Recruitment Dynamics and Dispersal of Coral Reef Species in a Network of National Parks and Marine Protected Areas in Hawai'i: Some Preliminary Findings

L.V. Basch[1, 2], J. Eble[2], J. Zamzow[2], D. Shafer[2#], and W.J. Walsh[3]

[1]U.S. National Park Service
[2] University of Hawai'i, Manoa
[3]Hawai'i State Department of Land & Natural Resources, Division of Aquatic Resources
#Current affiliation and address unknown.

Frontispiece: Finger Coral, *Porites compressa*, reef habitat on the Kona coast, Hawai'i Island, in which study sites were located.

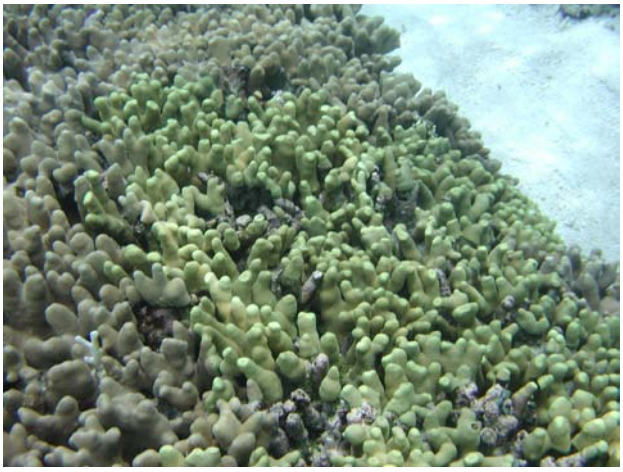


Table of Contents

List and captions of Figures and Tables 3
Abstract 6
Executive summary 7
Purpose 11
Background 11
Goals and Objectives 13
1. Life history and recruitment dynamics of coral reef fishes. 14
2. Temporal-spatial variation in life history parameters of coral reef fishes. 14
3. Life history and recruitment dynamics of invertebrates, including corals. 14
4. Near-shore Ecosystem structure and Oceanography of West Hawai`i. 15
Approach 15
Study Sites 15
Reef Fish 15
Coral Reef Invertebrates 16
Site Selection 16
Sampling Design 16
Methods - Invertebrates 20
Methods - Mobile Invertebrates 21
Methods - Sessile Invertebrates 22
Findings 26
Reef Fishes 26
Early Life History Strategies & Population Dynamics of select tropical reef fishes in Hawai`i 26
Other Fishes 32
Taxonomic trends – Mobile Invertebrate Recruits 33
Temporal Variability in Recruitment 38
Spatial Variability in Recruitment 40
Sessile Invertebrates – Corals 45
Life History of Benthic Reef Invertebrates 45
Multi-Species Patterns in Recruitment 46
Acknowledgements 54
References 55

List and captions of Figures and Tables

Map 1: WHAP and Recruitment sites.

Map 2: Invertebrate Recruitment sites.

Figure 1: Sampling array for mobile and sessile invertebrate recruits (note two Yellow Tang recruits above array at left; close-up of collectors at right) deployed at sites in Table 1.

Figure 2: Schematic of nested sampling design for invertebrate recruitment. Each rectangle represents paired replicate samplers on an array block. Each sampler on an array was approximately 20 cm from its identical sampler type (i.e., 2 sampler replicates (of each of 2-3 types: plates, brushes or scrub pads) per array block).

Figure 3: Terra cotta clay tile plate for sampling coral and other sessile invertebrate recruits. White tag notes experiment in progress, by whom, and contact information. Gray PVC lower plates were deployed below clay tiles to provide a gap or refuge habitat for recruitment of corals and other sessile reef invertebrates.

Figure 4: Species composition of fish collections for otolith analysis in the present study (as of 1/20/2004; n = 1584).

Figure 5: *Zebrasoma flavescens*, Yellow Tang or *Lau'ipala* juveniles (above) and representative otolith section (below) of recent recruit showing settlement mark (dark band) and white points marking larval daily increments (Scale bar = 25 µm).

Figure 6: Size frequency distribution of Yellow Tang sampled (n = 416).

Figure 7: *Acanthurus triostegus*, Convict Tang or Manini (left) and representative otolith section (right) of recent recruit showing settlement mark (dark band) and dark bands indicating larval daily increments (Scale bar = 25 µm).

Figure 8: Size frequency distribution of Manini sampled (n = 652).

Figure 9: *Abudefduf vaigiensis*, Indo-Pacific Sergeant Major or *Mamo*.

Figure 10: *Schindleria praematura* and *S. pietschmani*, Shindler's Fish (total length approximately 2 cm (two images above); representative otolith section (below) with dark points marking approximately daily larval growth increments; scale bar = 10 µm).

Figure 11: Number of taxa of reef invertebrate recruits for two consecutive sampling rounds separated by approximately 6 weeks.

Figure 12: Number of individuals of the most abundant taxa (other than snails and bivalves) for two consecutive sampling rounds separated by approximately 6 weeks.

Figure 13: Number of individuals of the two most abundant taxa, gastropods and bivalves, for two consecutive sampling rounds separated by approximately 6 weeks.

Figure 14: Number of species of gastropods, the most diverse higher taxon, by site, recruiting along the West Hawai'i island coast. Site names are as on Maps 1, 2.

Figure 15: Spatial variation among sites along the West Hawai'i island coast in recruitment of; (a) all bivalves (except purse shells); (b) Scallop # 5; (c) Purse shell bivalves, and (d) the gastropod *Vitricithina marmorata.*

Figure 16: Spatial variation within and among sites along the West Hawai'i island coast in number of recruits of: (a) the gastropod *Styliferina goniochila*; (b) Purse shell bivalves, and (c) the gastropod *Vitricithina marmorata.* Sites along the X axis are arranged from North to South from the origin. Note scale differences on Y axes. Site names are as on Maps 1, 2, Fig. 15.) N, C, and S are Northern, Central, and Southern subsites within sites at Waiakailio, Honokohau, and Manuka.

Figure 17: Seasonal patterns in occurrence of recruits in putative planktonic and non-planktonic reef invertebrate taxa.

Figure 18: Relative frequency of recruit taxonomic diversity among sites (of n = 224 total taxa).

Figure 19: NOAA GOES Satellite Sea Surface Temperature image illustrating onshore movement of oceanic warm gyre on west coast of Hawai'i Island.

Figure 20: Analysis of similarity (Anosim) of the taxonomic composition and abundance of recruit assemblages among sites along the West Hawai'i coast (blue=northern region, black=central region, grey=southern region) (Clarke and Warwick 2001).

Figure 21: Similarity of recruitment populations with distance among collectors.

Fig 22: Recruitment of taxa with pronounced seasonal reproductive/recruitment peaks among sites.

Tables

Table 1: Invertebrate recruitment sites, locations and number of arrays deployed.

Table 2: Comparison of differences in total number of species in major taxa observed, in two types of mobile invertebrate collector.

Table 3: Sampling sites and number of collectors per site.

Table 4: Number of common recruiting invertebrate taxa.

Table 5: Percent composition of recruits of common invertebrate taxa.

Table 6: Temporal variation in reef invertebrate recruitment. The total number of individuals per species are pooled from all collectors. Shaded cells indicate at least double the median abundance (dark shading= highest, lighter shading = second highest, that is at least 2 times the median value).

Table 7: Spatial Variability in Recruitment for the 20 most abundant reef species recruiting along the West Hawai'i coast.

Table 8: Spatial variability in recruitment for the 20 most abundant recruiting species among array pairs within sites with paired arrays at N, Central and S coast sites (Waikalio, Honokohau, and Manuka). Values in bold denote significant differences at a particular spatial scale (among sites or subsites).

Table 9: Numbers of seasonal vs. non-seasonal breeders for common reef invertebrates with putative planktonic and non-planktonic dispersal strategies.

Table 10: Interspecific concurrence in the relative abundance of recruits among species. Shaded cells indicate spatial concurrence among species at sites. Values in bold denote significant differences among sites.

Table 11: Nested ANOVA for common recruit taxa within and among sites having subsites.

Abstract

Recruitment Dynamics and Dispersal of Coral Reef Species in a Network of National Parks and Marine Protected Areas in Hawai'i: Some Preliminary Findings

Coral reefs provide tremendous ecological, cultural, economic, social, and aesthetic benefits. However, over the past several decades, Hawai`i coral reef fisheries have experienced significant declines, primarily as a result of overfishing and habitat degradation. Decreasing populations of ecologically, culturally, or economically important reef fish and invertebrates highlight the need to better understand factors that regulate life histories, recruitment, growth, and survival of key reef species.

The recruitment dynamics and dispersal of fish and invertebrates, including corals, and resulting population structure are significantly influenced by variation in oceanographic and ecological processes: e.g., flow patterns over tidal to inter-annual temporal scales, and are affected by reef topography and other complex shallow water nearshore conditions over successive years. This report characterizes temporal and spatial recruitment patterns and processes and some aspects of the oceanography in a network of National Parks and Marine Protected Areas (MPAs) off the Kona or west coast of Hawai`i Island. Using retrospective otolith analysis, we have improved understanding of how planktonic larval duration, larval growth rates, and size at settlement of herbivorous fish (important ecologically, in the commercial aquarium trade, and as food fish) can serve as indicators of potential survival success. This type of analysis, combined with fish population genetic and environmental-analytical chemical approaches by colleagues provides further resolution of questions regarding reef animal population sources and sinks, dispersal distances and rates, population connectivity and related phenomena. We examined temporal and spatial variation at several scales in the dispersion and recruitment of juveniles of reef invertebrates, including corals, which are of ecological, cultural, or economic importance.

Studying recruitment dynamics of reef animal groups within an existing MPA network off the West coast of Hawai'i Island allowed for assessment of underlying patterns and processes, and hence, provide information for assessing the design and effectiveness of networks of marine reserves. Most resource managers and scientists agree that such networks, managed effectively, and designed to withstand immediate and long-term threats, can help strengthen the persistence and resilience of reef systems against ecological or anthropogenic disturbances and simultaneously aid in long-term fisheries management. Indeed, many recently documented examples worldwide point to the effectiveness for resource managers of marine reserves built on fundamental scientific information such as the results presented in this report. Continuation of recruitment monitoring for corals will further develop our understanding of dispersal and recruitment dynamics on Hawaiian coral reefs, and will provide essential information for improved management of coral reefs in the Main Hawaiian Islands, and elsewhere.

Executive Summary

Recruitment Dynamics and Dispersal of Coral Reef Species in a Network of National Parks and Marine Protected Areas in Hawai'i: Some Preliminary Findings

Our overall goal was to support marine resource management through improved understanding of basic life history and growth, recruitment, dispersal patterns, and connectivity of populations of key coral reef functional groups in Hawai`i. This report describes some patterns of recruitment variation for several reef species over 9-10 sites and over time, along much of the west coast of the island of Hawai'i, within a network of National Parks and Marine Protected Areas (MPAs). Results are thus far preliminary because adequate understanding of recruitment variation in nearshore marine ecosystems requires data collected over multiple, consecutive years. We focused on several reef fish and invertebrates to better understand factors that regulate early life history patterns, and processes influencing recruitment, growth, and survival of key reef species. Our objectives included describing (1) early pre- and post-settlement life history and, where possible, recruitment dynamics of coral reef fishes, and (2) temporal-spatial variation in life history parameters of key coral reef fishes. We documented planktonic larval duration (PLD), size and age, and time at settlement of several reef fishes and determined that these life history variables are essential information, in combination with oceanographic and other ecological attribute data, to begin to understand processes underlying spatial and temporal variation in recruitment of these reef fish populations, which are important in the commercial aquarium trade, for traditional use, or for food. Otoliths (ear bones) from more than 1,580 juvenile fishes were dissected and archived from species collected around Hawai`i Island, including *Zebrasoma flavescens*, the Yellow Tang or *Lau'ipala*, *Acanthurus triostegus*, the Convict Tang or *Manini*, *Abudefduf abdominalis* and *A. vaigiensis*, and the Sergeant Major, or *Mamo*. Otoliths were mounted on glass slides (n=409), prepared for analysis (n=378), and baseline counts of annular rings made (n=314). In the first quarter of 2004, 250 additional otoliths from Yellow Tang and Manini were analyzed to explore temporal and spatial variation in early life history parameters. Summarizing data for these two species, one of the earlier Yellow Tang juveniles (the key target of the Aquarium Trade in Hawai'i) collected (June 2003, 38 mm Total Length) was approximately 90 days old, suggesting a spawning date around the second week in March. The earliest juveniles were captured between May 20-26 2003, and analyzed during the first quarter of 2004. It therefore appears that early March may be the onset of the reproductive season. Identification of the bounds of the adult reproductive season is important to managers when considering temporal protection efforts (e.g., enforcement of seasonal limits or closures). Planktonic Larval Durations (PLD; mean ± one standard deviation) of Yellow Tang (n=30) were determined to be 57.9 ± 5.2 days, ranging between 47-65 days. This PLD is significantly longer than that of many other reef fishes, although it is similar to other acanthurids (surgeon fishes) elsewhere. Long larval duration is characteristically associated with higher larval mortality. Early growth rates of Yellow Tang were determined to be 0.50 ± 0.06 mm Total Length (TL)/day. This is a relatively rapid early growth rate and allows Yellow Tang to settle at a relatively large size (33.8 ± 1.2 mm TL). The Convict Tang or Manini (*Acanthurus triostegus*) is a common traditional and recreational food fish in Hawai`i. Manini recruit primarily to tide pools and shallow nearshore areas, rather than recruiting directly to the reef, as with other acanthurids. This life history characteristic may make Manini more vulnerable to coastal pollution or fishing pressure, especially that which may concentrate in shallow tide pools. Manini are important nearshore grazers, and may help maintain a balance between algae and coral populations. Populations of Manini may be declining in the Main Hawaiian Islands (J.

Randall, pers. comm.). Randall suggested that Manini in Hawai`i have considerably longer PLDs than conspecifics elsewhere. Long PLDs are often associated with higher cumulative pre-settlement mortality in the plankton or water column, which has important implications for management. Randall determined larval duration by estimating the difference between time of first reproduction and the appearance of the first new recruits in tide pools. This method yielded a range of 71-83 days PLD. This has been frequency cited in the literature when discussing the unique population ecology of Hawaiian reef fishes. In particular, it is widely believed that coral reef fishes in Hawai`i have extraordinary long larval durations. This belief has never been challenged, however, and is supported by few data. The present work provides the first retrospectively determined larval duration information for Manini in Hawai`i, and begins to address this important issue in Hawaiian coral reef fish ecology. Over 652 otolith pairs were dissected from Manini in Hawai`i, 85 otoliths were mounted on slides, 70 were prepared for analysis, and 30 were analyzed. A settlement mark is visible in otoliths of most Manini; the mark is characterized by either a shift in increment width or optical focal plane. Manini in Hawai`i were found to have PLDs ranging from 48 – 61 days (n=30), with a mean (± one standard deviation) of 54 ± 4.3 days. This is significantly less than the earlier estimate of PLD by Randall, and is similar to the larval duration of Manini elsewhere. During the first quarter of 2004, many more otoliths were analyzed. This information, together with results from this study on other reef fishes in Hawai`i, suggests that reef fishes in Hawai`i may not necessarily have extraordinarily long PLDs. Manini grow approximately 0.52 ± 0.05 mm TL/ day (mean ± one standard deviation), similar to the fast rate determined for Yellow Tang. This fast growth rate allows Manini to settle at a relatively large size (32.0 ± 1.5 mm TL). Large size at settlement may have competitive and survival advantages in the intertidal nursery habitat. These findings significantly advance knowledge of Hawaiian reef fish ecology, with direct benefit to resource management.

One of us (JE) has extended studies (in collaboration with USNPS, UH and others) at the University of Hawai'i, Manoa, on reef fish (Yellow Tang) recruitment dynamics using population genetic and phylogeographic approaches (Eble et al. 2009, Christie and Eble 2009, Eble et al. in prep.). Other colleagues from the University of California Santa Barbara (in collaboration with USNPS and UH) studied otolith microchemistry in a common damselfish at Kona and other reefs throughout Hawai'i (Ruttenberg et al. 2008). These combined approaches improve our understanding of recruitment and connectivity and very much complement our life history work, oceanographic work by Storlazzi and Presto (2005), and reef habitat and population dynamics data collected by the West Hawai'i Aquarium Project (WHAP) and Hawai'i DLNR Division of Aquatic Resources (DAR).

Our 3rd objective focused on determining life history and recruitment dynamics of reef invertebrates, including corals. We studied invertebrates at 9-10 of the 23 DAR/WHAP sites; three sites are located at reefs within each of the north and south Kona regions while 3-4 are in the central Kona region (three of these are now actively studied; one was dropped because it was determined to be redundant). At each of these sites invertebrate recruits were sampled from a variety of artificial substrates that minimally impact the surrounding *Porites compressa* (finger coral)-dominated reef habitat. In addition, recruitment of opihi (limpets) on shore in the rocky intertidal zone was surveyed at 7 sites spanning the Kona coast. Opihi recruitment has generally been low and patchy, but recruits have been observed recently at low densities in adult habitats.

<u>Taxonomic patterns</u>: To date we have identified 250-300 taxa of marine invertebrates recruiting to the Kona reef system. The small sizes and early stages of development of recruits have made this

fundamental aspect challenging because these juvenile animals frequently lack the morphological characters required for identification to species. As a result, life history patterns, in the comparatively few species in which they are known with certainty, are often harder to define or infer without time-consuming larval or postlarval laboratory culture studies to yield adult-size individuals with recognizable features attributable to known species. Such work is beyond the scope of this study. Nonetheless, we have been able to at least tentatively identity and infer life history patterns for many species, and have been particularly successful with several molluscs in this regard. To date, data reveal striking differences amongst taxa in the number and diversity of recruiting individuals. More than 80% of recruits found in mobile invertebrate collectors are molluscs, with arthropod crustaceans (crabs, shrimps, and relatives) and echinoderms (sea urchins, sea cucumbers, and relatives) comprising 10% and 6% of total observations, respectively. Among the molluscs, total numbers of bivalves (oysters, clams, scallops) and gastropods (snails, nudibranchs) observed were nearly equal (52% and 48% respectively) though species diversity was considerably higher in gastropods by a ratio of nearly 9:1. As a taxon, gastropods dominate observed recruit diversity accounting for nearly 70% of the total species identified. Recruiting gastropod diversity to date reflects a total of 215 species representing 54 genera from 36 different families. Opihi are the only gastropod that is a targeted fisheries species. There was little or no recruitment of opihi and other target species including octopus, lobster, edible crabs, or other resource species throughout the study period.

Life Histories: Data indicate that most recruiting species appear to have a complex life history with one or more planktonic larval stages. Due to general similarities in larval types and potential larval dispersal capabilities within and among some taxa, it may be useful to use data from non-target species to make strong inferences about dispersal, recruitment and connectivity of species populations whose numbers of recruits are too low to allow for statistical analyses or rigorous conclusions.

Spatial patterns: Preliminary data and analyses suggest that, on average, variability of recruit abundance among reefs (> 1km scale) was three times greater than either regional (> 10km scale) or within site (paired array, 2m scale) differences, though patterns varied considerably among species. Nearly half of the 20 most abundant recruiting species showed significant spatial structure in recruit abundance at scales greater than 1km but less than 10km. Patterns of recruit availability among species vary considerably. Nonetheless, concurrent patterns of yearly, relative recruit abundance exist among species, with a number of sites receiving relatively higher or lower numbers of recruits across a wide range of taxa. In contrast with the relative paucity of recruiting invertebrates at central Kona sites, including Kaloko-Honokohau, Waikalio, the northern-most site, near Pu'u Kohola Heiau, is notable for its consistently diverse and abundant recruit populations. Of the 50 most abundant recruit species, 37 recruited at densities higher than the among site species average, with 13 species recruiting at 3 times the among site mean. Of the 224 distinguishable taxa of mobile recruiting invertebrates recorded to date, greater than 65% of taxa were observed to recruit at Waikalio, compared with an average of just over 43% for all sites and a low of 32% at both N. Keahou and Ke'ei, near Pu'u Honua O Honaunau, on the south Kona coast. Preliminary data suggests limited regional cohesion in recruitment within the central West Hawai'i region. This suggests that factors in addition to regional oceanography may be shaping recruitment patterns and community structure within the central Kona region. Similar low recruitment patterns between N. Keahou and Ke'ei might instead be attributed to similarities in either: 1) habitat; 2) disturbance regimes, or; 3) anthropogenic influences.

While identifying the cause(s) of low levels of recruitment is important, just recognizing its existence is helpful to marine resource management because, if these trends as well apply to key ecological, cultural, or resource species, then populations at these sites might be more vulnerable to anthropogenic impacts and may thus require targeted management. The identification of concurrent patterns of recruit availability among species is useful because it can aid in the identification of factors affecting multiple species, thus allowing resource managers to direct conservation efforts at an ecosystem level.

Ultimately, documenting large scale recruitment patterns over time will also aid in identifying optimal MPA placement and design by determining sensitive sites such as areas of low recruitment, perhaps reflecting limited settlement substrate availability or inconsistent larval transport via ocean currents, as well as identifying potential recruitment or diversity hot spots. Since no recruitment baseline previously existed, data thus far cannot determine if the absence or low numbers of many target and non-target reef invertebrate species is due to generally low recruitment levels, vagaries in ocean circulation patterns, recruitment limitation, or some other factor(s). Corals and opihi recruited in very low numbers to artificial and natural hard substrates, respectively, as in other studies (reviewed by Basch et. al. 2008, in prep.). Other species, and taxa with similar larvae, including crustaceans, octopus, and sea stars have recruited to substrates very similar to those sampled in this study. While we sampled several species of crustaceans, molluscs and echinoderms, very few octopus recruits have been recorded to date, and no lobster or crown-of thorns seastar recruits have been observed. It is likely that recruitment of species such as these is highly episodic or patchy in time and space, and that there is high pre- or post-settlement mortality.

Temporal patterns: Based on data collected, at present it appears that for the most commonly recruiting species on Kona reefs, most have planktonic larval stages that settle mainly in the spring-summer season, not unlike many other marine invertebrates elsewhere.

Our 4th objective focused on long-term data collection on near-shore ecosystem structure, including oceanography, off West Hawai`i. As part of other research by NPS, USGS, UH, and others, high spatial resolution imagery and benthic habitat characterization maps of the Kona reef tract and adjacent land areas are being developed as GIS layers. Ideally, these could be used to overlay data on the distribution, abundance and habitat selectivity (if any) of recruits of reef species, and ocean current patterns, for spatial analysis of dispersal distances, trajectories, rates (where possible), and other elements of connectivity among MPAs. A UH Manoa Geography Department graduate student who worked for the NPS Pacific Islands Coral Reef Program began to develop a spatial-relational database of the Kona reef tract. If this work can be continued in the future spatial analysis of multiple data sets could be done to further inform resource managers. USGS completed short term characterization of oceanographic patterns in the central Kona region. If funding becomes available further deployments of Acoustic Doppler Current Profilers, CTDs, temperature loggers and other instruments will provide future measures of local-scale current and related oceanographic patterns off the west Hawai'i coast.

Purpose

Background

Coral reefs in the Main Hawaiian Islands (MHI), as elsewhere, face extensive threats, including overfishing, habitat destruction, species invasions, pollution, and global climate change (Hixon et al. 2001, Williams et al. 2008). Over the past several decades, coral reef fisheries in Hawai'i have experienced significant declines, primarily as a result of overfishing (Birkeland and Friedlander 2001, Friedlander and DeMartini 2002, Williams et al. 2008), and Hawai'i Division of Aquatic Resources commercial catch data suggest that declines in a number of species have been going on for a considerably longer times than past several decades (W.J. Walsh, pers. obs.).

Declining stocks of coral reef fishes and invertebrates lead to impairment of the healthy structure, function and production of coral reef ecosystems. Moreover, by upsetting the delicate trophic balance on reefs, overfishing can contribute to degradation and loss of reef ecosystems. For example, declining populations of herbivorous fishes, or invertebrates such as sea urchins, can result in unchecked growth of algae, which can out-compete corals for space, and smother living reefs (e.g., Smith et al. 2002). Annual commercial harvest of aquarium reef fish (including herbivores) more than quadrupled from the 1970s to the 1990s, and was focused primarily on a few species (Miyasaka 1997, Walsh et al. 2003), making them vulnerable to overexploitation.

Lobster, crabs, other crustaceans, octopus, and opihi (limpets) are actively fished resources, yet very little is known about the condition of these and other populations of nearshore and reef invertebrates, much less the factors regulating their population dynamics in Hawai'i. While corals provide the key biogenic three-dimensional structure or biological architecture of reef communities, information about recruitment and local coral population dynamics in Hawaii exists for few locations and limited time periods. Likewise for other key ecological species such as *Acanthaster planci*, the Crown-of-Thorns sea star, a voracious predator on corals that may undergo episodic population outbreaks that decimate coral reefs (Birkeland and Lucas 1990). Moreover, development or other anthropogenic disturbances on the Kona coast, as elsewhere, may result in reproductive or recruitment limitation or complete failure in corals and other reef organisms.

Whether a reef system dies quickly by catastrophic disturbance or slowly by attrition – e.g., by no or low population replenishment via recruitment – the result is the same: loss of the reef, its ecological services and resources (Richmond 2001). Declining or low populations of fishes and invertebrates highlight the need to better understand factors that may regulate their recruitment, growth, and survival. Even in the absence of such information the precautionary principle should be invoked to protect resources which are threatened or for which status is uncertain, and trends suggest a problem may exist. In order to improve management of aquarium fisheries, the West Hawai`i Regional Fishery Management Area was created, and in the year 2000 35% of the Kona coastline was closed to commercial aquarium fish collecting, as mandated by Act 306 (W. Walsh, unpublished, Tissot et al. 2004). As populations recover, there is high stochasticity in recruitment, which may drive fluctuations in population abundance. Fish surveys in marine reserves off the Kona coast, conducted as part of the West Hawai`i Aquarium Project (WHAP) suggest that recruitment may be a significant factor in regulating fish population abundance within reserves (W. Walsh, unpublished, Tissot et al. 2004). The same can be expected for co-occurring populations of many reef invertebrates.

Recruitment typically varies on multiple spatial and temporal scales (Hughes et al. 2002, Parnell 2000), and may be primarily driven by highly variable and significant larval mortality (often close to 99%). Direct measures of larval mortality are hindered by logistical difficulties associated with large spatial and temporal scales of inquiry, and are prone to gross errors. Instead, variable early life history parameters of larval fish and invertebrates, including pelagic larval duration, larval growth rates, and size or numbers at settlement or recruitment, can serve as indicators of potential survival success (Rumrill 1990, Basch 1993, Basch 1996, Basch and Pearse 1996, Basch and Keesing 1996, Shafer 1998). In particular: 1) cumulative larval mortality may increase with longer time drifting in currents in the water column, i.e., Planktonic Larval Duration (PLD); 2) larval mortality may decrease with faster larval growth rates; and 3) early benthic mortality may decrease with larger size at settlement (reviewed in Rumrill 1990, Basch 1993, Basch and Keesing 1996, Basch and Pearse 1996, Schubart et al. 1995, Shafer 1998 and elsewhere). Understanding how these factors affect the temporal and spatial recruitment patterns and processes of coral reef organisms is important for effectively managing marine resources. This study provides baseline information on critical life history and ecological parameters for several coral reef animals in Hawai`i.

The importance of seasonal variation in ocean temperature to the population dynamics of tropical fishes has just begun to be explored (McCormick 1994, Shafer 1998), and temperature is a well known proximate factor influencing the life history and population dynamics of tropical (and higher latitude) marine invertebrates (Thorson 1950, Pearse 1974, Giese et al. 1987, Rumrill 1990). Recent work in Hawai`i demonstrated that the early life history of the common basalt goby, *Bathygobius coalitus*, is sensitive to seasonal fluctuations in ocean temperature (Shafer 1998, 2000). Specifically, larval duration increased, whereas growth rates and size at settlement decreased during cooler ocean temperatures. Determining if this is a widespread phenomenon among coral reef animals in Hawai`i has profound implications for our understanding of population dynamics of nearshore and reef organisms and for our efforts to manage them, especially in the context of episodic temperature shifts (e.g., El Niño Southern Oscillation events) and longer scale climate change (e.g., ocean warming).

Most resource managers and scientists agree that networks of Marine Protected Areas (MPAs) designed and managed effectively to withstand immediate and long-term threats can help stabilize against ecological disturbances as well as aid in long-term fisheries management (Allison et al. 2003, Ballantine 1997, Birkeland and Friedlander 2001, McClanahan and Kaunda-Arara 1996, NRC 2001, NCEAS 2001, and many others). No-take reserves within these MPAs could potentially serve both as sources of new recruits of corals, fish, and other organisms to colonize reefs damaged by anthropogenic impacts or natural disturbances, and as reservoirs of genetic and bio-diversity (Roberts 1997, 1998, Palumbi 2003). It is well documented that marine reserves can increase biodiversity and biomass within reserves (Halpern 2003). Moreover, “spillover effects” in which fish or other economically important organisms move outside the reserve have been demonstrated both theoretically (Hastings and Botsford 1999) and empirically (Roberts et al. 2001a, b, Williams et al. 2009). Because most marine species reproduce via broadcast spawning, releasing gametes which fertilize in the water column and develop into pelagic or demersal larvae, adults protected within reserves can repopulate areas outside reserves (“seeding effects”) (Hixon et al. 2001). Creating networks of reserves linked by larval dispersal thus can buffer an entire system against catastrophes (Gaines 2001).

One of the key questions to address in designing networks of reserves is the level of connectivity both between populations and processes in different reserves and between reserves and unprotected surrounding reefs (Roberts 1997). In practice, however, connectivity among populations is poorly

understood (Cowen et al. 2000, Palumbi 2003). Roberts (1997) used surface current patterns and larval dispersal periods to map "transport envelopes" in the Caribbean, as did Polovina et al. (1999) in the Northwest Hawaiian Islands. Recent research indicates that larval dispersal may not be as widespread as previously thought (Cowen et al. 2000, Shanks et al. 2003); thus, to ensure sustainability, reserves within a network would need to be larger or more closely spaced (Botsford et al. 2001; Mascia 2001, Halpern 2003). Additional methods are continually being developed to directly or indirectly assess the degree to which larvae are retained or exchanged, including tagging larvae (Jones et al. 1999), otolith analysis and microchemistry (Victor 1982, Wilson and McCormick 1998, 1999, Swearer et al. 1999; Radtke et al. 2001, Ruttenberg et al. 2008), and molecular techniques to estimate gene flow among populations (Hodges and Allendorf 1998; Barber et al. 2000; Bernardi et al. 2001, Palumbi 2003, Christie and Eble 2009, Eble et al. 2009).

While Marine Managed Areas with some form of state protection (e.g., gill net bans) presently cover about 29% of Main Hawaiian Island (MHI) reefs, only 0.4% of state waters are no-take reserves (W. Walsh, unpubl. data), and many fished species and essential habitats remain unprotected. Based on continuing declines in fished stocks (Williams et al. 2008), it is unlikely that the existing small, relatively isolated no-take reserves in the MHI are sufficiently inter-connected or effective to replenish each others' populations and ensure ecological persistence or sustainability of fisheries (Friedlander and DeMartini 2002, Birkeland and Friedlander 2001, Allison et al. 2003). As managers strive to increase protected areas and manage them on an ecosystem rather than individual species basis, it is important to understand recruitment of multiple species and components of the ecosystem.

To contribute to ongoing efforts to better understand how MPAs can and do function in conservation of different life stages of reef organisms, we collected baseline life history and recruitment information for several reef animal species in Hawai'i. We explored links between the effects of small changes in ocean temperature and the early life history and recruitment of reef fishes, in collaboration with the West Hawai'i Aquarium Project (WHAP). We have continued to collect data on recruitment of reef invertebrates of ecological or fisheries importance, particularly recruitment of corals. Reef building corals to a large extent determine the availability and resilience of critical habitat structure for life stages of many other reef organisms, from settlers to reef-associated adults. Studying recruitment dynamics of various functional groups within existing MPA networks can serve as a model for evaluating underlying patterns and processes, and hence, the effectiveness of networks of marine reserves.

Goals and Objectives

Our goals were: (1) to increase understanding of basic life history and growth, recruitment, dispersal, and connectivity of populations of key coral reef functional groups in Hawai`i. (2) To provide support for science-based resource management of coral reef ecosystems in Hawai`i. In particular, to look at patterns and factors underlying recruitment variation at multiple sites over time. (3) To better understand the recruitment and dispersal patterns of reef functional groups, as well as ecological connectivity between coral reefs on the Kona coast of the island of Hawai`i, and thereby to provide scientific information in support of the Hawai`i Island network of Marine Protected Areas.

Research to date has made significant progress, providing valuable information on the basic biology underlying recruitment of key reef organisms including fish, coral, and other invertebrates on the Kona coast. This information will help to determine how effective the current Fisheries Replenishment Areas are at protecting various life stages of key coral reef fish. Some oceanographic

data has been gathered (Storlazzi and Presto 2005, NPS unpublished data) to assist in identifying larval transport and dispersal patterns, potential source and sink areas, and related variation in environmental regimes. There is limited information in the literature for most Hawaiian taxa on spatial and temporal patterns of dispersal, recruitment, distribution and abundance of various life stages. The following primary research objectives were investigated:

1. Life history and recruitment dynamics of coral reef fishes.

We have determined basic life history information, including larval duration, average larval growth rate, and size at settlement, for target reef fishes. Knowledge of baseline life history information is important for understanding the life history and population dynamics of species, and related management concerns (see Background). This initial work has provided basic knowledge of these critical life history parameters for select coral reef fishes in Hawai`i. In addition, along with retrospective otolith analyses, NPS supported collection of tissue samples for genetic analyses, archived from (the same) collected fishes, and damselfish otolith environmental-microchemistry samples have been analyzed and reported by colleagues (Eble et al. 2009, in prep., Ruttenberg et al. 2008, Christie and Eble 2009). We anticipate that these complimentary and non-redundant approaches will greatly increase the resolution of key aspects of recruitment processes such as population sources, sinks, dispersal distances, and connectivity of target fish populations.

2. Temporal-spatial variation in life history parameters of coral reef fishes.

We examined temporal-spatial variation in larval growth rates, size at settlement, and larval duration for target reef fishes. Understanding factors that underlie variation in fish early life histories has important implications for understanding variability in survival and recruitment success. Understanding how water temperature affects the early life history of reef fishes has profound implications for our understanding of their population dynamics and for our efforts to manage them, especially in the context of episodic temperature shifts (e.g., El Niño) and climate change (e.g., ocean warming). We examined how larval growth rates, larval duration, and size at settlement vary with water temperature. Recruitment is highly variable across spatial scales. Low or limited recruit numbers at various sites and times may have constrained synoptic samples of fish with adequate replication. We used our existing data from the fish study period to suggest potential relationships between variable life history and environmental parameters and spatial and temporal patterns of recruitment.

3. **Life history and recruitment dynamics of invertebrates, including corals**.

We assessed coral recruitment in West Hawai`i over several years using settlement tiles. Scleractinian corals are a key functional group, in that they create much of the three-dimensional biogenic habitat structure for settlement and recruitment stages, and the habitat of later life stages of many other reef organisms. Several other invertebrate taxa were sampled from different settlement collectors to determine temporal and spatial variation in recruitment patterns and processes.

4. **Near-shore Ecosystem structure and Oceanography of West Hawai`i.**

As part of other collaborative research with NPS, USGS and others, high spatial resolution imagery and benthic habitat characterization maps of parts of the Kona reef tract were developed as GIS layers. It should be possible to overlay all available ecological data, including data from this study on the distribution and abundance of recruits of reef species for spatial analysis of dispersal distances, rates and other elements of connectivity across the Kona reef tract. GIS layers will supplement existing NPS spatial data and habitat characterization efforts done by WHAP. Oceanography data from (a) the literature on the study area; (b) satellites; (c) drifter studies or (d) oceanographic instrument deployments on the Kona reef that coincide with peak spawning or larval production events can be used in future work to further examine physical processes driving recruitment patterns observed in this study. Drifter data may be used to estimate dispersal trajectories and connectivity, while Acoustic Doppler Current Profilers, temperature loggers, CTDs and other instruments can provide measures of local-scale currents and other oceanographic factors driving recruitment and other reef ecological processes.

Approach

Study Sites

Prior to site selection we divided the West Hawai'i coast into three geographic regions. Divisions represented potential boundaries between different regional marine community assemblages as observed by the DAR Kona staff (W. Walsh, pers. obs.). The central region was bounded by Keahole Point on its northern end and Honaunau Bay on the southern end (roughly delimited by asterisks at Kaloko-Honokohau National Historic Park (NHP), slightly south of Keahole Point and at Pu'u Honua 'o Honaunau NHP; The northernmost asterisk is at Pu'u Kohola Heiau National Historic Site; Maps 1, 2).

Fish were sampled from the 23 existing WHAP study sites (Map 1) and from sites with contrasting temperature regimes on East Hawai'i and O'ahu islands. Corals and other invertebrates were sampled from 9-10 of the WHAP sites on and near the coasts of National Parks and MPAs along the West Hawai'i coast (Map 2). Opihi recruitment was sampled non-destructively at 7 intertidal sites along the Kona coast.

Reef Fish

Recruits of reef fish species were collected as available from the network of WHAP sites off Kona (Map 1) using small pole spears. Fish were placed in plastic bags marked with site and date, and transported on ice to the laboratory within hours of collection. In the laboratory fish were measured and fin clipped to obtain tissue samples for subsequent genetic analyses of population connectivity. All samples were then frozen until otoliths were dissected. Methods for otolith analysis appear below, with findings for reef fish life history and recruitment. Genetic analyses resulting from tissue samples collected in this project are completed or underway by Eble and others; these methods and findings are beyond the scope of this report. Otolith microchemistry work supported by NPS was done by Ruttenberg et al. (2008).

Coral Reef Invertebrates

Site Selection

Starting in 1999, the State of Hawai'i Division of Aquatic Resources (DAR) began conducting bimonthly surveys of 23 west Hawai'i near shore sites in order to examine the impact of the commercial aquarium trade on local reef fish populations (Tissot et al. 2004). Their criteria for site selection included a substratum with an abundance of finger coral (*Porites compressa)* at 10-18m. Finger coral typically dominates most areas of the West Hawai'i reef tract at 10-18m depth range. We chose to sample at 10 of the 23 DAR sites because they represent reasonably consistent habitats, on and near the coasts of National Parks and MPAs, spanning a wide geographic range and thus potentially contrasting oceanographic regimes, and because of access provided by the Hawai'i DLNR DAR and their vessel. Distance between adjacent invertebrate recruitment study sites ranged from approximately 6 to 25 km with an approximate average of 12 km (Maps 1, 2). The range in distance between the northern- and southern-most sites is approximately 125 km.

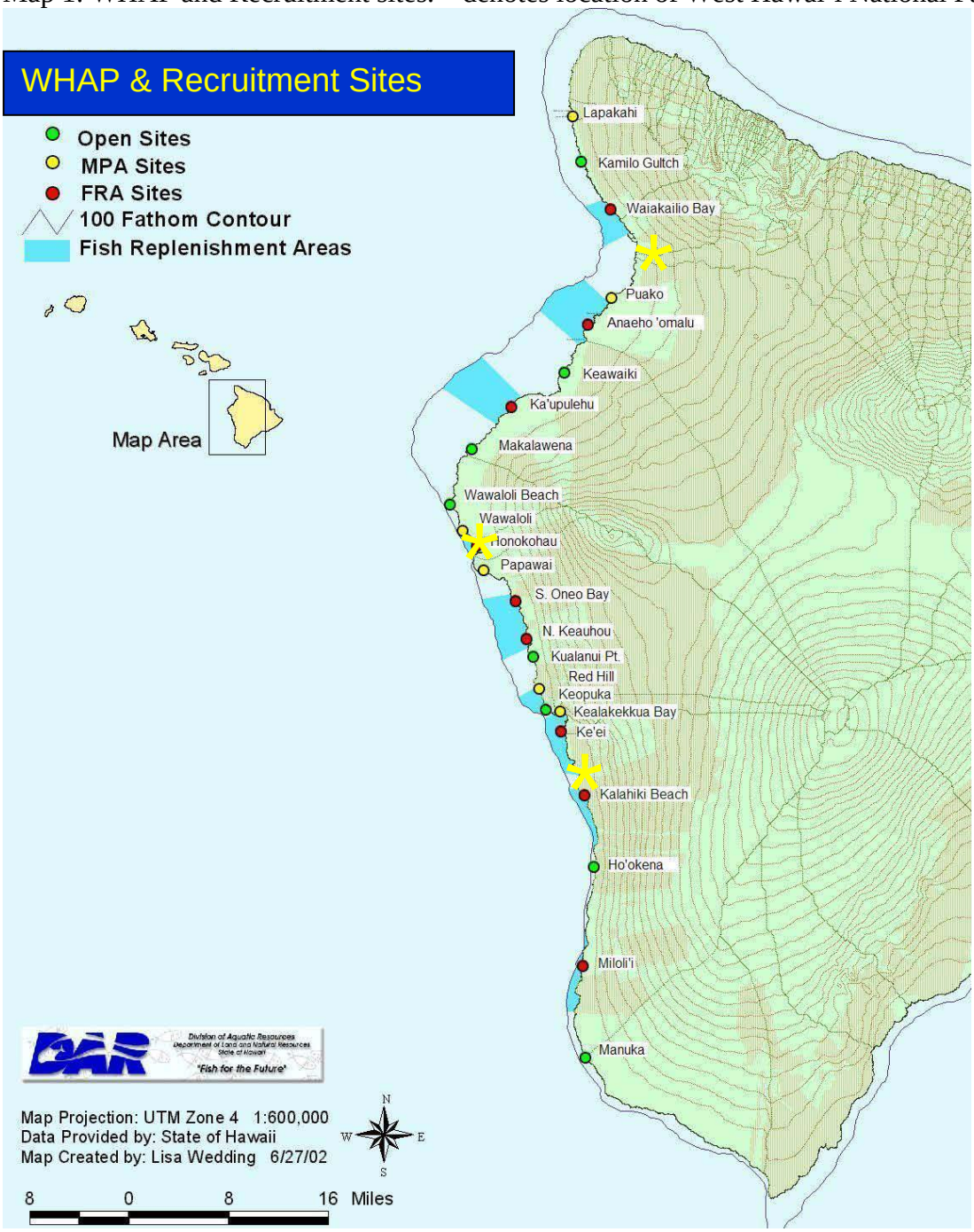
Sampling Design

Our sampling design compared recruiting populations of mobile and sessile invertebrates among paired recruitment collectors deployed at 9 or 10 West Hawai'i reef sites (Map 2). Sites were chosen for their proximity to WHAP sites, National Parks and MPAs, and to span nearly the full length of the Kona coastline, in order to assess at the ecosystem level, the full range of ecological and oceanographic conditions influencing recruitment patterns of coral reef invertebrates in the region. Study sites were selected within areas of comparable habitat and depth in order to minimize within- and between-site habitat variability while still maintaining unbiased placement of collectors within an area.

We developed a spatially nested sampling design specifically to examine the relative influence of large (10's of km), intermediate (1 to 10 km) and local (cm's to m's) scale factors affecting reef invertebrate recruitment by comparing recruit abundance and diversity among collectors within and among sites and regions (Fig. 2). Of the 10 DAR-WHAP sites selected, three were located within each of the northern and southern regions while four (initially, later reduced to three when one proved to be redundant) where established in the central region.

All but one site from each region received a single pair (two) of recruitment arrays (Fig. 1, left; one recruitment array of a pair; each array had two collectors of each type, for a total of 4 per site), with the remaining sites receiving 3 array pairs each to assess within-site recruitment variation at the local scale (1 – 10 m; Table 1, Fig. 2). When more than one array pair was placed at a site, array pairs were placed 30 meters apart within finger coral habitat (see frontispiece) between 10 and 14 meters depth in a line parallel to the reef slope, and placed consistently in relation to existing WHAP site transect marker pins cemented into the substratum. Individual arrays within a pair were placed between 1 and 2 meters apart with consideration to maintaining continuity in habitat.

Map 1: WHAP and Recruitment sites. * denotes location of West Hawai'i National Parks.



Map 2: Invertebrate Recruitment sites. * denotes location of West Hawai'i National Parks.

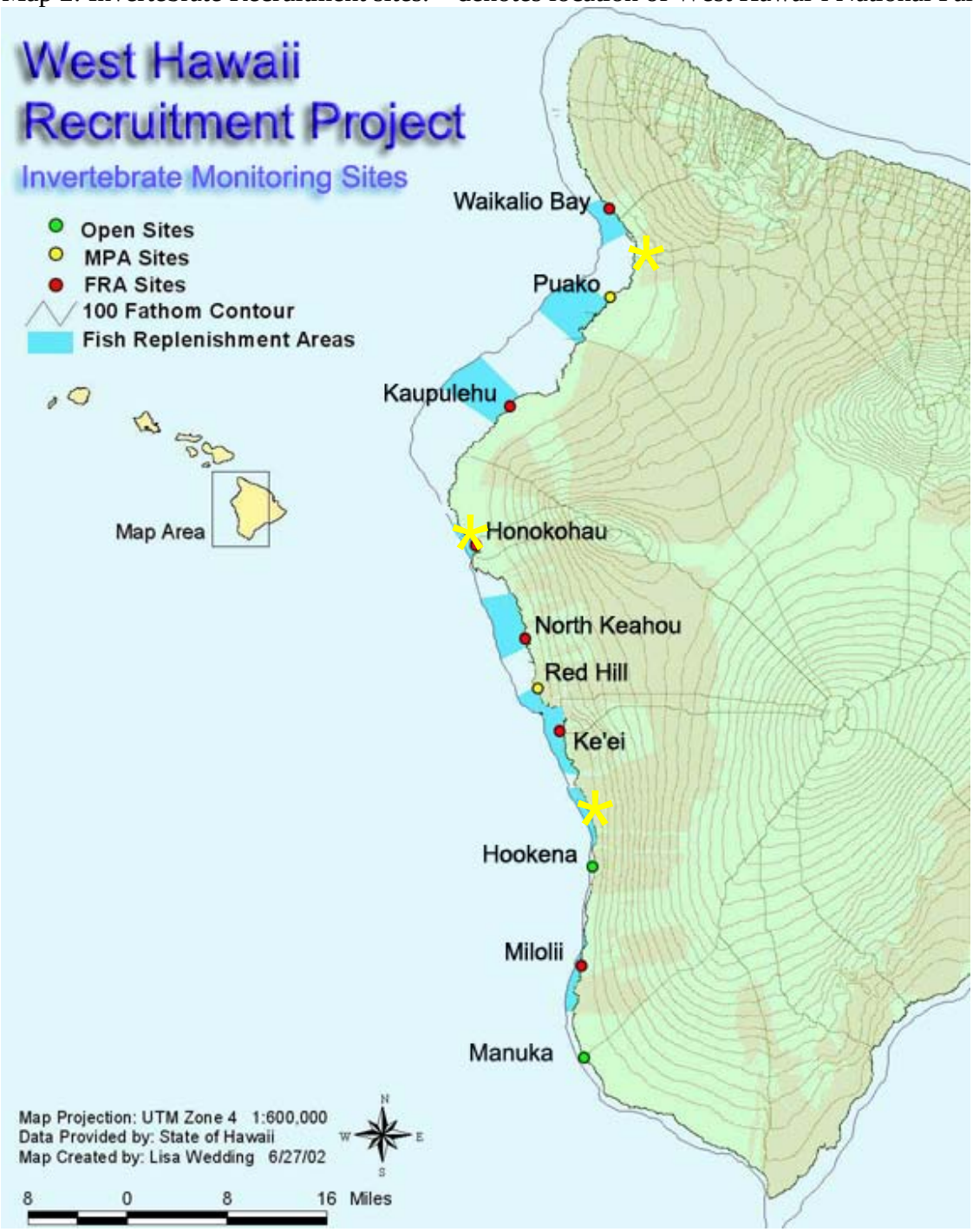


Figure 1: Sampling array for mobile and sessile invertebrate recruits (each array held two collectors of each type. Note two Yellow Tang recruits above array at left; close-up of collectors at right) deployed at sites in Table 1.

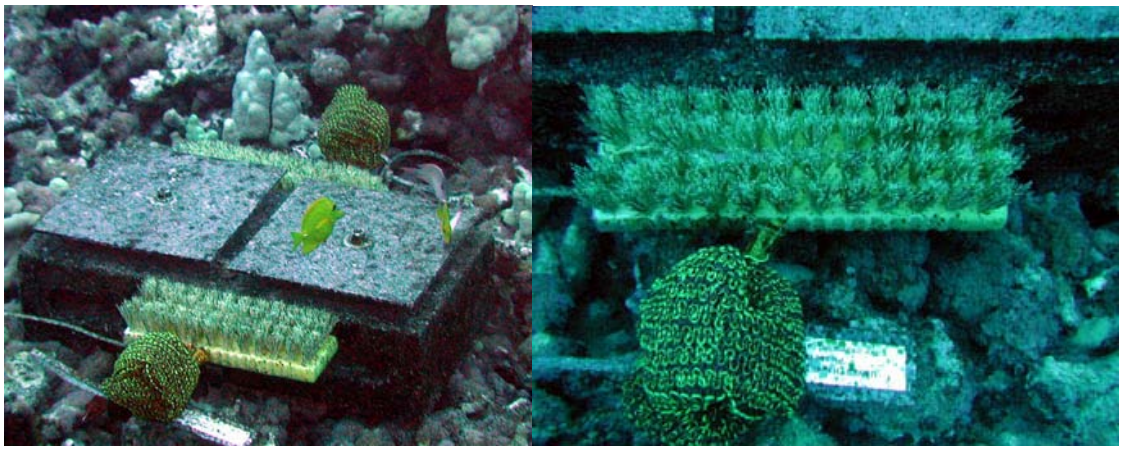
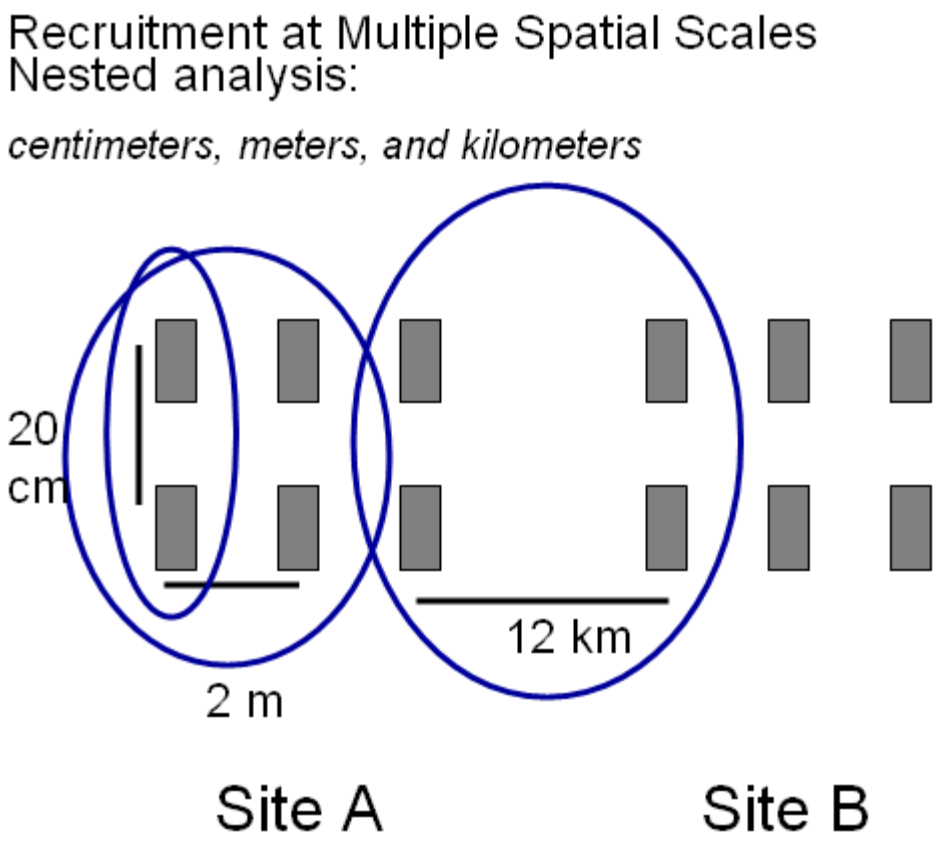


Table 1: Invertebrate recruitment sites, locations and number of arrays deployed.

Region	Site	Latitude	Longitude	Arrays
North	Waiakailio	20.04.435	155.51.871	6
	Puako	19.58.193	155.50.928	2
	Kaupulehu	19.50.637	155.58.858	2
Central	Honokohau	19.40.259	156.01.820	6
	N. Keahou	19.34.103	155.58.161	2
	Red Hill	19.30.273	155.57.184	2
	Keei	19.27.769	155.55.608	2
South	Hookena	19.22.149	155.53.844	2
	Milolii	19.10.038	155.54.795	2
	Manuka	19.04.603	155.54.238	6

Figure 2: Schematic of nested sampling design for invertebrate recruitment. Each rectangle represents paired replicate samplers on an array block. Each sampler on an array was approximately 20 cm from its identical sampler type (i.e., 2 sampler replicates (of each of 2-3 types: plates, brushes or scrub pads) per array block).



Methods - Invertebrates

Arrays for sampling mobile and sessile invertebrate recruits were constructed as long-term, stable, mounting platforms for multiple collector types (Fig. 1) thus providing the ability to target a diverse range of taxa with a single collection unit. The base of each array consisted of a hollow cement block (~ 19 x 40 x 9 cm) to which were affixed two 0.8 cm stainless steel bolts by drilling holes evenly spaced on the top of the blocks and epoxying bolts in holes. PVC plates (see Fig. 1) for observation of coral and other sessile invertebrate recruitment were attached to bolts using PVC pipe spacers between blocks and plates, washers and nuts. Attachment points for mobile invertebrate collectors where made by running two 1.3 cm diameter x 51 cm long parallel PVC rods through the openings in the cement block and then securing them with cable ties. All arrays were deployed in July 2003. Collectors for mobile invertebrates were retrieved and replaced every 6 weeks. Plates for corals and other sessile invertebrates were sampled at approximately six month intervals bracketing the coral spawning and larval settlement season for most known species in Hawai'i. Plates were photographed *in situ* with a 4.1 megapixel digital camera in a waterproof housing at intermediate times.

Methods - Mobile Invertebrates

Recruiting mobile invertebrates were sampled using two types of collectors: Rubbermaid® synthetic bristle scrub brushes (product number G231-12) and SOS Tuffy® synthetic dishwashing scrub pads (product number SWT-98130CLX). Both of these are and have been used successfully in numerous recruitment studies. The two collector types were attached in pairs to the PVC arms of each array with cable ties (Fig. 1). Every 6 weeks the collectors were replaced *in situ* with new ones. Collectors were retrieved *in situ*, placed in large re-sealable plastic bags (pre-labeled with site, array, replicate number, and date) and then placed on ice, transported to the laboratory within a few hours and refrigerated until processed and analyzed.

Recruits were removed from mobile invertebrate collectors by placing the retrieved collector in an 8 cup plastic container with fresh 5 um filtered seawater. The container and collector were then placed in a Fisher Scientific FS30 sonicator and sonicated for 10 minutes (as determined by Basch et al., unpubl.) The resulting sample was then filtered through a 64um mesh screen to remove excess seawater, transferred to individually labeled glass dishes with fresh seawater and kept refrigerated until examined. Identification and enumeration of specimens in samples was done using either a NIKON SMZ-2T Stereozoom or Leica MZ 125 binocular microscope. Specimens were identified to lowest taxon possible. A photographic library was made of representative individuals by photographing them with a digital camera mounted to a dissecting microscope. Specimens were also preserved as vouchers (in 70% ETOH) to aid in subsequent identification. Unknown animals were also photographed, then preserved as above for later identification using appropriate taxonomic literature or by consulting taxonomic specialists.

The current lack of information on developmental and morphological characteristics of the microscopic early life history stages, including juvenile recruits, of the majority of Hawaiian marine invertebrate taxa sometimes limited our ability to resolve specimens beyond genus or family. Verification of identifications was sought from taxonomic specialists; some unidentified samples were analyzed by researchers at the B. P. Bishop Museum, Honolulu, Hawai'i and at UH Hilo.

In conjunction with, and upon completion of, the first round of sampling we did a methodological experiment to compare data on mobile recruit populations found in the two types of mobile invertebrate collectors. The synthetic Tuffy scrubby collectors were observed to collect consistently fewer species and significantly lower numbers of individuals across a broad range of taxa than the plastic scrub brushes (Table 2). Tuffy collectors also required significantly more effort and time to process. Considering time constraints and the observed differences in composition and numbers of recruits collected between collector types, we decided to continue use of scrub brushes to sample the broadest range and numbers of mobile invertebrate recruits and to discontinue using Tuffy collectors.

Table 2: Comparison of differences in total number of species in major taxa observed, in two types of mobile invertebrate collector.

Taxa		Total Number of Species Observed	Divergence from Species Total	
			Brush	Scrubby
Phylum Arthropoda				
	Infraorder Anomura	1	0	0
	Infraorder Brachyura	9	0	-2
	Infraorder Caridea	2	0	0
Phylum Echinodermata				
	Class Echinoidea	5	-1	-2
	Class Ophiuroidea	8	-1	-1
Phylum Mollusca				
	Class Bivalvia	13	0	-4
	Class Gastropoda	52	-7	-7

Although very abundant in some samples, micro-invertebrate taxa with benthic adults such as polychaetes, copepods, and small peracarid crustaceans (tanaids, isopods and amphipods) were not identified or counted because these were not targeted species and this would have required considerable additional effort and time; since some of these taxa may be micro-predators on some newly settled recruits, the relative abundance of these micro-invertebrates was estimated using a DACOR scale (Dominant, Abundant, Common, Occasional, Rare) for each major taxon (e.g., amphipod) and sample. For this reason, when stated below in “Findings” that, e.g.,“80% of the recruits sampled are molluscs” such values represent the percent of all taxa that were enumerated, not including those whose relative abundance was estimated.

Recruitment of octopus was examined using bundles of PVC pipe (~ 1.5 cm inner diameter x ~ 60 cm length) placed in cavities in the reef; juvenile octopus have been observed to recruit into this type of pipe (L. Basch, pers. obs., Basch and Engle 1993) Preliminary data indicate that low numbers of octopus recruit to such pipes off Kona but more data are needed.

Recruitment of opihi on natural substrata on shore in the rocky intertidal was surveyed at 7 sites spanning the Kona coast. Observed recruitment of opihi has thus far been limited and more data are needed.

Methods - Sessile Invertebrates

Recruitment patterns of corals and other sessile invertebrates were examined initially using 17.8 x 17.8 x 0.6 cm PVC plates or tiles (n = 64) mounted in pairs to the top of each cement hollow block array. Tiles were cut from gray PVC sheets (purchased from Hawai’i Plastics Corporation). Each tile was drilled through the center and mounted on stainless steel bolts previously affixed to the cement block. A gap habitat or refuge was created between the undersurface of the tile and the cement block by mounting the tile on top of a 1.9 cm PVC spacer. Tiles were deployed with mobile invertebrate

collectors in September, 2003 and collected in May, 2004. Retrieved tiles where placed in large, resealable plastic bags on site and stored on ice until processed. Tiles where visually inspected at high magnification under a Nikon SMZ 2T binocular microscope. All taxa where identified to the lowest possible taxonomic group. Representative samples were photographed to aid in subsequent identification.

Analysis of samples retrieved from the 64 PVC plates indicated only four scleractinian (reef building) coral recruits, all on the underside of tiles, from the two northern-most sites. This extremely low level of recruitment may have been due in part to the timing of deployment of tiles in September, however, since some coral species in Hawai'i recruit at various times during the year (Richmond 2001 Table 8-1), there was sufficient time for development of biofilms and crustose coralline algae on PVC tiles that serve as settlement cues, and coral recruitment has occurred during this time in subsequent years, timing of tile deployment alone does not explain the very low number of observed coral recruits. It is likely that coral recruitment on Kona reefs was actually very low during the sampling period. While PVC tiles have been successfully used to examine scleractinian coral and other sessile invertebrate recruitment dynamics in various locations (e.g., Rogers et al. 1994, Soong et al. 2003) the paucity of coral recruits on PVC plates at our study sites led us to run trials using another previously used artificial substrate type -- terra cotta clay tiles. Terra cotta has been shown to be a suitable substrate for scleractinian coral recruitment at a number of widely divergent locations, including: Australia (Dunstan and Johnson 1998, Mundy 2000), the Red Sea (Glassom et al. 2003), and Hawai'i (Brown 2004, Kolinski 2004). Although coral recruitment has generally remained very low, corals recruited at all sites on clay tiles and we used them in subsequent deployments over the following 5 years

We deployed commonly available garden paving tiles (Fig. 3, SunShine Pavers: 20.3 x 9.5 x 1.3 cm) at 9 of the original 10 invertebrate recruitment sites, starting in May 2004 (Table 3). Based on prior experience we sought to balance several sampling considerations: increase statistical power -- the number of replicate tiles, further randomize their deployment spatially within uniform reef habitat and depth range, and limits on sample processing time. Given these considerations we chose to no longer sample the central site, Red Hill (between and close to other central sites, North Keahou and Ke'ei). Eliminating Red Hill allowed us to maintain sampling at three sites in each region and to increase replication at remaining sites without compromising our examination of local and regional spatial patterns in coral recruitment (Maps 1, 2, Table 1).

Figure 3: Terra cotta clay tile plate for sampling coral and other sessile invertebrate recruits. White tag notes experiment in progress, by whom, and contact information. Gray PVC lower plates were deployed below clay tiles to provide a gap or refuge habitat for recruitment of corals and other sessile reef invertebrates.

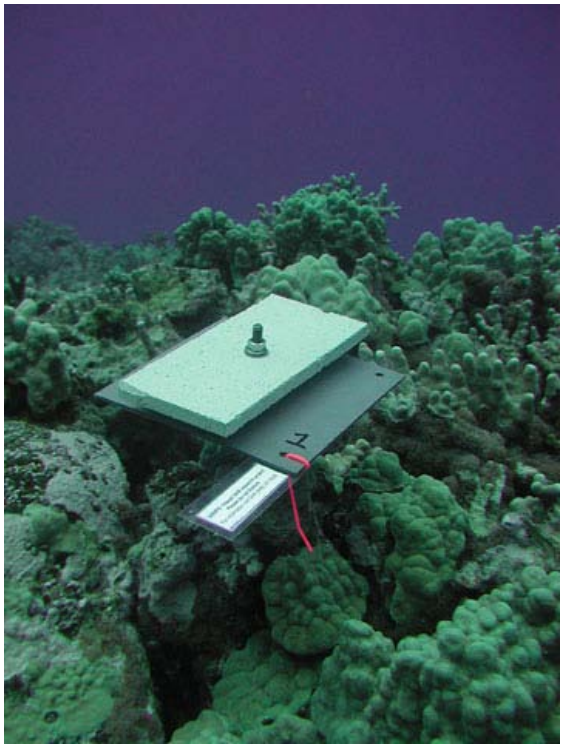


Table 3: Sampling sites and number of collectors per site

Region	Site	Terra cotta
North	Waiakailio	8
	Puako	8
	Kaupulehu	8
Central	Honokohau	8
	N. Keahou	8
	Ke'ei	8
South	Ho'okena	8
	Milolii	8
	Manuka	8

Terra cotta tiles were deployed on individual threaded steel rods mounted vertically in dead coral heads at randomly chosen points at each reef site. Each stainless mount consisted of a 0.8 cm diameter x 21 cm long threaded stainless steel rod to which we bolted one plastic PVC tile and one terra cotta tile using stainless steel nuts and washers (Fig. 3). The PVC tile was set to sit no more than 10 cm above the substrate once the threaded rod was inserted into holes drilled in the dead coral heads. The terra cotta tile was mounted on the threaded rod above the PVC plate with a 1.3 cm PVC spacer between the two in order to create a gap habitat or refuge for recruitment, since it was previously observed that most recruits

of several taxa were on the underside of plates and that tops of plates were covered mainly by crustose fleshy algae that were heavily grazed by herbivorous fishes and sea urchins. Mounting sites in dead coral were drilled with a pneumatic drill and a 1.3 cm carbide bit. Stainless threaded rods were affixed with epoxy (E6 EPCON System Epoxy) for multi-year deployment required for studies of this nature.

Terra cotta deployment sites where chosen randomly within a 50 m x 30 m area centered on existing DAR WHAP fish transect sites. In their study of reef fish populations, DAR established 4 permanent 25 m long transects per site with stainless steel pins marking the start and end points of each transect. Placement of tiles relative to the DAR transects allowed us to quickly locate tiles after long-term deployment. Tile locations were randomized prior to deployment by establishing random distance and compass bearings from a specified DAR transect pin using a random number generator. Criteria for placement were that we stay within the designated area, within uniform reef habitat and depth range, and that the plate mounting sites were dead coral that was robust enough to withstand disturbance from large storm swells.

Once in the field, if the selected randomized point was not suitable we surveyed within a radius of 2 m around the original point for a suitable mounting site. If no suitable site could be found we searched in another 2 m radius circle directly north of the original site. We were never required to look further than 1 step north for a suitable mounting point.

Terra cotta tiles were deployed initially in May, 2004. To estimate coral recruitment during the summer-fall, when many coral species spawn, settle and recruit, tiles were deployed for 6 months. The first batch of tiles was retrieved in November 2004 and subsequent batches at approximately 6 month intervals, and were processed and analyzed for taxonomic composition, numbers, and sizes of coral recruits.

We predicted that the density of recruiting invertebrate taxa would vary concurrently at scales greater than 10m. We tested our predictions by comparing total recruitment per collector within and among reefs and regions. A comparison of total recruitment among collectors at different spatial scales allowed us to identify how scale-dependant factors may be shaping the diversity and abundance of recruiting populations (Fig. 2). We conducted comparisons in two ways: 1) by examining the data for differences on a taxon-by-taxon basis; and 2) by comparing overall recruitment patterns among sites.

Individual species comparisons were conducted using a nested one-way analysis of variance with collectors nested within site. Only data from sites with multiple array pairs were included in this comparison. An examination of among and within site variation on a species-by-species basis can provide some insight into how individual species recruitment patterns differ in response to environmental factors and thus how management may need to formulate its response with respect to species or taxa of interest.

A multivariate comparison of overall recruitment patterns (of multiple species) among sites can provide some insight into ecosystem level processes by testing for the presence of large-scale factors impacting the recruitment dynamics of numerous, disparate species. The strength of the multivariate approach is its ability to reveal the presence of factors potentially influencing: 1) local community structure; 2) larger biogeographic regions; and, 3) establishment and placement of Marine Protected Areas (MPAs). This analysis was conducted with the full data set using the analysis of similarity

algorhythm (PRIMER multivariate statistical package, Clarke and Warwick 2001). To avoid biasing data in favor of abundant recruiters, each taxon data set was recalculated as a percent of the median total number of recruits among all sites.

Findings

Reef Fishes

Early Life History Strategies and Population Dynamics of Select Tropical Reef Fishes in Hawai`i

Populations of tropical reef fishes in Hawai`i are in decline. Little is known about their life history and population dynamics. For reef fishes elsewhere, populations can be driven by variable recruitment success. Recruitment typically varies on multiple spatial and temporal scales, and may be primarily driven by highly variable and significant larval mortality (sometimes as great as 99%). Mortality is due to planktonic predation, inadequate larval nutrition, or advection by currents of larvae away from suitable settlement and recruitment habitats. Variation in early mortality may drive variation in recruitment, and thus, the population dynamics of reef fishes in Hawai`i. Variable early life history parameters, including pelagic larval duration and larval growth rates may significantly influence survival, and hence, recruitment success. Specifically, cumulative larval mortality may increase with longer larval duration and larval mortality may decrease with faster larval growth rates. In addition to a basic knowledge of these species-specific life history parameters, it is important for managers to understand their variability. Factors which control variation in these key life history parameters may ultimately regulate mortality, recruitment, and population abundance. Variation in life history parameters can, and likely do, vary temporally and spatially.

During this study important knowledge of basic life history parameters was developed for key herbivorous reef fishes in Hawai`i using retrospective otolith analyses. Otoliths from more than 1580 fishes were dissected and stored from a range of important reef fish species collected around Hawai`i Island, including the yellow tang, convict tang, sergeant major, and other reef fishes (Fig. 4). During 2003 subsets of these otoliths were mounted on glass slides (n=409), prepared for analysis (n=378), and baseline counts made (n=314). During the first quarter of 2004, 250 additional otoliths from yellow tang and manini were analyzed in order to explore temporal and spatial variation in early life history parameters.

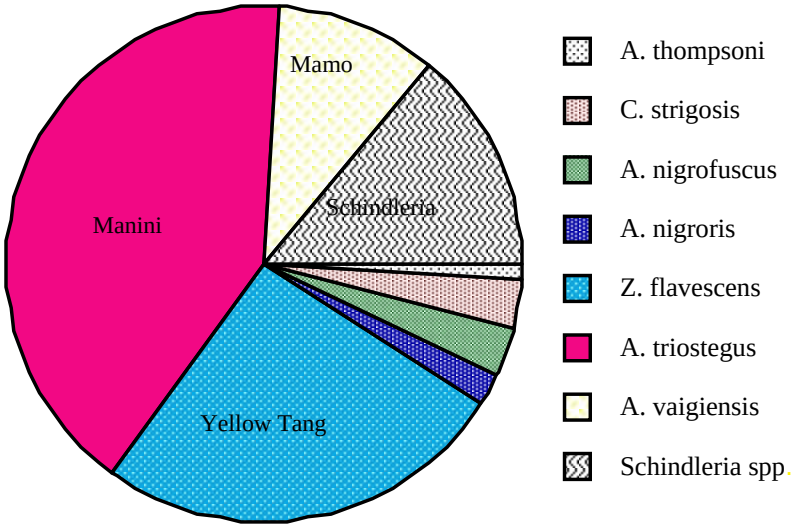
During the study, two UH Manoa graduate students were trained in retrospective otolith techniques in the otolith lab at UHM. Collaborative work done with Amber Whittle resulted in the production of two chapters of her dissertation, and was featured in part, during her Ph.D. defense. This co-authored work is being prepared for publication. Another student, Jeremy Claisse examined annual otolith increments in adult reef fishes at West Hawai'i for a HCRI project focused on later fish life stages that is complimentary to this study. A collaboration was also initiated between D. Shafer and E. DeMartini of NOAA Fisheries. This study is expected to help determine if there is a chemical signature in otoliths that can be used to retrospectively determine the origins of adult reef fishes (Main Hawaiian Islands vs. the Northwest Hawaiian Islands). This work may later be refined to examine specific geographic origins of fishes within the Main Hawaiian Islands. It is complimentary with another study in progress mentioned above with researchers at the University of California Santa Barbara (in collaboration with USNPS and UH) using otolith microchemistry to detect environmental signatures

indicative of population source(s), sinks(s) and connectivity in a common damselfish at Kona and other reefs throughout the Main Hawaiian Islands.

Yellow tangs (Fig. 5) are the primary target of the commercial aquarium fishery in Hawai`i, and are the most economically valuable inshore fishery in the state (Walsh et al. 2003). Yellow tangs are important algal grazers, and may help maintain a balance between algal and coral populations. Yellow tangs settle directly onto the reef. Although their recruitment is known to be variable and patchy (Tissot et al. 2004), nothing was known prior to this study about their early growth rates, planktonic larval duration, or other basic life history parameters.

To date, over 416 otolith pairs have been dissected from recently recruited juvenile yellow tang (Fig. 6), 70 otoliths have been mounted to slides, 54 have been prepared, and 30 have been analyzed. Optimum otolith preparation techniques were developed for the yellow tang, and involve carefully grinding and polishing a thin section that represents a transverse section through the otolith including the core. Otoliths of yellow tang are extremely difficult to analyze due to their complex three dimensional structure. A settlement mark is apparent in the otoliths of most yellow tangs examined. The settlement mark in the sagittae of yellow tangs is distinguished by an abrupt change in increment width from narrow pre-settlement to wider post-settlement daily increments (Fig. 5).

Figure 4: Species composition of fish collections for otolith analysis in the present study (as of 1/20/2004; n = 1584).



One of the earlier yellow tang juveniles collected (38 mm, June 10, 2003) was approximately 90 days old, suggesting a spawning date around the second week in March. The earliest juveniles were collected toward the end of May (May 20-26 2003), and were analyzed during the first quarter of 2004. It appears that early March may be the onset of the reproductive season. Identification of the bounds of

the adult reproductive season is important to managers when considering temporal protection efforts (e.g., seasonal limits, enforcement).

Mean (± one standard deviation) larval durations of yellow tang (n=30) were determined to be 57.9 ± 5.2 days, ranging between 47-65 days. This larval duration is significantly longer than that of many other reef fishes, though is similar to those of acanthurids (surgeon fishes) elsewhere. Long larval duration may be associated with higher larval mortality. Early growth rates of yellow tang were determined to be 0.50 ± 0.06 mm total length/day. This is a relatively rapid early growth rate and allows the yellow tang to settle at a relatively large size (33.8 ± 1.2 mm TL).

Figure 5: *Zebrasoma flavescens*, Yellow Tang or *Lau'ipala* juveniles (above) and representative otolith section (below) of recent recruit showing settlement mark (dark band) and white points marking larval daily growth increments (Scale bar = 25 µm).

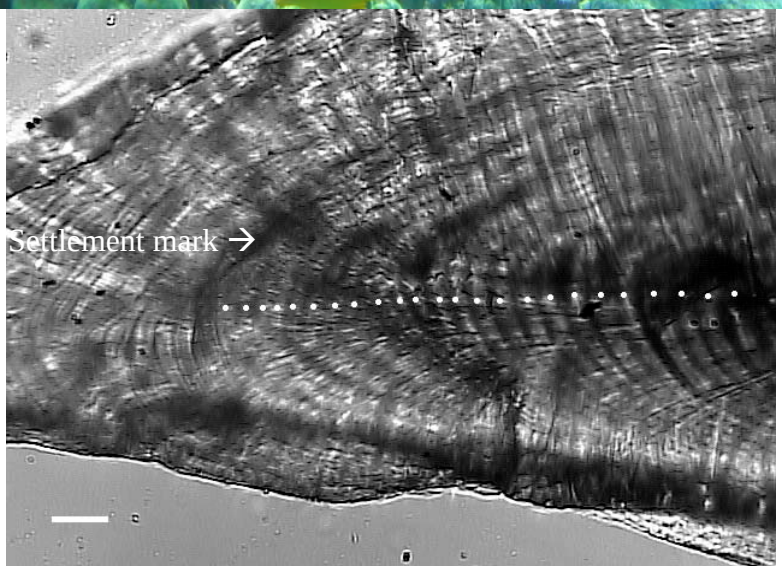


Figure 6: Size frequency distribution of Yellow Tang sampled (n = 416).

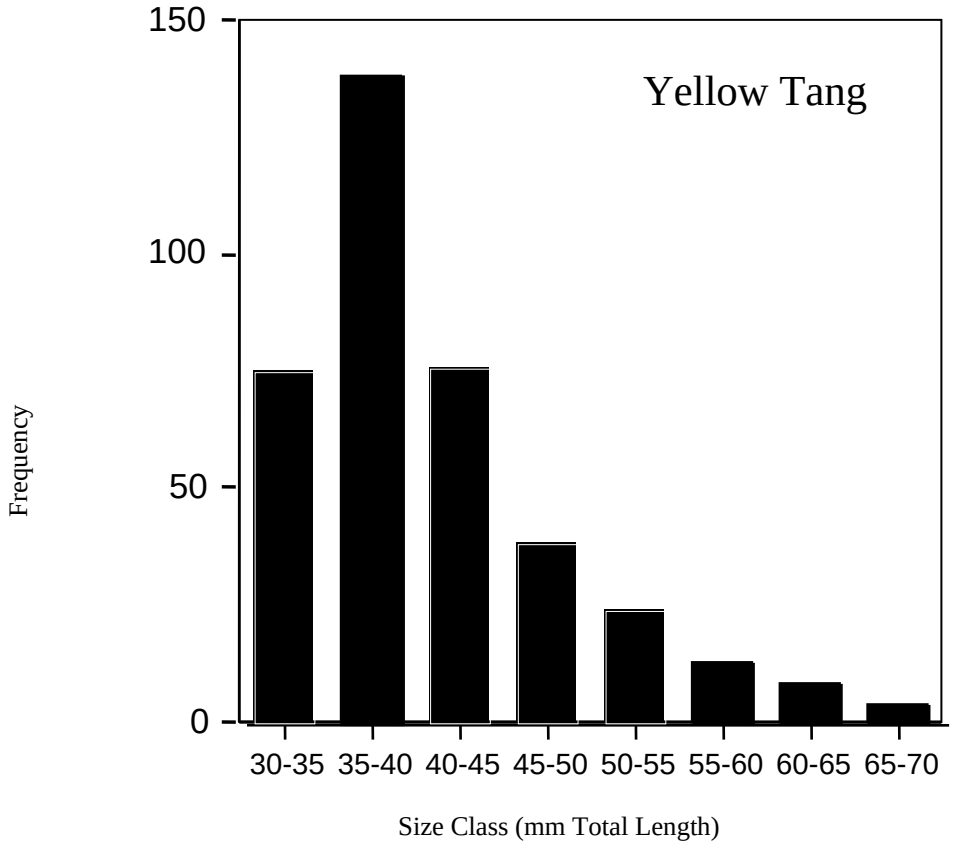
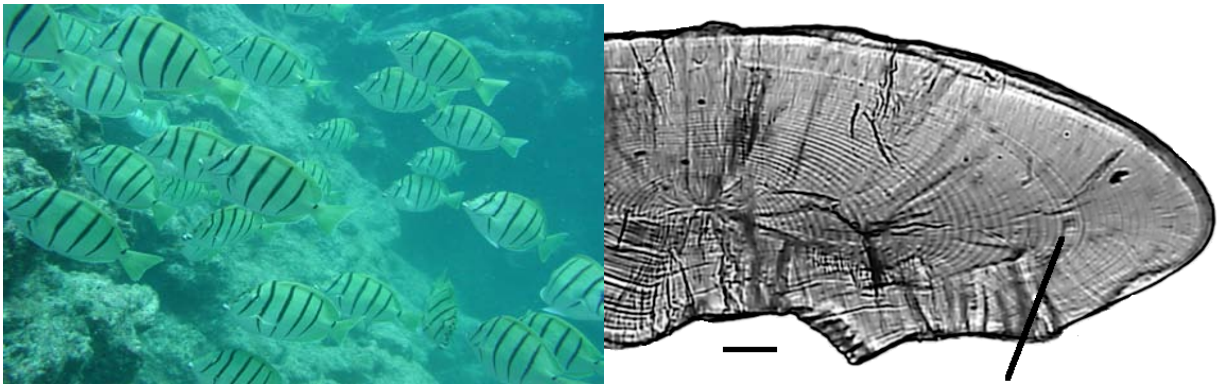


Figure 7: *Acanthurus triostegus*, Convict Tang or *Manini* (left) and representative otolith section (right) of recent recruit showing settlement mark (dark band) and dark bands indicating larval daily increments (Scale bar = 25 µm).



Manini is a common food fish in Hawai`i. Most of what biologists and managers know about manini in Hawai`i comes from an impressive body of work conducted in the late 1950s by Jack Randall. Manini recruit to tide pools and shallow nearshore areas, instead of recruiting directly to the reef, as in other acanthurids. This life history characteristic may make manini more vulnerable to shoreline

pollution, especially that which can concentrate in shallow tide pools. Manini are important nearshore grazers, and may help maintain a balance between algae and coral populations. Populations of manini may be declining in the Main Hawaiian Islands.

Randall suggested that manini in Hawai`i have considerably longer larval durations than conspecifics elsewhere. Long larval durations may be associated with higher cumulative planktonic mortality, which has important implications for management. He determined larval duration by estimating the difference between the time of first reproduction and the appearance of the first new recruits in the tide pools. This method yielded a range of 71-83 days for larval duration. This work has been cited in the literature with great frequency when discussing the unique population ecology of Hawaiian reef fishes. In particular, it is widely believed that coral reef fishes in Hawai`i have extraordinary long larval durations. This belief has never been challenged, however, and is supported by very little data. Data from this project provide the first retrospectively determined larval duration information for manini in Hawai`i, and begins to address this important issue in Hawaiian coral reef fish ecology.

Over 652 otolith pairs have been dissected from recent recruits of manini in Hawai`i (Fig. 8), 85 otoliths have been mounted on slides, 70 have been prepared for analysis, and 30 have been analyzed. Optimum otolith preparation techniques were determined to be similar to those developed for the yellow tang. A settlement mark is visible in sagittae of most manini, characterized by either a shift in increment width or optical focal plane.

Manini in Hawai`i were found to have larval durations ranging between 48 – 61 days (n=30), with a mean (± one standard deviation) of 54 ± 4.3 days. This finding is significantly shorter than the earlier estimate made by Randall, and is similar to the larval duration of manini found elsewhere. During the first quarter of 2004, 100 more otoliths were analyzed. This information, together with results from this study on other reef fishes in Hawai`i, suggests that reef fishes in Hawai`i may not necessarily have extraordinary long larval durations.

Manini grow approximately 0.52 ± 0.05 mm TL/ day (± one standard deviation), which is similar to the fast rate determined for the yellow tang. This fast growth rate also allows manini to settle at a relatively large size (32.0 ± 1.5 mm TL). Large size at settlement may have competitive and survival benefits in the intertidal nursery habitat.

Figure 8: Size frequency distribution of Manini sampled (n = 652).

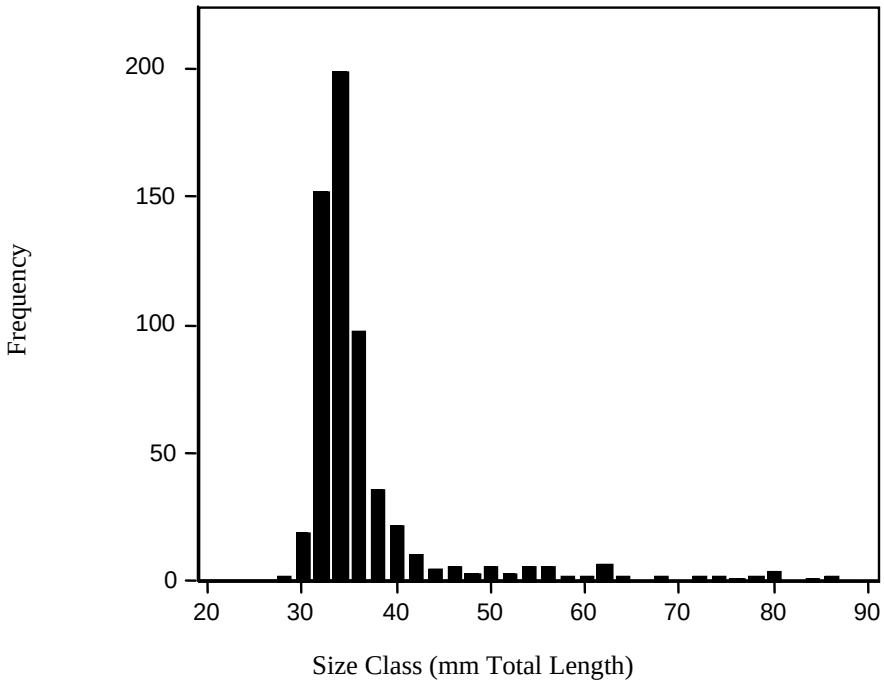


Figure 9: *Abudefduf vaigiensis*, Indo-Pacific Sergeant Major or *Mamo*.

Abudefduf abdominalis and *A. vaigiensis* are similar congeneric pomacentrids (damselfishes) in Hawai`i. *A. abdominalis* is endemic, whereas *A. vaigiensis* may be a more recent arrival to the islands. According to Jack Randall, *A. vaigiensis* may be displacing *A. abdominalis* in Hawai`i, however this needs to be confirmed with quantitative sampling. Collections of new recruits made on the south shore of O`ahu and on the Kona coast of Hawai`i Island during 2003 (n > 158) only contained *A. vaigiensis* (D. Shafer pers., obs.). This same result was independently confirmed by a collector from NOAA NMFS (E. Demartini, pers. comm.). Retrospective life history analysis of endemic and recent

immigrant species offer a tremendous opportunity to identify points of departure in the life history between competing species. Of course, recruits of *A. abdominalis* must first be collected.

Otoliths from 158 *A. vaigiensis* have been dissected, and 30 have been mounted on slides, prepared and analyzed. A settlement mark can be vaguely identified in the sagittae of *A. vaigiensis*. Often the settlement mark can be identified as an abrupt shift in increment widths, or as a phase shift in optical properties of daily increments.

Abudefduf vaigiensis demonstrate relatively linear growth to at least 30 mm TL, with average daily growth rates of about 0.4 mm/day (relatively slower than growth rates of *A. triostegus* and *Z. flavescens*). Larval duration of *A. vaigiensis* averages 18.9 ± 5.3 days, and is considerably shorter than larval durations of the target acanthurids of this study. Shorter larval durations may reduce exposure time to high pelagic mortality during larval life. The tradeoff may be shorter sizes at settlement and higher mortality in juvenile nursery areas or the reef. Shorter larval durations, over the short term, may limit dispersal of an alien species. Shorter larval durations may be associated with lower pelagic mortality rates, and may facilitate recruitment success.

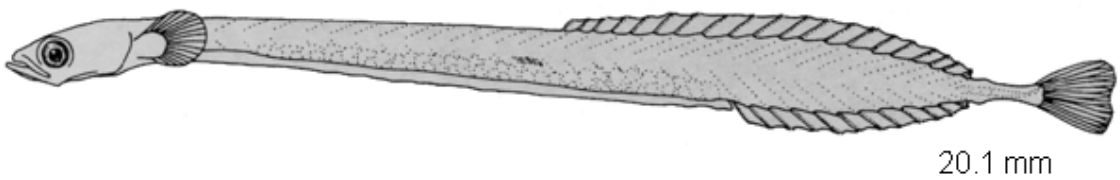
Schindler's fishes, in the family Gobiidae, are progenetic. They mature and reproduce with a larval-fish-like morphology (Fig. 10). Schindler's fishes occur in very dense patches in nearshore habitats adjacent to reefs (e.g., reef flats and fore reefs off Kaua'i, O'ahu, and Hawai'i islands, Basch unpublished data).

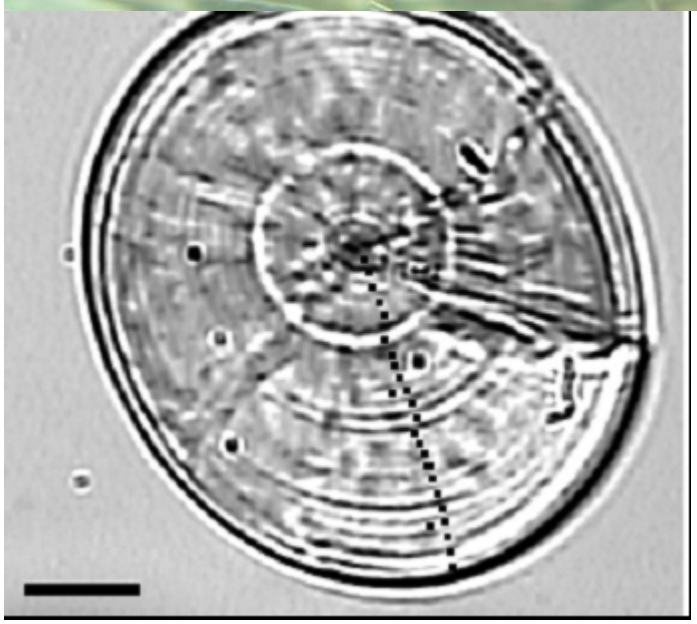
Otoliths from 224 Schindleria were dissected, mounted to slides, prepared, and analyzed. This study found that *Schindleria spp*. may mature and reproduce at ages as young as 20 days old! Growth rates are also rapid at about 0.5-0.6 mm/day. Significant abundance, short generation times, and fast growth rates suggest that *Schindleria spp*. may play an important role in the trophic structure and energy budget of nearshore reef ecosystems.

Other Fishes

Otoliths have been dissected and stored from other species of acanthurids including 10 *A. thompsoni*, 45 *C. strigosis*, 52 *A. nigrofuscus*, and 27 *A. nigroris*.

Figure 10: *Schindleria praematura* and *S. pietschmani*, Shindler's Fish (total length approximately 2 cm (two images above); representative otolith section (below) with dark points marking approximately daily larval growth increments; scale bar = 10 µm).





Taxonomic trends – Mobile Invertebrate Recruits

Results show striking differences amongst taxa in the number and diversity of recruiting individuals. More than 80% of the recruits found in the mobile invertebrate collectors were identified to

be from the phylum Mollusca (Table 4, Fig. 10) with individuals from the phyla Arthropoda and Echinodermata comprising 10% and 6% of total observations, respectively (Table 4, Fig. 10, 12).

Figure 11: Number of taxa of reef invertebrate recruits shown for two typical consecutive sampling rounds separated by approximately 6 weeks.

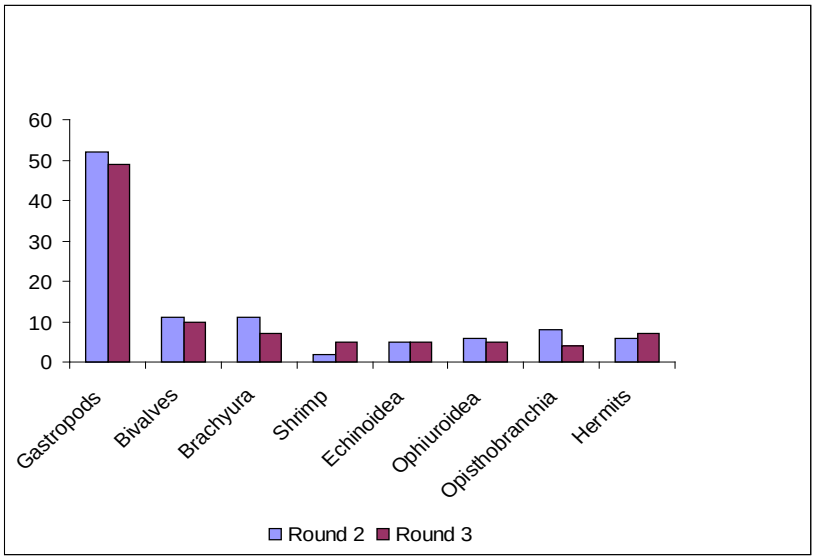
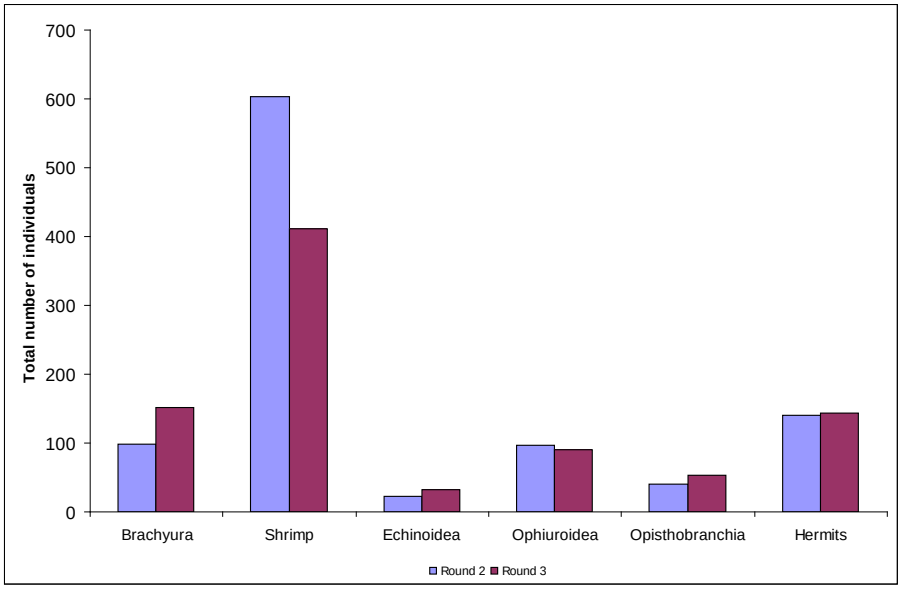


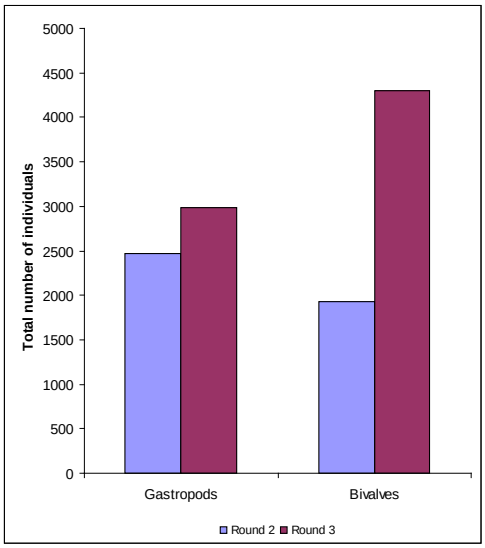
Figure 12: Number of individuals of the most abundant higher taxa (other than snails and bivalves) shown for two typical consecutive sampling rounds separated by approximately 6 weeks.



Within the phylum mollusca, total numbers of bivalves and gastropods observed were nearly equal (52% and 48% respectively) although species diversity was considerably higher in gastropods by nearly a 9:1 ratio. The discrepancy between absolute number of individuals and number of species

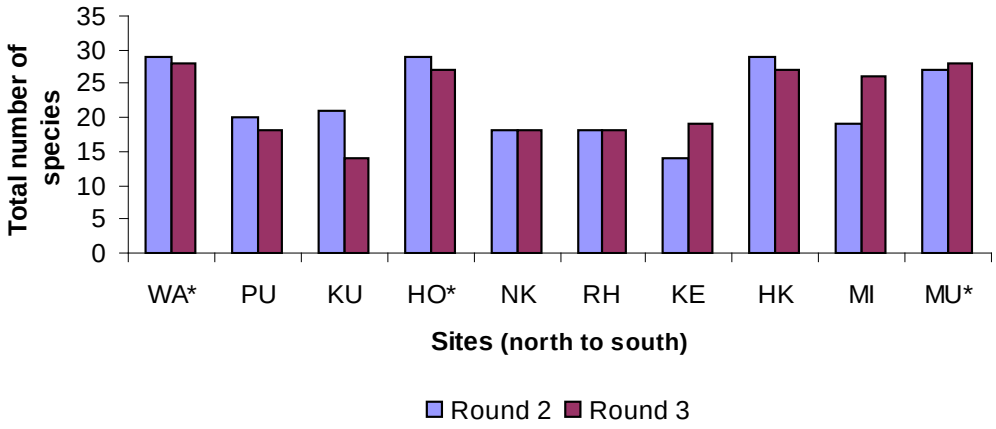
observed is due to the high number of observations of an unidentified bivalve recruit from the oyster family Ostreidae (subsequently identified as Ostreidae 1). Ostreidae 1 was by far the most dominant recruit taxon identified, comprising 38% of the total number of individuals observed, far outnumbering the next most abundant species, the gastropod *Tricolia variabilis* (subclass Prosobranchia, family Phasenallidae), which comprised 8.5% of the total (Table 5, Fig. 13).

Figure 13: Number of individuals of the two most abundant higher taxa, gastropods and bivalves, shown for two typical consecutive sampling rounds separated by approximately 6 weeks.



As a taxon, gastropods dominated observed recruit diversity, accounting for nearly 70% of the total species identified. Recruiting gastropod diversity consisted of a total of 215 species representing 54 genera from 36 different families (Table 4). Average gastropod species abundance was just under 2% compared to an average of just under 0.8% for all non-gastropod species (excluding the prolific recruiter Ostreidae 1). Many of the identified gastropod species were observed infrequently, with 68 species observed less than 5 times. This trend was maintained in higher order taxa as well with the 50 most abundant species comprising more than 94% of the total number of individuals observed (Table 4). The number of species of gastropods was generally similar among sites and sampling periods (Fig. 14)

Figure 14: Number of species of gastropods, the most diverse higher taxon, by site, recruiting along the West Hawai'i island coast. Site names are as on Maps 1, 2.



As with higher order variability, gastropod families varied considerably in diversity and abundance. Average relative abundance of gastropod families found within the 50 most abundant species was nearly 3% of the total observed but varied between a maximum of 8.4% (family: Phasianellidae) and a minimum of 0.14% (family: Triphoridae). An average of 2 species was identified from each gastropod family with many families represented by only a single species. However, low within-family diversity was not consistent with low relative abundance (i.e., Phasianellidae). The Rissoidae was the most diverse (and second most abundant) gastropod family, represented by 5 identified species (Table 5).

The above results indicate, in terms of the taxonomic composition, that most recruits were molluscs, and that most species recruiting were gastropods. Since none of the originally targeted species (e.g., opihi, octopus, crabs, lobster, Crown-of-Thorns seastars) occurred in sufficiently high numbers to observe temporal or spatial trends in recruitment, we focused mainly on some of the most abundant species in recruitment samples, molluscs, to assess patterns in recruitment of reef invertebrates.

Table 4: Number of common recruiting invertebrate taxa.

	Family	Genus	Species
Phylum Arthropoda			
Class Malacostraca	12	17	50
Phylum Echinodermata			
Class Echinoidea	3	4	19
Class Ophiuroidea	1	NA	NA
Phylum Mollusca			
Class Bivalvia	11	12	24
Class Gastropoda	36	54	215

Table 5: Percent composition of recruits of common invertebrate taxa.

Taxa	**% of Total**
Phylum Arthropoda	**7.84**
Class Malacostraca	
Order Decapoda	
Infraorder Anomura	
Family Galatheidae	
Galatheidae sp 1	0.34
Infraorder Brachyura	
Family Majidae	
Majidae sp 2	0.14
Family Portunidae	
Phlameda charyodis	0.82
Family Xanthidae	
Xanthidae sp 2	0.7
Xanthidae sp 3	0.12
Unknown Megalops	0.12
Unknown Zoea	0.18
Infraorder Caridea	
Family Alpheidae	

Alpheid sp 1	0.12
Family Palaemonidae	
Palaemonidae sp 1	4.37
Palaemonidae sp 2	0.93
Phylum Echinodermata	**3.29**
Class Echinoidea	
Echinoid sp 1	1.23
Echinoid sp 2	0.32
Class Ophiuroidea	
Family Ophiocomidae	
Ophiocomidae sp 1	0.22
Ophiocomidae sp 1b	0.26
Ophiocomidae sp 2	0.61
Ophiocomidae sp 2b	0.52
Ophiocomidae sp 3	0.13
Phylum Mollusca	**82.95**
Class Bivalvia	43.14
Family Isognomonidae	
Isognomon perna	2.73
Family Mactridae	
Mactirdae sp 3	0.14
Family Ostreidae	
Ostrea sanwichensis	0.81
Ostreidae sp 1	38.02
Family Pectinidae	
Pectinidae sp 2	0.77
Pectinidae sp 3	0.67
Class Gastropoda	39.81
Subclass Opisthobranchia	
Family Aplysiidae	
Aplysiidae sp 5	0.18
Subclass Prosobranchia	
Family Architectonicidae	
Architectonicidae sp 1	0.25
Family Atydae	
Atys semistriata	0.62
Diniatys dentifer	0.13
Family Cerithiidae	
Bittium impendens	2.71
Cerithium egenum	0.66
Cerithiidae sp 1	1.56
Family Columbellidae	
Euplilca ionida	0.57
Mitrella sagitta	0.60
Zafrona striatula	0.10
Family Costellariidae	
Vexillum tusum	0.96
Family Dialidae	
Cerithidium diplax	0.11
Diala varia	0.34
Styliferina goniochila	4.24
Family Eulimidae	
Eulimidae sp 4	1.02
Eulimidae sp 7	0.30
Family Phasianellidae	
Tricolia variabilis	8.48

Family Rissoidae	
Merelina granulose	0.58
Merelina hewa	0.12
Rissoina miltozona	1.77
Rissoina pulchella	0.13
Vitricithna marmorata	5.57
Family Thaididae	
Drupa elata	0.28
Family Triphoridae	
Viriola fallax	0.14
Family Trochidae	
Thalotia ocellata	6.89
Trochus intextus	0.63
Family Turridae	
Carinapex minutissuma	0.89
Cummulative percent of total	**94.07**

Temporal Variability in Recruitment

Many species examined exhibited temporal variability in recruit abundance between sampling dates (Table 6). Often the variability appears to follow a trend of increasing then decreasing abundance likely reflecting reproductive seasonality. Although there was no overall concurrent pattern amongst the majority of species, 18 appear to exhibit late Fall recruitment peaks (i.e., Ostreidae sp. 1 and the snail *Styliferina goniochila*) while another 16 species where observed to recruit in increasing numbers through the Spring (i.e., *Tricolia variabilis* and *Thalotia ocellata*). Summer 2004 data (not shown) indicate recruitment patterns of several species likely reflect summer peaks in reproductive activity.

Table 6: Temporal variation in reef invertebrate recruitment. The total number of individuals per species are pooled from all collectors. Shaded cells indicate at least double the median abundance (dark shading= highest, lighter shading = second highest, that is at least 2 times the median value).

Taxa	**10/22/2003**	**12/1/2003**	**1/22/2004**	**3/2/2004**	**4/12/2004**	**5/25/2004**	**Recruit peak**
Phylum Arthropoda							
Class Malacostraca							
Infraorder Anomura							
Galatheidae sp 1	19	18	9	18	27	13	**None**
Infraorder Brachyura							
Majidae sp 2	6	2	0	19	12	5	**Spring**
Phlameda charyodis	28	36	39	52	51	43	**None**
Xanthidae sp 2	38	81	17	18	46	12	**Fall**
Xanthidae sp 3	0	10	3	4	11	7	**None**
Unknown Megalops	4	11	3	7	3	6	**Fall**
Unknown Zoea	7	0	4	35	10	0	**Spring**

Infraorder Caridea							
Alpheid sp 1	5	1	2	6	18	4	**Spring**
Palaemonidae sp 1	598	389	77	100	69	109	**Fall**
Palaemonidae sp 2	0	0	19	28	17	24	**Spring**
Phylum Echinodermata							
Class Echinoidea							
Echinoid sp 1	3	18	161	142	39	8	**Winter/Spring**
Echinoid sp 2	6	8	19	31	24	8	**Spring**
Class Ophiuroidea							
Ophiocomidae sp 1	43	7	3	7	1	6	**Fall**
Ophiocomidae sp 1b	0	12	10	26	24	4	**Spring**
Ophiocomidae sp 2	44	48	9	39	39	8	**None**
Ophiocomidae sp 2b	1	23	14	84	29	5	**Spring**
Ophiocomidae sp 3	1	4	11	16	2	7	**Winter/Spring**
Phylum Mollusca							
Class Bivalvia							
Isognomon perna	61	144	93	121	65	46	**Fall**
Mactridae sp 3	0	0	0	21	18	2	**Spring**
Ostrea sanwichensis	84	61	35	48	10	11	**Fall**
Ostreidae sp 1	1507	3838	1962	2652	905	399	**Fall**
Pectinidae sp 2	7	163	12	5	5	6	**Fall**
Pectinidae sp 3	206	0	0	0	0	0	**Fall**
Class Gastropoda							
Aplysiidae sp 5	0	10	4	7	18	3	**Spring**
Atys semistriata	40	55	8	8	10	31	**Fall**
Diniatys dentifer	0	0	1	5	14	14	**Spring**
Bittium impendens	163	184	34	49	72	275	**Spring**
Cerithium egenum	113	40	1	11	17	19	**Fall**
Cerithiidae sp 1	0	124	83	156	71	30	**Spring**
Euplilca ionida	38	19	31	33	27	27	**None**
Mitrella sagitta	34	44	28	20	41	19	**None**
Vexillum tusum	24	75	39	66	55	36	**Fall**
Cerithidium diplax	0	0	20	8	3	2	**Winter**
Diala varia	4	85	3	0	2	2	**Fall**
Styliferina goniochila	429	563	143	64	52	44	**Fall**
Eulimidae sp 4	50	10	8	25	15	54	**Summer?**
Eulimidae sp 7	0	49	43	0	0	0	**Fall**
Tricolia variabilis	497	120	103	282	345	1271	**Spring**
Merelina granulosa	9	112	25	18	6	0	**Fall**
Merelina hewa	0	4	4	3	3	22	**Spring**
Rissoina miltozona	34	193	99	95	54	50	**Fall**
Rissoina pulchella	0	0	6	23	9	1	**Spring**
Vitricithna marmorata	521	775	87	71	72	156	**Fall**
Drupa elata	5	13	10	17	19	19	**None**
Viriola fallax	3	11	0	20	5	3	**Winter**
Thalotia ocellata	223	281	40	95	96	421	**Spring**
Trochus intextus	27	37	16	15	34	54	**None**
Carinapex minutissuma	49	62	22	54	36	40	**None**

Spatial Variability in Recruitment

For the 20 most abundant recruiting species, differences in recruit abundance among adjacent collectors accounted for the majority of within species variability observed (Table 7). The three most abundant arthropods and several species of gastropods were observed to exhibit very strong differences in recruit abundance among reefs. These patterns were not as clear when comparing net recruitment among collectors from only the three array pair sites (Waikalio, Honokohau, and Manuka) (Table 8). On average, variability in recruit abundance amongst reefs (>1km) was three times greater than either regional (>10km) or within site-paired array (2m) differences, though patterns varied considerably amongst species.

Variation within four of the top 20 species was higher between arrays within a pair than among site or among region variability. Of the four, three are gastropods with restrictive dispersal potential (*Thalotia ocellata, Rissoina miltozona,* and *Caranipex minutissimus*) and the fourth is an unidentified bivalve scallop of the Family Pectinidae (Pectinidae sp. 3). *T. ocellata, R. miltozona,* and Pectinidae sp. 3 were not observed to vary significantly among array pairs within a site (10m). *C. minutissimus* was the only species of the 20 most abundant ones that exhibited significant variation both among and within array pairs. Another seven species showed stronger variation among array pairs than among sites while also exhibiting generally low levels of variation between arrays within a pair.

Only the bivalve species *Isognomon perna* exhibited stronger partitioning at the regional level (>10km) than among or within reefs. For the remaining 19 species examined, all but two (Ostreidae sp.1 and *Tricolia variabilis*) showed little to no regional differentiation in recruit abundance (Table 8).

Some taxa (e.g., bivalves) had higher numbers of recruits at northern sites, with recruitment decreasing to the south, while other taxa (e.g., the snail *Vitricithina marmorata* showed no clear spatial trends in recruitment (Fig. 15).

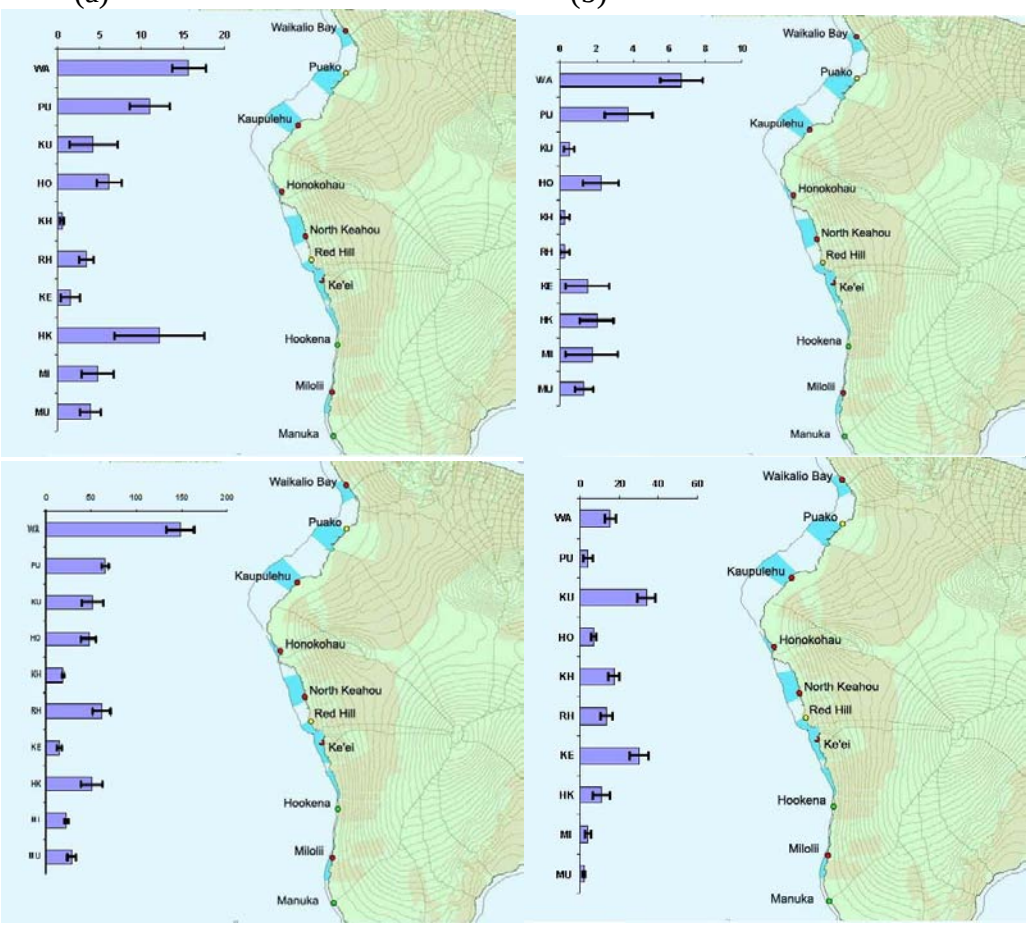
There was generally low variation in numbers of recruits within sites for many of the most common taxa; however some species (e.g., the gastropod *Styliferina goniochila*) showed less spatial coherence within sites, i.e., had one or more subsites with greater variance (Fig. 16).

Table 7: Spatial Variability in Recruitment for the 20 most abundant reef species recruiting along the West Hawai'i coast.

	% Total Variance			
Taxa	**Region**	**Site**	**Array**	**Error**
Phylum Arthropoda				
Class Malacostraca				
Infraorder Brachyura				
Phlameda charyodis	0	40.84	9.03	50.13
Xanthidae sp 2	0	66.45	0	33.55
Infraorder Caridea				
Palaemonidae sp 1	0	66.47	7.11	26.42
Phylum Echinodermata				
Class Echinoidea				
Echinoid sp 1	3.02	0	0	96.98
Class Ophiuroidea				
Ophiocomidae sp 2	3.4	0	0	96.6
Phylum Mollusca				
Class Bivalvia				
Isognomon perna	19.54	15.99	0	64.47
Ostrea sanwichensis	0	21.34	0	78.66
Ostreidae sp 1	24.96	36.89	26.01	12.14
Pectinidae sp 2	7.24	28.18	15.33	49.25
Pectinidae sp 3	0	14.85	42.5	42.66
Class Gastropoda				
Bittium impendens	0	88.34	0	11.66
Cerithium egenum	12.82	30.61	0	56.57
Cerithiidae sp 1	0	50.09	12.69	37.22
Vexillum tusum	22	0	0	78
Styliferina goniochila	0	26.38	6.19	67.43
Tricolia variabilis	21.42	36.42	17.32	24.84
Rissoina miltozona	0	13.7	22.66	63.64
Vitricithna marmorata	0	59.39	9.88	30.73
Thalotia ocellata	7.19	9.2	24.72	58.89
Carinapex minutissuma	0	11.59	40.92	47.49
Mean contribution to variance	6.0795	30.8365	11.718	51.3665

Figure 15: Spatial variation among sites along the West Hawai'i island coast in recruitment of; (a) all bivalves (except purse shells); (b) Scallop # 5; (c) Purse shell bivalves, and (d) the gastropod *Vitricithina marmorata.*

(a) (b)



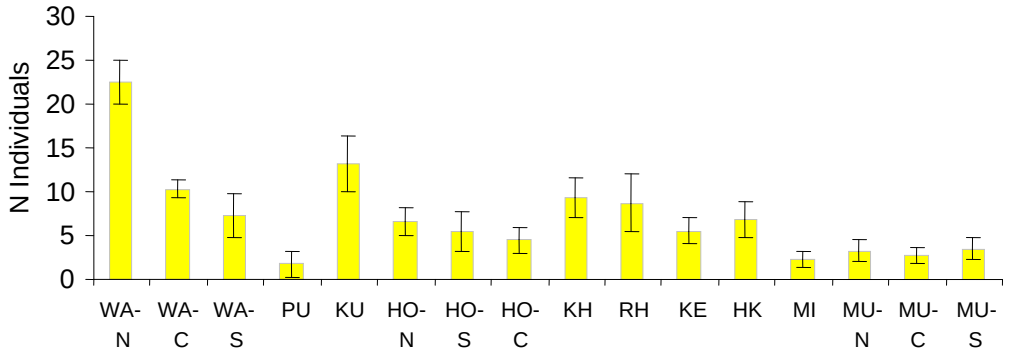
(c) (d)

Table 8: Spatial variability in recruitment for the 20 most abundant recruiting species among array pairs within sites with paired arrays at N, Central and S coast sites (Waikalio, Honokohau, and Manuka). Values in bold denote significant differences at a particular spatial scale (among sites or subsites).

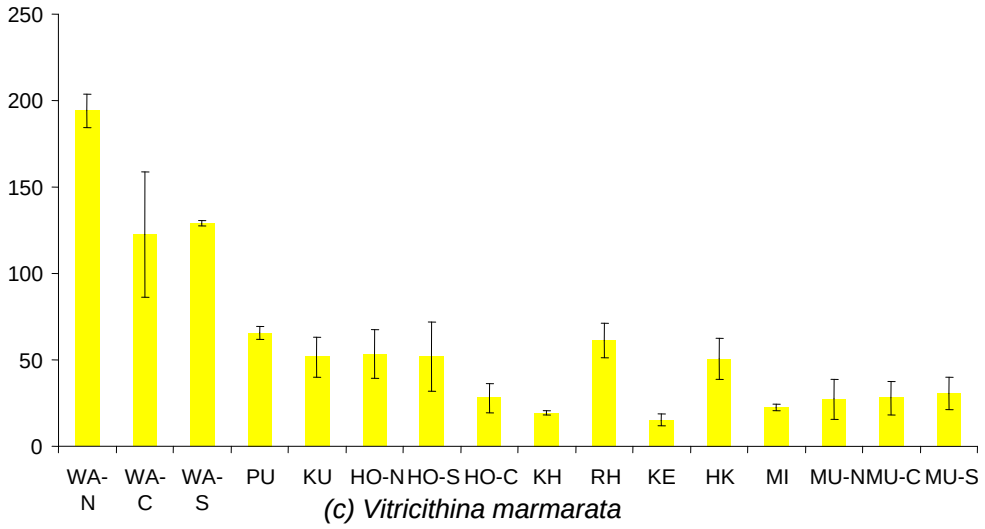
			Nested ANOVA		% Total Variance		
Taxa			***Site***	***Sub-site***	***Site***	***Sub-site***	***Error***
Phylum Arthropoda							
	Class Malacostraca						
		Infraorder Brachyura					
		Phlameda charyodis	0.358	**0**	4.94	56.82	38.24
		Xanthidae sp 2	**0.021**	0.824	21.4	0	78.6
		Infraorder Caridea					
		Palaemonidae sp 1	0.117	**0.018**	26.79	25.68	47.53
Phylum Echinodermata							
	Class Echinoidea						
		Echinoid sp 1	0.148	**0.005**	24.25	32.79	42.96
	Class Ophiuroidea						
		Ophiocomidae sp 2	0.336	0.295	3.06	6.53	90.41
Phylum Mollusca							
	Class Bivalvia						
		Isognomon perna	0.07	0.387	22.72	1.93	75.35
		Ostrea sanwichensis	0.103	0.261	20.09	6.83	73.07
		Ostreidae sp 1	**0.006**	**0.024**	67.22	10.8	21.98
		Pectinidae sp 2	**0.002**	0.631	55.34	0	44.66
		Pectinidae sp 3	**0.047**	0.27	30.88	5.58	63.54
	Class Gastropoda						
		Bittium impendens	0.204	0.608	6.49	0	93.51
		Cerithium egenum	**0.002**	0.563	56.57	0	43.43
		Cerithiidae sp 1	0.119	**0.034**	24.92	22.6	52.48
		Vexillum tusum	0.132	0.259	16.59	7.23	76.18
		Styliferina goniochila	0.273	**0.015**	9.8	32.48	57.71
		Tricolia variabilis	**0.047**	**0.017**	42.65	20.33	37.02
		Rissoina miltozona	**0.04**	0.666	21.36	0	78.64
		Vitricithna marmorata	**0.001**	0.702	56.3	0	43.7
		Thalotia ocellata	0.147	0.914	4.45	0	95.55
		Carinapex minutissuma	0.384	**0.025**	2.06	31.69	66.25

Figure 16: Spatial variation within and among sites along the West Hawai'i island coast in number of recruits of: (a) the gastropod *Styliferina goniochila*; (b) Purse shell bivalves, and (c) the gastropod *Vitricithina marmorata.* Sites along the X axis are arranged from North to South from the origin. Note scale differences on Y axes. Site names are as on Maps 1, 2, Fig. 15.) N, C, and S are Northern, Central, and Southern subsites within sites at Waiakailio, Honokohau, and Manuka.

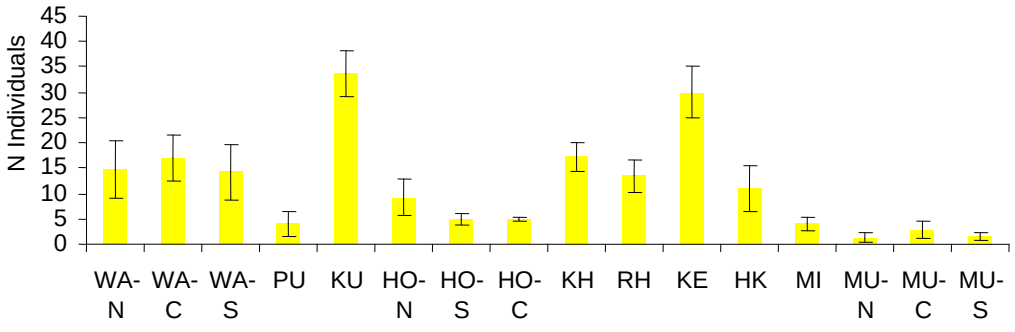
(a) Styliferina goniochila
(snail)



(b) Purse shell



(c) Vitricithina marmarata
(snail)



Sessile Invertebrates -- Corals

A total of only four corals recruited at the two northernmost sites, Waiakailio and Puako, during the first sampling year of this study. This is an extremely low level of annual recruitment. Data from twice annual sampling over the following four years (to be presented in Basch et al. manuscript in prep.) subsequently indicated marginally higher coral recruitment, at the same order of magnitude, with higher rates at the same northern sites, and predominantly Summer-Fall seasonality, supporting an annual reproductive pattern for Hawaiian corals (Jokiel 1987). Given the high intra- and inter-annual variance in coral and other invertebrate recruitment rates typically reported from sites around the world, it is recommended that time series data for coral recruitment continue to be collected to determine if observed coral recruitment off West Hawai'i island remains lower than at most other sites in the Hawaiian islands and worldwide where coral recruitment rates have been reported, and if data indicate that there is actually strong limitation of coral recruitment on West Hawai'i reefs. This data is critical to inform management at the regional ecosystem level for the entire Kona reef tract, given the tremendous ecological, economic and cultural importance of this area and the threats to it.

Life History of Benthic Reef Invertebrates

The existence of seasonal variability in reproductive activity and recruitment is well documented in many marine invertebrate taxa, and in systems at all latitudes (Giese et al. 1987, M. Strathmann 1987. By varying reproductive activity, marine species can take advantage of seasonal conditions that specifically favor the survival, growth, development, or recruitment of their respective larvae or juvenile recruits (Basch 1993, 1996, Basch and Tegner 2007). While seasonal patterns of reproduction and recruitment are known for many invertebrates around the world, less is known about most of the Hawaiian fauna (Kay 1979). However many corals, other invertebrates, and reef fishes in Hawai'i are Spring-Summer spawners which, following a planktonic larval development period, often recruit in Summer-Fall (Walsh 1987 Kolinski and Cox 2003). This variability in recruitment may coincide with mesoscale oceanographic circulation patterns including cool core gyres that form during trade wind periods off the west Hawaii Island coast.

The contrasting reproductive strategies of planktonic and non-planktonic dispersing species establishes a potential basis for explaining differences among species in recruitment and their response to environmental conditions. Identifying the cause(s) of congruous recruitment patterns among multiple species in an area can benefit resource managers by: 1) identifying environmental factors important for the maintenance of a large number of species or individuals, and; 2) supporting hypotheses regarding species ecological requirements based on characterization of one or a few physiological or behavioral traits.

Planktonic dispersers are sometimes thought to optimize the timing and location of gamete or larval dispersal in favor of increased dispersal potential, which would benefit local populations periodically subject to strong disturbance or local extinction by recolonization of planktonic dispersing larvae. Non-planktonic dispersers have been thought to respond differently to environmental factors by selecting for conditions specifically suited to meet their unique life cycle or local environmental requirements. Resulting benthic populations may have localized or lower levels of recruitment relative to species with planktonic larvae.

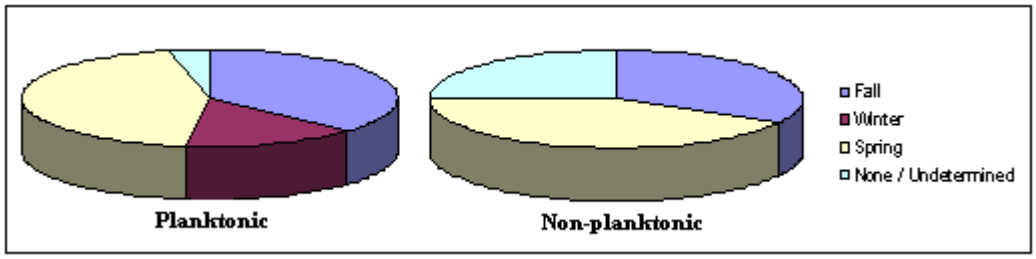
Considerable variation was found in the patterns of recruit abundance among the species collected during our study. Might species reproductive strategy determine optimal timing of recruitment or other aspects of reproduction? Of the 50 most abundant species we collected, we identified 38 species that could be classified as having either non-planktonic or planktonic dispersal. Classification was based on published data. When species-specific data was not available, or when species identification was not fully resolved, classification of planktonic or non-planktonic dispersal was only made if strong generalities existed within families or genera.

There is no apparent difference between planktonic and non-planktonic species in the ratio of seasonal to non-seasonal dispersers (Table 9). Each group had 4-5 times more seasonal than non-seasonal species. This is consistent with reproductive patterns for marine invertebrates globally. Similarly, there were no apparent differences in the timing of seasonal reproduction between dispersal categories with the exception that several (but not most) likely planktonic dispersers exhibited peak recruit abundance in the winter, and recruits of most species occurred in Spring, regardless of dispersal type, suggesting Winter-Spring reproductive peaks (Figure 17). The lack of any obvious difference in patterns of recruit abundance between dispersal categories suggests other factors may be playing a more important role in determining optimal reproductive strategy including: 1) food resource availability and utilization, 2) larval behavior, or 3) planktonic larval duration.

Table 9: Numbers of seasonal vs. non-seasonal breeders for common reef invertebrates with putative planktonic and non-planktonic dispersal strategies.

	Reproductive strategy	
Dispersal strategy	*seasonal*	*non-seasonal*
planktonic	21	5
non-planktonic	10	2

Figure 17: Seasonal patterns in occurrence of recruits in putative planktonic and non-planktonic reef invertebrate taxa.



Multi-Species Patterns in Recruitment

Identification of concurrent patterns of recruitment among several co-occurring species is useful because it helps to determine environmental factors affecting multiple species, thus allowing resource managers to focus conservation efforts on areas with environmental conditions conducive to the recruitment, survival, or maintenance of a number of species. Identifying community scale recruitment

patterns can also aid in identifying optimal MPA placement by identifying sensitive sites such as areas of low recruitment, as well as identifying potential recruitment or diversity hot spots.

Nearly half of the 20 most abundant species showed significant differences in recruit abundance at scales greater than 1km but less than 10km (Table 8). Patterns of recruit abundance among species vary considerably. Nonetheless, concurrent patterns of annual, relative recruit abundance exist among species (Table 10) with a number of sites receiving relatively higher or lower numbers of recruits across a wide range of taxa.

Within 3 of the 4 central sites, half of the 50 most abundant species recruited in lower densities than the among site species average. The fourth (Red Hill) exhibited average relative recruitment. The two central sites, North Keahou and Ke'ei, exhibited the lowest relative recruit abundance (Table 10, Fig. 18). A number of the 50 most abundant species were not found in recruit populations at either site (7 at N. Keahou and 6 at Ke'ei). The remaining species, while found in recruit populations at both sites, were observed to recruit in considerably lower numbers, with 16 and 15 species respectively recruiting at densities 1/3 that of the among site species average.

Contrasting the relative paucity of recruiting invertebrates at the central study sites, Waikalio, the northern-most study site, is notable for its consistently high diversity and abundance of recruits. Of the 50 most abundant recruit species, 37 recruited at densities higher than the among site species average, with 13 species recruiting at 3 times the among site mean (Table 10). Of the 224 distinguishable taxa recorded during the survey period, greater than 65% were observed to recruit at Waikalio, compared with an average of just over 43% of taxa for all sites and a low of 32% at both N. Keahou and Ke'ei (Figure 18).

The contrasting abundance and diversity of recruiting reef invertebrates among sites may be due to the influence of near- and off-shore oceanographic forcing. While the "passive particle" concept of planktonic marine larval transport has come under some scrutiny (Swearer et al. 1999, Jones et al. 1999, Taylor and Hellberg 2003) the effects of oceanography on the dispersal and dispersion of recruits of species with planktonic larvae cannot be discounted.

Oceanographic patterns off the West Hawai'i island coast are quite complex, exhibiting strong seasonal fluctuations in current direction and strength (Wyrtki et al. 1969, Lobel 1989, Storlazzi and Presto 2005). The seasonal increase in the strength of the trade winds causes the formation of large scale oceanic gyres off the leeward (west) coast of the islands of Hawai'i and Maui particularly during the summer months (Fig. 19, Lobel and Robinson 1988). Since the embryos or larvae of many reef animals are in the plankton during the summer season, it is probable that their survival and potential transport to reef habitats suitable for recruitment is in part influenced by the dynamics of gyres. Onshore-offshore movement of these gyres may influence spatial and temporal variation in the transport and supply of coral reef invertebrate larvae which are competent to recruit to the reef, similar to coincident patterns of onshore gyres and the recruitment of reef fishes in summer on the West Hawai'i coast (Figure 20, Tissot et al. 2004). Variation in recruitment may also be affected by coastline aspect, bathymetry, and benthic habitat type. Resulting spatial and temporal differences in the hydrographic regime along the West Hawai'i reef tract creates the potential for among site differentiation in recruitment, and consequently, of the near shore community structure and composition due to spatio-temporal differences in the abundance and composition of recruiting larvae.

Table 10: Interspecific concurrence in the relative abundance of recruits among species. Shaded cells indicate spatial concurrence among species at sites. Values in bold denote significant differences among sites.

Taxa	Waikalio	Puako	Kaupulehu	Honokohau	Keauhou	Red Hill	Ke`ei	Ho'okena	Milolii	Manuka
Phylum Arthropoda										
Class Malacostraca										
Infraorder Anomura										
Galatheidae sp 1	**3**	2.67	0.33	**4.33**	0.33	0	0.33	0.33	1.67	2.44
Infraorder Brachyura										
Majidae sp 2	1.25	2.63	1.5	0.63	0.38	0.38	0.75	1.5	1.13	0.88
Phlameda charyodis	0.99	0.95	1.07	0.8	1.01	1.26	0.63	1.14	0.57	1.37
Xanthidae sp 2	2.21	**12.15**	0.31	1.23	**5.23**	0.92	0.77	1.08	0.15	0.72
Unknown Zoea	0.86	0.86	0	2.29	0	0	2.57	**27.43**	**4.29**	1.14
Infraorder Caridea										
Alpheid sp 1	1.86	1.29	**3**	0.71	0	1.29	0	1.71	0	0.29
Palaemonidae sp 1	1.73	1.28	0.94	0.88	2.31	0.98	0.68	1.02	0.61	1.18
Palaemonidae sp 2	**5.02**	1.87	**3.07**	0.4	0.67	0.27	0.67	1.6	1.33	0.27
Phylum Echinodermata										
Class Echinoidea										
Echinoid sp 1	**3.28**	1.17	1.05	0.62	0.82	0.82	0.93	1.17	1.57	0.95
Echinoid sp 2	1.38	0.92	1.69	0.56	0	0.46	1.23	1.85	1.08	0.77
Class Ophiuroidea										
Ophiocomidae sp 1	2.74	0	0	1.05	0.32	0.63	1.26	1.89	0.95	1.58
Ophiocomidae sp 1b	1.56	0.33	1.17	0.33	1	1	0.33	1.5	1.17	0.44
Ophiocomidae sp 2	1.22	1	1.58	0.69	1.25	1	0.33	0.92	0.83	1.06
Ophiocomidae sp 2b	1.13	0.87	1.04	0.41	0.96	1.13	0.35	1.13	1.22	0.93
Phylum Mollusca										
Class Bivalvia										
Isognomon perna	2.51	1.05	1.03	0.97	0.14	0.72	0.47	1.7	0.68	1.16
Mactirdae sp 3	1.47	0	**3.2**	1.6	0.4	1.2	0	0.8	1.2	0.4
Ostrea sanwichensis	**3.5**	1.04	0.92	2.46	0.12	1.04	0.69	**3.69**	0.58	0.96
Ostreidae sp 1	**3.23**	1.02	1.82	0.92	0.74	1.49	0.59	1.51	0.66	0.98
Pectinidae sp 2	**5.75**	2	0.38	1.13	0.13	0.25	1.88	1.25	0.88	0.83
Pectinidae sp 3	**3.48**	0.72	0.96	1.04	0.24	0.24	2.28	1.68	0.72	1.44
Class Gastropoda										
Aplysiidae sp 5	**4.46**	0.46	0.92	1.08	0	2.77	0	1.85	0	1.23
Architectonicidae sp 1	**3.44**	**6.33**	0.33	0.67	0	1	0	1	1.67	1.11
Atys semistriata	**7.03**	**3.45**	0.36	1.09	1.09	0	0.91	0.36	0.73	1.27
Bittium impendens	1.16	**8.16**	0.94	0.38	1.87	0.81	1.92	1.06	0.7	0.56
Cerithium egenum	0.9	0.73	1.71	1.1	0.73	1.59	0.24	2.69	0.61	**3.51**
Cerithiidae sp 1	1.13	0.47	1.28	0.51	0.17	1.14	0.28	1.14	1	1
Euplilca ionida	1.02	1.12	0.98	0.88	0.28	1.53	2.65	0.28	0.28	**3.86**
Mitrella sagitta	1.61	1	0	1.18	1	0.27	1.73	1.18	1	0.82
Vexillum tusum	1.21	1.18	0.46	0.65	1.69	1.28	1.54	0.56	0.82	0.72

Diala varia	**24.33**	**24**	0	0	0	2	1	0	1	1
Styliferina goniochila	1.24	0.43	1.27	0.76	1.25	1.64	0.64	1.32	0.53	0.6
Eulimidae sp 4	**5.62**	0.09	0.35	0.14	0	2.35	1.48	1.13	0.87	1.3
Eulimidae sp 7	0.67	0	0	0.44	**13.33**	**6.67**	**20.67**	1.33	0.67	**5.11**
Tricolia variabilis	0.31	0.16	0.09	0.85	0.45	2.92	**3.77**	1.15	1.72	2.83
Merelina granulosa	2.07	2.5	0.9	0.47	1.6	1.1	0.3	2.3	0.9	0.27
Merelina hewa	0.55	**7.09**	0	0.91	1.09	**3.82**	1.09	1.09	0.55	0.18
Rissoina miltozona	0.64	1.44	0.9	1.15	1.04	1.46	0.25	2.25	0.96	0.57
Rissoina pulchella	1.2	1.2	1.2	0.8	1.2	2.1	0	0	0	0.1
Vitricithna marmorata	1.2	0.89	2.21	0.28	1.14	0.89	1.96	1.11	0.61	0.42
Drupa elata	0.9	0.77	0.39	1.03	2.52	0.19	1.35	1.35	0.97	1.23
Viriola fallax	**3.67**	1	2	1	0.5	0	0	1	2	0.17
Thalotia ocellata	**5.17**	1.4	0.29	1.29	0.09	0.56	0.57	0.9	1.82	1.1
Trochus intextus	1.77	1.44	2.54	0.9	0.42	1.1	0.08	1.1	0.34	0.48
Carinapex minutissuma	1.65	1	0.44	0.75	1.13	0.5	1	1.63	1	1.1
Median cumulative relative abundance	**1.63**	**1.03**	**0.94**	**0.87**	**0.7**	**1**	**0.685**	**1.16**	**0.88**	**0.97**

Figure 18: Relative frequency of taxa recruiting to various study sites (of n = 224 total taxa).

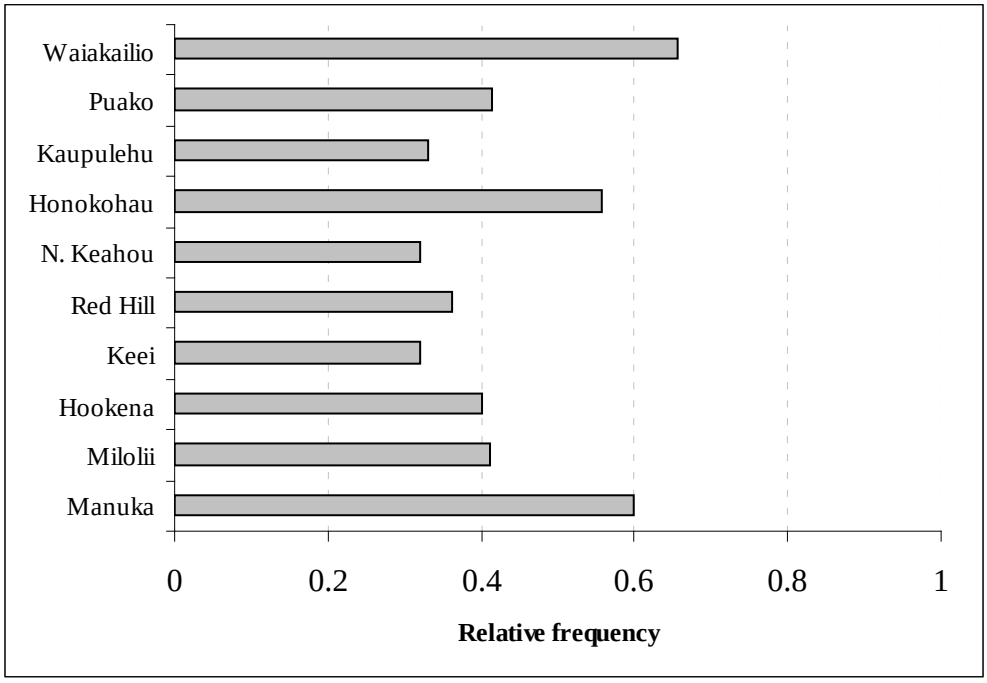
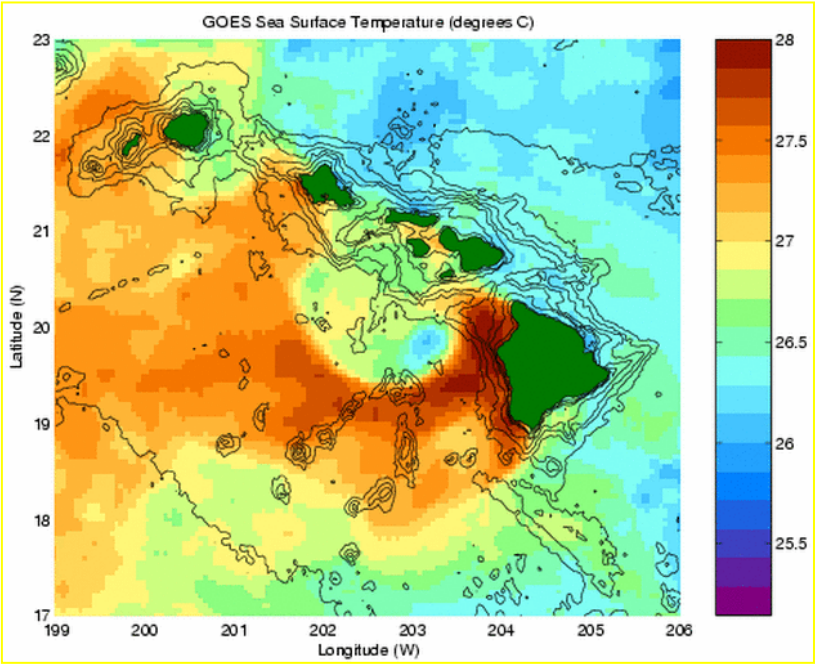


Figure 19: Example of NOAA GOES Satellite Sea Surface Temperature image illustrating nearshore presence of oceanic cool core eddy on west coast of Hawai'i Island in summer (18-19 August, 2003).



A comparison of the taxonomic composition and abundance of the full assemblage of recruits among array pairs reveals similarities, both within sites, and among adjacent sites within a region (Figure 20). As well, there is a clustering of six sites (one northern, two central, and three southern) highlighting similarity in their recruit assemblages. Two pairs of sites stand out from the average and from each other.

North Keahou and Ke'ei seem to be alike not only in their overall lower than average abundance of recruits but also in the overall taxonomic composition of their respective recruit assemblages. The fact that Red Hill, which is situated approximately an even distance between the two, shows more similarity in recruitment to sites considerably further north and south, suggests limited regional spatial cohesion within the central West Hawai'i coast. This suggests that factors other than regional oceanography may be influencing recruitment and community structure within the central region. Similar low recruitment patterns between N. Keahou and Ke'ei might instead be attributed to similarities in either their: 1) suitable habitat available for recruitment, 2) disturbance regimes, or 3) anthropogenic influences. While identifying the cause(s) of low recruitment is important, just recognizing its existence is helpful to marine resource management because, if these trends apply as well to targeted resource species having similar life histories, then their populations at these sites might be more vulnerable to extraction or other anthropogenic impacts and may thus require targeted management.

While Waikalio, the northern-most site, has already been identified as particularly unique, Puako, the next site to the south, appears to be more or less average in terms of the diversity and abundance of its recruit assemblage (with respect to the most abundant species). The similarity between the two sites must then be a product of overall similarities in diversity and abundance amongst the full set of species observed. Are these similarities due to the impact of regionally unique factors or, are they simply due to the impact of distance on recruit assemblage structure with more distant populations exhibiting decreased similarity?

A graph of similarity of recruit populations versus distance among collectors (Figure 21) shows a strong negative correlation ($R^2=.89, P=.03$) with similarity among recruit assemblages decreasing with increasing distance. Manuka and Ho'okena are further from Honokohau than are Waikalio and Puako to one another. Yet, recruitment patterns at Manuka and Ho'okena are quite similar to Honokohau while Waikalio and Puako can be noted for their dissimilarity. Distance alone does not appear to be enough to explain differences in recruiting populations among sites, suggesting the potential that the northern region may be under the influence of unique regional factors. The lack of similarity between Kaupulehu and the two northern most sites suggests Kaupulehu is not subject to the same environmental factors influencing recruitment further north on the West Hawai'i coast. Recruitment at Kaupulehu less similar to Puako (the next closest northern site) than the adjacent southern site (Honokohau), south of Keahole Point. Due to known effects elsewhere of large coastal points or promontories on coastal oceanography, in designing project sampling it was hypothesized that Keahole Point represented a potential cause of spatial differences in recruitment between regions. The similarity in recruitment patterns between Kaupulehu and Honokohau suggests otherwise.

Figure 20: Analysis of similarity (Anosim) of the taxonomic composition and abundance of reef animal recruit assemblages within and among sites along the West Hawai'i coast (blue=northern region, black=central region, grey=southern region) (Clarke and Warwick 2001).

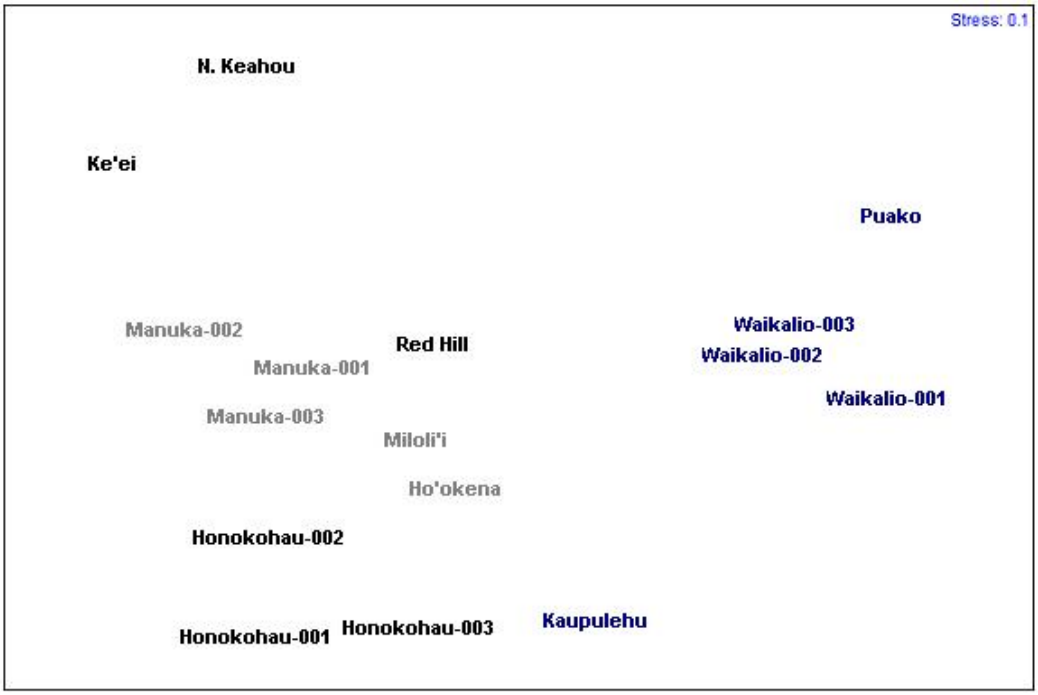


Figure 21: Similarity of recruitment populations with distance among collectors.

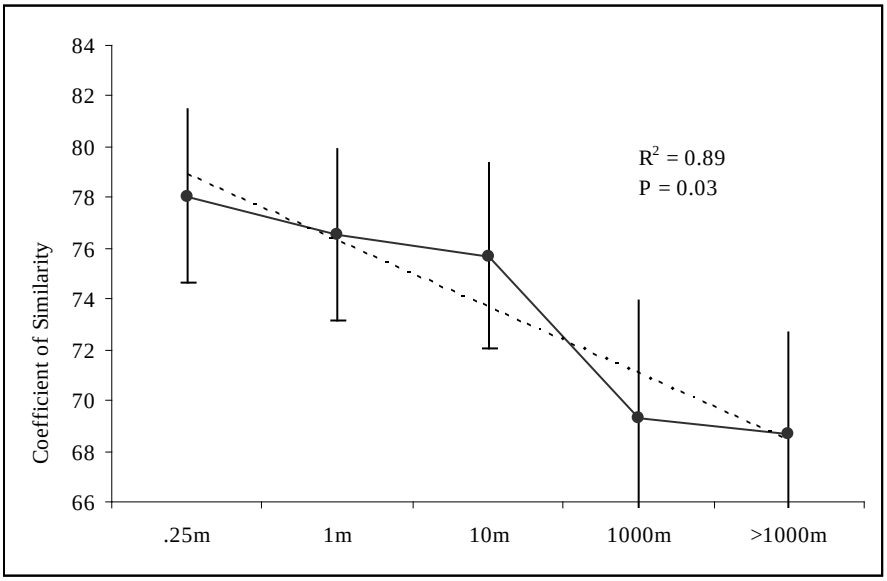


Table 11: Nested ANOVA for common recruit taxa within and among sites having subsites.

NESTED ANOVA (P Values)

Site	*Styliferina goniochila*	*Vitricithina marmorata*	Purseshell	Caridea	*Bittium imperidens*	*Rissoina miltozona*	Scallop 5
Honokoha	u.503	0.243	0.288	0.444	0.699	0.071	0.366
Manuka	0.899	0.665	0.968	0.133	0.11	0.044	0.911
Waikalio	0.001	0.928	0.081	0.024	0.748	0.274	0.531

The pattern of similarity in recruitment among subsites proximate to one another within sites Figures 20, 21) is supported by nested ANOVA. There was no significant within site variation at most sites for common recruit taxa, i.e., no difference in numbers of recruits at sub-sites, within sites (Table 11).

If the occurrence of spatially distinct, seasonal oceanographic regimes has an impact on larval availability among sites, then recruitment patterns may vary concurrently for taxa with similar life histories or reproductive timing. This, in turn, may play an important role in determining the composition of local reef invertebrate populations: i.e., sites subject to pronounced seasonal shifts in oceanographic regimes may more often have recruitment of species whose peaks in reproductive timing are in phase with these seasonal shifts in oceanographic regime.

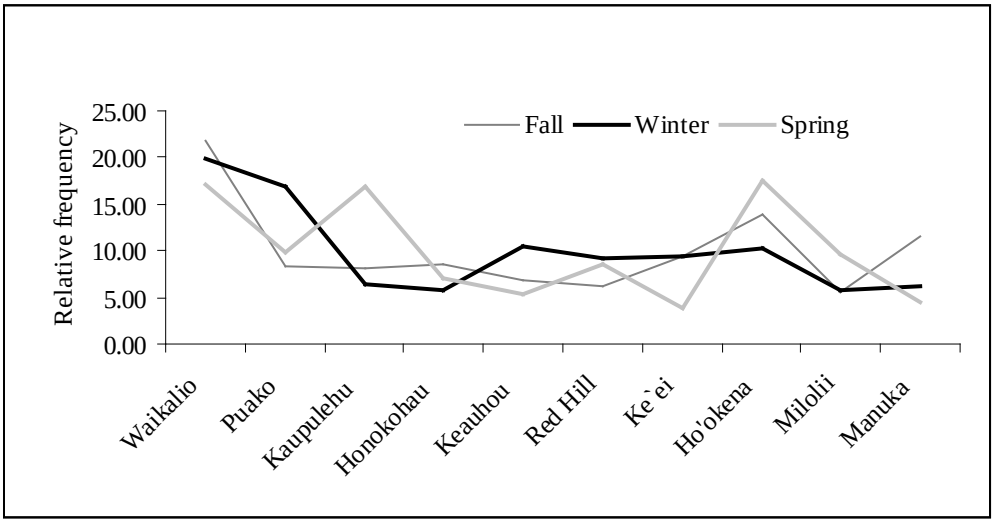
Five of the six most abundant bivalves exhibited a recruitment pulse from mid to late Fall (Table 6). Four of these taxa exhibit three times the among site average recruitment at Waikalio while the fourth (*I. perna*) exhibited 2.5 times the among site average. The only bivalve not recruiting proportionally higher at Waikalio was an unidentified member of the family Mactridae (Mactridae sp. 3) which exhibits a spring peak in reproductive activity (Table 10). Reproductive timing and the concurrent presence or absence of cool core gyres near the coast during trade wind periods at this time of year are linked with increasing productivity and biological enhancement, suggesting the potential importance for recruitment of these factors co-occurring.

The patterns of recruitment we observed in the most abundant bivalves do not hold true for other taxa. A comparison of spatial recruitment patterns from species exhibiting pronounced seasonal peaks in reproductive intensity shows Waikalio to be receiving the majority of recruits throughout the sampling period, with no apparent bias to seasonal differences in the reproductive activity among species (Figure 22). With the exception of spring recruiters, the relative frequency of recruit abundance at Waikalio is typically at least twice that of any other site. Waikalio appears to consistently receive recruits from species with considerably different reproductive seasonality, which may explain the high species diversity observed at Waikalio.

Recruitment is the basic process that supplies, replenishes and maintains populations of coral reef animals. Marine recruitment studies, to provide rigorous, meaningful scientific information useful for resources management require multiple, successive years of data in order to discern natural

variations among years and potential human influences, or the effectiveness of management actions on variation in recruitment. Given the extremely low levels of recruitment found in this study for corals and many other species, and the apparent low levels of recruitment of target species, it would be beneficial for management to minimize other ecosystem stressors, and to continue recruitment studies, with a focus on corals, over several years to provide a baseline of recruitment variation under changing environmental regimes, particularly increase in sea surface temperatures and decrease in pH associated with ocean climate change (Hoegh-Guldberg 1999, Wilkinson 1999) and their known effects on corals and many other reef organisms whose recruitment, survival, and growth depend on maintenance of their calcified skeletons.

Fig 22: Recruitment of taxa with pronounced seasonal reproductive/recruitment peaks among sites.



Acknowledgements

We gratefully acknowledge the U.S. Department of Commerce, NOAA (Grant numbers: NA160A2412, NA03NOS4260044) through the Hawaii Coral Reef Initiative Research Program (HCRI-RP) for support in initiating this study and the U.S. Department of the Interior, National Park Service through the University of Hawai'i, Manoa, Pacific Cooperative Studies Unit (PCSU) and Hawai'i-Pacific Islands Cooperative Ecosystem Studies Unit (H-PI CESU) for continued support for collection of recruitment data time series to inform resource management decision-making at a regional-ecosystem scale. Findings and products mentioned in this report do not imply endorsement by the U.S. Government or other entity. This report was submitted in another format to HCRI-RP. We greatly appreciate the support or assistance in various capacities of the following individuals: USNPS, B. Harry, J. Martin, G. Bell, D. Kawaiaea, S. Beavers, S. Bond, E. Brown, B. Saldua, R. Boston; HCRI-RP, M. Hamnett, R. Minato, K. Davidson, J. Christiansen, and the HCRI-RP Management Committee; Hawai'i DLNR DAR: B. Carman, S. Cotton, I. Williams, W. Devick, D. Polhemus, F. Oishi, R. Nishimoto; West Hawai'i Aquarium Project; University of Hawai'i, Manoa (UHM), C. Birkeland, C. Zabin; UHM Pacific Cooperative Studies Unit and Hawai'i-Pacific Islands Cooperative Ecosystem Studies Unit, D. Duffy, L. Wedding, L. Hara, L. Kinoshita and staff; University of Hawai'i, Hilo, M. DeMaintenon; Bishop Museum, S. Godwin; Team MPA RACE: **R**ecruitment **A**nd **C**onnectivity **E**xperiment.

References

Allison GW, Gaines SD, Lubchenco J, Possingham HP. 2003. Ensuring persistence of marine reserves: Catastrophes require adopting an insurance factor. Ecological Applications. 13(1); S8-S24.

Ballantine WJ 1997. 'No-take' marine reserve networks support fisheries. *In* DAHancock, DC Smith, A Grant and JP Beumer (eds). Developing and Sustaining World Fisheries Resources: The State and Management. Second World Fisheries Congress, Brisbane, Australia. Pp. 702-706.

Barber PH, Palumbi SR, Erdmann MV, Moosa MK. 2000. A marine Wallace's line? Nature 406:692-693.

Basch LV. 1993. Nutrition and the ecology of some marine invertebrate early life history stages. Ph.D. dissertation, UC Santa Cruz. xii + 233 pp.

Basch LV 1996. Effects of algal and larval densities on development and survival of asteroid larvae. Marine Biology 126: 693-701.

Basch LV, Pearse JS. 1996. Consequences of larval feeding environment for settlement and metamorphosis of a temperate echinoderm. Oceanologica Acta 19 (3-4): 273-285.

Basch LV, Keesing J. 1996. Ecology of marine benthic invertebrate juveniles. Oceanologica Acta 19: 466-467.

Basch LV, Engle JM. 1993. Biogeography of *Hemisquilla ensigera californiensis* (Crustacea: Stomatopoda) with emphasis on Southern California Bight populations. Pp. 211-220, in: Third California Islands Symposium: Recent Advances in Research on the California Islands, FG Hochberg, ed. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Basch LV, Tegner MJ. 2007. Reproductive responses of sea urchin *Strongylocentrotus purpuratus* populations to environmental conditions across a coastal depth gradient. Bull. Marine Science 81 (2): 255-282.

Basch L, Leemhuis A, White J, Walsh WJ. 2008. Recruitment Dynamics of Scleractinian Corals in a Network of National Parks and Marine Protected Areas: West Coast Hawai'i Island. Abstract, Proceedings 11th International Coral Reef Symposium, Ft. Lauderdale, Fl.

Bernardi G, Holbrook SJ, Schmitt RJ. 2001. Gene flow at three spatial scales in a coral reef fish, the three-spot dascyllus, *Dascyllus trimaculatus*. Marine Biology 138:457-465.

Birkeland C, Friedlander AM. 2001. The importance of refuges to reef fish replenishment in Hawaii. Honolulu: The Hawaii Audobon Society. 19pp.

Birkeland C, Lucas JS.1990. *Acanthaster planci*: major management problem of coral reefs. CRC Press, Boca Raton, Florida. 257 p.

Botsford LW, Hastings A, Gaines SD. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecology Letters 4:144-150.

Brown EK. 2004. Reef coral populations: Spatial and temporal differences observed at six reefs off West Maui. Ph.D. Thesis, University of Hawai'i, 277 p.

Christie MR, Eble JA. 2009. Isolation and characterization of 23 microsatellite loci in the yellow tang, *Zebrasoma flavescens* (Pisces: Acanthuridae). Molecular Ecology Resources, 9 (2): 544 – 546.

Clarke KR, Warwick RM. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E, Plymouth, UK.

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB. 2000. Connectivity of marine populations: Open or closed? Science 287:857-859.

Dunstan PK, Johnson CR.1998. Spatio-temporal variation in coral recruitment at different scales on Heron Reef, southern Great Barrier Reef. Coral Reefs Volume 17 (1): 71-81

Eble JA, Toonen RJ, Bowen BW. 2009. Endemism and dispersal: comparative phylogeography of three surgeonfishes across the Hawaiian Archipelago. Mar. Biol. 156 (4): 689-698.

Friedlander AM, DeMartini EE. 2002. Contrasts in density, size, and biomass of reef fishes between the Northwestern and the Main Hawaiian Islands: the effects of fishing down apex predators. Marine Ecology Progress Series 230: 253–264**.**

Gaines SD.2001. Catastrophes: where the unlikely becomes probable. In: AAAS Annual Meeting. San Francisco.

Giese AC, Pearse JS, Pearse, VB, editors. 1987. Reproduction of Marine Invertebrates Vol. IX: General Aspects: Seeking Unity In Diversity. Boxwood Press, Pacific Grove, CA. 211p.

Glassom D, Zakai D, Chadwick-Furman NE. 2003. Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. Mar. Biol.144 (4): 641-651.

Halpern B. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications Vol. 13, Supplement: Marine Reserves, pp. 117-137.

Hastings A, Botsford LW. 1999. Equivalence in yield from marine reserves and traditional fisheries management. Science 284:1537-1538.

Hixon MA, Boersma PD, Hunter ML, Jr, Micheli F, Norse EA, Possingham HP, Snelgrove PVR. 2001. Oceans at Risk: Research Priorities in Marine Conservation Biology. In: Soulé ME, Orians GH eds) Conservation Biology: Research Priorities for the Next Decade, p 307. Covelo, CA: Island Press.

Hodges MH, Allendorf FW. 1998. Population genetics and pattern of larval dispersal of the endemic Hawaiian freshwater amphidromous gastropod *Neritina granosa* (Prosobranchia: Neritidae). Pacific Science 52:237-249.

Hoegh-Guldberg O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50:839-866.

Hughes TP, Baird AH, Dinsdale EA, Harriott VJ, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL. 2002. Detecting regional variation using meta-analysis and large scale sampling: latitudinal patterns in recruitment. Ecology 83:436-451.

Jokiel PL. 1987. Ecology Biogeography and Evolution of Corals in Hawaii. Trends in Ecology & Evolution 2:179-182.

Jones GP, Milicich MJ, Emslie MJ, Lunow C. 1999. Self-recruitment in a coral reef fish population. Nature (London) 402:802-804.

Kay A. 1979. Hawaiian marine shells, Reef and shore fauna of Hawaii, section 4; Bishop Museum Press, Honolulu, Hawaii. 653 p.

Kolinski SP. 2004. Sexual reproduction and early life history of *Montipora capitata* in Kaneʻohe Bay, Oʻahu, Hawaiʻi. Ph D. Dissertation Dept of Zoology. University of Hawaiʻi. 151p.

Kolinski SP, Cox EF. 2003. An Update on Modes and Timing of Gamete and Planula Release in Hawaiian Scleractinian Corals with Implications for Conservation and Management Pacific Science 57 (1): 17-27.

Lobel PS. 1989. Ocean current variability and the spawning season of Hawaiian reef fishes. Environmental Biology of Fishes 24:161-172.

Lobel PS, Robinson AR. 1988. Larval fishes and zooplankton in a cyclonic eddy in Hawaiian waters. Journal of Plankton Research 10:1209-1223.

Mascia MB. 2001. Designing effective coral reef marine protected areas. IUCN. 22pp.

McClanahanTR, Kaunda-Arara B. 1996. Fishery recovery in a coral reef marine park and its effects on the adjacent fishery. Conservation Biology 10:1187-1199.

McCormick MI.1994. Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the northern Great Barrier Reef Lagoon. Mar Ecol Prog Ser 103: 1-15.

Miyasaka A. 1997. Status report, aquarium fish collections, fiscal year 1994-95. Division of Aquatic Resources, Department of Land and Natural Resources, State of Hawaii. Honolulu, Hawaii, USA. 10 p.

Mundy CN. 2000. An appraisal of methods used in coral recruitment studies. Coral Reefs 19: 124-131.

National Center for Ecological Analysis and Synthesis. 2001. Scientific Consensus Statement on Marine Reserves and Marine Protected Areas. Santa Barbara: University of California, Santa Barbara.

NRC (National Research Council). 2001. Marine Protected Areas: Tools for Sustaining Ocean Ecosystems. National Academy Press, Washington, D.C.

Palumbi S R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. Ecological Applications 13:S146-S158.

Parnell PE. 2000. The effects of circulation, larval planktonic period, adult distribution and pollution on benthic recruitment in Hawaiian waters. Ph.D. Dissertation, Oceanography Department, University of Hawai'i, Manoa. xx + 274 pp.

Pearse JS. 1974. Reproductive patterns of tropical reef animals: three species of sea urchins. Proc. 2nd Intl. Coral Reef Sym. 1:235–240

Polovina JJ, Kleiber P, Kobayashi DR.1999. Application of TOPEX-POSEIDON satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands, 1993-1996. Fishery Bulletin 97:132-143.

Radtke RL, Kinzie RA, Shafer DJ. 2001. Temporal and spatial variation in length of larval life and size at settlement of the Hawaiian amphidromous goby *Lentipes concolor*. Journal of Fish Biology 59:928-938.

Richmond RH. 2001. Reproduction and recruitment in corals: critical links in the persistence of reefs. Chapter 8, pp. 175-197 in: C. Birkeland (Ed.), Life and Death of coral reefs. 3rd printing, Kluwer Academic Publ., Boston. 536 p.

Roberts CM.1997. Connectivity and management of Caribbean coral reefs. Science (Washington D C) 278:1454-1457.

Roberts CM. 1998. Sources, sinks, and the design of marine reserve networks. Fisheries 23:16-19.

Roberts CM, Halpern B, Palumbi SR, Warner RR. 2001a. Reserve networks: why small, isolated protected areas are not enough. Conservation Biology in Practice. 2(3): 13-19.

Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R. 2001b. Effects of marine reserves on adjacent fisheries. Science 294:1920-1923.

Rogers C, Garrison G, Grober R, Hillis Z-M, Franke MA. 1994. Coral reef monitoring manual for the Caribbean and Western Atlantic. National Park Service, Virgin Islands National Park, and USGS, St. John, USVI.

Rumrill, SS. 1990. Natural mortality of marine invertebrate larvae. Ophelia 32: 163-198.

Ruttenberg B, Hamilton S, Warner R. 2008. Spatial and temporal variation in the natal otolith chemistry of a Hawaiian reef fish: prospects for measuring population connectivity. Canadian J. Fish. Aquatic Sci. 65 (6): 1181-1192.

Schubart CD, Basch LV, Miyasato G. 1995. Recruitment of *Balanus glandula* Darwin (Crustacea: Cirripedia) into empty barnacle tests and its ecological consequences. J. Exp. Mar. Biol. Ecol. 186: 143-181.

Shafer DJ.1998. Early life history growth and settlement dynamics of a tropical reef fish (Gobiidae: *Bathygobius coalitus*). Ph.D. Dissertation, Department of Zoology, University of Hawai‘i

Shafer DJ. 2000. Evaluation of periodic and aperiodic otolith structure and somatic-otolith scaling for use in reconstruction of the early life history of a tropical marine goby, *Bathygobius coalitus.* Marine Ecology Progress Series 199: 217-229

Shanks AL, Grantham BA, Carr MH. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecol. Applications 13 Supplement: Marine Reserves: 159-169.

Soong K, Chen M, Chen C, Dai C, Fan T, Li J, Fan H, Kou K, Hsieh H. 2003. Spatial and temporal variation of coral recruitment in Taiwan. Coral Reefs 22(3): 224-228.

Smith J E, Hunter CL, Smith CM. 2002. Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. Pacific Science 56(3): 299-315.

Storlazzi C, Presto K. 2005. Coastal Circulation and Water Column Properties along Kaloko-Honokohau National Historical Park, Hawaii PART I: Measurements of waves, currents, temperature, salinity and turbidity: April-October 2004 U.S. Department of the Interior U.S. Geological Survey Open-File Report 2005-1161. 30 p.

Strathman MF. 1987. Reproduction and development of marine invertebrates of the Northern Pacific Coast. University of Washington Press, Seattle, WA. 670 p.

Swearer SE, Caselle JE, Lea DW, Warner RR. 1999. Larval retention and recruitment in an island population of a coral-reef fish. Nature 402:799-802.

Taylor, MS, Hellberg ME. 2003. Genetic Evidence for Local Retention of Pelagic Larvae in a Caribbean Reef Fish. Science 299: 107-109.

Thorson G**.**1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev., 25: 1-45.

Tissot BN, Walsh WJ, Hallacher LE. 2004. Evaluating effectiveness if a Marine Protected Area Network in West Hawai'i to increase productivity of an aquarium fishery. Pacific Science 58 (2): 175-188.

Victor BC.1982. Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. Mar. Biol. 71: 203-208

Walsh WJ.1987. Patterns of recruitment and spawning in Hawaiian [USA] reef fishes. Environmental Biology of Fishes 18:257-276.

Walsh WJ, Cotton SP, Dierking J, Williams ID. 2003. The commercial marine aquarium fishery in Hawai`i 1976-2003. In: Friedlander A.M. (ed) Status of Hawai`i's Coastal Fisheries in the New Millennium. Proceedings of a Symposium sponsored by the American Fisheries Society, Hawai`i Chapter. pp. 132-159.

Wilkinson CR. 1999. Global and local threats to coral reef functioning and existence: Review and predictions. Marine and Freshwater Research 50:867-878.

Williams ID, Walsh WJ, Schroeder RE, Friedlander AM, Richards BL, Stamoulis KA. 2008. Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. Environmental Conservation 35: 261-272.

Williams ID, Walsh WJ, Claisse JT, Tissot BN, Stamoulis KA. 2009. Impacts of a Hawaiian marine protected area network on the abundance and fishery sustainability of the yellow tang, *Zebrasoma flavescens*. Biol. Cons. 142:1066-1073

Wilson DT, McCormick MI.1997. Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. Mar. Ecol. Prog. Ser. 153: 259-271

Wilson DT, McCormick MI.1999. Microstructure of settlement-marks in the otoliths of tropical reef fishes. Mar. Biol. 134: 29-41

Wyrtki K, Graefe V, Patzert W.1969. Current observations in the Hawaiian archipelago. Honolulu, HI: Hawaii Institute of Geophysics. 97 pp.