denotes "coastal" pattern of farthest east and west data ensembles not addressed in this study.

Many fundamental ecological processes involve preferences made at the individual level, e.g., mate choice, foraging behavior, and habitat selection. The quantification of such preferences has received much attention from scientific researchers (Cock, 1978; Lechowicz, 1982; Confer and Moore, 1987) and typically involves simultaneous examination of some measure of what resources an individual uses and, equally importantly, some measure of what resources are available to that individual. Many selectivity or electivity indices have been put forth, including well-known approaches such as the Forage Ratio (Savage, 1931), Ivlev's Electivity Index (Ivlev, 1961), Jacob's Electivity Index (Jacobs, 1974), Linear Index (Strauss, 1979), Manly-Chesson Alpha (Manly et al, 1972; Chesson, 1978; 1983), and Relativized Electivity (Vanderploeg and Scavia, 1979). These methods were initially developed for, and have primarily dealt with, foraging studies; but these techniques have also been applied to habitat selection behavior (e.g., Morrissey and Gruber, 1993; Lukoschek and McCormick, 2001; Carreras et al., 2004; Cardona et al., 2005). Despite much scientific literature on this topic, no single index prevails. Quite often, multiple indices are calculated and contrasted (e.g., Brodeur, 1998; Govoni et al., 1986; León and Bjorndal, 2002). Lechowicz (1982) evaluated many indices and recommended Relativized Electivity, which was used by Lukoschek and McCormick (2001) to characterize goatfish habitat; the Linear Index has been used to characterize habitat in juvenile lemon sharks (Morrissey and Gruber, 1993), and the Manly-Chesson Alpha is perhaps the most widely used forage index as an alternative to the now deprecated Ivlev's Electivity Index (Cock, 1978; Chesson, 1978; Lechowicz, 1982). In this study Relativized Electivity, the Linear Index, and Manly-Chesson Alpha are applied and contrasted to characterize habitat preference in loggerhead sea turtles.

The calculation of Relativized Electivity, the Linear Index, and Manly-Chesson Alpha (henceforth designated RE, LI, and MCA, respectively) for habitat characterization requires data on the utilization (u) and availability (a) of a particular habitat variable. The subscripts i and j are added to each of the RE, LI, MCA, u, and a to indicate category i within each habitat variable j. Utilization of a particular habitat variable was simply derived by tabulating values from the merged satellite track data for each of the

j environmental variables into frequency distributions. After standardization these became the u_{ij}. Availability in this analysis was defined as the distribution of values available over a spatiotemporal grid encompassing the satellite track data; in other words, this is the distribution of values assumed to be available to the individual in some sequential process. After using NMDS to specify bounds of 150°E–130°W longitude, it is seen that more than 99% of the remaining satellite track data lies between 27°N and 44°N latitude. For each of the j environmental variables examined, all weekly or monthly pixel values within this spatial grid over the January 1997–December 2006 time period were tabulated into frequency distributions of availability; after standardization these become the a_{ij}. The u_{ij} and a_{ij} were tabulated identically into N_j uniform bins representing the categories i, as input to the selectivity indices. An attempt was made to use the objective bin-size methodology of Scott (1979); however, this was unsuccessful and resulted in unworkably small bin sizes, likely based on issues related to pseudoreplication mentioned below. Bin sizes were determined qualitatively to maintain sufficient resolution so as to not obscure distributional patterns in the data.

In an approach similar to Kinzie (1988), the two cumulative frequency distributions of the raw, unbinned u_{ij} and a_{ij} were first statistically compared for each of the j habitat variables using a Kolmogorov-Smirnov (KS) test, which uses the maximum vertical distance between the two overlaid cumulative frequency distributions, referred to as $D_{\max}$ (Zar, 1984). The KS test is particularly attractive for use in habitat studies because it is sensitive to both location and shape, therefore amenable to the types of the continuous and nonsymmetrical habitat variables typically encountered in biological studies (Pacheco and Henderson, 1996). The KS test was modified in two ways for this specific application. The first modification was to use a one-sample KS test to compare the u_{ij} to the a_{ij}, in a manner analogous to comparing one sample distribution to an extrinsic and invariant distribution, e.g., comparison to a normal distribution. In this case, the comparison of u_{ij} from the tracks is made to an underlying a_{ij} distribution made up of many hundreds of thousands of background pixels of information aggregated over a large spatial grid over many years. Utilization of this large n for a_{ij} in the calculation of statistical significance is unjustified as a result of pseudoreplication (Hurlbert, 1984); i.e., this large n sampled from the spatiotemporal grids does not reflect n independent values because of spatial correlation, pixel-based interpolation, arbitrary resolution, and temporal binning of the data. The approach taken here is to treat these background distributions a_{ij} as extrinsic and invariant. The second modification of the KS test is to similarly adjust the degrees of freedom (henceforth df) corresponding to the u_{ij} distribution. The df were conservatively adjusted to reflect the sample sizes of tagged individuals contributing to each cumulative frequency distribution, since pseudoreplication is again a potential problem, for the same reasons just described. Additionally, there is obvious lack of independence in the data as a result of many satellite "hits" along a continuous track-line coupled with the extraction of the matching environmental data from spatially and temporally discrete grids for each "hit." This adjustment of df is comparable to approaches taken elsewhere to alleviate the effects of pseudoreplication in autocorrelated datasets (Clifford et al., 1989; Pyper and Peterman, 1998). The Bonferroni correction factor was used to calculate the significant $D_{\max}$ values for n=16 tests. For the N_{KS} variables which had statistically significant differences in u_{ij} and a_{ij} using the modified KS test, further analysis was performed with the preference indices RE_{ij}, LI_{ij} and MCA_{ij}, which were calculated using the following equations:

$$RE_{ij} = \frac{\dfrac{\dfrac{u_{ij}}{a_{ij}}}{\sum_{i=1}^{N_j} \dfrac{u_{ij}}{a_{ij}}} - \dfrac{1}{N_j}}{\dfrac{\dfrac{u_{ij}}{a_{ij}}}{\sum_{i=1}^{N_j} \dfrac{u_{ij}}{a_{ij}}} + \dfrac{1}{N_j}}$$

$$LI_{ij} = u_{ij} - a_{ij}$$

$$MCA_{ij} = \frac{\dfrac{u_{ij}}{a_{ij}}}{\sum_{i=1}^{N_j} \dfrac{u_{ij}}{a_{ij}}}$$

Pelagic habitat was characterized by the selectivity curves using seasonal 0.1° latitude/longitude climatological fields as a predictive baseline. A high-resolution lookup table was created for each selectivity curve to enable prediction for each pixel of the grids. A multivariate habitat map was constructed using each of the LI selectivity curves as an additive component towards the final habitat preference index. Weighting of the component LI with weights *W* was explored. The meta type habitat index, *H*, was created from the standardized LI of the N_{KS} significant variables as follows:

$$H = \sum_{k=1}^{N_{KS}} LI_k \times W_k$$

Seasonal values of *H* were mapped across the entire North Pacific Basin. Suitable habitat was delineated by an arbitrary threshold value determined from inspection of the overall *H* frequency distributions and locations of tracked loggerheads.

The performance of the multivariate habitat prediction was tested using more recently available raw satellite track data for loggerhead sea turtles in late 2006 and early 2007.

Data subsequent to July 2006 were not included in the habitat characterization study and served as an ideal test of habitat utilization. Habitat index values were calculated for the test dataset of tracks after merging the five environmental variables to the newer data, and this distribution was compared to the original distribution using a two-sample Kolmogorov-Smirnov test. The distributions should be similar if the habitat characterization is robust.

7.4 Results

As of the time of this analysis in mid-2006, 186 tracks ranging in duration from 1.25 to 945.3 days have been recorded (Table 7.1), with total distance traveled ranging from 13.6 to 17906.5 km (integrated along entire track). The average track spanned 257.9 days and covered 5648.9 km, for an average speed of 21.9 km per day. A broad size range of wild and captive-reared loggerheads were tagged and released, ranging from 25.6 to 89.1 cm SCL at locations across the North Pacific (Figure 7.1). The mean size of tracked individuals was 48.3 cm SCL. Individuals did not simply radiate from a single point of release and there were strong indications of directed orientation that was qualitatively similar between years and size classes of individuals.

The NMDS analysis suggested that data ensembles in the easternmost and westernmost regions of the North Pacific Basin were exhibiting different characteristics with respect to latitudinal distributions (Figure 7.3). Season of the year and turtle size did not correlate to any pattern in the resulting NMDS ordination scatterplot. Subsequent analyses were performed on the pelagic subset of satellite tags (*n*=135) between 150°E and 130°W longitude. There was no strong indication from the latitudinal analysis of further data groupings based on size, longitude or season; therefore, all pelagic track data was aggregated for this analysis of habitat.

The modified KS statistical tests indicated that 5 of the 16 environmental variables examined were significantly different in utilization and availability (Table 7.2). SeaWiFS chlorophyll a, Pathfinder SST, and 3 IGRF-10 magnetic field variables (total force, declination, and inclination) had strongly different cumulative frequency distributions. The largest $D_{\max}$ values occurred at 0.1050 milligrams chlorophyll a per cubic meter, 19.85 degrees C sea surface temperature, 44136.5 nanoteslas magnetic total force, 12.1485 degrees magnetic declination, and 53.897 degrees magnetic inclination.

Table 7.2 - Summary of modified Kolmogorov-Smirnov (KS) statistical tests comparing cumulative frequency distributions of utilization and availability of 16 environmental variables merged with pelagic loggerhead sea turtle satellite track data. Asterisks denote significance at $p<0.05$ (*), $p<0.01$ (**), and $p<0.001$ (***) levels of probability, corresponding to Bonferroni adjusted critical values for Dmax of 0.1535, 0.1717, and 0.1948, respectively. In a KS test, Dmax represents the largest absolute vertical distance between any 2 horizontal locations on an overlaid cumulative frequency distribution plot. This value where Dmax occurs is presented below.

Environmental variable	Kolmogorov-Smirnov D_{max} value	Value at D_{max}	Significance
SeaWiFS chlorophyll-a	0.3596	0.1050	***
Pathfinder sea surface temperature	0.2985	19.8500	***
IGRF-10 magnetic declination	0.2669	12.1485	***
IGRF-10 magnetic total force	0.1998	44136.5	***
IGRF-10 magnetic inclination	0.1866	53.8970	**
AVISO geostrophic u-component	0.1516	4.5000	ns
Smith & Sandwell bathymetry	0.1486	-5485	ns
AVISO sea surface height	0.1476	171.5	ns
Pathfinder sea surface temperature gradient	0.1303	0.1350	ns
ERS/QuikSCAT winds u-component	0.1106	-0.0212	ns
IGRF-10 magnetic orthogonality index	0.1097	0.0786	ns
ERS/QuikSCAT winds v-component	0.1002	-0.0042	ns
AVISO geostrophic v-component	0.0707	-8.5	ns
ERS/QuikSCAT winds total magnitude	0.0665	0.1859	ns
Smith & Sandwell bathymetric EW gradient	0.0300	-315	ns
Smith & Sandwell bathymetric NS gradient	0.0133	-625	ns

Example selectivity curves for Pathfinder SST are shown in Figure 7.4. Note that RE and LI can vary in both positive and negative directions, indicative of preference and avoidance, respectively. MCA is always positive and is intended to measure biologically based preference over the range of resources sampled (Chesson, 1978, 1983). The utilization and availability distributions for SST are also shown as an example (Figure 7.4). The simplicity and well-behaved nature of the LI index are appealing, as is the intuitive logic of an index which can be negative for resources not preferred. The odd behavior of the RE index in the negative domain is not clearly understood, and it is also unclear why the region of preference is much broader than both LI and MCA would indicate; the raw utilization distribution is more consistent with the shapes of the LI and MCA curves (Figure 7.4). For these reasons, further analyses focused on the LI results. LI curves for SeaWiFS chlorophyll a, IGRF-10 magnetic force, IGRF-10 magnetic declination, and IGRF-10 magnetic inclination are shown in Figure 7.5.

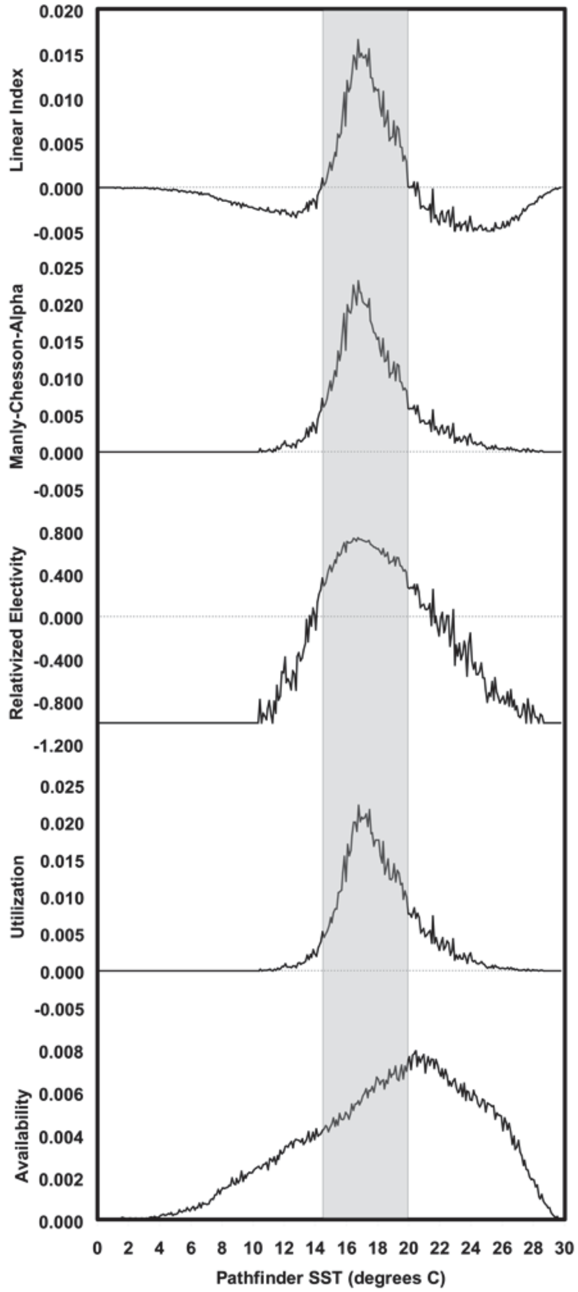


Figure 7.4. Availability, utilization, and loggerhead sea turtle selection curves estimated for Pathfinder SST per 0.1°C bins. Availability represents overall frequency distribution from 150°E–130°W longitude, 27°N–44°N latitude, January, 1997 - December, 2006. Utilization represents overall frequency distribution from data merged to all pelagic satellite tracks. RE refers to the Relativized Electivity index, MCA refers to the Manly-Chesson-Alpha index, and LI refers to the Linear Index. Shaded region represents positive values of the LI (14.45°C–19.95°C) for reference.

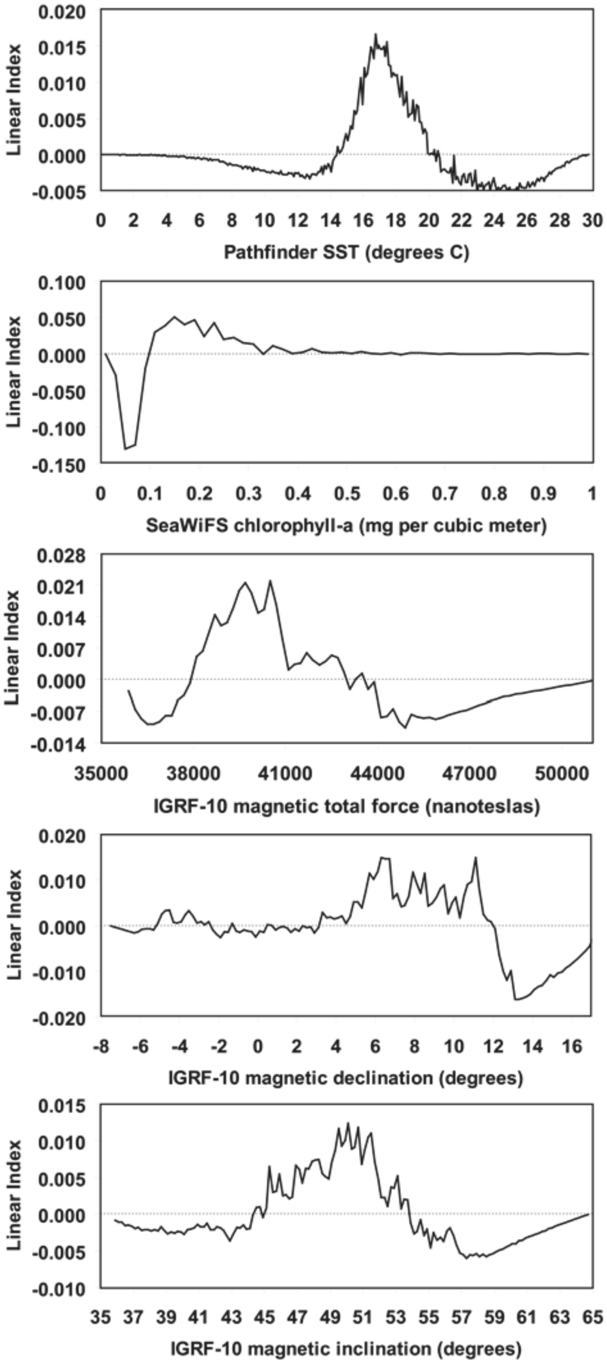
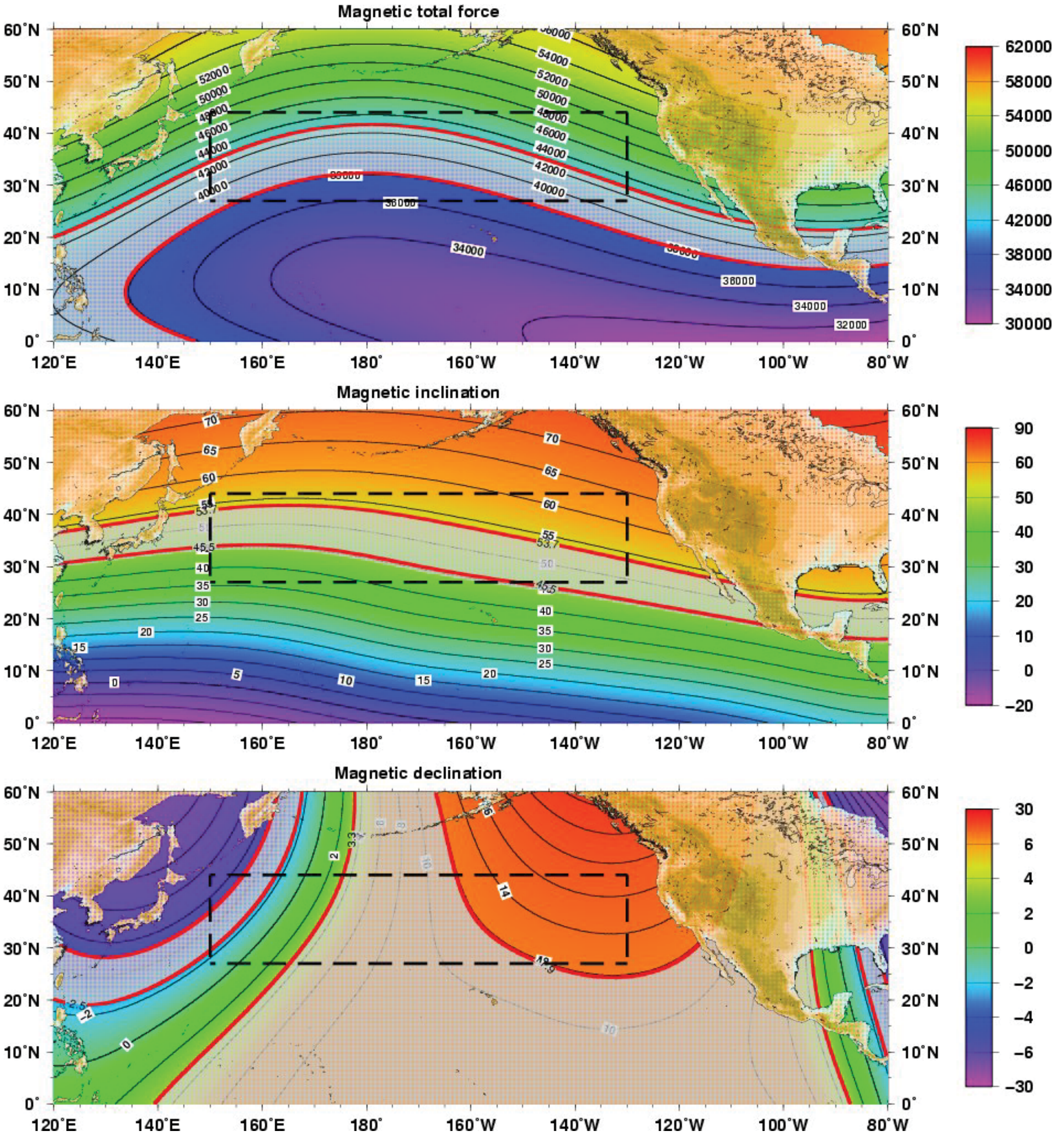


Figure 7.5. Linear Index (LI) for the five statistically significant environmental variables from the modified Kolmogorov-Smirnov test. LIs are shown for Pathfinder SST, SeaWiFS chlorophyll a, IGRF-10 magnetic force, IGRF-10 magnetic declination, and IGRF-10 magnetic inclination.

Positive values of LI were used to delineate habitat ranges for each of the five statistically significant variables. Loggerhead sea turtle pelagic habitat was therefore defined by Pathfinder SST values from 14.45°C to 19.95°C, SeaWiFS chlorophyll a values from 0.11 mg per cubic meter to 0.31 mg per cubic meter, IGRF-10 magnetic force values from 38100 nanteslas to 42900 nanoteslas, IGRF-10 magnetic declination values from - 5.1° to - 2.5° and 3.3° to 11.9°, and IGRF-10 magnetic inclination values from 44.5° to 53.7° (Table 7.3). Since the spatial patterns of magnetic field data are not familiar to the average reader, the habitat ranges and overall patterns for the three IGRF-10 magnetic variables are shown in Figure 7.6 for an example month (May 2007). It should be noted that the earth magnetic field data used in this study change very slowly over time, termed secular variation; however, the differences over the time scale of this analysis are barely perceptible to the human eye when plotted as in Figure 7.6.

Table 7.3 - Environmental variable range of values for pelagic habitat definition of loggerhead sea turtles, based on criteria of positive Linear Index.

Variable	Range definition for habitat
Pathfinder SST	14.45°C to 19.95°C
SeaWiFS chlorophyll-a	0.11 mg per cubic meter to 0.31 mg per cubic meter
IGRF-10 magnetic force	38100 nanteslas to 42900 nanoteslas
IGRF-10 magnetic declination	-5.1° to -2.5°, 3.3° to 11.9°
IGRF-10 magnetic inclination	44.5° to 53.7°


Magnetic total force

Magnetic inclination

Magnetic declination

Figure 7.6. Example IGRF-10 earth magnetic field grids (total force, inclination, and declination from top to bottom, respectively) from May 2007. Loggerhead sea turtle pelagic habitat ranges for each variable are outlined in red and stippled in gray. Dashed line delineates grid used for pelagic habitat study, 150°E–130°W longitude, 27°N–44°N latitude.

The multivariate habitat index, *H*, is shown for seasonal climatological grids in Figures 7.7–7.10. Four versions of habitat are shown, utilizing the LI differentially. In the first habitat map, the LI of all five environmental variables are simply summed in unweighted fashion (Figure 7.7). In the second habitat map, only the LI of Pathfinder

SST is used (Figure 7.8). In the third habitat map, the LI of Pathfinder SST and SeaWiFS chlorophyll a are used (Figure 7.9). In the fourth habitat map, the LI of all five environmental variables are summed in weighted fashion (Figure 7.10). Various weighting factors were explored. Since utilization of three components of the earth magnetic field is likely redundant in the habitat index, an attempt was made to weight these component LI correspondingly less than SST and chlorophyll a LI. Temperature is likely linked to more fundamental metabolic or innate responses and received a higher weight than the component likely related to forage (chlorophyll a). A tentative weighting scheme of (1.0, 0.5, 0.1, 0.1, 0.1) is presented here for the calculation of H from component LI of SST, chlorophyll a, IGRF-10 magnetic force, IGRF-10 magnetic declination, and IGRF-10 magnetic inclination, respectively (Figure 7.10).

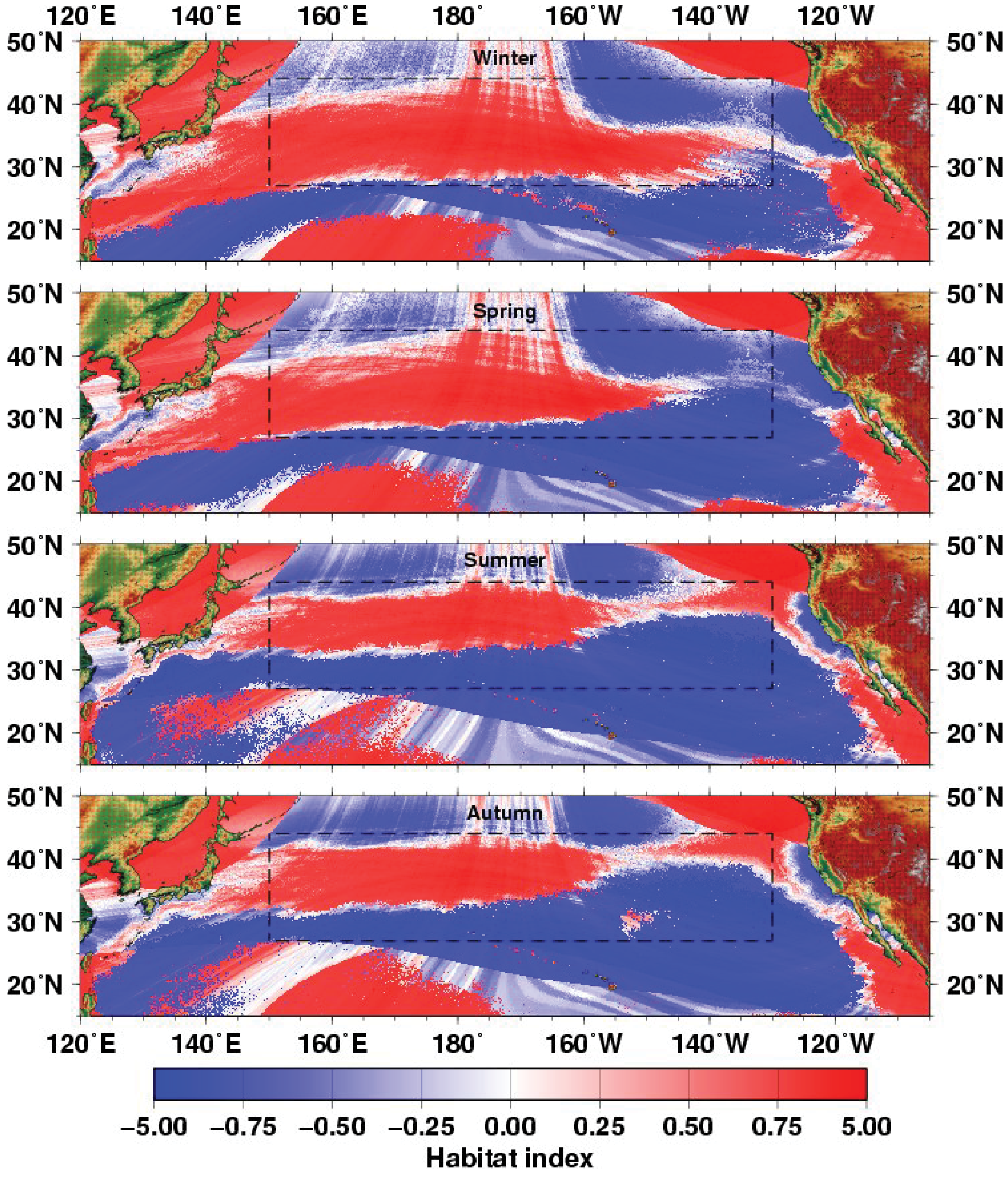


Figure 7.7. Seasonal climatological habitat map for pelagic loggerhead sea turtles in the North Pacific Ocean. Multivariate habitat index is derived from the LI selection curves for Pathfinder SST, SeaWiFS chlorophyll a, IGRF-10 magnetic force, IGRF-10 magnetic declination, and IGRF-10 magnetic inclination. All five variables combined equally for the final habitat index.

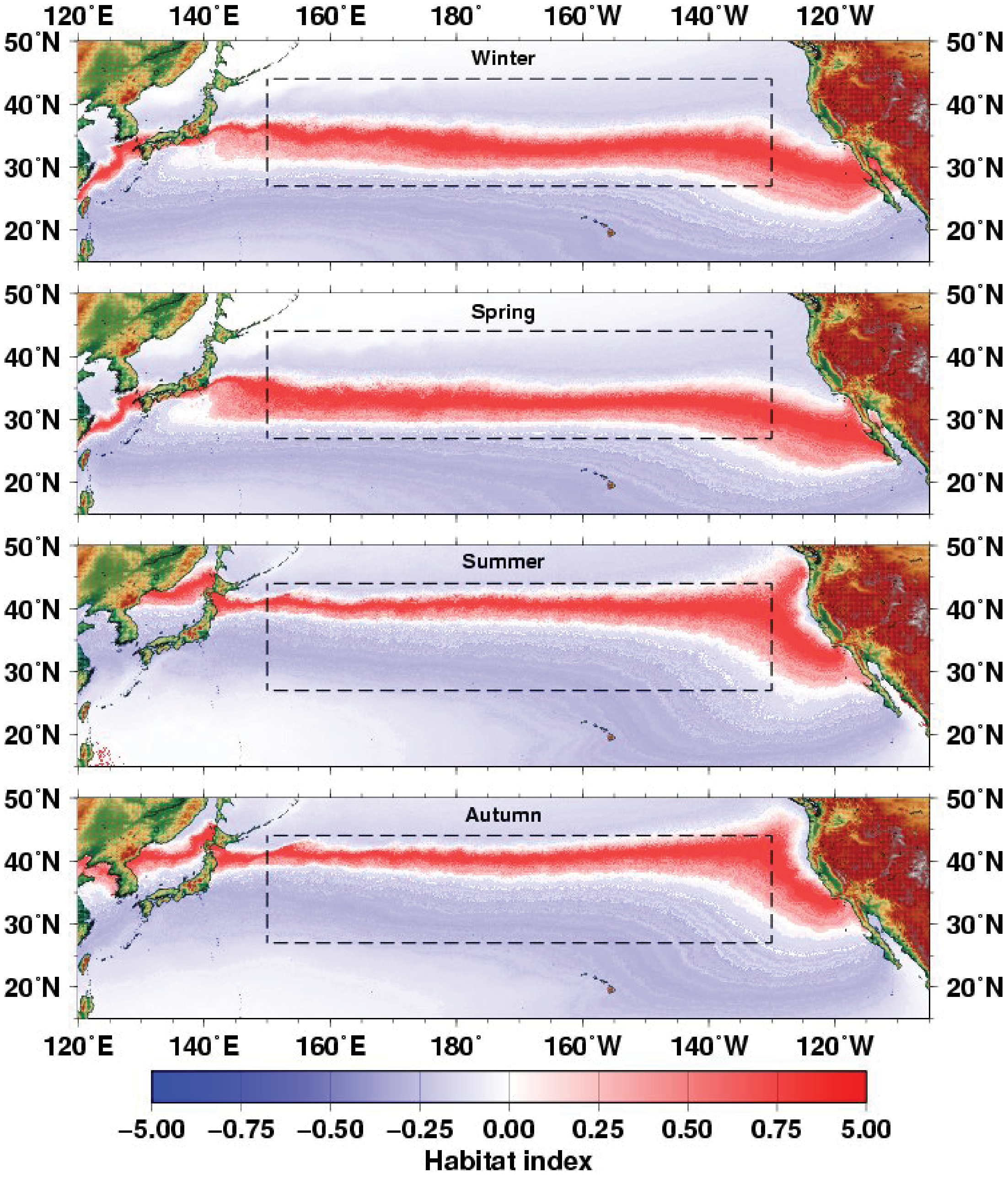


Figure 7.8. Seasonal climatological habitat map for pelagic loggerhead sea turtles in the North Pacific Ocean. Habitat index is derived from the LI selection curve for Pathfinder SST only.

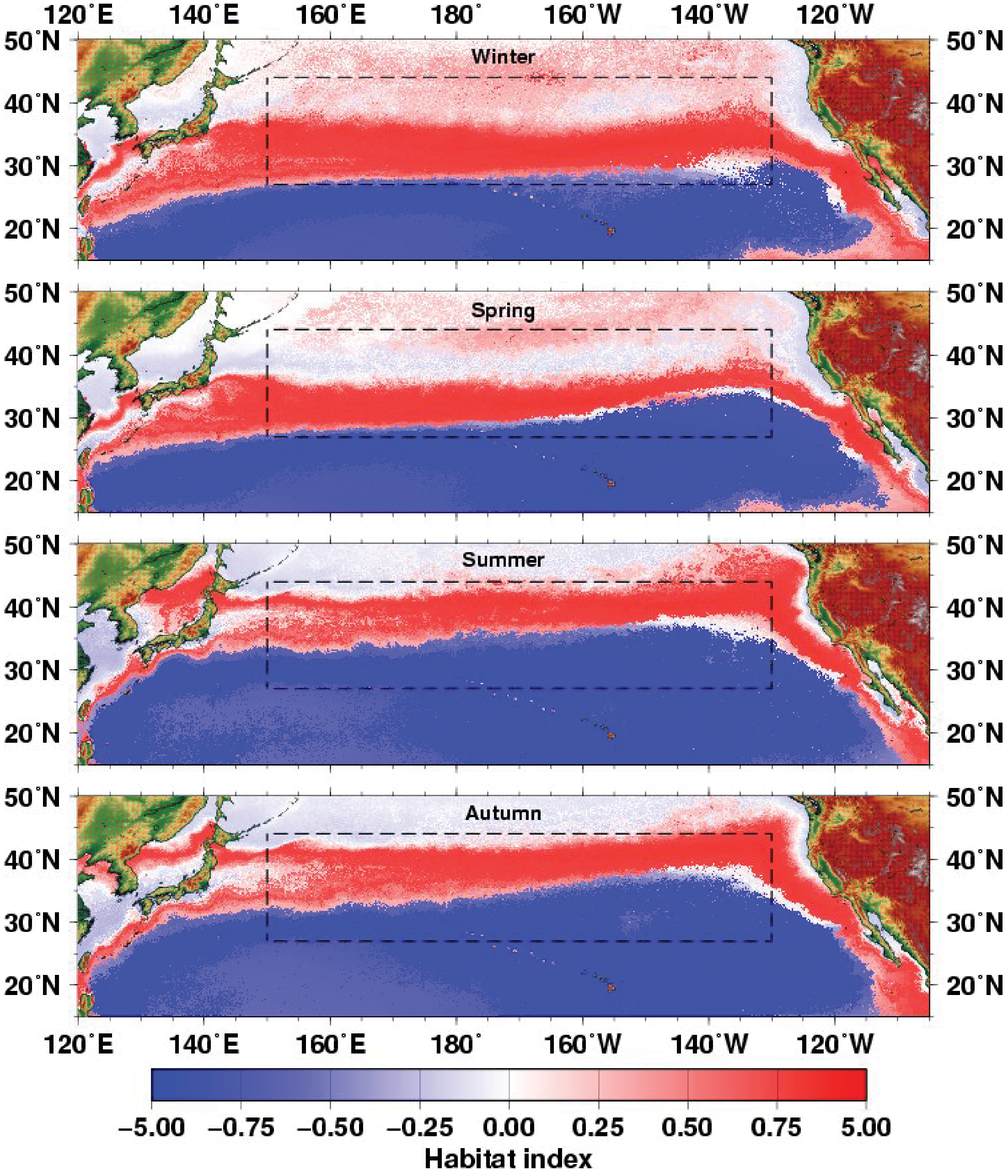


Figure 7.9. Seasonal climatological habitat map for pelagic loggerhead sea turtles in the North Pacific Ocean. Multivariate habitat index is derived from the LI selection curves for Pathfinder SST and SeaWiFS chlorophyll a.

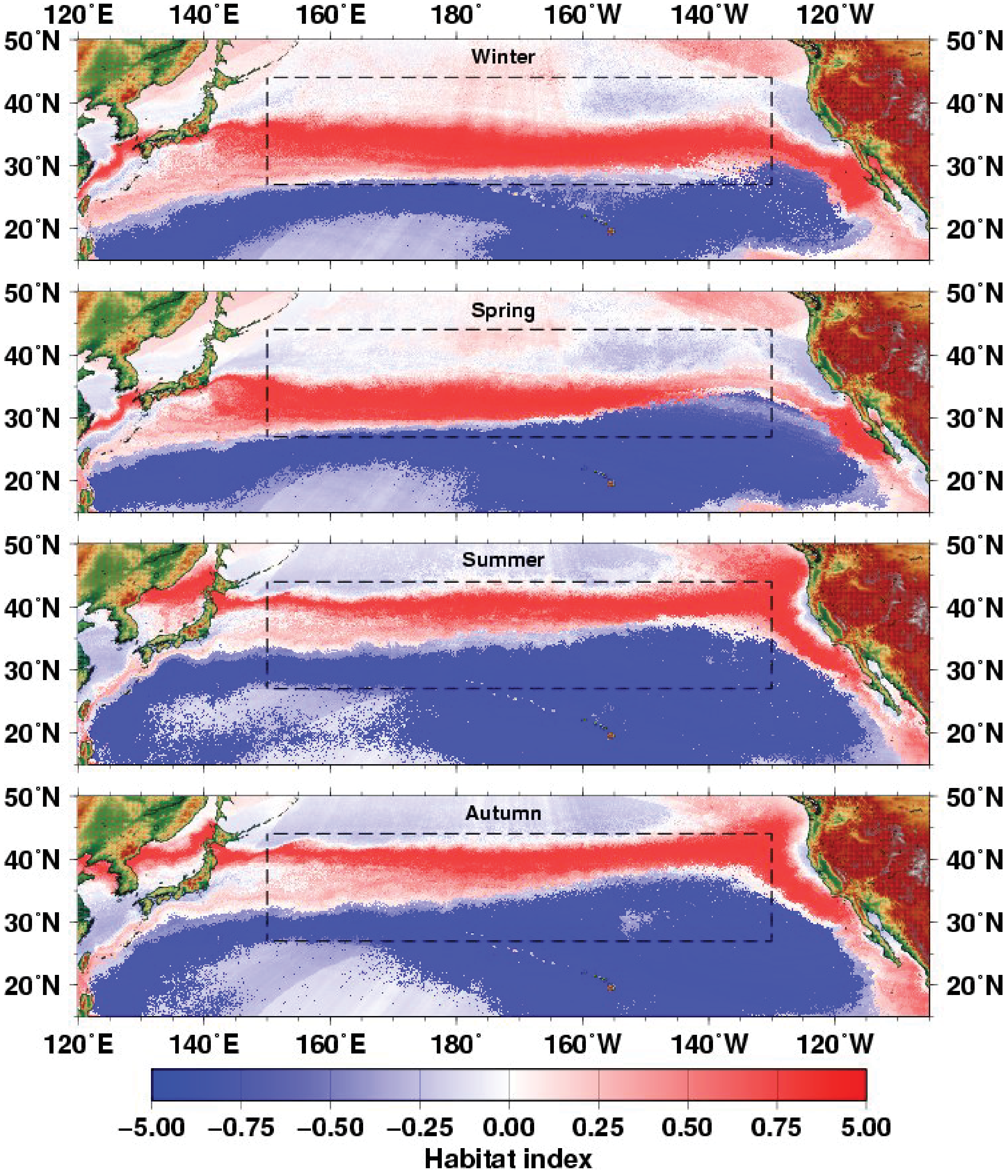


Figure 7.10. Seasonal climatological habitat map for pelagic loggerhead sea turtles in the North Pacific Ocean. Multivariate habitat index is derived from the LI selection curves for Pathfinder SST, SeaWiFS chlorophyll a, IGRF-10 magnetic force, IGRF-10 magnetic declination, and IGRF-10 magnetic inclination. Five variables combined with weights of 1.0, 0.5, 0.1, 0.1, and 0.1, respectively for the final habitat index.

Loggerhead sea turtle satellite track data in late 2006 and early 2007 primarily occurred within the delineated habitat predicted by the multivariate *H* index. The two-sample

Kolmogorov-Smirnov test indicated that the cumulative frequency distribution of weighted *H* values from the original track data was not significantly different from the cumulative frequency distribution of the newer 2006–2007 track data not used in the habitat characterization ($D_{\max} = 0.1295$, $p > 0.05$, $N_1 = 135$, $N_2 = 66$, $D_{0.05} = 0.2037$). The percent distributions of the weighted habitat index are shown in Figure 7.11.

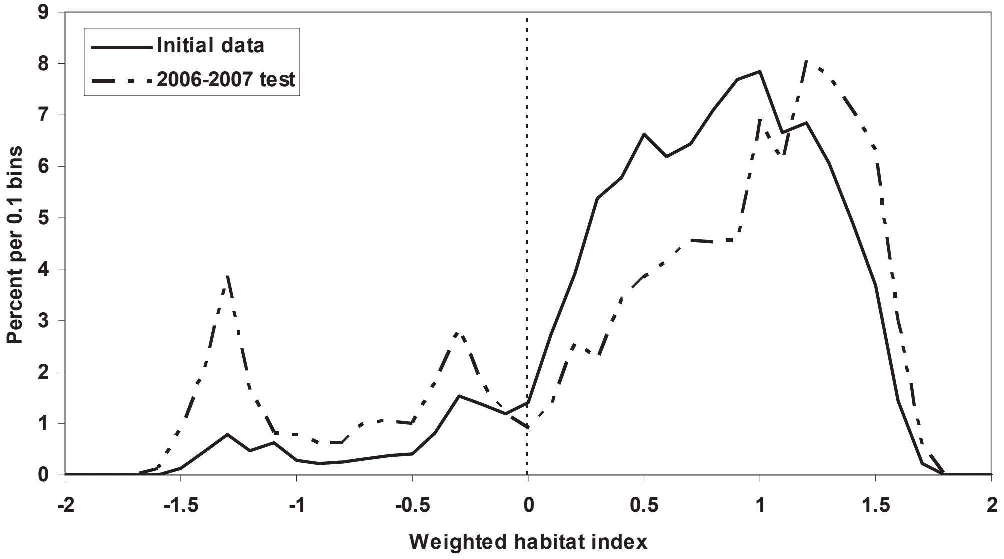


Figure 7.11. Percent distributions of the weighted habitat index for the initial data used in this study (solid line) and the 2006-2007 test data (dashed line). A two-sample Kolmogorov-Smirnov test indicated that the distributions were not significantly different ($D_{\max} = 0.1295$, $p > 0.05$, $N_1 = 135$, $N_2 = 66$, $D_{0.05} = 0.2037$). The vertical dotted line separates presumed avoidance from preference.

7.5 Discussion

Quantitative evaluation of habitat preference may be improved by analytical tools developed in the foraging field of study. Both of these processes are shared elements of the broader field of resource selection, and common approaches can apply (Manly et al., 2002). With the now widespread use of satellite tags and other data-intensive approaches, it will be very useful to apply methodologies that can distill the massive amounts of data into simplified and ecologically meaningful results. Resource selection indices should be further explored as a technique in satellite tag research, and may have broad applicability toward habitat-related issues such as mitigation of protected species interactions with fisheries, Marine Protected Areas, Essential Fish Habitat, and ecosystem management. The quantification of habitat is a critical element of successful management of highly migratory species (Cañadas et al., 2005; Louzao et al., 2006). Some researchers have used Ivlev's Index of Electivity to characterize habitat preference (Carreras et al., 2004; Cardona et al., 2005; Revelles et al., 2007a), despite this approach being considered deprecated for use in forage studies (Cock, 1978; Chesson, 1978; Lechowicz, 1982) because of statistical concerns. The implications of this are unclear, yet caution is warranted since resource utilization, whether forage or habitat, is a single process with much literature on relevant analytical tools and their performance or lack thereof. The Linear Index of Strauss (1979) is promoted here as a tool for habitat characterization since it offers a simple, objective means of determining preferred or non-preferred ranges for a particular environmental variable, and the index is well-behaved over a finite negative to positive range of values.

The finding that SST and chlorophyll a characterize the loggerhead sea turtle pelagic habitat is consistent with earlier studies based on fewer turtles over a smaller temporal and spatial range (Polovina et al., 2000, 2004, 2006). In particular the preferred range of surface chlorophyll a habitat identified in this study (0.1–0.3 mg per cubic meter) is interpreted as identifying the Transition Zone Chlorophyll Front (TZCF) as an important loggerhead turtle foraging habitat. The TZCF is a basin-wide surface chlorophyll a front that represents the boundary between the warm, vertically stratified, low surface chlorophyll a water of the subtropical gyre and the vertically mixed cool, higher surface chlorophyll a Transition Zone water (Polovina et al., 2001). The TZCF is defined to be located at surface chlorophyll a level of 0.2 mg per cubic meter and thought to represent a zone of surface convergence that would concentrate the buoyant, surface prey of loggerheads (Polovina et al., 2001; Parker et al., 2005). Forage issues have been shown to be a strong determinant of habitat selection in other pelagic animals such as leatherback sea turtles (Houghton et al., 2006) and sea lions (Fowler et al., 2006). Pathfinder SST and SeaWiFS chlorophyll a are possible proxies to forage availability and abundance; furthermore, these two candidate variables display the most temporal and spatial variability, relative to the IGRF-10 variables, and correlate well to the seasonal and interannual patterns observed in the data. For example, when summarized against latitude for individual years, the satellite tracks appear to correspond closely to interannual and seasonal variability in SST (Figure 7.12) and chlorophyll a (Figure 7.13). Forage fields in the North Pacific are not as well known as in the North Atlantic (Hays, 1996), yet relevant ecosystem level approaches are beginning to clarify the relationships between physical oceanography, productivity, and forage availability for higher trophic level organisms in the North Pacific pelagic environment (e.g., Batten et al., 2006).

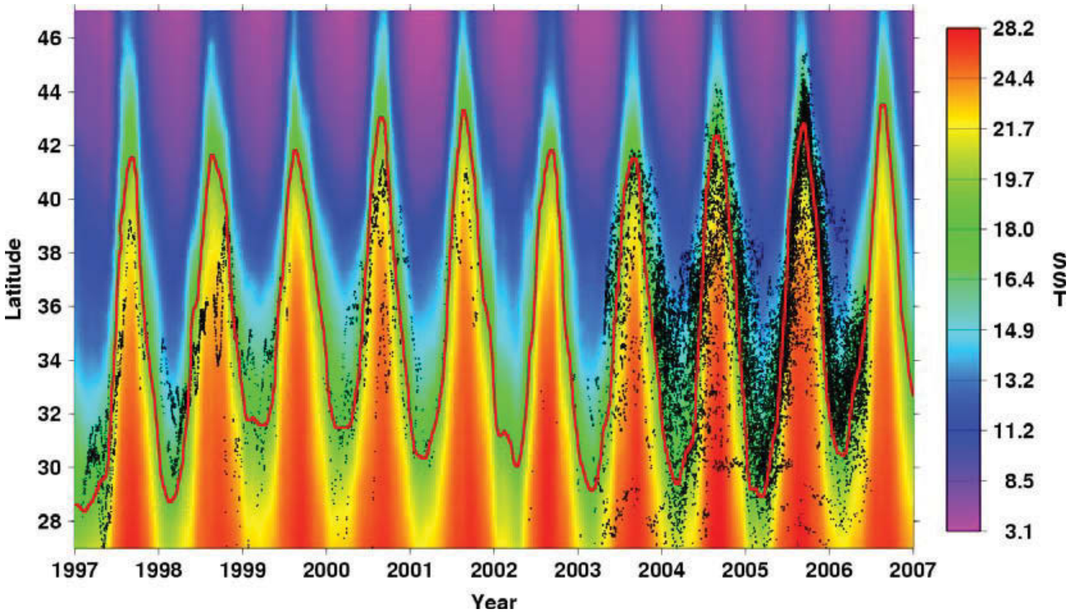


Figure 7.12. Mean Pathfinder SST (°C) by latitude (*y*-axis) and time (*x*-axis). All loggerhead sea turtle satellite track data are also shown (black dots) for the corresponding latitude and time of the satellite fix (spanning January 1997–July 2006). Mean SST is from 180°–160°W longitude, thick red line is the 18.5° isotherm for reference.

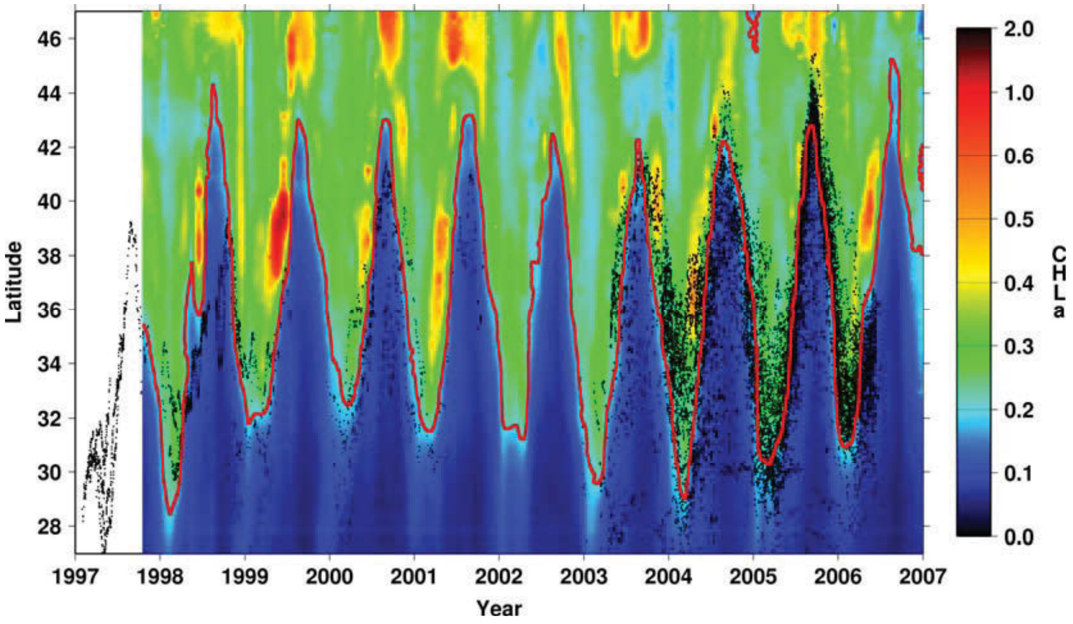


Figure 7.13. Mean SeaWiFS chlorophyll a concentration (mg per cubic meter) by latitude (*y*-axis) and time (*x*-axis). All loggerhead sea turtle satellite track data are also shown (black dots) for the corresponding latitude and time of the satellite fix (spanning January 1997–July 2006). Mean chlorophyll a is from 180°–160°W longitude, thick red line is the 0.2 mg per cubic meter isoline for reference. SeaWiFS data is available from September 1997 onward.

Many aspects of life history often reflect evolutionary adaptations or trade-offs in 3 important areas: foraging/growth, reproduction, and avoiding predators. It follows that habitat selection can be related to one or all of the above. Reproduction is not likely a factor in loggerhead pelagic habitat since mating and nesting occur in coastal areas. It remains possible that loggerhead habitat selection is related to predator avoidance, since this has been found to be important in certain green sea turtle habitat studies (Heithaus et al., 2007, in press). Clearly, more work is needed on the predator/prey dynamics of pelagic loggerhead sea turtles, from both perspectives. It should be noted, however, that tiger sharks and great white sharks, 2 likely predators in this general region, are not known to be foraging heavily in the pelagic North Pacific (Holland et al., 1999; Weng et al., 2007). It remains likely that foraging issues are the primary determinant of loggerhead pelagic habitat selection in this portion of their life history.

The importance of SST implies that preferred habitat may be seriously impinged on by trends in ocean temperature, for example El Niño Southern Oscillation events, climate change, or global warming may reposition migratory pathways, and possibly remap critical intersections with high-seas fisheries. The issue of bycatch mitigation is extremely important, as the incidental take of sea turtles has closed or severely restricted fishing activities where interactions occur. The pelagic habitat maps presented here may be useful for reducing interactions with high-seas fisheries, in conjunction with real time products such as the PIFSC TurtleWatch Program (http://www.pifsc.noaa.gov/eod/turtlewatch.php).

In addition to the two oceanographic variables, three magnetic variables also emerged as potentially defining loggerhead habitat. This is the first treatment of loggerhead habitat in the Pacific that brings into consideration the potential importance of magnetic variables. In laboratory studies performed with Atlantic loggerhead sea turtle hatchlings, magnetic total force and magnetic inclination have been shown to be detectable (Light et al., 1993; Lohmann and Lohmann, 1996). Detection of magnetic declination *per se* has not been documented in this species, yet the plausibility of determining declination is discussed by Lohmann and Lohmann (2006). Organisms which have the ability to detect true-north, via stellar navigation for example, could easily determine magnetic declination by comparing the true-north information with a magnetic compass. Such magnetic compasses have been found to be very widespread throughout the animal kingdom, including sea turtles (Wiltschko and Wiltschko, 1995).

Pelagic orientation in the North Pacific Ocean may be the closest example of "swimming the isoline" hypothesis of Lohmann and Lohmann (2006), who suggested the possibility of sea turtles simply swimming along some constant value in the earth magnetic field. For example, the apparent curvature of loggerhead tracks in mid-basin in the North Pacific Ocean (Figure 7.1) may correspond to individuals following isolines or contours (lines of constant value) of magnetic total force or magnetic inclination, both of which have slightly domed shapes (Figure 7.6). Individuals following either the ~ 40000 nanotesla magnetic total force contour or the ~ 50° magnetic inclination contour could maintain relative proximity to the observed migratory pathway. These values are markedly different from values that would be practical for loggerhead sea turtles in the Atlantic. Likewise, there are many differences in oceanography between the two basins, and localized adaptation or individual learning is therefore likely since this species is found to be genetically heterogeneous over its range (Bowen et al., 1994). While magnetic fields are clearly used by some sea turtles, experimental evidence suggests that other navigational aids must also be important (Luschi et al., 2007). The parameterization of loggerhead pelagic habitat with several environmental variables as conducted in this analysis is clearly supported by scientific findings to date. Future studies need to carefully quantify the navigational mechanisms used at different portions of the life history, since hatchlings have different behavioral and ecological needs than older stages.

The futility of an organism using any single environmental variable for habitat orientation is best seen with IGRF-10 magnetic declination. While this variable was statistically significant, individually it is very unlikely to explain the observed distributional pattern of loggerhead sea turtles (Figure 7.6, lower panel), since the habitat bounds extend zonally into regions of the Pacific Ocean where loggerhead sea turtles do not occur (Dodd, 1988; Eckert, 1993). While exact orientation cues used in real-time by pelagic loggerhead sea turtles remain unknown, it would seem likely and evolutionarily advantageous to have more than a single navigational aid. It is plausible that certain variables serve as a general guide, locating the organism crudely in preferred regions, coupled with variables which are more detailed spatially, for fine-tuning of position. Magnetic fields could be the general cue, with oceanography serving as the specific cue. Such polyphasic navigational models have been proposed by Bingman and Cheng (2005), whereby different models of navigation are used by an organism depending on immediate data availability and its ecological needs. The concept of bi-coordinate magnetic maps (Lohmann and Lohmann, 2006) was explored here with the IGRF-10 index of orthogonality (between total force and inclination), but this variable was not found to correspond to habitat utilization. Considering the similarity of magnetic total force and inclination fields in the North Pacific (Figure 7.6), a bi-coordinate system that uses magnetic declination and either magnetic total force or magnetic inclination would perform nearly as well as a Cartesian coordinate system such as latitude and longitude. Clearly, more work in this area is needed, both descriptive and experimental.

The sea surface height and related variables were not found to be significant in characterizing pelagic habitat. These features are not deemed unimportant, only not amenable to being a habitat descriptor. Geostrophic features are known to be very important towards foraging habitat (Polovina et al., 2006). Bathymetric variables were also unuseful descriptors of pelagic habitat, although as mentioned below may be more useful when examining the coastal behavior and habitat characterization. Wind is potentially a very important variable locally, but like sea surface height, does not seem to be a likely habitat cue basin-wide.

The final weighting scheme for the pelagic habitat characterization is tentatively proposed to effectively merge the five environmental variables in a meaningful way. The magnetic information brings interesting new patterns to the predicted habitat, e.g., the mid-basin deformation may be critical towards separating purely latitudinal or SST patterns from the influence of other habitat variables. Interestingly, bifurcations in habitat appear when SeaWiFS chlorophyll a is included in the habitat, as well as significant habitat range extensions. Such bifurcations, broadening/narrowing, and gradients of the habitat index offer much in the way of hypothesis-testing for future work.

Tagging data analyzed by other researchers have suggested that sea turtle pelagic movement can be significantly passive (Luschi et al., 2003, Revelles et al., 2007b). However, even post-hatching loggerheads have well-developed swimming skills (O'Hara, 1980; Davenport and Clough, 1986) and have been characterized as "smart" drifters (Witherington, 2002) with alternating periods of passive floating and directed swimming based on suitability of forage and habitat. A similar finding for biphasic behavior was found in Mediterranean adult loggerhead sea turtles (Bentivegna et al., 2007). Subadult and juvenile loggerhead sea turtles in the North Pacific are thought to be actively swimming most of the time (Polovina et al., 2000, 2004). Satellite track analysis should incorporate ocean currents to better understand movement dynamics (Gaspar et al., 2006), and the tag unit itself would benefit from nonmagnetic-interference means of determining the orientation of the sea turtle, i.e., what direction is the sea turtle facing, and also how much swimming effort is being expended (e.g., flipper beats). Hays et al. (2004) used a small sensor for measuring and storing green sea turtle flipper beats during diving behavior; unfortunately, this device involves powerful rare-earth magnets (Wilson and Liebsch, 2003) which could potentially interfere with magnetic navigation. Crittercam has also proven useful for measuring sea turtle flipper beat frequency (Hays et al., 2007) and, coupled with a simple compass in view of the camera, could provide the necessary data although this approach requires very time-consuming extraction of data via frame-by-frame visual inspection. Ideally, a small electronic package would record, summarize, and compress the pertinent data into a format that could then be transmitted in the Argos satellite data stream as described by Myers et al. (2006). Specialized bio-loggers have proven to be very useful for understanding swimming behavior in other taxa such as finfish (e.g., Kawabe et al., 2004) and birds (e.g., Ropert-Coudert et al., 2006). In comparison to these taxa, sea turtles are an optimal platform for this type of work (size, carapace for attachment points, epipelagic habitat, and behavior), which will allow a better understanding of the relationship between swimming behavior and background current fields.

Our future work on loggerhead sea turtle pelagic habitat will evaluate the role of ocean currents on the distribution and abundance of pelagic loggerhead sea turtles, as well as the role of other variables not examined in this study, such as ocean current convergence, wind stress curl, and ocean productivity. Further work with the *H* index, and how to effectively apply diverse LI simultaneously is also needed. The presently used availability measure covers a large time and space domain of values; undoubtedly, this is a crude measure and, as more behavior is incorporated into the habitat selection process, the availability measure should be refined accordingly. The track randomization approach of Heithaus et al. (2002, 2006) offers much promise towards characterization of microhabitat using tracking information. This effort should also coincide with further analyses on the spatial autocorrelation in the environmental data grids, possibly with variogram approaches to quantify this (e.g., Liebhold and Sharov, 1998). The subsurface aspect of pelagic habitat will also be investigated, since pelagic diving behavior is common (Polovina et al., 2003), and diving behavior can be a critical component of habitat selection behavior in pelagic organisms (e.g., Sims et al., 2005; Sale et al., 2006). Application of an ecosystem approach which takes into account the vertical distribution of forage will be important in this regard (e.g., Batten et al., 2006). Coastal behavior of loggerhead sea turtles will also be quantified in a subsequent study. Pelagic foraging behavior off the coastline of Baja California Sur appears to be a specialized pattern related to high concentrations of pelagic red crabs, *Pleuroncodes planipes*, and is not a subset of normal pelagic behavior (Peckham and Nichols, 2003; Etnoyer et al., 2006). Coastal behavior in the western Pacific may be primarily related to nesting and dispersal from nesting areas (Kamezaki et al., 2003; Cheng and Chen, 1997) and may require a more focused, regional study such as that done by Schofield et al. (2007). Bathymetry, proximity to shore, shoreline type, and forage availability may be more important coastal habitat variables.

7.6 Conclusion

Satellite track data for 186 loggerhead sea turtles in the North Pacific Ocean was merged to remotely sensed environmental data in an analysis to characterize pelagic habitat. Five statistically significant variables were identified out of the sixteen environmental variables examined using a modified KS test. Two of the oceanographic variables have strong seasonal, interannual, and spatial patterns (sea surface temperature and chlorophyll a concentration), while three others were strongly spatial and relatively static (earth magnetic force, earth magnetic declination, and earth magnetic inclination). Habitat selectivity for these variables was quantified using the Linear Index preference curve methodology established in the foraging literature. The output from the selectivity curves was used to predict a multivariate loggerhead sea turtle habitat index across the pelagic North Pacific.

Chapter 8: Synthesis and discussion

The goals of this thesis were to demonstrate the utility of computer simulation modeling and animal-borne tags towards understanding movement dynamics in the marine environment. In Chapter 1 the existing methodologies to study movement are reviewed and evaluated with respect to marine applications. Additionally, some historical perspective is presented for certain larval fish applications in the Hawaiian Archipelago. Chapter 2 reports findings from a set of simulations over a broad spatial and temporal scale to examine seasonal, interannual, and spatial correlates of retention and transport. In this chapter it is demonstrated that these important movement attributes (retention and transport) are strongly dependent on both the biology of the organism (i.e., pelagic larval duration) and many aspects of the environment. Chapter 3 incorporates an additional dimension of larval behavior in the vertical plane to examine the effects of diel vertical migration on horizontal transport. These modeling results are then developed further in 2 subsequent chapters with investigations bridging physical connectivity with ecological connectivity to address biogeographic patterns and metapopulation structure. Chapter 4 presents an application of transport modeling to address a historically intriguing question regarding physical linkages between Johnston Atoll and the Hawaiian Archipelago. Oceanographic transport mechanisms were found to exist for propagules originating from Johnston Atoll with a certain threshold of pelagic larval duration. In Chapter 5, a broader analysis of physical linkages throughout the archipelago is accomplished, leading to tabulated probabilities for all pair-wise connectivities in the region and modeled metapopulation structure using these connectivities in a multigeneration simulation. Next, 2 types of tagging data (conventional and electronic) are presented for very different organisms, a deepwater demersal fish in Chapter 6 and the pelagic juvenile stage of a sea turtle in Chapter 7.

These two chapters show how these types of data can be used to understand movement and habitat usage for species and areas which are very difficult to study by conventional means.

The findings of this thesis will be beneficial to the target species of study and resource managers. Modeling and tagging approaches are appealing for the many practical reasons described in Chapter 1. However, the conservation issues are perhaps more important in many applications. Presently, access and extraction are problematic for many areas and species in the Hawaiian Archipelago, primarily due to the difficulties in obtaining scientific research permits in heavily managed ecosystems. These issues often relate to concerns of anthropogenic damage to fragile habitats and/or excessive mortality of organisms from species with very low abundances. Techniques which are noninvasive to the environment and nonlethal to the organisms under study will inevitably be required in ecological studies. Targeted surveys in space and time, determined from predictive modeling, could also minimize disturbance to the ecosystem while optimizing scientific content per unit of research effort. Resource managers could also use the same information to minimize human interactions to particularly vulnerable stages of the life history. For example, the results from Chapter 2 and Chapter 3 could be used to improve designs of larval surveys, and results from Chapter 7 could be used to reduce interactions between loggerhead sea turtles and fishermen, ship traffic, and other potentially deleterious anthropogenic effects. The ongoing management issues with bottomfish in the Hawaiian Archipelago will benefit from the findings of Chapter 6, primarily towards implementing and understanding the efficacy of marine protected areas. Research with loggerhead sea turtle and opakapaka tagging data is continuing with additional analyses of the data by the thesis candidate, particularly as the organism movement relates to anthropogenic interactions and resource management.

These chapters have focused on movement by either passive transport in ocean currents or active swimming behavior. Other means of organism movement over long distances should not be ignored and are mentioned here for reference. Some of these mechanisms may be particularly important with respect to biogeography and range expansions. Rafting or otherwise piggybacking on natural or anthropogenic objects (trees, pumice, carcasses, drifting seaweed, marine debris, ballast water) has been shown to have important consequences (e.g., Hobday, 2000; Jokiel, 1989). Other oceanographic mechanisms exist such as internal waves, surface slicks, eddies, tidal currents, coastal trapped waves, etc. (Pineda and López, 2002; Shanks, 2006). The occurrence of these mechanisms in the Hawaiian Archipelago warrants further study. Many fine scale processes very close to shore or very near the bottom are undoubtedly very important for larval and adult movement of certain species. The next generation of computer simulations for pelagic organism movement will likely include many of these processes, as the appropriate hydrographic models and data become available. For example, tidal current data in Hawaii is becoming available (Dr. Mark Merrifield, University of Hawaii, personal communication) and will be incorporated into models of nearshore larval transport in subsequent research.

The need for quantitative studies of larval connectivity remains vitally important towards understanding population maintenance and the process of speciation. Effective management relies on knowledge of population structure. Biophysical modeling such as performed in this thesis should be examined in conjunction with genetic analyses and field surveys. Some genetic studies have shown evidence of strong genetic connectivity for species with lengthy PLD (e.g., Schultz et al., 2007). Other genetic studies have discovered that substantial genetic differentiation (i.e., precursor to speciation) can occur for species with relatively short PLDs (Bird et al., 2007) as well as for species with lengthy PLDs (Taylor and Hellberg, 2003; Bowen et al., 2006; Ramon et al., in press). The lack of correlation between PLD and genetic connectivity or range size may be an indication that larval behavior or other specific differences in larval ecology contribute towards retention and transport (Lester and Ruttenberg, 2005; Rocha et al., 2007). Recent studies suggest olfactory cues may inhibit dispersal in certain species due to homing towards natal odors (Gerlach et al., 2007). Auditory cues have been shown to be very important as well (Simpson et al., 2008). Active larval swimming and the use of long-range cues or navigational ability (see Leis, 2007 for review) will be important additions to transport modeling once the mechanisms are clearly determined and the spatio-temporal distribution of the relevant cues are mapped. This will allow parameterization of more complex Lagrangian modeling (e.g., Codling et al., 2004; Paris et al., 2007) or probabilistic models (e.g., Armsworth et al., 2001), which can include key demographic processes as well.

The ‘surface current vicariance’ hypothesis of Veron (1979) mentioned in Chapter 1 is very intriguing since it provides a framework with which to examine physical transport of propagules and genetic differentiation. Such evolutionary processes are very difficult to examine with observational data due to studies in historically narrow time windows. However, some evidence of the range extensions and subsequent hybridizations consistent with Veron’s hypothesis exist in the Hawaiian Archipelago. For example, the damselfish *Abudefduf vaigiensis* is a recent colonizer to the Hawaiian region and has been observed hybridizing with the endemic *A. abdominalis* (Maruska and Peyton, 2007). Many other fish hybridizations have been observed in Hawaii (Pyle and Randall, 1994; Randall, 2007). These opportunistic range expansions and successful interbreedings underlie Veron's hypothesis. The continuous formation and removal of oceanographic barriers and bridges is hypothesized to drive biogeographic patterns. The utilization of very long time series of ocean circulation data could enable modeling of this 'reticulated evolution', and this is a research direction the thesis candidate is actively pursuing.

In conclusion, organism movement was quantified using computer simulation modeling and animal-borne tags. These techniques are presented as effective tools towards understanding movement dynamics in species which are otherwise difficult to study. The findings presented here will be useful to other researchers, and will benefit the target species of study. Numerous future directions of research are presented and will be explored subsequent to this thesis.

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Appendix

Publications and submissions by candidate:

Kobayashi, D.R. Accepted with revision, 'Limited horizontal dispersal mediated by vertical migration behavior: Larval transport modeling in the Hawaiian Archipelago with layered current fields', *Pacific Science*.

Kobayashi, D.R. Accepted with revision, 'Larval retention versus larval subsidy: Marine connectivity patterns within and around the Hawaiian Archipelago', *Marine Ecology Progress Series*.

Gilman, E. & Kobayashi, D.R. In Press, 'Reducing seabird bycatch in the Hawaii longline tuna fishery', *Endangered Species Research*.

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Oral presentation, 25 January 2008, International Sea Turtle Symposium, Loreto, Baja California, Mexico. 'Habitat of loggerhead sea turtles in the North Pacific Ocean using tags and satellite data'.

Oral presentation, 20 December 2007, Loggerhead Sea Turtle Expert Panel, Honolulu, HI, USA. 'Habitat of loggerhead sea turtles in the North Pacific Ocean using tags and satellite data'.

Oral presentation, 17 August 2007, Tri-national Fisherman Exchange, Honolulu, HI, USA. 'Habitat of loggerhead sea turtles in the North Pacific Ocean using tags and satellite data'.

Oral presentation, 15 August 2007, Hawaiian Archipelago Marine Research (HAMER) Workshop, Honolulu, HI, USA. 'Marine connectivity patterns in Hawaii'.

Oral presentation, 26 July 2007, Hawaii Conservation Conference, Honolulu, HI, USA. 'Marine connectivity patterns in Hawaii'.

Oral presentation, 13 June 2007, WPRFMC SSC Meeting, Honolulu, HI, USA. 'Growth rate of the Hawaiian deepwater snapper opakapaka (*Pristipomoides filamentosus*): Insights from a large-scale tagging program'.

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Oral presentation, 5 February 2007, Northwestern Hawaiian Islands Joint Symposium, Honolulu, HI, USA. 'Simulation studies of larval transport in the Hawaiian Archipelago'.

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Poster presentation, 12 December 2005, 16th Biennial Conference on the Biology of Marine Mammals, San Diego, CA, USA. 'Mortality and injury of cetaceans in the Hawaii-based longline fishery, 1994-2004'.

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Oral presentation, 2 November 2004, Northwestern Hawaiian Islands Science Symposium, Honolulu, HI, USA. 'Seasonal and interannual variability in larval transport and oceanography in the Northwestern Hawaiian Islands using satellite remotely sensed data and computer simulation'.

Oral presentation, 19 October 2004, PICES 13th Annual Meeting, Honolulu, HI, USA. 'Seasonal and interannual variability in larval transport and oceanography in the Northwestern Hawaiian Islands using satellite remotely sensed data and computer simulation'.

Poster presentation, 14 October 2004, PICES 13th Annual Meeting, Honolulu, HI, USA. 'Using a generalized additive model to predict Bigeye (*Thunnus obesus*) CPUE at the Palmyra fishing grounds'.

Oral presentation, 2 June 2004, MMPA Workshop, Honolulu, HI, USA. 'A description of the relationships between marine mammals and the Hawaii-based longline fishery from 1994-2003'.

Poster presentation, 24 May 2004, 55th Annual Tuna Conference, Lake Arrowhead, CA, USA. 'Using a generalized additive model to predict Bigeye (*Thunnus obesus*) CPUE at the Palmyra fishing grounds'.

Poster presentation, 15 February 2004. ASLO Meeting, Honolulu, HI, USA. 'Predicting bigeye tuna (*Thunnus obesus*) longline catch at Palmyra Atoll using a generalized additive model'.