

**COMMUNITY STRUCTURE, LIFE HISTORY, AND MOVEMENT
PATTERNS OF PARROTFISHES: LARGE PROTOGYNOUS FISHERY
SPECIES**

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ABSTRACT

Populations of large protogynous coral reef fishes such as parrotfish are diminishing worldwide. Management strategies to mitigate anthropogenic stressors on these fish are hampered by a paucity of basic biological data, and reproductive and population dynamics models that are inadequate for the complex socio-sexual systems exhibited by these fish. This study provides critical biological information on community dynamics, life history and movement patterns of parrotfishes, and provides input on more effective management strategies.

Fishing pressure and habitat degradation are important stressors on parrotfish communities in Oahu, Hawaii. Parrotfish communities were dominated by small, unfished species and smaller size classes of all species. Good quality reef habitat, characterized by higher proportions of live coral cover and more rugose benthic topography, were positively associated with scarid communities. Oahu parrotfish populations, particularly fished species, are stressed, and current management strategies should be modified to better mitigate anthropogenic stressors.

Life history characteristics of parrotfish also indicate that current management regimes in Hawai'i should be modified. The current minimum size limit of parrotfish catch in Hawai'i is 12 inches in fork length, yet 50% of *Scarus rubroviolaceus* are immature until they reach almost 13.5 inches in fork length. Life history data suggest that management strategies should be employed to

protect large female and male parrotfish, so as to prevent reductions in egg production or sperm limitation. Current reproductive and population dynamics models ignore alternative mating strategies as indicated by the presence of non-sex-changed males. These males may be important to sex ratios and reproductive dynamics, and the degree to which these males occur in a population may be an indicator of overexploitation.

Movement and behavioral patterns of *Scarus rubroviolaceus* suggest that marine reserves may be an effective management strategy to complement the current management regime in Hawai'i. Individuals have discrete home ranges and are site attached. However, individuals make long distance forays from their home ranges (at least 400 m), indicating that small reserves may not fully protect all individuals. There may also be sex-specific biases in movement patterns and in reproductive and sleeping site locations, which should be considered in marine reserve design.

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CHAPTER 1

General Introduction

Many modern fisheries management models and tools were developed for managing broadcast spawning, gonochoristic (distinct sexes) species, but have been applied to the full spectrum of fish reproductive strategies. The reproductive biology of fishes is extremely diverse, and species exploited in fisheries include long-lived viviparous species, brooding species, sex changing species, and others. With such diverse life histories, “one size” does not fit all, and some fisheries management tools (e.g. minimum size limit of catch and Spawning Stock Biomass Per Recruit models) have been widely implemented, sometimes with poor fit for fish species with differing reproductive modes (Russ 1991, Munro 1996, Alonzo & Mangel 2004). The limited success of these approaches may be due primarily to a lack of alternative models, management tools and basic biological information that would support more effective management strategies.

Hermaphrodites are among the reproductive guilds for which fishery management has been problematic. Hermaphroditism is a common reproductive mode, particularly among coral reef fishes, present in almost 50% of reef fish families (Sadovy 1996). There is considerable evidence that hermaphrodites may be particularly vulnerable to fishing pressure and other anthropogenic stressors compared to their gonochoristic counterparts (Sadovy 1996, Armsworth 2001, Alonzo & Mangel 2004, Birkeland & Dayton 2005). As ubiquitous, yet susceptible members of reef fisheries, hermaphrodites warrant concentrated

efforts to obtain basic biological information and improve fisheries models and management input for this group.

Hermaphroditism and Sex Change

Differences in gonad structures suggest that hermaphroditism has originated many times among teleost fish (Smith 1975). The extraordinary plasticity in teleost sexuality, including reproductive patterns (gonochorism, hermaphroditism, parthenogenic reproduction, etc.), is attributable to the labile nature of teleost gonads. Teleosts generally lack sex chromosomes, and both female and male gonadal somatic cells arise from the same origin. It has been suggested that hermaphroditism may merely be a delayed expression of larval or juvenile sexual differentiation (Shapiro 1987).

Protogynous hermaphroditism, where individuals begin life as female and can change sex to male, is particularly common among coral reef fishery species. Protogynous hermaphrodites may be monandric (all males are derived from sex changed females) or diandric (some portion of males are non-sex-changed). Prematurational sex change has also been described for some protogynous hermaphrodites, where individuals pass through an ovarian stage and develop testes, before reaching sexual maturity (Francis 1992). Because true diandric males could still exhibit some vestigial ovarian tissue, diandric males and males derived from prematurational sex change are difficult if not impossible to distinguish positively (Francis 1992).

The first models to predict the circumstances under which hermaphroditism would be expected to arise were provided by Ghiselin (1969). Ghiselin's Size Advantage Model predicted that protogynous hermaphroditism would be advantageous over gonochorism when the reproductive function of one sex has a size-related advantage, such as in sexual selection for large males. Numerous models have been developed to modify the Size Advantage Model and better understand the timing and nature of sex change from mature females to males (Warner 1975, Warner et al. 1975, Munoz & Warner 2003, Munday et al. 2006, Clifton & Rogers 2007). This has been the most intensely studied aspect of protogynous hermaphrodite biology, largely because these dynamics powerfully influence our ability to estimate parameters relating to population dynamics and reproductive output.

The mechanism by which sex change occurs has also received considerable attention. All the currently proposed hypotheses include inhibition or induction by cues related to social group dynamics: male inhibition of females' endogenous tendency to change sex (Robertson 1972), sex or size ratio cues (Shapiro 1991), or combined effects of inhibition by males and induction by smaller females (Ross et al. 1983).

Because social cues are so closely associated with sexual identity, protogynous hermaphroditism is often associated with complex social dynamics and unique behavioral characteristics. Factors influencing the presence and extent of diandric or prematurationally sex-changed males in populations of protogynous hermaphrodites are poorly understood, but abiotic environmental conditions and

social conditions seem critical (Robertson 1972, Francis 1992, Munday et al. 2006). Likewise, sex change from female to male seems to be triggered by local hierarchical, social interactions (Warner et al. 1975, Robertson & Warner 1978, Warner & Hoffman 1980, DeMartini et al. 2005, Oldfield 2005).

For protogynous hermaphrodites sexual dichromatism occurs such that females and primary males (diandric and prematurationally sex changed males) often have drab coloration (hereafter called initial phase (IP)), and large, primarily sex-changed, males are more colorful (hereafter called terminal phase (TP)). It is suspected, but not confirmed, that IP males may be able to change to TP coloration after reaching a large size. Mating systems where a TP male defends a spawning and/or feeding territory from other males and maintains a harem of females within that territory are typical of protogynous hermaphrodites. However, even for a social structure such as this, numerous variations may occur, even intraspecifically, due to local social and environmental conditions (Warner & Hoffman 1980, Shapiro 1991, deGirolamo et al. 1999).

Study Species and Study Location

Parrotfish (Scaridae) were chosen for this research because of their ecological importance as bioeroders, their economic importance in commercial, artisanal, and recreational fisheries worldwide, and the paucity of current information on these species, particularly in Hawai'i. There are over 90 species of parrotfish worldwide, in 10 genera, and half of these species are in the genus *Scarus* (Streelman et al. 2002). The family exhibits a broad size range, with

maximum sizes of individual species from 20 cm (*Leptoscarus vaigiensis*) to 150 cm (*Bolbometopon muricatum*).

Hawai'i hosts seven species of parrotfish, three of which are endemic. These species are found throughout the islands. Hawaiian parrotfish range in maximum size from ~30 cm (*Scarus psittacus*) to over 70 cm (*Scarus rubroviolaceus*) total length (TL). All Hawaiian scarids are sexually dimorphic, exhibit the general scarid socio-sexual system, and at least some species have mature initial phase males. The degree to which these fish are exposed to fishing pressure depends on the human population (highest on Oahu where fishing pressure is greatest) and differs among species, with the largest species being most targeted.

Despite their ecological and economic importance, very little is known about the basic life history, reproductive biology and population dynamics of Pacific scarids, and even less is known that is specific to Hawai'i. In Hawai'i there is growing concern over the status of scarid populations. Anecdotally, stakeholders (fisheries managers, fishermen, and conservationists) are noticing declines in both the numbers and sizes of parrotfish. However, there is no reliable baseline population-level information because these data are incomplete and difficult to interpret. Non-reporting by licensed and non-licensed commercial fishermen is a major problem. There are no adequate data on recreational or subsistence fishing for any fish species, and for inshore fishes such as parrotfish, the vast majority of the catch probably results from recreational fishing (Smith 1993).

Existing fisheries management regulations in Hawai'i include a minimum size limit for catch, covering all parrotfish species as one group, and placed at 12 inches fork length (FL). Management based on minimum size limits should be supported by reproductive data, with size limits set to ensure that at least some of the population of each species harvested attains sexual maturity before being exposed to fishing pressure. It is inappropriate to combine species of different sizes at sexual maturity, which probably have very different life history and reproductive regimes, under the same size limit management strategy. Larger, slow-growing and late-maturing species are probably more vulnerable to fishing pressures than smaller, fast-growing and early-maturing species (Jennings et al. 1999a, Jennings et al. 1999b) and should therefore be managed differently. Research on the biology of parrotfish, particularly in terms of demographic and life history studies, is urgently needed to support efforts in conservation and management of exploited parrotfish species.

Objectives of the Present Study

Given the extraordinary complexities related to sexual identity and mating systems for protogynous hermaphrodites, it is no wonder that fisheries scientists struggle to understand life history and population dynamics of these species, much less provide appropriate management recommendations. This dissertation contributes to the growing body of knowledge on the biology of protogynous hermaphrodites by introducing information on poorly studied species of the parrotfish (Scaridae) family, primarily *Scarus rubroviolaceus*. This research was

conducted in Hawai'i, an area where parrotfishes have been virtually unstudied. This dissertation uses this basic biological information to explore the role of anthropogenic stressors, such as fishing pressure and habitat degradation, on protogynous hermaphrodites, and provides suggestions for management strategies to mitigate these impacts. This dissertation is composed of three sections that address the following questions: (1) What is the present status of parrotfish communities in Hawai'i, and what anthropogenic factors are influencing these communities? (Chapter 2), (2) How do life history characteristics shape the response of *S. rubroviolaceus* to anthropogenic stressors, and how can fisheries managers use this information to more effectively manage stocks of this species? (Chapter 3), (3) What are the movement and social patterns for *S. rubroviolaceus*, how do they affect population and distribution dynamics, and how do these results inform management decisions? (Chapter 4).

CHAPTER 2

Community Structure and Habitat Associations of Parrotfishes on Oahu, Hawai'i

INTRODUCTION

Parrotfish (Family: Scaridae) play an important role in coral reef ecosystems throughout the tropics, functioning both as bioeroders and algal consumers (Choat 1991, Bellwood et al. 2004, Mumby 2006). They are also an important component of many small-scale commercial, artisanal and subsistence coral reef fisheries (Smith 1993, Page 1998, Jennings et al. 1999b). There is growing concern about the status of scarid populations in many parts of their geographic range. Because of their life history and behavioral traits, parrotfish may be particularly susceptible to detrimental effects of fishing pressure. These fishes are sequential hermaphrodites, with the ability to change sex from female to male. Since individuals primarily begin life as females and only some individuals change sex, populations of sequential hermaphrodites have female-biased sex ratios. Parrotfish are also easily caught while resting at night, and the widespread use of SCUBA to harvest parrotfishes has also increased catches substantially (Smith 1993, Jennings et al. 1999b). Because of its greater impact, spearing fish while using SCUBA has been prohibited in some countries, but it remains legal in Hawai'i.

The abundance of reef associated herbivorous fish may be reduced when the physical structure of the reef deteriorates due to coral mortality and/or anthropogenic nutrient-driven phase shifts from coral-dominated environments to algal-dominated environments (Done 1992, Williams & Polunin 2001). Numerous studies have documented the importance of topographic structure or cavities in reef environments as refugia from predation, particularly for juvenile fish (Risk 1972, Roberts & Ormond 1987, Williams et al. 2001). Therefore, although algal dominated reef communities initially increase the food supply, they may ultimately impede population growth of herbivorous fish by reducing topographic relief, and there may be an algal threshold above which herbivores cannot control algae (Williams & Polunin 2001, Williams et al. 2001). With reduced herbivore abundance the problem of algal overgrowth of coral can be exacerbated (Conklin & Stimson 2004, Mumby 2006).

Because parrotfish are dominant herbivores throughout the tropics and management of their populations is important to maintain overall reef health, we must understand the structure of parrotfish communities and how those communities interact with degraded habitats. Studies investigating habitat associations with scarid community characteristics (e.g. biomass, species richness) have often produced conflicting or inconclusive results. For example, Bell & Galzin (1984) and Tolimieri (1998) found significantly higher numerical abundance of scarids with greater coral cover. However, Gust (2002), Hart et al. (1996), and Ohman & Rajasuriya (1998) found no significant correlations between benthic habitat measures, including coral cover, and scarid abundance.

No consistent, broad-scale pattern of family-level trends in scarid-habitat associations is evident from these studies, and patterns found in the reported studies may largely reflect regional differences or study methodology or both.

The present study investigates parrotfish-habitat associations in Hawai'i over a relatively large geographic area. Hawai'i has seven species of scarids, three of which are endemic (Table 2.1). All seven species are found throughout the Hawaiian archipelago. These species range in maximum total length (Ledlie et al.) from ~30 cm (*Scarus psittacus*) to over 70 cm (*S. rubroviolaceus*) and exhibit dimorphic coloration (termed initial phase and terminal phase). This study was designed to describe the community structure of parrotfish on Oahu, Hawai'i (including species composition, biomass and numerical abundance) and to investigate the parrotfish associations with various habitat characteristics. A secondary goal of this study was to predict the potential effects that continued habitat degradation might have on parrotfish communities in Hawai'i.

METHODS

Study Site

Previous fish assemblage analyses in Hawai'i indicate that scarids are the second most abundant reef fish family by weight in the Main Hawaiian Islands (Friedlander et al. 2003). No prior attempt has been made to thoroughly characterize parrotfish populations around any of the Hawaiian islands, and few

studies have been conducted to characterize populations of any Hawaiian nearshore fisheries species.

The field portion of this study was conducted around the island of Oahu (Figure 2.1) from November 2005 through to March 2007. Oahu has the most dense human population of the islands in Hawai'i and correspondingly has some of the most heavily fished reefs and most degraded habitat (Smith 1993). Oahu has a few small marine reserves offering various degrees of protection from fishing, and these reserves were included as potential sampling sites in this study.

Sampling Design

Sampling followed a hierarchical stratified random design with two levels: island sector and habitat type. Oahu was first categorized into four sectors (north, south, windward and leeward), which roughly correspond to the directions of exposure to seasonal swells. Coarse-scale habitat types were classified by GIS-based benthic habitat maps developed by the National Oceanic and Atmospheric Administration's National Ocean Service (NOAA/NOS) (Coyne et al. 2003). These maps were developed using orthorectified aerial photographs and hyperspectral imagery, and have been used in other fish community-habitat associations (Friedlander & Brown 2003). Three major bottom types representing potential parrotfish habitat were sampled: hard bottom colonized by coral (CH); uncolonized hard bottom (UH); and macroalgae (MA). Within each of these habitat types, random starting points for underwater visual censuses were generated using the Animal Movement extension to ArcView 3.2 (Hooge &

Eichenlaub 1997). The random point generator was restricted to only create points that were at least 100 m distant from the edge of a habitat type.

A total of 140 transects were conducted, with a minimum of 20 transects for each sector (Samoilys & Carlos 2000) (see Figure 2.1 for locations of all transects). The number of transects conducted on each shoreline and within each habitat were representative of the potential area available (Table 2.2). Only habitat patches larger than the transect size were sampled. In the West sector, for example, there were only a few small areas of CH habitat available to sample, and none of these permitted transects through contiguous CH habitat, so no transects of this kind were conducted in this sector.

Survey Methods

Prior to surveys, divers were trained to estimate fish size under water using fish models of known length (Bell et al. 1985, Friedlander et al. 2003). A team of two divers conducted 5 m x 100 m transect surveys, at a relatively constant depth as indicated with a depth gauge, within a habitat type. For each transect, parrotfish data were recorded (number, species, total length (TL) to the nearest cm, and initial or terminal color phase). Biomass for parrotfishes on each transect was computed by converting length to weight using the allometric length-weight conversion: $W = aL^b$, where length (L) is expressed in centimeters, weight (W) is expressed in grams, and a and b are constants of allometric growth, obtained through a related study on scarid life history in Hawai'i (Howard et al. unpublished data).

Benthic habitat characteristics were recorded using a 1 m² quadrat, with 25 point intercepts (Friedlander & Brown 2003). The substrate beneath each quadrat point was identified and recorded. Benthic macroorganisms were identified to the species level. For statistical purposes during analyses, substrate features were grouped into 7 live categories (live coral, crustose-coralline algae, sponge, filamentous turf, non-turf macroalgae, tunicate, and non-scleractinian anthozoans), and 3 other categories (sand, dead coral rubble and rock). Rugosity measurements were taken using a 10 m chain made of small links (1.3 cm length) draped carefully to follow the contours of the substrate. The distance along the chain's substrate contour divided by the linear horizontal distance measured with a taut transect tape yielded a rugosity index that could be used to compare habitats at different sites (McCormick 1994). The results of this index ranged from 0-1, with smaller numbers reflecting greater topographic relief. So that larger numbers would represent greater rugosity, the inverse of these results were used. Benthic habitat data and rugosity measurements were made at fixed intervals of 10, 30, 50, 70, and 90 meters along the 100 m transect tape.

Data Analysis

Demographic and habitat-related data were analyzed using one-way Analysis of Variance where appropriate, and nonparametric approaches were used for non-normal distributions. Correlation coefficients were used to evaluate relationships between specific habitat variables and scarid numbers and

biomasses. Since multiple correlations were conducted, sequential Bonferroni tests were used to attain an overall alpha of 0.05 (Rice 1989).

PRIMER (Plymouth Routines in Multivariate Ecological Research) (Clarke & Gorley 2005) multivariate software was used to identify environmental trends in the demographic characteristics of these species (Ohman & Rajasuriya 1998, Clarke et al. 2006). For multivariate statistics, both habitat and scarid community data were 4th root transformed to adjust for non-normality of the data. Bray-Curtis similarity was used to create a rank similarity matrix on habitat characteristic measures and to construct Multi Dimensional Scaling (MDS) ordinations. An MDS ordination is a visual configuration of the samples in two or three dimensions which can satisfy all conditions imposed by the similarity matrix, with relative distance between samples in the configuration relating to relative similarity between those samples (Clarke & Warwick 2001). To test for significant differences among groups, ANOSIM (Analysis of Similarities) permutation tests were performed (Clarke & Warwick 2001). RELATE functions were used to test for specific associations between habitat variables and scarid community structure (Clarke & Warwick 2001). This approach uses a modified Spearman rank correlation with statistic Global rho (values -1 to 1) (Clarke & Warwick 2001).

RESULTS

Habitat Characteristics

Benthic habitat data collected confirmed that the *a priori* habitat delineations indicated by the NOS benthic habitat maps were appropriate. One-way ANOVA indicated that areas designated as CH did have significantly more live coral cover than the other habitat types ($p < 0.001$). They also contain significantly higher percent cover of tunicates (Kruskal-Wallis $p = 0.019$) and non-scleractinian anthozoans (zoanthid and octocoral) (Kruskal-Wallis $p = 0.026$). The habitats designated as MA had significantly more macroalgae than the other habitat types (ANOVA $p < 0.001$). Filamentous turf best characterized UH habitats. However, ANOSIM analysis revealed a high degree of overlap in habitat attributes between these coarse-scale habitat types, with a Global R of 0.132 ($p < 0.001$), where a measure of 1 is total dissimilarity and 0 is complete overlap. This overlap probably occurs because benthic features such as depth, sand, rubble and rock were indistinguishable among the 3 coarse-scale habitat types (Table 2.3). In comparing the three major habitat types, CH habitat was significantly more rugose than other habitat types, using one-way ANOVA, $p = 0.017$. Sector identity, as a proxy for exposure, was not significantly correlated with any habitat characteristics within habitat types.

Scarid community structure

Six of the seven scarid species found in Hawai'i were observed during our surveys. The only species not observed was *Calotomus zonarchus*, which is uncommon in the Main Hawaiian Islands except for Kauai. Fifty-four percent of the surveys revealed no parrotfish of any species. The three main fishery species (*Scarus rubroviolaceus*, *Chlorurus perspicillatus*, and *Calotomus carolinus*) made up only a small part of the overall scarid community. *Scarus psittacus* occurred on 36%, *Scarus dubius* on 7%, *Chlorurus spilurus* on 17%, *S. rubroviolaceus* on 14%, *C. perspicillatus* on 1%, and *C. carolinus* on 6% of all transects.

The stratified random sampling design can be used in conjunction with the area of available habitat based on NOAA/NOS benthic maps, to estimate parrotfish numbers and biomass around Oahu. However, such maps are restricted by water clarity and light penetration to relatively shallow depths. Therefore, they usually do not classify habitat type deeper than 30 m. Because these maps formed the *a priori* basis of our stratification scheme, our survey locations were restricted to habitats included in these maps. Estimates of fish abundance therefore applied only to the habitat types included in these maps, and did not include deeper or unclassified habitats. Within classified habitats, the estimated numerical abundance of all scarid species combined was 277.3 scarids/ha \pm 82.6 fish/ha. Based on the potential reef area calculated from the NOS benthic habitat maps for all three habitat types around Oahu (24,127 ha) and the relative numerical abundances and biomasses of scarids for each habitat type, by extrapolation there are approximately 6,690,417 \pm 1,992,890 scarids in coastal waters around Oahu

(see also Table 2.4, 2.5). The biomass of all scarid species combined was estimated at 13.07 ± 4.05 kg/ha. We also predict a combined potential biomass of $315,340 \pm 97,714$ kg of scarids for all of Oahu (Table 2.5). For estimates of numerical abundance and biomass of the 6 scarid species quantified within classified habitats, see Table 2.5.

The Oahu scarid community is numerically dominated by small fish. In this study, the most numerically abundant species are two of the smallest species, *S. psittacus* and *C. spilurus* (Figure 2.2). Within species, the relative size of individuals was small, and the majority of individuals were reproductively immature (Figure 2.2). Initial/Terminal color phase ratios varied considerably among species: *S. psittacus* 77:1, *S. dubius* 22:0, *S. rubroviolaceus* 7:1, *C. carolinus* 23:1, *C. spilurus* 120:1, *C. perspicillatus* 3:1.

Scarid-habitat Association

To investigate multivariate associations between scarid community structure and habitat characteristics, a RELATE test was conducted using PRIMER multivariate statistical software to test the null hypothesis that there is no relationship between the scarid community characteristics and specific habitat variables. Scarid biomass was not significantly associated with habitat type ($\rho = -0.01$, $p = 0.991$), but was significantly associated with scarid numerical abundance ($\rho = 0.28$, $p = 0.01$). Since significance was not found in relation to scarid biomass, only scarid numerical abundance was used in the remaining multivariate analyses. All multivariate statistical procedures used the 10 substrate

categories, rugosity, and depth as habitat variables. A BIO-ENV computation determined which environmental characteristics, including depth and rugosity, most strongly correlated with scarid numerical abundance. This computation was set to test for each habitat variable and all combinations of 1-5 variables for whatever combination or single variable that best predicts the relationship. Live coral and non-scleractinian anthozoans, together, showed the strongest correlation, with a Spearman rank correlation coefficient of 0.422.

While multivariate statistics were used to investigate associations of parrotfishes with specific habitat characteristics, non-parametric tests were used to investigate relationships with the three coarse-scale habitat types. Kruskal-Wallis tests indicated some association between coarse-scale habitat type and scarid community measures (Figure 2.3). CH habitat is associated with significantly higher scarid numerical abundance, greater biomass, greater species richness and greater species diversity than the other habitat types investigated. The majority of scarid biomass seems to be associated with CH habitat on the windward shore exposure of Oahu (Mood's median $\chi^2 = 9.78$, $p = 0.020$), but there is considerable variation among species (Figure 2.4a, 2.4b).

Congruent with the BIO-ENV analysis on scarid numerical abundance, there were weak, but significant, positive correlations between scarid numerical abundance and rugosity, percent live coral cover, substrate diversity and percent cover of crustose coralline algae. There were significant, but weak, negative correlations between scarid numerical abundance and proportion of sand, and non-turf macroalgae. Most of these correlations were heavily influenced by the

two most abundant species; *S. psittacus* and *C. spilurus*. Species-specific analyses were performed using biomass rather than numerical abundance to reflect the importance of size structure in the population and for the fishery. Total scarid biomass was correlated in the same pattern as that for numerical abundance, except substrate diversity was not significant under serial Bonferroni tests. The biomass of *S. dubius*, the rarest species, was significantly, but weakly, positively correlated with rubble, and *C. spilurus* was the only species with biomass significantly positively correlated with non-scleractinian anthozoa (Table 2.6).

DISCUSSION

This study provides the first thorough, broad-scale investigation of scarid communities in Hawai'i, and presents important evidence for the role of habitat characteristics in scarid distributions. Many reef fish-habitat association studies that included parrotfish have shown little or no evidence of associations between various habitat variables and scarid community measures (Ohman & Rajasuriya 1998, Tolimieri 1998, Gust 2002), suggesting that ecological characteristics of parrotfish (such as social structure or vagility) may limit their habitat associations. If this were true, reef fish assemblage-habitat association studies may have reduced power to detect these associations where parrotfish predominate. The current study has shown weak but significant associations between parrotfish

communities and habitat characteristics, suggesting that the inclusion of scarids in fish assemblage-habitat association studies will not diminish the power of such analyses to detect overall patterns.

Since the studies mentioned above have not detected significant habitat associations for scarids in other locations, the differences in results among studies may reflect regional differences or differences in methodology, such as the geographic scale of the study, or some combination thereof. In the present study, live coral cover was positively associated with scarids, but negative correlations occurred with non-filamentous macroalgae. This contrasts with a study conducted in American Samoa (Sabater & Tofaeono 2007) where investigations reported no significant relationship between scarids and coral cover and a positive relationship with fleshy macroalgae. While similar in overall methodology, the study in American Samoa covered an area about 14% of that of the Oahu study, and benthic habitat data were collected using a video camera rather than with quadrats.

One of the notable trends in the present study was the patchy distribution of scarids around Oahu. However, habitat associations at a coarse scale (i.e. CH habitat) were obvious. Scarid communities were also influenced by specific habitat characteristics. Most notably, live coral cover and substrate diversity, all of which are typical of healthy, diverse reef substrates, were positively correlated with the numerical abundance of scarids. The range of rugosity encountered was low, but evidence indicated that rugosity was an important factor in shaping the scarid communities studied.

Our data also indicated the importance that fishing pressure may have on the local distribution and abundance of scarids. For example, no scarids were found on 54% of transects surveyed, even though many of these surveys were in locations that appeared to contain relatively healthy reefs. In contrast, Hanauma Bay Nature Preserve is the largest no-take reserve on Oahu, and parrotfish biomass in that reserve was ten times that of healthy coral reefs elsewhere on Oahu, as calculated in this study. This suggests that heavy fishing pressure may be an important factor limiting the ability of coastal scarids to exploit the relatively few patches of favorable habitat around Oahu.

Degradation of coastal fish habitat continues in Hawai'i. Our data suggest that increased algal abundance and decreased rugosity resulting from a reduction in live coral cover will be detrimental to parrotfish populations. Importantly, the scarid community on Oahu is dominated by small individuals. However, for one species, *S. rubroviolaceus*, there are few small individuals and the size distribution is less skewed. This could be a result of habitat degradation, where shelter spaces have been lost, reducing the abundance of smaller and more vulnerable fish (Ledlie et al. 2007). However, Poisson distributions were found for both *S. psittacus* and *C. spilurus*, two unfished species of parrotfish, so it is unlikely that the lack of small *S. rubroviolaceus* individuals is a result of habitat loss. Ontogenetic shifts in habitat preference are also unlikely in scarids (Green 1996, Gust 2004). However, shifts in fish communities to a greater relative abundance of smaller species with earlier maturation and faster growth rates have been demonstrated when these communities are exposed to heavy fishing pressure

(Jennings et al. 1999a, Hawkins & Roberts 2003). It seems credible that a similar phenomenon may be occurring on Oahu reefs.

Parrotfish populations around Oahu, particularly fished species, continue to be stressed. It is evident that parrotfish communities in Hawai'i are structured by habitat and probably by fisheries influences, and future management and conservation efforts should address both issues. Scarid-habitat associations detected were generally weak. These correlations may have been confounded by effects of differentially distributed fishing activity. Failure of some previous studies to find habitat associations for scarids may either indicate regional differences or different behavior of other species. This study demonstrates that specific habitat characteristics, such as topographic relief, are important to maintain numerical abundance and biomass of parrotfishes.

Table 2.1. Hawaiian scarid species, their total length and geographic range, provided by FishBase.

Species	Maximum Total Length (cm)	Geographic Distribution
<i>Scarus psittacus</i>	30	Indo-Pacific
<i>Scarus rubroviolaceus</i>	70	Indo-Pacific
<i>Scarus dubius</i>	35.6	Hawaiian Endemic
<i>Chlorurus spilurus</i>	40	Indo-Pacific
<i>Chlorurus perspicillatus</i>	60.9	Hawaiian Endemic
<i>Calotomus carolinus</i>	54	Indo-Pacific
<i>Calotomus zonarchus</i>	33	Hawaiian Endemic

Table 2.2. Transects conducted around Oahu by shoreline and habitat type.

	North	South	Leeward	Windward	Total
Colonized hard bottom	7	17	0	13	37
Uncolonized hard bottom	16	17	11	10	54
Macroalgae	5	21	9	14	49
Total	28	55	20	37	140

Table 2.3. Summary of averages and ranges of habitat characteristics found in each habitat type. Rugosity is shown as the inverse of the rugosity index, so that a larger number indicates greater rugosity.

	Rugosity	Substrate diversity	Depth (m)	Live coral cover	Sand	Rubble	Rock	Sponge	Tunicate	Non-scleractinian anthozoa	Non-turf macroalgae	Filamentous turf algae	Crustose coralline algae
Coral-colonized hard bottom (CH)	1.22	1.70	7.89	14.6%	19.5%	1.4%	0.28%	0.66%	0.09%	1.7%	11.3%	42.3%	8.08%
	1.08 – 1.88	0.29 – 1.70	0.6 – 16.5	0% - 58.4%	0% - 88%	0% - 11.2%	0% - 4%	0% - 4%	0% - 0.8%	0% - 24.8%	0% - 50.4%	0% - 81.9%	0% - 35.2%
Uncolonized hard bottom (UH)	1.16	1.15	7.70	4.3%	28.1%	1.3%	0.61%	0.28%	0%	0.17%	10.9%	49.5%	4.7%
	1.02 – 1.45	0.23 – 1.60	0.9 – 18.6	0% - 35.2%	0% - 98.4%	0% - 14.4%	0% - 8%	0% - 2.4%	0% - 0%	0% - 3.2%	0% - 36.8%	1.6% - 95.2%	0% - 24.8%
Macroalgae (MA)	1.16	1.27	7.66	4.9%	26.3%	2.3%	0.53%	0.25%	0.02%	0.21%	27.4%	34.6%	3.6%
	1.04 – 1.52	0.36 – 1.66	0.6 – 29	0% - 49.6%	0% - 85.6%	0% - 19.2%	0% - 12.2%	0% - 2.4%	0% - 0.79%	0% - 5.6%	0% - 75.2%	0% - 83.2%	0% - 16.5%

Table 2.4. Numerical abundance and biomass of scarids for each coarse scale habitat type

	Area of Reef (hectare)	Average No. Fish/ha	Estimated Fish No.	Average Biomass	Estimated Biomass
CH	4554.82	892 ± 316	4,062,899 ± 1,439,323	38.3 kg/ha ± 15	174,450 kg/ha ± 68,322
MA	8165.72	127.8 ± 46.7	1,043,579 ± 381,339	6.77 kg/ha ± 4.06	55,282 kg/ha ± 33,153
UH	10662.10	44.5 ± 22.3	474,463 ± 237,765	3.65 kg/ha ± 1.17	38,917 kg/ha ± 12,475

Table 2.5. Estimated numerical abundances and biomasses for scarid species around Oahu

	Total Scarid	<i>S. psittacus</i>	<i>S. rubroviolaceus</i>	<i>S. dubius</i>	<i>C. carolinus</i>	<i>C. spilurus</i>	<i>C. perspicillatus</i>
Numerical abundance	6,690,417 ± 1,992,890	4,955,686 ± 1,551,366	226,794 ± 63,213	72,140 ± 32,571	86,375 ± 33,054	1,324,572 ± 33,054	24,213 ± 17,951
Biomass	315,340 ± 97,714 kg	64,298 ± 12,281 kg	169,613 ± 69,486 kg	3,901 ± 1,653 kg	8,637 ± 4,874 kg	43,911 ± 13,101 kg	25,116 ± 23,756 kg

Table 2.6. Summary of Spearman Rank correlations between habitat variables and scarid community variables. Modified Bonferroni adjustments were used to determine significant levels at alpha = 0.05. Significance is indicated in bold, with an asterisk.

	Rugosity	Substrate diversity	Non-scleractinian anthozoa	Filamentous turf algae	Live coral cover	Sand	Rubble
Total scarid numerical abundance	0.41*	0.29*	0.21	0.17	0.48*	-0.30*	0.009
Total scarid biomass	0.42*	0.24	0.24	0.16	0.52*	-0.32*	0.025
<i>Scarus psittacus</i> biomass	0.36*	0.068	0.17	0.13	0.44*	-0.25	0.008
<i>Scarus dubius</i> biomass	0.077	0.041	0.029	0.04	0.068	-0.11	0.30*
<i>Scarus rubroviolaceus</i> biomass	0.29*	-0.061	0.13	0.16	0.24	-0.21	0.016
<i>Calotomus carolinus</i> biomass	0.21	0.12	-0.024	0.044	0.095	-0.14	0.005
<i>Chlorurus spilurus</i> biomass	0.42*	0.29*	0.38*	-0.093	0.44*	-0.14	0.058
<i>Chlorurus perspicillatus</i> biomass	0.25	0.086	0.027	0.026	0.14	-0.10	-0.061

	Depth	Rock	Sponge	Tunicate	Non-turf macroalgae	Crustose coralline algae
Total scarid numerical abundance	-0.063	-0.047	0.19	0.111	-0.32*	0.33*
Total scarid biomass	-0.040	0.050	0.16	0.040	-0.34*	0.42*
<i>Scarus psittacus</i> biomass	-0.054	-0.009	0.23	0.14	-0.27*	0.30*
<i>Scarus dubius</i> biomass	-0.12	0.055	0.041	-0.053	0.009	0.060
<i>Scarus rubroviolaceus</i> biomass	0.107	0.009	0.12	-0.076	-0.24	0.28*
<i>Calotomus carolinus</i> biomass	-0.23	-0.053	-0.073	-0.05	-0.008	0.23
<i>Chlorurus spilurus</i> biomass	-0.13	-0.016	0.23	0.007	-0.18	0.37*
<i>Chlorurus perspicillatus</i> biomass	-0.14	-0.038	0.005	-0.023	-0.043	0.175

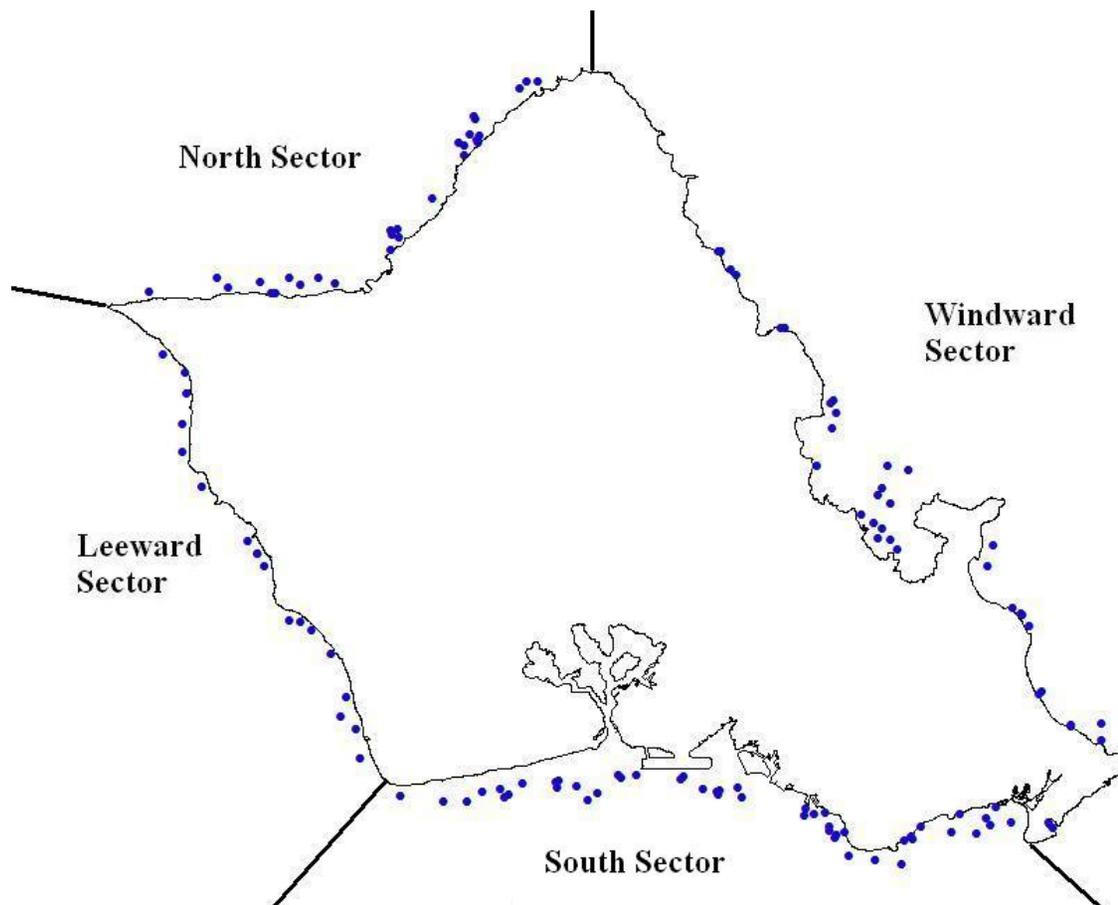


Figure 2.1. Locations of underwater visual surveys of parrotfish around Oahu.

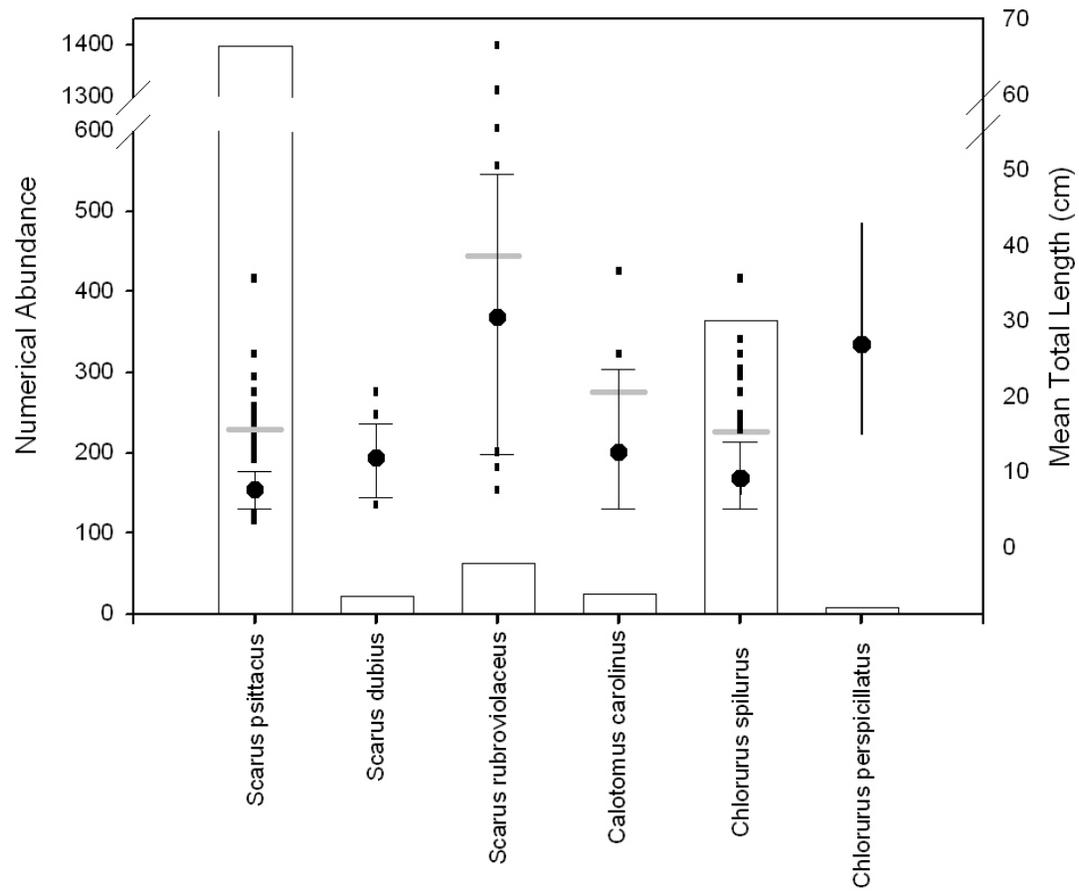


Figure 2.2. Relative numerical abundance of scarid species on Oahu in bars. Black circles represent mean total length with ± 1 (standard deviations: s.d.) confidence intervals, and gray horizontal bars represent the mean total length at sexual maturity (L_m) for that species (obtained from FishBase (Froese & Pauly 2008)).

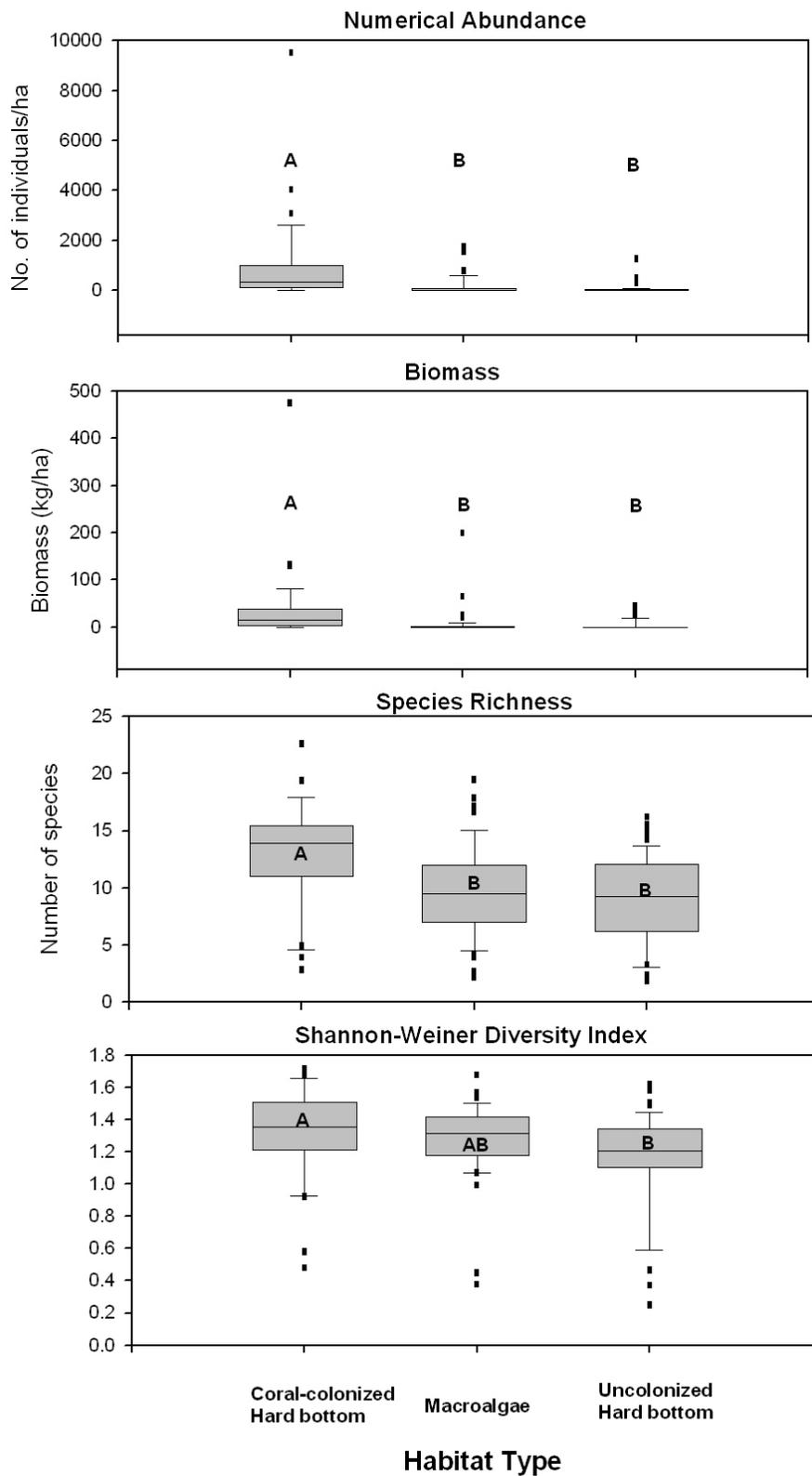


Figure 2.3. Scarid community structure characteristics associated with coarse-scale habitat type.

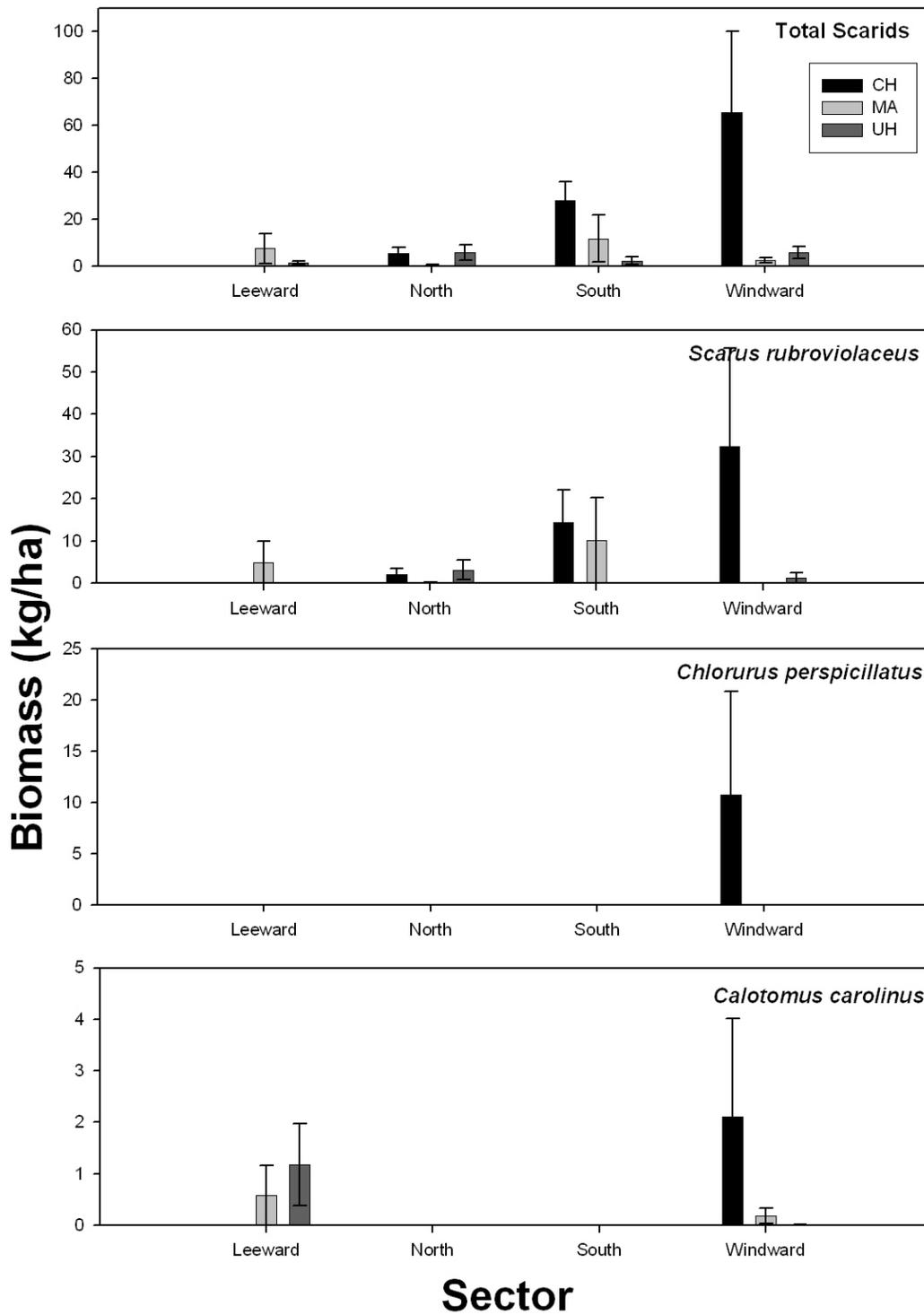


Figure 2.4a. Mean scarid biomass (kg/ha ± 1 SE) from census transects conducted on each shoreline of Oahu and in 3 coarse-scale habitat types. Species are presented in vertical order of decreasing maximum size (TL), and Y axis scales are different among species.

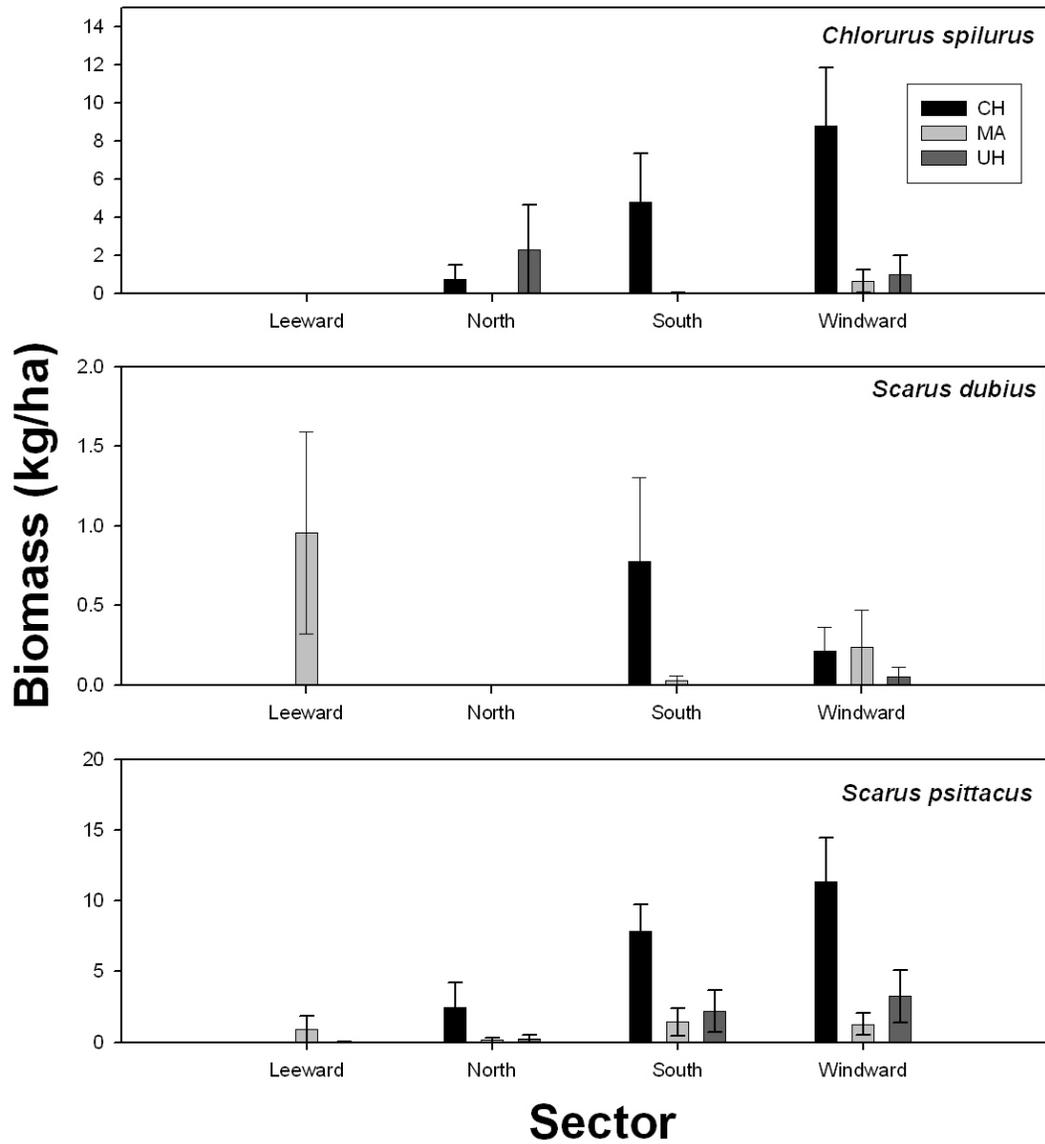


Figure 2.4b. Mean scarid biomass (kg/ha ± 1 SE) from census transects conducted on each shoreline of Oahu and in 3 coarse-scale habitat types. Species are presented in vertical order of decreasing maximum size (TL), and Y axis scales are different among species.

CHAPTER 3

Life History of a Large Protogynous Hermaphrodite, *Scarus rubroviolaceus*: Implications for Fishery Management

INTRODUCTION

Protogynous hermaphroditism is a common reproductive mode among coral reef fishes. Typically protogynous hermaphrodites begin life as females, with the capability to change gender later in life (Choat & Robertson 1975, Thresher 1984). Among the most prominent coral reef fish exhibiting this type of reproductive mode are parrotfish (Scaridae). Scarids, particularly the larger species, are ecologically important inhabitants of coral reefs, serving ecological functions as bioeroders and algal consumers (Choat 1991, Bellwood et al. 2004, Mumby 2006, Hamilton et al. 2008), and providing economic value in coral reef fisheries worldwide (Jennings et al. 1999a).

Parrotfish of the genus *Scarus*, including 51 species, generally exhibit three morphological phases related to their socio-sexual structure: a juvenile phase, an initial phase (IP), and a terminal phase (TP) (Robertson & Warner 1978). The juvenile phase includes newly recruited individuals that are sexually undifferentiated. IP females are capable of transitioning into TP males. The transition between phases seems to be dependent upon individual physiological status (health, size, etc.) and environmental conditions (social and abiotic) (Choat & Robertson 2002). Sexual development, however, is extremely plastic, and

variations on this pattern occur, including: (1) diandry, in which some individuals begin life male and do not change sex, and (2) pre-maturational sex change, in which immature females change sex without leaving the initial phase (Choat & Robertson 1975, Robertson & Warner 1978, Thresher 1984).

TP male individuals often exhibit territorial behavior and protect their territories, which encompass the home ranges of groups of females (termed harems) from intrusion by other males. These territories may encompass preferred spawning sites and/or preferred feeding habitat attractive to females (Thresher 1984). In species and populations where IP males exist, these males may act as “sneakers”, which, because of their similar appearance to females, receive little aggression from the TP males, and are able to sneak into spawning events initiated by the TP male and release their sperm alongside the territorial male (Robertson & Warner 1978). Some species also exhibit group spawning where several IP males will spawn simultaneously with a female.

Because of their ecological importance on coral reefs, life history estimates are important for understanding population dynamics and determining the extent of the ecological role of scarids on coral reefs. For fisheries species, estimates of their age structure, longevity, reproductive biology, and growth rates are also needed to understand and manage fishery effects on scarid populations (Choat et al. 1996). Sequential hermaphrodites such as scarids, particularly species with sexes that differ in size, may be especially sensitive to fishing pressures (Jennings et al. 1999b, Armsworth 2001, Alonzo & Mangel 2004). Fishing intensity has been correlated with decreased mean size and decreased

number of TP males for some scarid species (Hawkins & Roberts 2003), but the role of fishing mortality in modifying reproductive and life history characteristics is not well known. Furthermore, the limited information on parrotfish life histories, particularly across varied environmental regimes and for large-bodied species, provides little basis for fishery management and conservation. The goal of the present work is to provide an in-depth study of the reproductive biology, age and growth of a large parrotfish species, *Scarus rubroviolaceus* (maximum length ~70 cm), to investigate fisheries management implications for large sequential hermaphrodites such as this species, and to compare life history information for this species in Hawai'i to that in other locations.

METHODS

Specimens of *Scarus rubroviolaceus* were collected from the island of Oahu between March 2005 and April 2007. Specimens were obtained from fish markets, spearfishing tournaments, fish traps, and by spearing in the field. Attempts were made to obtain a full size range for both IP and TP fish. For each fish, whole body wet weight, length (Standard Length (SL), Fork Length (FL), and Total Length (TL)), phase (juvenile, initial or terminal), liver wet weight, and gonad wet weight were determined. Except for gonad weight, all weights were measured to the nearest 0.1 g, and all lengths were measured to the nearest millimeter. Gonad weights were measured to 0.01 g. The gonads were examined

macroscopically to determine sex and preserved in Dietrich's fixative (10 % formalin, 30 % ethanol, 2 % glacial acetic acid in distilled water) (Gray 1954). Sagittal otoliths were removed, washed with ethanol, and stored dry before processing for age and growth analysis.

Age and Growth

Sagittal otoliths were processed and analyzed, using techniques established for scarid ageing on other species (Choat et al. 1996, Gust et al. 2002, Choat et al. 2003). Both sagittae for each fish were weighed to the nearest 0.01 mg. Transverse sections, including the centrum, were ground with a Crystal Master 8 jewelry grinder and wet/dry silicon carbide 1000 grit abrasive paper. Sections were mounted to microscope slides and covered for protection using thermoplastic resin (CrystalBond). Increment counts of sectioned otoliths were made under a dissecting microscope with transmitted light. Each sample was blindly processed so that no information relating to the size or phase of fish would bias increment counts. Increments for each otolith were counted on two independent occasions by a single observer (Howard). If these counts were incongruent, a third round of increment counting was conducted. The second otolith was processed and analyzed in the same manner as the first if the third count did not match one of the previous counts.

Age validation was conducted by injecting the musculature of live fish with 50 mg/ml tetracycline hydrochloride in a sterile saline solution for every kilogram of fish (McFarlane & Beamish 1987). These fish were kept in 2 275

gallon tanks, monitored, and reared for 15 months after injection. To maximize the number of individuals raised in each tank, we collected small immature specimens of 4 parrotfish species: *S. rubroviolaceus*, *Calotomus carolinus*, *Chlorurus spilurus*, and *Scarus psittacus*. The few *S. rubroviolaceus* and *C. carolinus* individuals collected did not survive the rearing period. Therefore, we have validation results only for *C. spilurus* and *S. psittacus* - species that represent the two dominant genera in Hawai'i. Thirteen *S. psittacus* and 7 *C. spilurus* survived the full rearing period, and their otoliths were collected for processing. Otoliths were removed, stored and processed using the same techniques described above, taking care not to expose otoliths to light for extended time periods to avoid degrading the tetracycline fluorescence. Otoliths were examined microscopically with an Olympus BX-51 fluorescent microscope, using a U-MWB2 filter cube (EX460-490, DM500, EM520IF) to visualize the oxytetracycline (OTC) marks, and photographed with an Optronics Macrofire color digital camera (Cappo et al. 2000).

Growth was analyzed by fitting the von Bertalanffy growth function (VBGF) to increment data. The model was fitted under 3 conditions: (1) all individuals grouped together, (2) individual curves for each life history type (IP female, IP male and TP male), and (3) individual curves for each sex. Because there was a lack of juveniles in the data set, the model was fitted and constrained through the known size at settlement (12 mm) (Bellwood & Choat 1989, Grandcourt 2002). Growth trajectories of the sexes and of different life history types were compared qualitatively, and quantitative differences of size at age for

each group were compared with general linear models (GLM) (Munday et al. 2004). Older age classes were not included in GLMs because of insufficient numbers of individuals in these age classes for all life history types. Longevity estimates were obtained from the maximum increment count on the otoliths.

Reproductive Biology

The gonadosomatic index ($GSI = \text{gonad weight} * 100 * \text{somatic weight}^{-1}$) was determined for each fish. A higher GSI indicates greater reproductive investment (greater weight of gonads relative to somatic weight) and therefore greater reproductive capacity. The hepatosomatic index condition factor was also determined for each individual ($HSI = \text{liver weight} * 100 * \text{somatic weight}^{-1}$). A high HSI indicates that a female has adequate lipid stores to be invested in reproduction.

Histology was conducted on all female fish. Tissues were dehydrated in ascending grades of ethanol, embedded in paraffin, sliced in 5 μ m thick transverse sections, and stained with Mayers Hematoxylin and Eosin stain (Humason 1967, Gillanders 1995). Each individual was categorized based on an 8 class scheme (Table 3.1). Oocyte stage terminology follows Wallace and Selman (1981). Determination of maturity was based on the most advanced oocytic stage present (West 1990).

A preliminary histological study examined oocyte distribution and development throughout the length of the ovary and compared between lobes. Serial sectioning of 6 individuals was conducted and the percent cover of each

oocyte stage was determined for each section. Homogeneous development along the length and between ovarian lobes was found. This allowed for more selective tissue sampling (medial sections only) for the rest of the histological work. Oocyte size ranges for each stage were also determined by measuring 200 oocytes of each stage under high-powered compound microscopes with micrometers (Figure 3.1).

The fraction of IP individuals that were male was determined. Because targeted individuals in the fishery were not random, ratios of IP:TP fish were obtained from demographic data from Oahu in a related study (Howard et al, Chapter 2). Functional sex ratio was then determined by estimating the percentage of IP individuals that are male from the present study and applying that percentage to the number of total IP in the demographic study. Ratios of females to males (including IP and TP) were then obtained. Proportions of IP that were male and sex ratios were compared to the only other known study to document these aspects of reproduction for this species, from the Seychelles (Grandcourt 2002).

Batch fecundity analyses were conducted by sampling proximal, medial and distal sections of one ovarian lobe, using the gravimetric method of fecundity estimation (Murua et al. 2003). Each section was patted dry and weighed to the nearest 0.01 g. Counts were made of all hydrated ova in each sample. The average number of ova per gram ovary (AO) for the three samples was determined for each individual as:

$$AO = (SSC * SSW^{-1}) * 3^{-1}$$

where SSC = subsample count and SSW = subsample weight

Batch fecundity (BF) was then determined as:

$$BF = AO * GW$$

where GW is gonad weight.

RESULTS

A total of 499 specimens of *S. rubroviolaceus* were collected, including 390 IP, 104 TP, and 5 individuals that had transitional color morphology (intermediary of IP and TP coloration). The collected fish ranged from 15.0 to 64.8 cm in length (FL), between 70.0 g and 5443.1 g in weight, and from <1 to 22 years in age. Details of age and size ranges of collected fish are shown in Table 3.2.

Gonads were bi-lobed and varied greatly in weight (Table 3.3). Ovaries of mature fish often included oocytes in all stages of development with no dominant stage, confirming an asynchronous spawning mode, as has been demonstrated in other scarids (Robertson & Warner 1978, Thresher 1984, Gust 2004).

Life History Types

All females exhibited the IP coloration and all TP individuals were male. Since IP fish were caught across a broad size range, and no obvious gender

indicators biased sampling, the proportion of IP males in the collection was assumed to be representative of the population, and provides some indication of the degree to which alternative reproductive strategies (e.g: group spawning or “sneaking males”) are being employed. Twenty percent of the IP fish in this study were male. This is double the only other known reproductive information on this species, from the Seychelles (Grandcourt 2002). When applied to the demographic data (Howard et al., Chapter 2), the present study suggests that the sex ratio on Oahu is 2.3 females per male. This is a significant female bias ($\chi^2 = 25.5, p < 0.001$). However, this is a less female-biased sex ratio than would typically be expected from a protogynous hermaphrodite, and it is much less female biased than that found in the Seychelles study (4.5:1) for the same species (Grandcourt 2002).

As a proxy for reproductive investment, GSI is markedly different among the three life history types. One-way ANOVA of logged GSI with Tukey’s pairwise comparisons shows that reproductive investment of each life history type is significantly different from the others, with IP males having highest GSIs on average, followed by females, and TP males having the lowest.

Temporal Reproductive Patterns

The GSI reveals that this species is reproductively active year-round with a peak during April – June (Figure 3.2). The frequencies of gonad classes for mature females show gravid and postovulatory females throughout the year and females with gonads classified as spawning during January, March and May

(Figure 3.3). Lunar periodicity in spawning activities, as determined by the timing of occurrences of gravid females relative to the lunar cycle, was not found.

Maturity, Female Size and Reproductive Output

The smallest mature female was 30.5 cm FL or 2 years of age. All females were mature by 43 cm FL or 5 years of age. Fifty percent maturity was estimated at 34 cm FL and an age of about 4 years (Figure 3.4). Batch fecundity estimates of *S. rubroviolaceus* ranged from 2,645 ova for a 4 year old female to 437,231 ova for an 11 year old. Batch fecundity was best explained with a power function (Figure 3.5), but this model only explained 28.9% of the variation in batch fecundity estimates.

While the overall pattern for this species is year-round reproductive activity, this pattern seems to be heavily influenced by the largest females in the population. Larger females are reproductively active over a longer time frame (Figure 3.6). Reproductive activity declines sharply after the peak spawning period for smaller, mature females. Furthermore, of all of the fish collected with gonads classified as recovering, 87% of these were medium size fish while only 11.1% were large females. Larger females may not only be producing proportionally more eggs in a batch, but they may be spawning over a longer time frame, or even with greater frequency than their smaller counterparts.

Other factors were also investigated for their influence on reproductive output in females. Condition played an important role in batch fecundity. Of the variation in batch fecundity estimates, 34.9% is attributable to H.S.I. ($p = 0.005$).

The strength of this factor may be masking a stronger relationship between fish length and batch fecundity. The importance of maternal size in reproductive output was also investigated in terms of egg size. There was no relationship between maternal size or maternal condition, as expressed in H.S.I., and egg size.

Age Validation

Growth of fish in tanks was variable. Over the period of captivity, *S. psittacus* individuals showed a small but significant increase in both length and weight (mean growth of 2.79 cm and 18.23 g) in 2-sample t-tests. *C. spilurus* did not show a significant change in either length or weight during the rearing period. For both species, otoliths contained a tetracycline mark near the outer edge of the otolith, followed by an opaque ring, and then a translucent area (Figure 3.7). This implies that the otolith rings are forming on an annual basis. For all fish, the tetracycline mark (injected in September) appeared on the outer edge of the opaque band. Otoliths from reared fish were collected in the winter of the following year, and a translucent area appears on the margin of the otoliths. This suggests that the formation of the opaque band occurs in late spring or early summer as was found in Australian scarids (Choat et al. 1996). Since scarid species studied elsewhere have been successfully validated, we assume that the species used in our study are representative of all Hawaiian scarids, and that sagittal increments in Hawaiian scarids are representative of the yearly age of the fish.

Age and Growth

A total of 182 otoliths from individuals ranging in size from 15.0 cm to 64.8 cm were processed. The otoliths of *S. rubroviolaceus* in Hawai'i showed consistent and regular increment patterns of alternating broad translucent areas and narrow opaque areas. Sagittal weight showed a positive relationship with age increments (Figure 3.8). Sagittal growth at a relatively constant rate confirms that these otoliths are growing throughout the life of the fish.

This species exhibits asymptotic growth. The greatest number of increments (age) recorded was 22 years. A general linear model (GLM) using otolith weight as a response and FL and gender as predictors showed small, significant sex-specific differences in sagittal weight-fish length relationships ($F = 11.83$, $p = 0.001$), but no significant interaction with phase (comparing IP females and IP males to TP males). Males tended to have a smaller otolith for a given fish size when compared to females. A similar model conducted with age of fish instead of otolith weight was used to investigate relationships with the mean size of fish for a given age, and no significant differences were found between any of the life history types or between genders. Size at age plots (VBGF) were partitioned into various life history types (IP female, IP male and TP male). There were no obvious differences in the growth curves among the three life history strategies (Figure 3.9).

Latitudinal Variation in Life History Parameters: Comparisons with Other Studies

Based on the mean annual sea surface temperatures at Oahu, Seychelles, and American Samoa (Figure 3.10), we predicted: 1) greater growth rates in the Seychelles and American Samoa than in Hawai'i (Atkinson & Sibly 1997, Choat et al. 2003), 2) greater maximum size in Hawai'i than in the other studies (Atkinson & Sibly 1997), 3) greater maximum age in Hawai'i than in the other studies (Choat & Robertson 2002, Choat et al. 2003), and 4) greater size at maturity in Hawai'i (Atkinson & Sibly 1997). Unfortunately the sample size in the American Samoa study is rather small ($n = 6$), so we focus our comparisons between the present study and the Seychelles study. Growth and reproductive parameters for the present and Seychelles studies are illustrated in Table 3.4. All the predicted trends in latitudinal variations in life history characteristics appeared to be supported by these studies. It should be noted, however, that the k parameter, as determined by fitting the VBGF, represents a growth rate toward L_{∞} . Comparing k parameters with different L_{∞} values may be problematic.

DISCUSSION

Native Hawaiian traditional knowledge indicates that the peak spawning season for parrotfish in Hawai'i occurs from May through July (Poepoe et al. 2003). Our data are supportive of this time frame. The reproductive biology of this species and local management are less congruent, however. Fisheries

management regulations in Hawai'i include a minimum size limit for catch, covering all parrotfish species as one group, and placed at 12 inches fork length (FL). Management based on minimum size limits should be supported by reproductive data, with size limits set to ensure that at least some of the population of each species harvested attains sexual maturity before being exposed to fishing pressure. Our data suggest that 50% maturity, a level that is typical for minimum size limit management, does not occur for *S. rubroviolaceus* until it reaches 13 inches FL. At 12 inches, only about 11% of the population of this species is expected to have reached reproductive maturity.

Management strategies of large protogynous hermaphrodites such as *S. rubroviolaceus* should emphasize the importance of leaving large females in the reproductive population (Birkeland & Dayton 2005, Pears et al. 2006) and retaining adequate mature males to prevent sperm or male limitation that might result from unregulated size-selective fishing that targets the largest size classes (Alonzo & Mangel 2004). Reduced numbers of TP males and smaller size at sex change have been identified as major vulnerabilities of protogynous hermaphrodites in relation to fishing pressure (Russ 1991, Armsworth 2001, Hawkins & Roberts 2003).

In the present study, large females seem to be reproductively active for longer time periods and to produce more eggs. They may also be spawning more frequently than smaller individuals. The largest and oldest fish encountered are female, suggesting that some females retain their sexual identity throughout their lifetime. The egg production capabilities of these individuals are then

disproportionately important to the spawning stock. Protecting a few large females may be more beneficial to the future of populations of large hermaphrodites than protecting more, smaller individuals.

The low skew in sex ratio for this species on Oahu has important ramifications for both reproductive output and socio-sexual dynamics. Protogynous hermaphrodites are characterized by strongly female-biased sex ratios (Choat & Robertson 1975, Sadovy 1996). If reproductive output is limited by egg production, lower female abundance may foretell a breakdown in future recruitment. A study detailing the demography and community structure of scarids on Oahu has already documented a noticeable paucity of young (<2 year old) *S. rubroviolaceus*, despite an abundance of young individuals of other, unfished scarid species around the island (see Howard, Chapter 2).

The decreased sex ratio skew is, in part, due to a very high incidence of IP males in the population. While these patterns of low sex skew and high IP abundance could merely reflect a species-specific phenomenon, the sex ratio for *S. rubroviolaceus* in the Seychelles is much more skewed (4.5 females per male), and the proportion of IP males is half that found in Hawai'i (Grandcourt 2002). Fishing pressure in the Seychelles is much less intense than that on Oahu. Spearfishing, one of the primary modes of catching parrotfish in Hawai'i, is prohibited in the Seychelles. Also, as a proximate measure of fishing intensity, the Seychelles have far fewer people/km of shoreline than occur on Oahu: 165.2 people/km compared to 5031.1 people/km on Oahu. It is apparent that on Oahu

intense fishing activity is depleting fish numbers, and it may be altering the socio-sexual structure and population dynamics of this species.

It has been proposed that sex determination in species exhibiting diandry may be labile and controlled by the same mechanisms as those that control sex change (i.e.: local social hierarchy) (Francis 1992, Yoshikawa 2003). Therefore, for a juvenile fish settling on the reef, if the cue responsible for inhibiting sex change in females is the presence of a large TP male, and there are no TP males in the area of the newly settled recruit, then the recruit will not be inhibited and may prematurely change sex and become an IP male. If this process occurs, then conditions of high fishing mortality that target large TP males may lead to a higher proportion of IP males in the overall population. Supporting this idea, Gust (2004) discovered a higher proportion of *Chlorurus sordidus* IP males in areas of the Great Barrier Reef with higher natural mortality. Also, IP males are often associated with a prevalence of group spawning rather than pair spawning, and group spawning is a behavioral trait frequently associated with over-exploitation in protogynous hermaphrodites (Hamilton et al. 2008).

Predominance of IP males as a reproductive strategy may not only be a response to intense fishing pressure, but it may also influence the population's future response to fishing pressure. (Alonzo & Mangel 2004, Hamilton et al. 2008). When mating groups are small and large TP males are targeted by the fishery (as is the case in the present study in Hawai'i), sperm limitation and male limitation may strongly restrict successful mating by protogynous hermaphrodites (Alonzo & Mangel 2004). However, models of reproductive output and of

population dynamics for protogynous hermaphrodites have yet to include diandry, so the role of increased occurrence of IP males for preventing sperm or male limitation is unknown.

Many scarid ecological studies have assumed that all IP individuals are females, based on the few studies investigating scarid reproductive demography where IP male proportions were small. Therefore, many of these studies may have missed important variations in IP male abundances and grossly overestimated female abundances. The phenomena of decreased sex ratio and high incidence of IP males merit further investigation. If these phenomena prove to be widespread side effects of exploitation, then the proportion of IP males in a population of large protogynous hermaphrodites may be an indicator of population health, and management plans will need to address these issues.

Studies on other scarids have shown variation in growth attributable to sexual identity (vanRooij et al. 1995, Choat et al. 1996, Munday et al. 2004). It has been suggested that these differences may result from differential gonadal investment, with IP males and females investing more in gonadal development than TP males, and therefore having slower growth. In the present study, sex-specific differences were only minor and not significant. Gust and colleagues found marked differences in growth rates of scarids related to habitat differences (2002). Since specimens from the present study were collected around all of Oahu, which contains considerable variety in type and quality of habitats, sex-specific growth differences may be masked by noise from habitat differences.

While there are limited data on the life history of this species elsewhere, this study is the first to investigate *S. rubroviolaceus* in Hawai'i, at a higher latitude than the earlier studies (Figure 3.10). This is also the first study to provide comprehensive reproductive information on *S. rubroviolaceus*, or to validate age increments in parrotfish in Hawai'i. The information presented here is critical, not only for management and conservation of this species, but also for understanding fishery impacts on large protogynous hermaphrodites in general.

Table 3.1. Histological characteristics of stages of development in *Scarus rubroviolaceus* ovaries.

Stage	Microscopic characteristics
Immature	Oogonia and primary growth oocytes present only, no atresia
Developing	Primary growth, cortical alveoli and few early vitellogenic oocytes present only
Fully Developed	Primary growth, cortical alveoli and advanced vitellogenic oocytes present; atresia of vitellogenic oocytes may be present
Gravid	All oocyte stages present. Hydrated oocytes un-ovulated; minor atresia and postovulatory follicles may be present
Spawning	Ovulated ova and/or recent postovulatory follicles present; minor atresia of advanced vitellogenic oocytes
Postovulatory	Primary growth through advanced vitellogenic oocytes; remnant hydrated oocytes may be present; postovulatory follicles common; minor atresia of advanced vitellogenic oocytes
Spent	Primary growth and cortical alveoli oocytes present; vitellogenic oocytes in advanced stages of atresia; postovulatory follicles may be present
Recovering	Oogonia and primary growth oocytes dominate; other oocytes may be present in late stages of atresia; muscle bundles may be present; thicker ovarian membrane than immature fish

Table 3.2. Age and size ranges for each life history type of *S. rubroviolaceus*.

		n	Minimum FL (cm)	Maximum FL (cm)	Minimum Age	Maximum Age
IP	Female	311	15.0	64.8	<1	22
	Male	79	28.2	52.0	2	10
TP		104	30.9	61.5	3	18
Transitional	Ovary	1	38.5		5	
	Testis	4	40.0	43.5	3	8

Table 3.3. Gonad size ranges for *S. rubroviolaceus*

		Gonad weight (g)
IP	All Female	0.0015 – 153.47
	Mature Female Only	0.7407 – 153.47
	Male	0.3156 – 153.46
TP		0.1077 – 78.019
Transitional	Ovary	2.0507
	Testis	5.6296 – 24.0345

Table 3.4. Von Bertalanffy growth parameters as estimated for *S. rubroviolaceus* in 2 locations (Grandcourt 2002, Allsop & West 2003).

Study		Annual Mean Sea Surface Temperature	K (year ⁻¹)	L _∞ (cm, FL)	t ₀ (years)	r ²	n	Size at Maturity (FL, cm)	Maximum age	Maximum size fish sampled (FL)
Grandcourt 2002	All	27.8 °C	0.431	30.8	-0.092	0.648	54	25	20	42
	Females		0.589	29.0	-0.072	0.754	45			
Present study	All	25.4 °C	0.288	51.2	-0.809	0.589	182	34	22	64.8
	Females		0.307	50.7	-0.558	0.666	116			
	IP Males		0.611	41.7	-0.096	0.272	27			
	TP Males		0.359	52.0	-0.271	0.271	35			

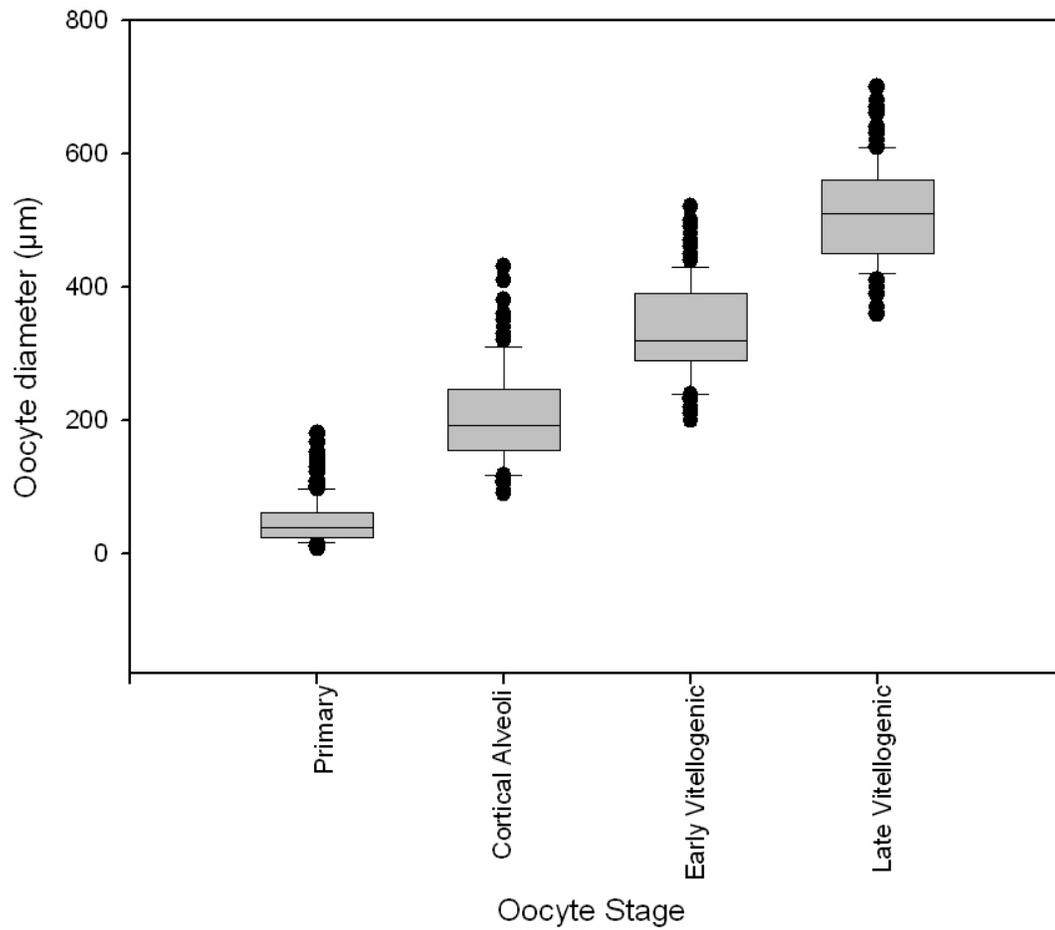


Figure 3.1. Oocyte size distribution for each stage of oocyte development.

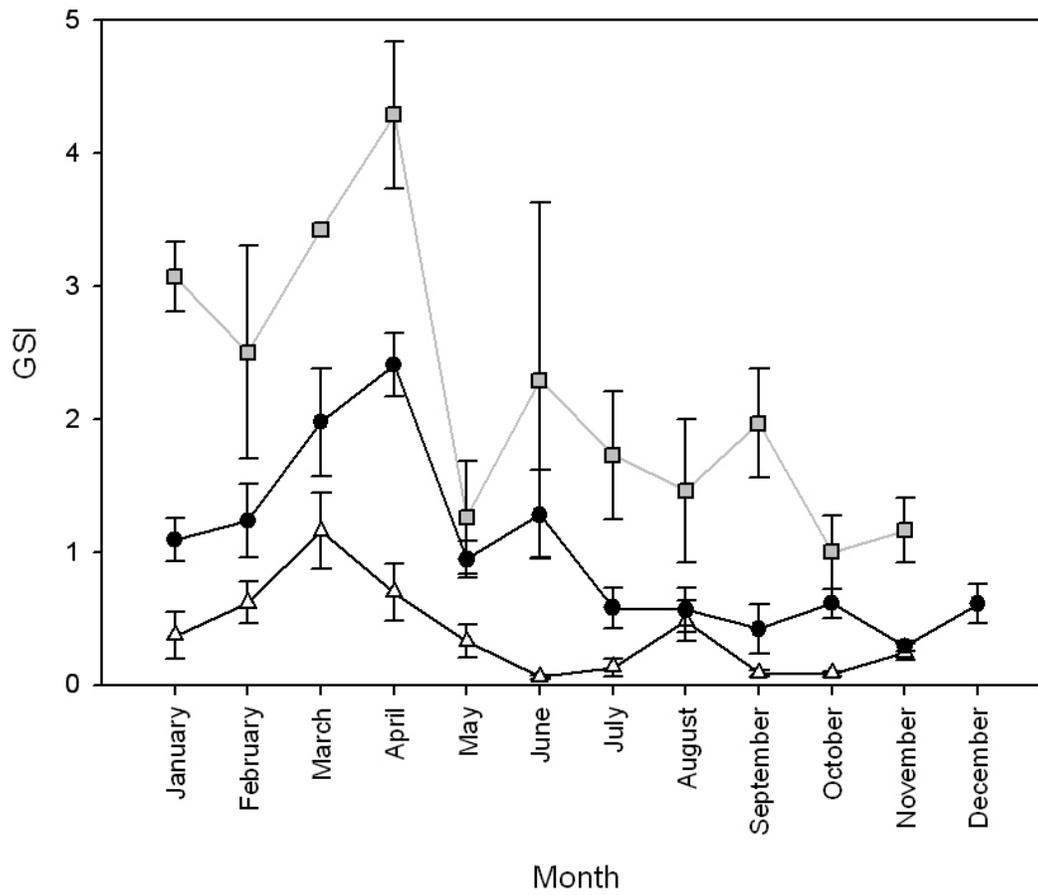


Figure 3.2. Spawning seasonality: mean monthly GSI \pm SE of IP male (gray squares), females (black circles) and TP males (white triangles)

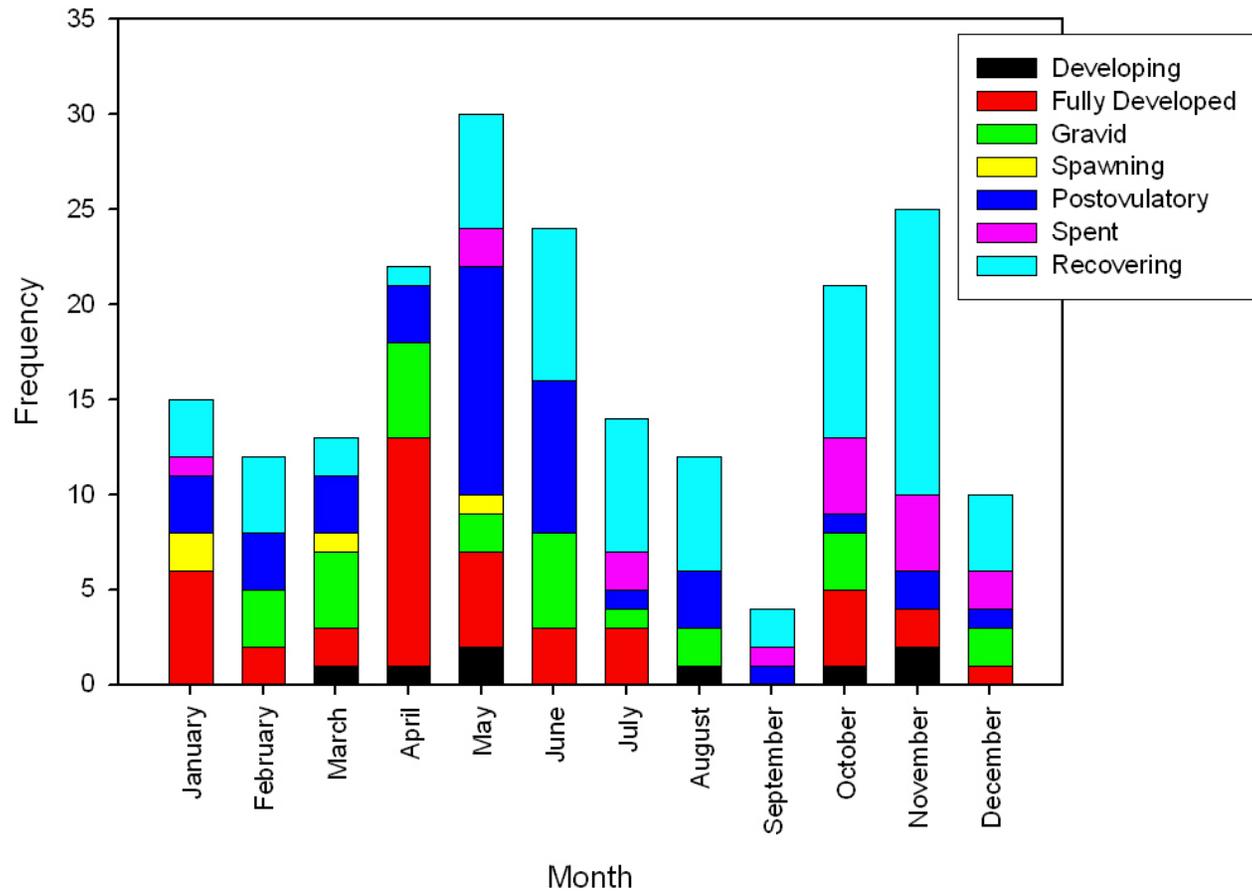


Figure 3.3. Seasonal variation in frequency of occurrence of each gonad class of mature females.

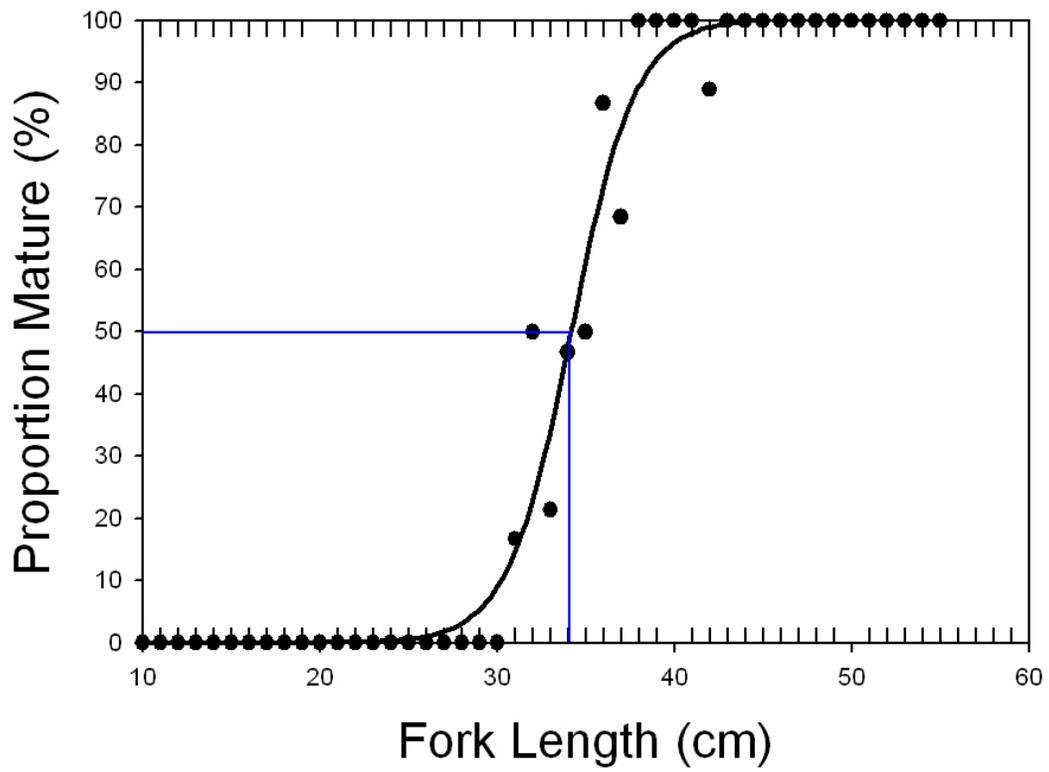


Figure 3.4. Maturity estimates. Reference lines indicate length at 50% maturity.

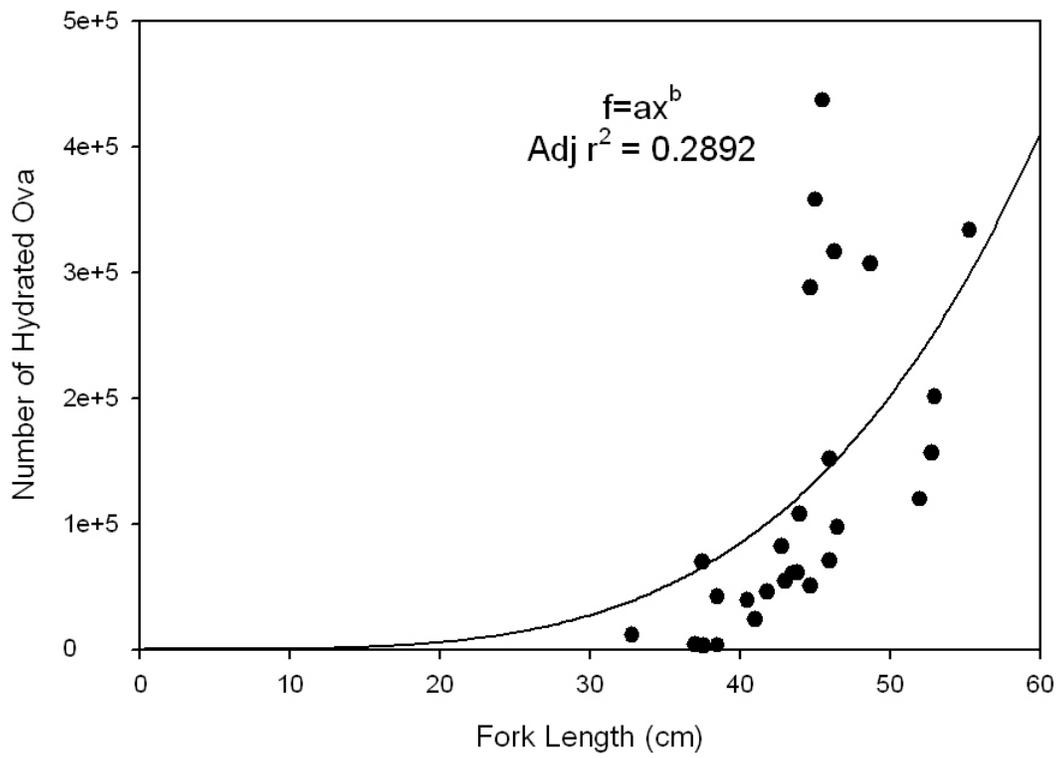


Figure 3.5. Batch fecundity relationship to female size. A model of power function provided best fit to the data.

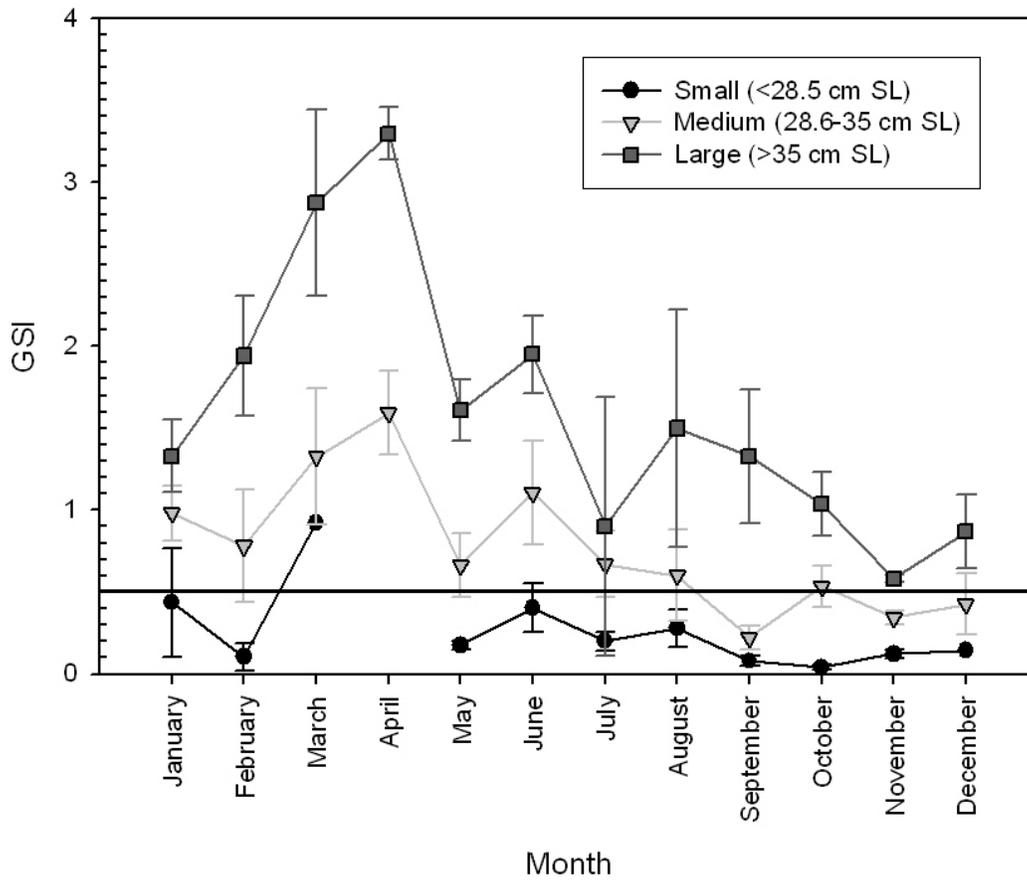


Figure 3.6. Seasonal GSI range for three size classes of females. The smallest size class includes females beginning to mature; the medium size class includes smaller mature females; the large size class consists of large mature females. The black horizontal line indicates the point below which females are reproductively inactive (immature and recovering). GSI values above the line represent all active reproductive classes (developing, fully developed, gravid, spawning, postovulatory and spent).

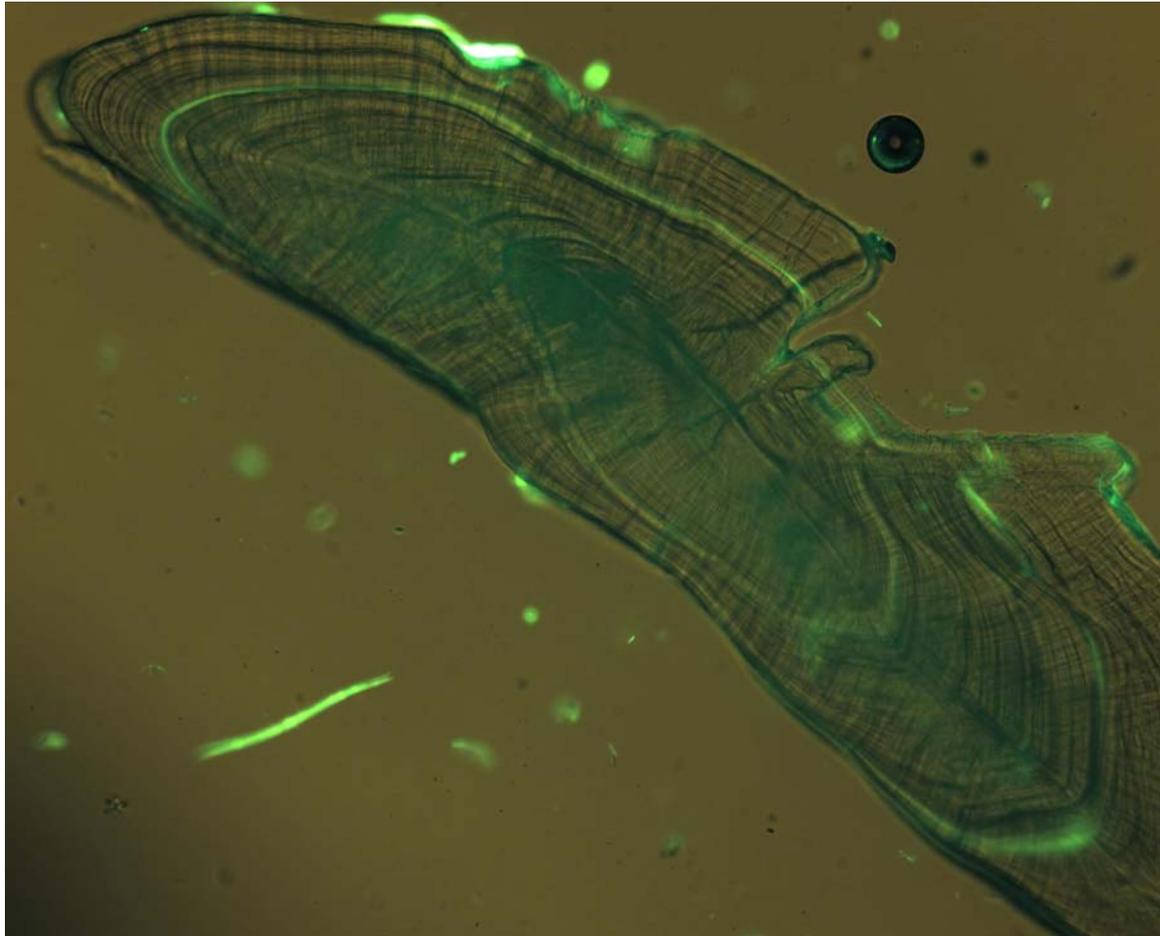


Figure 3.7. Image of sectioned otolith. Green tetracycline band near the perimeter of the otolith is the tetracycline mark. Following this mark is an opaque band and a translucent region, indicating that the bands are formed on an annual basis.

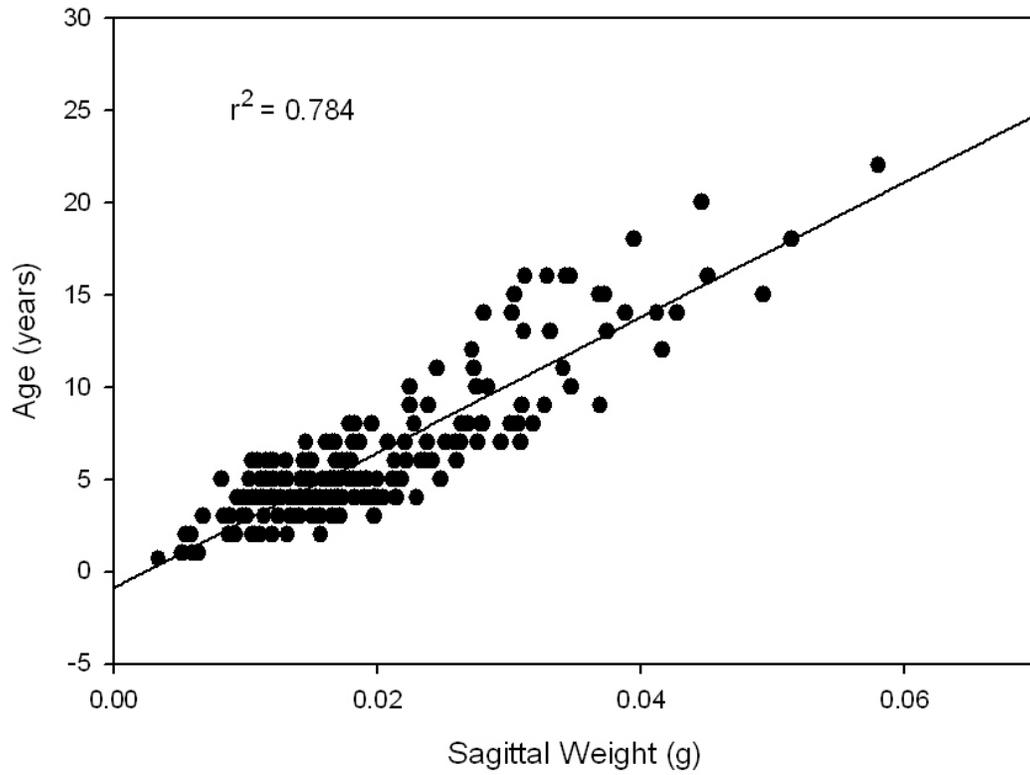


Figure 3.8. Least squares linear regression of sagittal increments (age) on sagittal weight.
 $y = -0.878 + 366.48x$

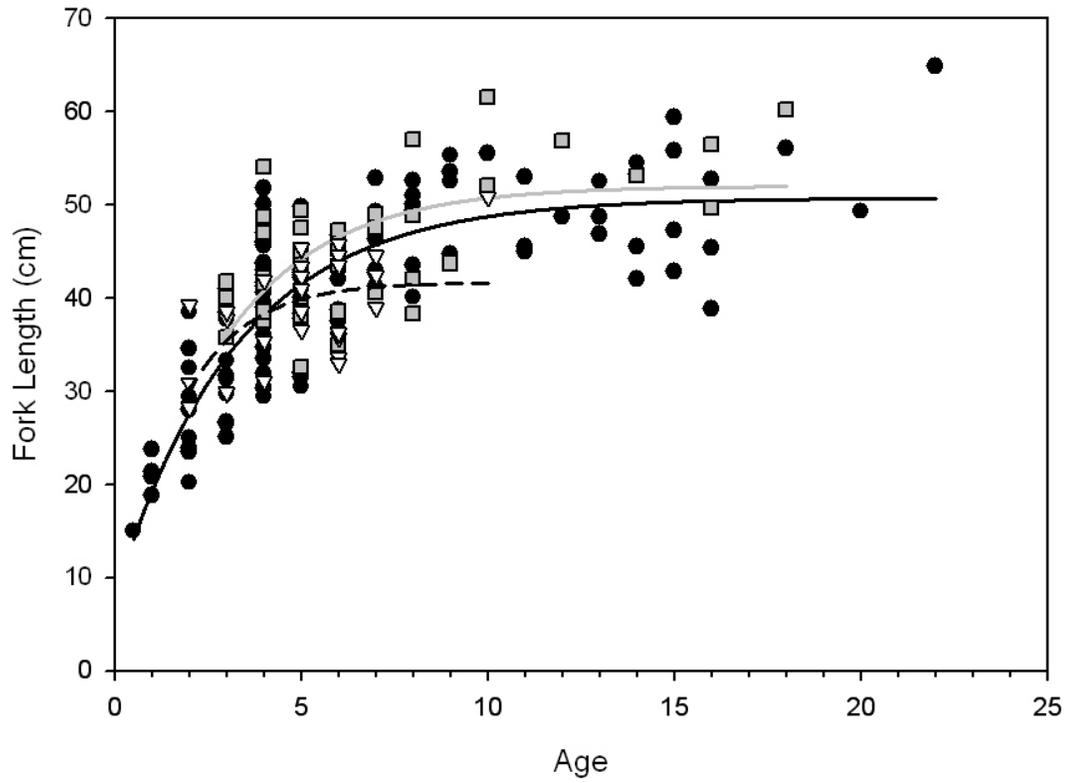


Figure 3.9. Von Bertalanffy growth curves fitted to data for each life history type. Black circles and solid black line represent females; gray squares and gray line represent TP males; and white triangles and black dotted line represent IP males.

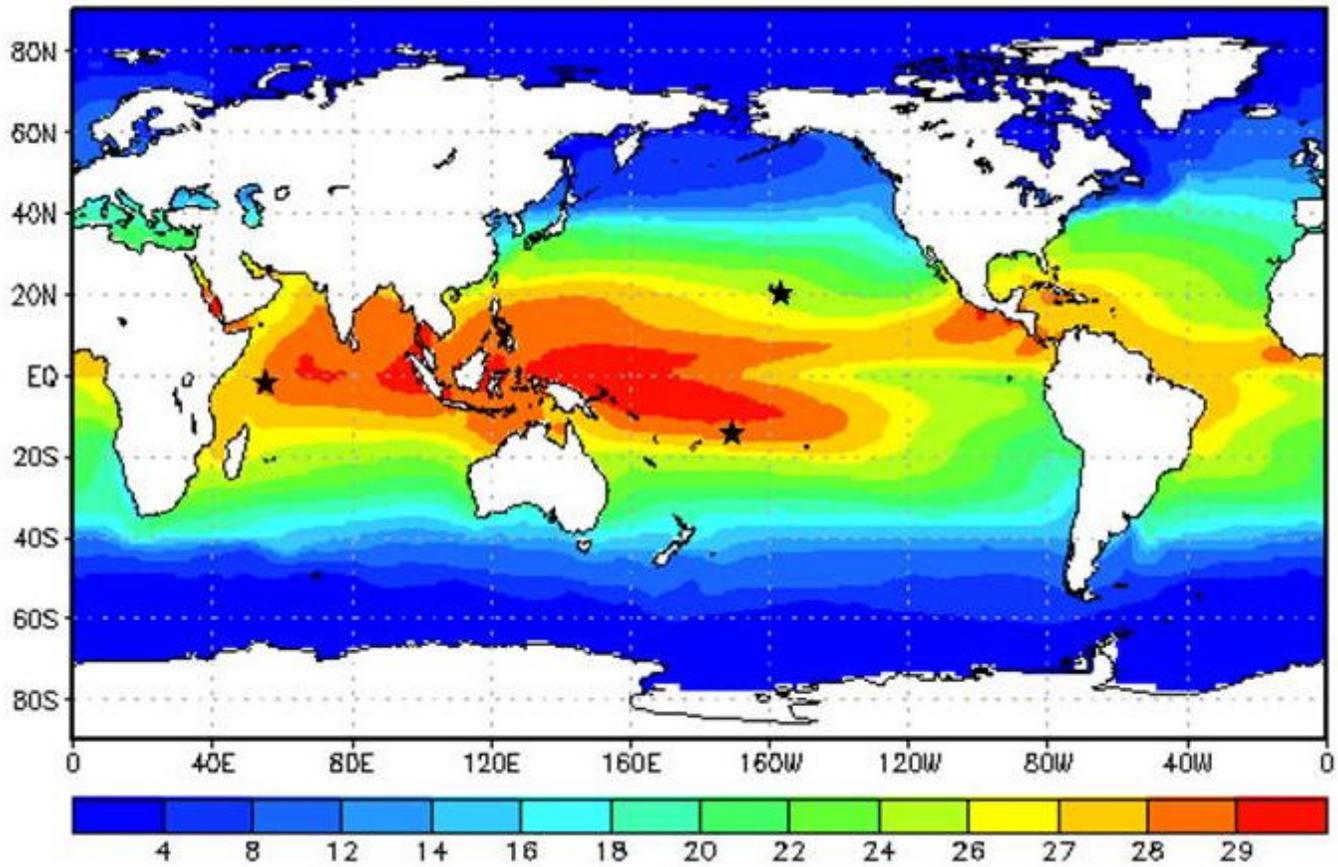


Figure 3.10. Mean annual sea surface temperatures. Black stars indicate the three locations mentioned (from left to right): Seychelles, American Samoa, and Hawai'i.

CHAPTER 4

Home Range and Movement Patterns of the Redlip Parrotfish (*Scarus rubroviolaceus*) in Hawai'i: Implications for Management

INTRODUCTION

Activity patterns and use of space are among the most important components of the demography and population biology of animals (Heupel et al. 2006). This information is valuable for understanding basic population biology and social dynamics of animals, and it is critical for development of effective strategies in fisheries and wildlife management (Hooge & Eichenlaub 1997, Zeller 1997). In active tracking studies, tagging devices enable researchers to follow the exact movements of an individual in real time, but require extensive man-hours of labor. Passive tracking studies use ultrasonic transmitters attached to the animal and *in situ* receivers that can record signals from the transmitter without the researchers' presence. While active tracking is useful for obtaining home range or territory information and fine-scale behavioral data, passive tracking is helpful in estimating repeated movement patterns, site fidelity, emigration and dispersal rates, or mortality, and has the added benefit of obtaining information on multiple individuals concurrently (Heupel et al. 2006). The combination of both active and passive tracking permits a more comprehensive

analysis of animal movement and behavior, including detailed, but short duration observations, as well as long-term, large-scale, continuous monitoring (Bolden 2001).

Passive and active tracking studies in marine ecosystems have become increasingly important to address demographic, behavioral and management questions (Heupel et al. 2006, Righton & Mills 2006). Analyses of animal home range and movements have provided valuable information on the effectiveness of marine reserves, and may be used to estimate spillover of individuals into fishery areas (Zeller 1997, Kramer & Chapman 1999, Eristhee & Oxenford 2001, Kaunda-Arara & Rose 2004b, Meyer & Holland 2005). Such information may also help determine sensitive habitats (e.g. spawning aggregations) and migration patterns that may make a species particularly vulnerable to fishing pressure (Zeller 1998).

Coral reef fish commonly show high site fidelity, long-term site attachment, territoriality and complex social structures, all of which shape population dynamics and distribution patterns (Bardach 1958, Ogden & Buckman 1973, Jones 2005, Righton & Mills 2006). Notable among coral reef fishes is the parrotfish family (Scaridae). Parrotfish are important bioeroders and algal consumers on coral reefs and help to maintain healthy reef ecosystems throughout the tropics (Done 1992, Williams & Polunin 2001, Mumby 2006). Parrotfish, particularly the larger species, are also economically valuable for fisheries and tourism (Smith 1993, Page 1998, McClanahan et al. 1999). Parrotfish are sequential protogynous hermaphrodites and exhibit two color phases: initial phase

(IP) fish which are primarily females with a small proportion of males, and terminal phase (TP) fish which are all males. TP males are typically territorial, with one male defending a territory against other males and maintaining a harem of females within that territory. Parrotfish spawn throughout the year, are more reproductively active during summer months, and some species may undergo migrations to specific spawning sites (Thresher 1984). The population dynamics of these harem, protogynous hermaphrodites is strongly influenced by social structuring, making information on use of space extremely valuable for these fish (Alevizon & Landmeier 1984).

Despite the economic and ecological importance of scarids, relatively little information is available on their movement and spatial activity patterns. Almost all the studies investigating territoriality or home range in parrotfish have been conducted on Caribbean species, have had a strict sociobiology focus, and mostly investigated smaller, less vagile species. (Table 4.1 contains a summary of scarid territoriality studies.) Information on the movement patterns of large scarid species that are a major component of tropical fisheries is limited, and their social structures and population dynamics are poorly understood.

Few studies have investigated *S. rubroviolaceus*, despite its prominence in recreational, artisanal and commercial fisheries throughout its distribution (Connell et al. 1998, Page 1998, Jennings et al. 1999b, McClanahan et al. 1999, Grandcourt 2002, Ong 2007). Kaunda-Arara and Rose (2004b) used mark-recapture techniques to study this species off the coast of Kenya and calculated the distance moved between locations, but with only one recapture, analyses were

limited. The only other movement study conducted on this species to date used passive and active tracking in Hanauma Bay, Hawaii (Ong 2007). However, this study had a limited sample size and was conducted in a small, enclosed bay, which might not be representative of most coastal reef settings in Hawaii. The present study expands on these prior investigations by using relatively large sample sizes of fish, using both active and passive tracking, using a study site that is more representative of Hawaiian coastal reefs, and using a large array of acoustic receivers.

The objective of this study was to describe the home ranges and movement patterns of *Scarus rubroviolaceus* on a typical coastal reef tract along the Kona Coast of Hawaii. We predicted that (H₁) home range size would increase with depth of home range, (H₂) home range size would increase with fish length (Mumby & Wabnitz 2002, Jones 2005), (H₃) fish would appear on the nearest receivers to their home range on a consistent, diurnal basis (Ong 2007), and (H₄) any movements beyond the home range would occur near dawn and would be related to reproductive behavior (Ong 2007). This study provides comprehensive and vital information for understanding social patterns, distribution and population dynamics of this species, and provides a basis for effective management strategies for this large scarid and for related valuable fisheries species.

METHODS

Study site

This study was conducted from April through August 2007, on a 6.81 ha reef tract called Wawaloli on the Kona Coast of the Big Island of Hawaii. The bulk of the study was conducted on the reef slope, and the habitat was fairly consistent across the study area. This site was chosen because of minimal fishing influence (pers. obs.).

At this site, the reef flat (0-5 m depth) is characterized by pavement with moderate to low cover of live coral. The reef slope ranges from 5 to 35 m depth and is characterized by rubble, boulders with moderate to high cover of live coral, and high live coral cover aggregations (particularly *Pocillopora meandrina*, *Montipora capitata*, *Porites compressa*, and *Porites lobata*). Beyond the slope is a steep drop-off into open ocean (Ortiz & Tissot 2008).

Characterization of Scarid Assemblage at Wawaloli

Numerical abundance and biomass estimates were obtained using underwater visual censuses (UVC). Six replicate belt transect censuses (100 m x 5 m) were conducted in the Wawaloli area. Starting points for transects were randomly selected from within the tract area. Depths of transects ranged from 5 to 17 m. Benthic habitat data were also collected on these transects using 1 m² quadrats with 25 point intercepts. Rugosity was measured by draping a 10 m long chain along the contours of the substrate and dividing the measurement of

distance covered by the chain by the distance the chain would have covered on a completely flat surface (McCormick 1994). Rugosity measurements and quadrat measurements were conducted at 10, 30, 50, 70, and 90 m marks along the 100 m transect tape. For more detailed methods of the UVC see Chapter 2.

Tagging and Night Surveys

During April and May, SCUBA divers captured resting parrotfish at night with hand nets. The position of each tagged fish was recorded with a GPS unit towed at the surface, attached to a float. For each captured parrotfish, color phase was recorded and fork length (FL) was measured to the nearest millimeter. Each individual was tagged with a unique color/location combination of visual t-bar tags (Floy Tag, Seattle) and then released at its capture location. Nighttime resting locations of previously tagged fish that were re-sighted during subsequent nighttime surveys were recorded. No juvenile phase fish were tagged.

A subset of tagged fish was also implanted with acoustic transmitters. Fish were caught using the same techniques as used for conventional tagging and raised slowly from depth to minimize trauma from decompression. On a boat, individuals were anaesthetized with MS-222 (0.1 g/L) solution, a small incision was made into the peritoneal cavity, and a sterilized Vemco V-7 ultrasonic transmitter (20.5 mm long x 7 mm diameter) was implanted, using standard field surgical procedures. Incisions were sealed with Vetbond tissue adhesive, and fish were allowed to recover in an onboard saltwater recovery tank. Each fish receiving an acoustic transmitter also received a unique color combination of

visual t-bar tags. Once the fish was active and appeared to be successfully recovered from surgery, it was slowly returned to depth and then returned to the capture site. See Table 4.2 for information on tagged fish.

Daytime Active Tracking

Active tracking of tagged individuals was conducted by a snorkeler with a towed GPS unit. Fish location was recorded every 5 seconds, and synchronized watches allowed divers to record specific behaviors linked to GPS locations. Unlike SCUBA divers, the presence of snorkelers did not appear to affect scarid behavior. Preliminary studies tracking focal individuals for time periods longer than 1 hour indicated that tracking periods of 20 minutes were amply representative of an individual's primary movement patterns. Afterwards, attempts were made to maintain individual tracks at least 20 minutes long. A track was ended if visual contact could not be maintained, even if lost temporarily (e.g.: limitations caused by chasing behaviors among fish or by benthic topography).

The Animal Movement Analysis Extension (AMAE) for ArcView was used for geospatial analysis of the tracking data (Hooge & Eichenlaub 1997). Site fidelity tests were used within the AMAE program to determine whether the fish movement was significantly different from random Monte Carlo walks. Only those fish showing site fidelity were used in home range analyses (Powell 2000). Because of the large number of location data points for each individual fish, the active tracking data were reduced to 60-second time intervals for analysis. (One

individual was reduced to 90-second time intervals because of an extremely large number of location data points.) Further subsampling was not done because the primary home range estimator used, Kernel Home Range (KHR), does not require serial independence of observations, and such subsampling may actually be counterproductive (DeSolla et al. 1999). KHR provides probability contours, showing the probability that the individual will occupy a particular space. In this study we define home range as the area in which an individual conducts its typical daily activities, and quantify this with 95% probability contours (Powell 2000, Eristhee & Oxenford 2001, Rechisky & Wetherbee 2003, Righton & Mills 2006). The core utilization area is that part of an individual's home range that is particularly important and most heavily utilized (Powell 2000). We use a 50% probability contour, within each utilization distribution, to define the core area for each individual (Jones 2005, Righton & Mills 2006). We implemented KHR using Least Squares Cross Validation (LSCV) to determine the smoothing factor, as this is generally considered the most robust and descriptive home range analysis available (Seaman & Powell 1996, Powell 2000, Righton & Mills 2006). We also present Minimum Convex Polygons (MCP) because of their prevalence in tracking literature and their utility in comparisons with other studies. MCPs are constructed by creating the smallest polygon that encompasses all location points for an individual. They are relatively easy to estimate, but they are strongly influenced by outliers and sample size.

Minimum Sample Size Determination

Minimum sample size of location fixes was determined with bootstrapping analyses in AMAE, and only those fish meeting these sampling requirements were included in the site fidelity and home range analyses (Righton & Mills 2006). Seventeen individuals had very large sample sizes (>200 points after the previously mentioned reduction). For these individuals, a random sampling of points starting with 5, and increasing until reaching the total number of points for that individual, was used to create a MCP based on that sample size of points used. One hundred repetitions at each sample size were performed, and the average area of MCP for each was determined. Observation-area curves were then created for the average area of MCP vs. sample size.

Home Range Analysis

Variables calculated for home range were the 95% KHR contour area (home range area, m^2), 50% KHR contour area (core area, m^2), MCP area (m^2), average depth of core area (m), and deepest part of home range area (m). The deepest part of the home range was chosen as an indicator rather than the average depth of home range because of the variability in home range shape and variability of depth, and the difficulty in obtaining accurate depth measurements throughout these large home ranges. To determine temporal variations in KHR, areas were estimated on subsets of location points corresponding to month or to time of day (early morning: sunrise to 11:00, midday: 11:01 to 15:00, and late afternoon: 15:01 to sunset).

For regression and other statistical analyses, MCP areas, 95% KHR areas, 50% KHR areas, and average depth of core were all log transformed to allow for assumptions of equal variances. To test the first two proposed hypotheses ((H₁) home range size would increase with depth of home range, (H₂) home range size would increase with fish length), a general linear model (GLM) was used to assess the individual and interactive effects of phase, FL of fish, and depth of home range, with area of home range as the response factor. A second GLM was conducted to test for relationships between phase, FL of fish, and 50% core depth on the 50% core area. Non-parametric tests were used where parametric tests were inappropriate, and all regression values are shown as adjusted r^2 .

Passive Tracking

Prior to tagging, 21 Vemco VR1, VR2 and VR2W acoustic receivers were range tested and deployed. Receivers were secured to the substrate and suspended in mid-water with a float. Receivers were located, in part, to cover shallow-, mid- and deep-water areas across the study site, and specific locations were chosen for appropriate substrate available to securely attach the receivers. Receivers detected signals up to 20 m away in shallow locations and up to 40 m away at deeper sites. The maximum receiver range was used in error estimates in the analyses. The high number of receivers used allowed for considerable overlap of many receivers despite their limited range. The receiver network is illustrated in Figure 4.1. Receivers were deployed from April through December 2007.

Information on individual fish sizes, release dates and last recorded transmissions are shown in Table 4.3.

RESULTS

Characterization of Scarid Assemblage at Wawaloli

The underwater visual censuses at Wawaloli provided an estimate of mean scarid numerical density of $140 \text{ fish ha}^{-1} \pm 41$ (S.E.) and biomass of $93.6 \text{ kg ha}^{-1} \pm 23.9$ (S.E.). The numerical density of *Scarus rubroviolaceus* was $106.7 \text{ fish ha}^{-1} \pm 32.5$ (S.E.). The estimated total number of *S. rubroviolaceus* in the study area is $726.6 \text{ fish} \pm 221.3$ (S.E.), with biomass of $555.0 \text{ kg} \pm 149.1$ (S.E.).

Daytime Active Tracking

Thirty of the 41 t-bar tagged *S. rubroviolaceus* were resighted during the sampling period. A total of 1,370 tracking sessions were conducted, with a total track time of 9,903 minutes and 242,270 location fixes for all fish. Twenty-one (13 TP and 8 IP) individuals were consistently tracked and had met the minimum sample size determined in the study. All these fish except for one TP individual showed site fidelity.

Minimum Sample Size Determination

Observation-area curves were created for the average area of MCP vs. sample size (Figure 4.2). We chose a conservative minimum sample size for home range determination to be the size where the observation-area curve approaches an asymptote at 1% or less change in area (Odum & Kuenzler 1955). Minimum sample sizes for individuals ranged from 39 to 134 points, with an average of 74. We deemed that, for this study, a minimum of 74 points was appropriate to be included in home range analyses. This is consistent with the recommendation of >50 location points per home range by Seaman et al. (1999). Although our decision is conservative, other individuals had very few data points and were obvious outliers when compared to more thoroughly sampled fish.

Home Range Analyses

The 20 fish with adequate sample size and showing site fidelity were used in home range analyses (Table 4.4). Kernel home ranges and MCPs for all fish used in analyses are shown in Figures 4.3 and 4.4. (Home range border colors correspond in each figure, and home range numbers represent ID numbers of individuals in Table 4.4). Large TP male territories tended to encompass one to a few IP home ranges.

IP individuals had significantly smaller home ranges than TP fish (Kruskall Wallis test: $p = 0.031$). The best model to predict home range size included phase and depth of home range, explaining 71.6% of the variation in home range size, with depth being the most important factor ($F = 49.80$, $p <$

0.001, regression of home range area and depth shown in Figure 4.5). The addition of FL did not improve the fit of the model, and FL alone did not have a significant relationship with home range size ($F = 0.73$, $p = 0.408$). Fork length only had a significant relationship with home range area (95% KHR) for IP *S. rubroviolaceus* alone (slope = -0.0251, Adj. $r^2 = 41.1\%$, $p = 0.05$). There was also no relationship between the size of the fish and the deepest part of the home range for IP, TP or all parrotfish combined.

Individual home range locations were relatively stable, but there were also some changes in home range shape over the course of the study, and over the course of the day. There are no apparent patterns in these temporal changes, and KHR areas were not significantly different among subsets of points containing adequate sample size (>74). One TP individual disappeared from our surveys part-way through our study. Afterwards, a neighboring TP male expanded his territory by 11.9%, to include much of the area formerly occupied by the missing TP male (Figure 4.6a & 4.6b). Together, these results indicate that these fish are maintaining discrete, long-term territories/home ranges, but territory borders are dynamic.

Tagging and Night Surveys

Nine of the 12 TP (75%) and 4 of 8 IP (50%) used in home range analyses were actually tagged within their home range. The remaining fish were tagged in locations that ranged from 1 to 116 m from their home range. Over the course of 13 potential resighting nights (19.32 hours), 11 tagged fish were resighted. Home

range information was collected for 7 resighted fish, 3 of which were resighted within their home ranges. Three resightings were fish without tracks. One of these fish was resighted next to the area where it was tagged, while the other two ranged from 44 m to 308 m away from the original tagging location.

Passive Tracking

Fourteen of the 17 fish tagged with acoustic transmitters were detected on acoustic receivers (Table 4.3). The timing of recorded transmissions among all fish strongly suggests diurnal activity (Figure 4.7). One individual was recorded continually throughout day and night, but this probably occurred because the receiver was located immediately adjacent to the fish's nighttime resting area. Otherwise, very few transmissions were recorded during nighttime hours. There were no recordings of an individual fish at night from more than one receiver. Such recordings would have suggested substantial nighttime activity.

Eight fish that had enough active tracking points for home range analyses were also acoustically tagged. For these fish, most of the recorded acoustic transmissions were within the general area of the home range. Three of these had receivers inside their home range, while 4 had receivers immediately adjacent to their home range. Occasional long forays, up to about 350 m away from the home range, occurred for many of the fish. For fish whose home range had not been identified, movements up to about 400 m away from their original tagging locations were evident. The majority of movement activity away from the fish's home range tended to occur near dusk (e.g. Figure 4.8). An individual's long

forays often were not in the same direction, which could have suggested a repetitive migration pattern. Forays occurred both parallel and perpendicular to the reef slope. Large females seemed to make more and longer forays than TP males or small females, although there were too few individuals to warrant statistical analysis.

Most *S. rubroviolaceus* exhibited high site fidelity over the course of the study. Individuals continued to be recorded at receivers near their home range (e.g. Figure 4.9). However, for two IP fish for which a large number of transmissions were recorded throughout the study, there was a shift in the predominant receiver receiving the signals. Both fish shifted from (a) having most hits recorded by receivers that were slightly deeper but close to their home range during summer months (May through August), to (b) having most hits at shallower receivers that were also close to their home range in fall and winter months (September through December). While both receivers were near the estimated home range of the animal, there is an obvious shift in time spent in deeper vs. shallower parts of the home range (Figure 4.10). Other fish did not show any measurable shift in receiver detections.

DISCUSSION

Only two of the four proposed hypotheses on movement patterns in *Scarus rubroviolaceus* were supported by this study. Our findings did indicate a strong

positive relationship between home range size and depth (H_1). This relationship may be related to parrotfish compensating for decreased algal quality or quantity at depth (Hessen et al. 2002), but further research is needed to verify depth-related differences in habitat quality. The second hypothesis (home range size would increase with fish length) has been demonstrated in other studies on reef fish, including parrotfish. These previous studies have shown strong, positive relationships between fish length and territory size (Zeller 1997, Mumby & Wabnitz 2002, Jones 2005). The present study, however, did not find this relationship. H_3 proposed that fish would appear on the nearest receivers to their home range on a consistent, diurnal basis (Ong 2007), and diurnal activity was confirmed by the present study (Figure 4.7). Finally, H_4 anticipated that any movements beyond the home range would only occur near dawn and would be related to spawning migrations, as predicted by Ong (2007). While the presence of spawning migrations could not be refuted by the present study, there was no evidence to support it, and the majority of long-distance movements in this study occurred at dusk, when there was no apparent spawning activity.

Long-term, discrete, and reliable home ranges or territories seem to be the norm for *Scarus rubroviolaceus*, but other strategies may also exist. Small shifts in location of home ranges were evident for some individuals (Figure 4.10). Territory borders may be somewhat dynamic and influenced by local social conditions (Figure 4.6a & 4.6b). This suggests that analyses of territory size and distribution for this species should incorporate dynamics of nearby fish and resources, and studies documenting only a few individuals may be insufficient or

misleading. Furthermore, not all TP male parrotfish may be territorial. One TP male in our study did not exhibit site fidelity.

S. rubroviolaceus is a large parrotfish and may be exhibiting greater mobility than previously studied scarid species. While we detected movements of up to ~400 m within our study area, fish may have made movements beyond the area (6.84 ha) of our receiver array. Long distance movement of individual fish may be rare, but may also be underrepresented in most movement studies because resightings or recaptures are limited to a small reef area (Kaunda-Arara & Rose 2004a).

Parrotfish reproductive behavior can show tremendous intra- and inter-specific variability (Thresher 1984), and little reproductive information is available on *Scarus rubroviolaceus*. Ong (2007) interpreted the repeated absence of *S. rubroviolaceus* from its home range in Hanauma Bay, Oahu for a period near dawn as reproductive migrations out of the bay (Ong 2007). In the present study, only 2 fish (1 each of IP and TP) seemed to exhibit a pattern such as Ong described: consistently detected on receivers adjacent to their home ranges, except for frequent absences for 30-90 minute time periods, close to dawn. While fish could potentially be traveling at dawn to spawn in very deep waters, our data cannot confirm this. We were unable to place receivers deeper than 35 m, and even with the best visibility, our active tracking data would not have reliably observed behavior beyond this depth. However, only two fish in our study showed the pattern Ong described, and spawning by some TP males was observed within their territories during the present study. Therefore, mass spawning

migrations for this species at this site seem unlikely. With an open coastline, the Wawaloli site may simply offer more varied spawning options than the enclosed bay of Ong's study, with some individuals migrating and some individuals remaining in or near their home range to spawn.

Protogynous hermaphrodites, such as parrotfish, are particularly vulnerable to fishing pressure (Sadovy 1996, Jennings et al. 1999b, Armsworth 2001), and data from the present study provide critical information for parrotfish fishery management. The high degree of site fidelity seen in this fish makes it a good candidate for management through Marine Protected Areas (MPAs). However, conscious and deliberate MPA design would be required. Water depth is a key factor influencing home range size and thus impacting the social structure and potentially the density of these fish. The long forays in the late evening may well be attempts to find appropriate shelter sites for sleeping, as is seen in other parrotfish species (Dubin & Baker 1982). If parrotfish are fished at night while sleeping, as is the case in Hawaii, then MPA design needs to account for both daytime and nighttime habitat use. Furthermore, data from the present study suggest that large females may be more likely to sleep outside their home ranges or make more frequent or longer forays. Since large females of protogynous hermaphrodites are disproportionately influential to the spawning stock biomass (Birkeland & Dayton 2005), protecting home ranges and sleeping sites for these females may be particularly important. MPAs large enough to encompass daytime and nighttime movements of sufficient numbers of parrotfish to offset fishing impacts may not be feasible, and additional measures may be necessary to

complement even well-designed MPAs. Because of the vulnerability of parrotfish to fishing at night, the success of MPAs for parrotfish management in Hawaii would be greatly enhanced if nighttime spearfishing with SCUBA were banned, as it has been in American Samoa, Queensland (Great Barrier Reef, Australia), Palau, Fiji, French Polynesia, the Seychelles, and elsewhere in the tropics.

Table 4.1. Scarid movement/territory studies. *Maximum size estimates obtained from fishbase.org.

Study	Location	Species	Total Length (cm)*	Sample Size	Observation period	Observation # per individual	Method of Territory Estimate	Territory size estimate (m ²)
(deGirolamo et al. 1999)	Mediterranean	<i>Sparisoma cretense</i>	50.0	7	20 min – 2 hr	6-12	Hand drawn maps of aggressive interactions with neighbors	189-587
(Mumby & Wabnitz 2002)	Caribbean	<i>Scarus iserti</i>	35.0	25	20 min	1	Hand drawn map of locations at 1 min interval	41-120
		<i>Sparisoma aurofrenatum</i>	28.0	25				82-319
		<i>Sparisoma chrysopterum</i>	46.0	17				170-324
		<i>Sparisoma rubripinne</i>	47.8	17				168-1400
		<i>Sparisoma viride</i>	64.0	27				91-289
(Marconato & Shapiro 1996)	Caribbean	<i>Sparisoma radians</i>	20.0	22	30-60 min	1	Hand drawn map of aggressive interactions with neighbors	unspecified
(Dubin 1981)	Caribbean	<i>Scarus taeniopterus</i>		22	unspecified	unspecified	unspecified	120-500
(Munoz & Motta 2000)	Caribbean	<i>Sparisoma aurofrenatum</i>	28.0	10	unspecified	unspecified	Largest length and width based on observation of aggression	240 ± 137.4
		<i>Sparisoma chrysopterum</i>	46.0	7			Largest length and width based on observation of change in direction of movement	4371.5 ± 5869.5
(Ong 2007)	Hawai'i	<i>Scarus rubroviolaceus</i>	70.0	5	1- 4 hours	Variable: total of 17-22 hours per fish	Minimum Convex Polygon	2635 ± 2183

Table 4.2. Tagged fish statistics.

Tag Type	Number of fish tagged	Number TP fish	Number IP fish	Size range of fish tagged FL (cm)	Average FL of fish tagged (cm)
T-bar Tags	41	23	18	29-61	44.4
Acoustic Tags	17	9	8	29-58	43.6

Table 4.3. Summary of acoustic transmitter data for *Scarus rubroviolaceus*. * The active tracking portion of this study observed this fish for more than a month after the last detection recorded.

Fish	FL (cm)	Phase	Date acoustic tagged released	Last recorded transmission	Total days passively tracked	Total transmissions detected	# receivers visited	# transmissions recorded
Ch-F	51	TP	5/29/2007	11/21/2007	194	5138	5	5138
ChCh-F	48	IP	5/29/2007	11/11/2007	184	42	7	42
F-Ch	58	TP	5/29/2007	n/a	0	0	0	0
F-F	39	TP	5/23/2007	11/19/2007	180	4897	5	4897
FF-F	47	IP	5/23/2007	11/5/2007	166	26	10	26
P-Ny-P	43.5	TP	5/24/2007	6/4/2007	11	41	10	41
Ny--	29	IP	5/24/2007	11/20/2007	180	363	4	363
W--	37.5	IP	5/30/2007	11/18/2007	172	82	1	82
W-F	52	TP	5/31/2007	6/15/2007*	15	4	2	4
W-W	39	TP	5/23/2007	n/a	0	0	0	0
WW-W	36	IP	5/23/2007	11/19/2007	180	6500	12	6500
WW-Y	43	IP	5/30/2007	11/20/2007	174	293	3	293
W-Y	45	TP	5/24/2007	11/7/2007	167	2	1	2
Y-W	45	TP	5/24/2007	n/a	0	0	0	0
YY-W	42	IP	5/30/2007	11/7/2007	161	44	8	44
Y-Y	48	TP	5/24/2007	9/15/2007	129	325	2	325
YY-Y	39	IP	5/23/2007	5/26/2007	3	2	2	2

Table 4.4. Summary of active tracking data for the 20 individuals used in home range estimates. ID numbers correspond to those shown for home ranges in Figures 4.3 and 4.4.

	FISH									
	P-G	P-P	R	R-R	R/RRR	W	WW-W	Y-G	Y-Y	YY-W
Phase	TP	TP	TP	TP	TP	IP	IP	TP	TP	IP
ID #	8	17	9	11	19	1	13	5	18	16
FL (cm)	61	42	46	49	53	37.5	36	44	48	42
# tracking events	81	7	77	86	80	61	80	78	80	21
Span of active tracking (days)	90	13	107	85	80	45	53	78	53	22
Sample Size (# fixes at 60 or 90 min interval)	417	88	563	431	330	574	508	408	803	239
MCP area (m ²)	3029.9650	439.2202	3395.1712	3901.7720	4641.5583	1252.3808	1783.4791	7008.3601	11255.7389	7008.3601
Kernel 95% area (m ²)	1981.989	342.709	842.545	1645.834	994.869	479.438	732.959	2391.097	1093.682	908.502
Kernel 50% area (m ²)	166.111	39.967	59.240	179.641	149.519	23.709	65.660	178.873	273.111	249.984

	FISH									
	B-R	Ch-F	ChCh-F	F-Ch	F-F	G-P	GG-G	GG-P	GG-TB	Ny
Phase	TP	TP	IP	TP	TP	TP	IP	IP	IP	IP
ID #	12	7	2	6	15	10	20	4	3	14
FL (cm)	45	51	48	58	39	50.5	40	39	41	29
# tracking events	3	77	64	34	36	51	14	75	74	79
Span of active tracking (days)	22	51	47	53	49	85	56	78	85	54
Sample Size (# fixes at 60 or 90 min interval)	75	463	445	321	269	548	84	415	438	590
MCP area (m ²)	1178.1770	3196.0374	492.3532	3872.9412	2970.6546	10258.6080	652.7378	6147.4173	2159.5446	8253.0324
Kernel 95% area (m ²)	1500.429	713.142	256.009	711.064	1072.171	3699.976	758.651	782.54	700.980	1065.562
Kernel 50% area (m ²)	112.092	161.356	46.949	137.231	123.002	946.153	243.484	246.275	93.517	161.935

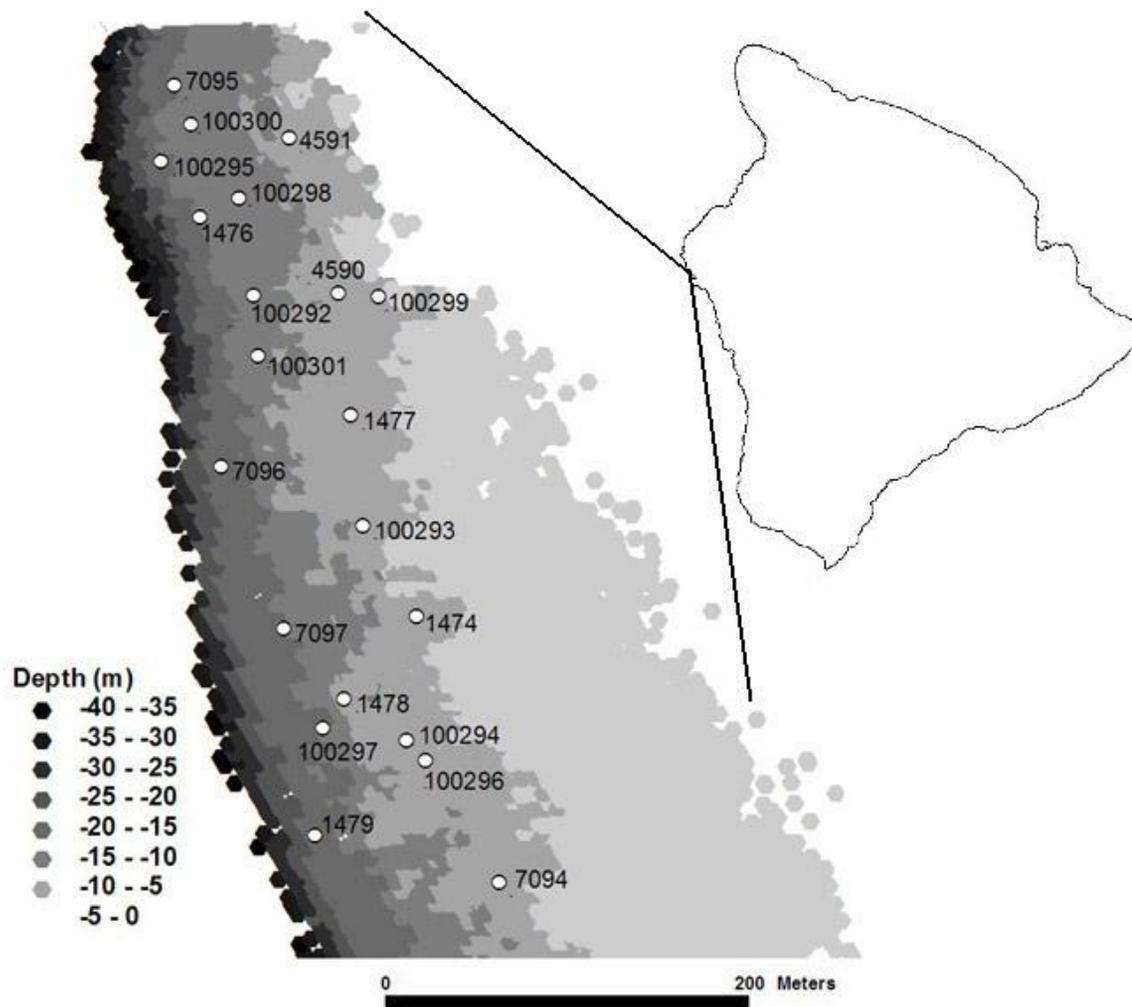


Figure 4.1. Hawai'i Island with inset of Wawaloli site. Bathymetry from Shoal lidar data is designated on the inset by a gray gradient. Dots indicate locations of receivers in the array.

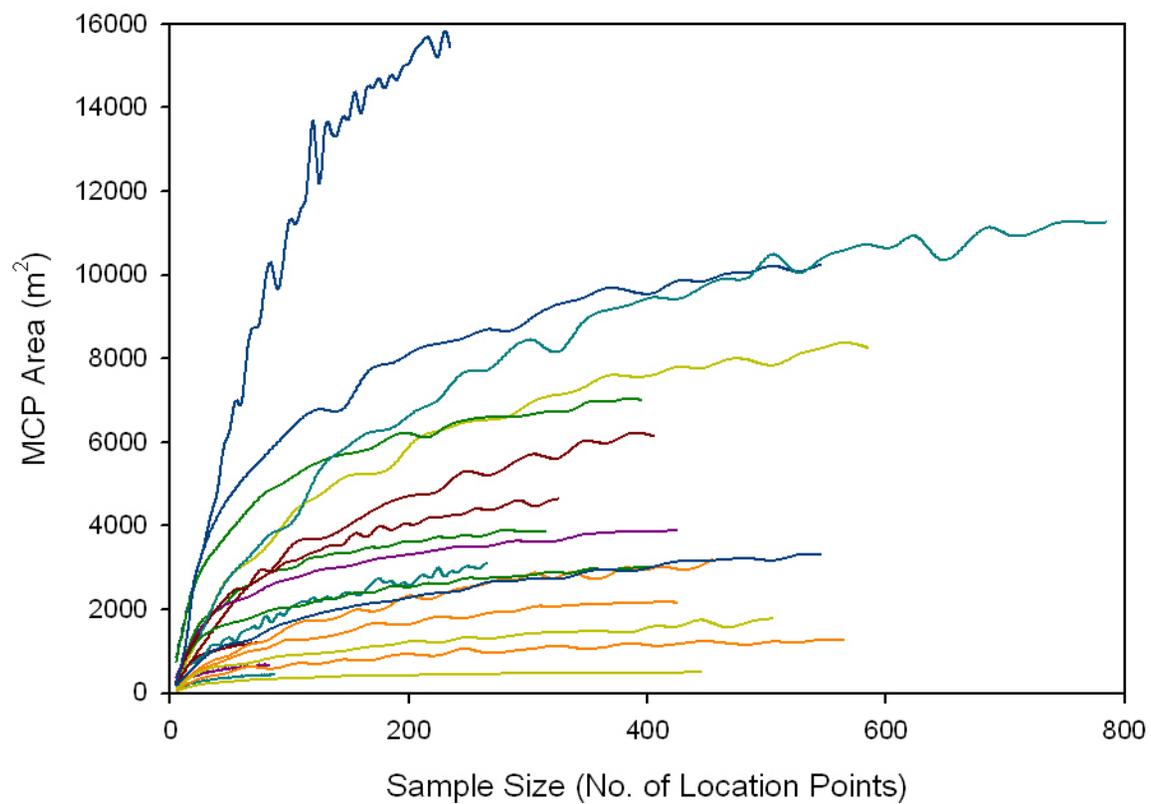


Figure 4.2. Observation-Area Curve for the 20 *S. rubroviolaceus* individuals with adequate sample size of location fixes. Each point indicates an average from bootstrapping procedures with 100 replicates.

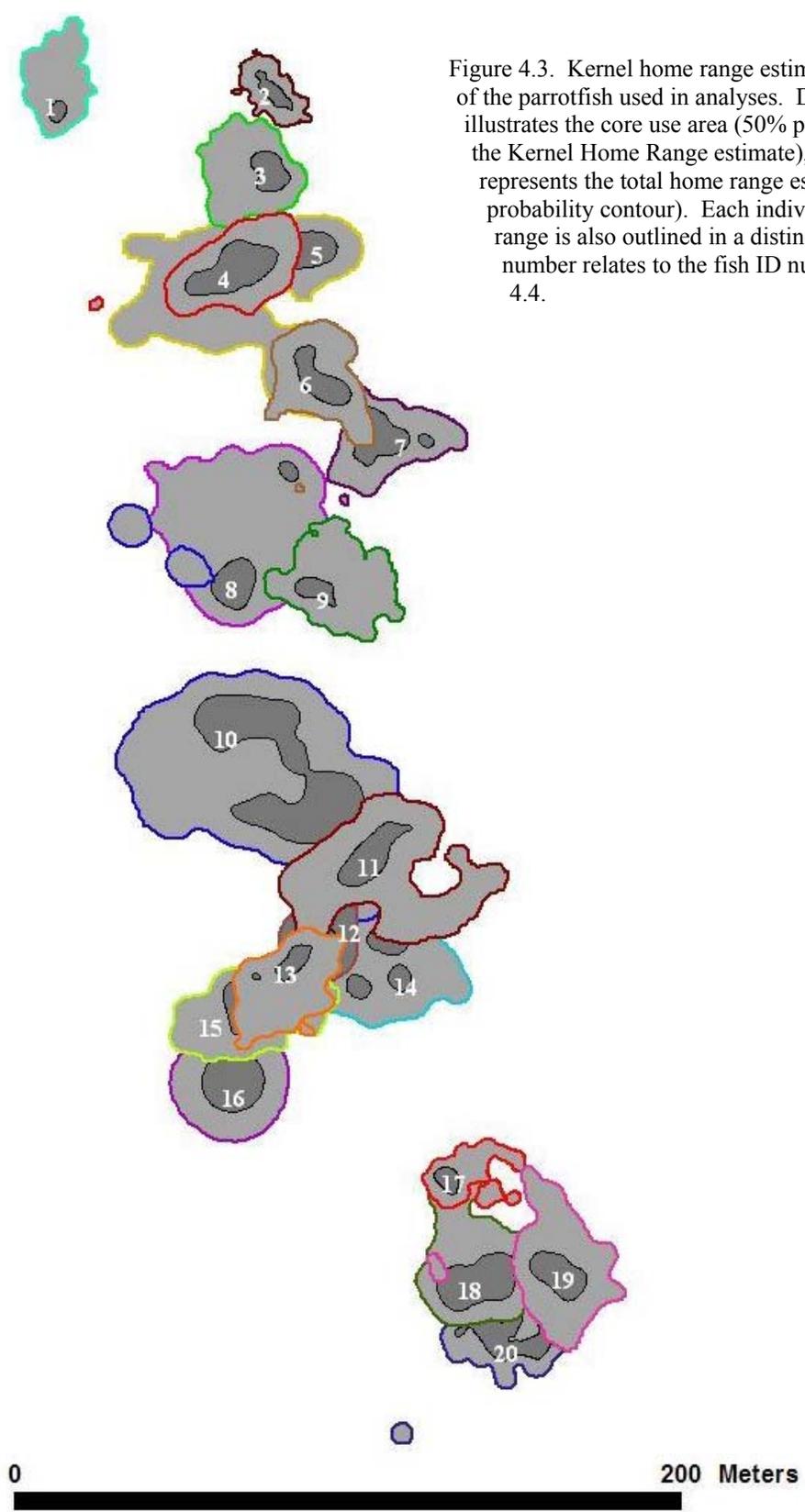


Figure 4.3. Kernel home range estimates for each of the parrotfish used in analyses. Dark gray illustrates the core use area (50% probability in the Kernel Home Range estimate), and light gray represents the total home range estimated (95% probability contour). Each individual home range is also outlined in a distinct color and the number relates to the fish ID number on Table 4.4.

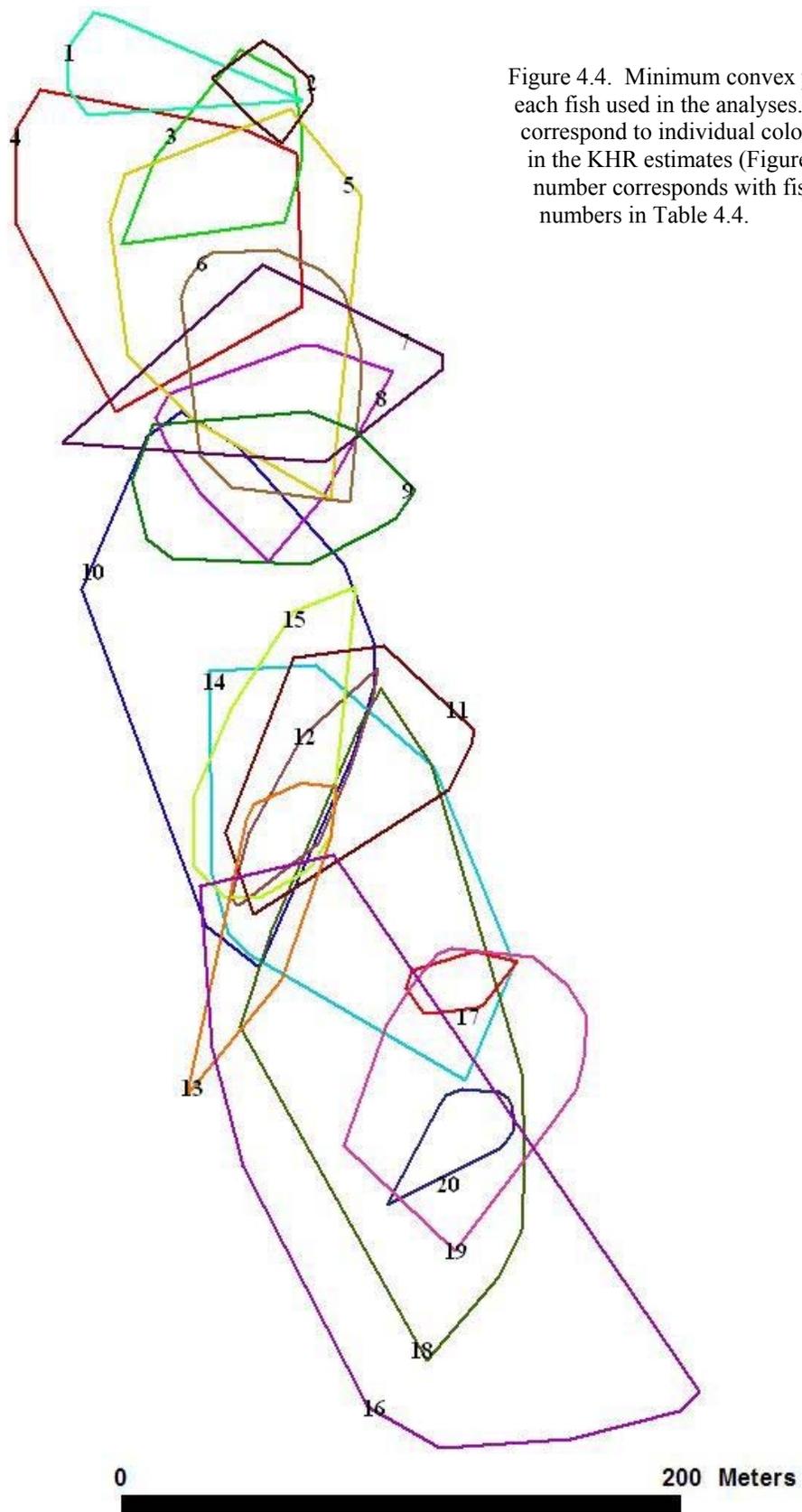


Figure 4.4. Minimum convex polygons for each fish used in the analyses. Colors correspond to individual colors illustrated in the KHR estimates (Figure 4.3) and number corresponds with fish ID numbers in Table 4.4.

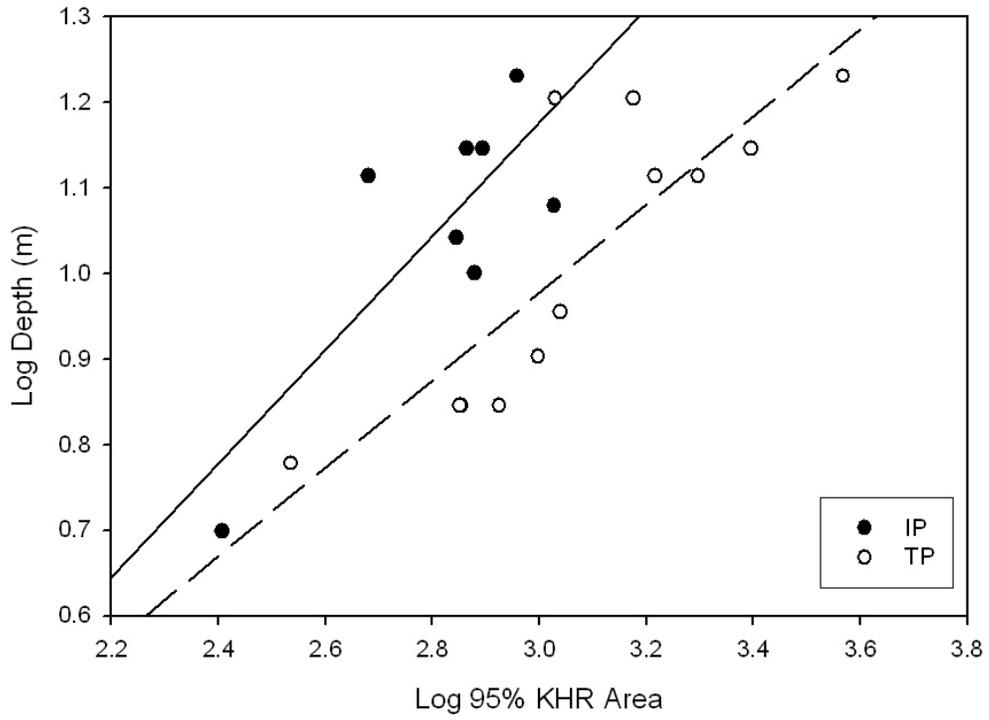


Figure 4.5. Regression of home range area (95% KHR) and home range depth for IP and TP *S. rubroviolaceus*.

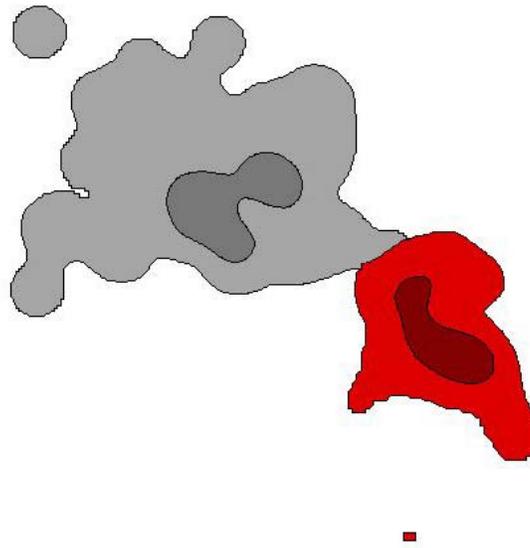


Figure 4.6a. Kernel home ranges for the individual that left its territory (in red) and the neighboring male (in gray)



Figure 4.6b. The new home range established by the neighboring male after the disappearance. The previously occupied territory location is illustrated by the red outline.

Diurnal Activity of *Scarus rubroviolaceus* (WW-Y)

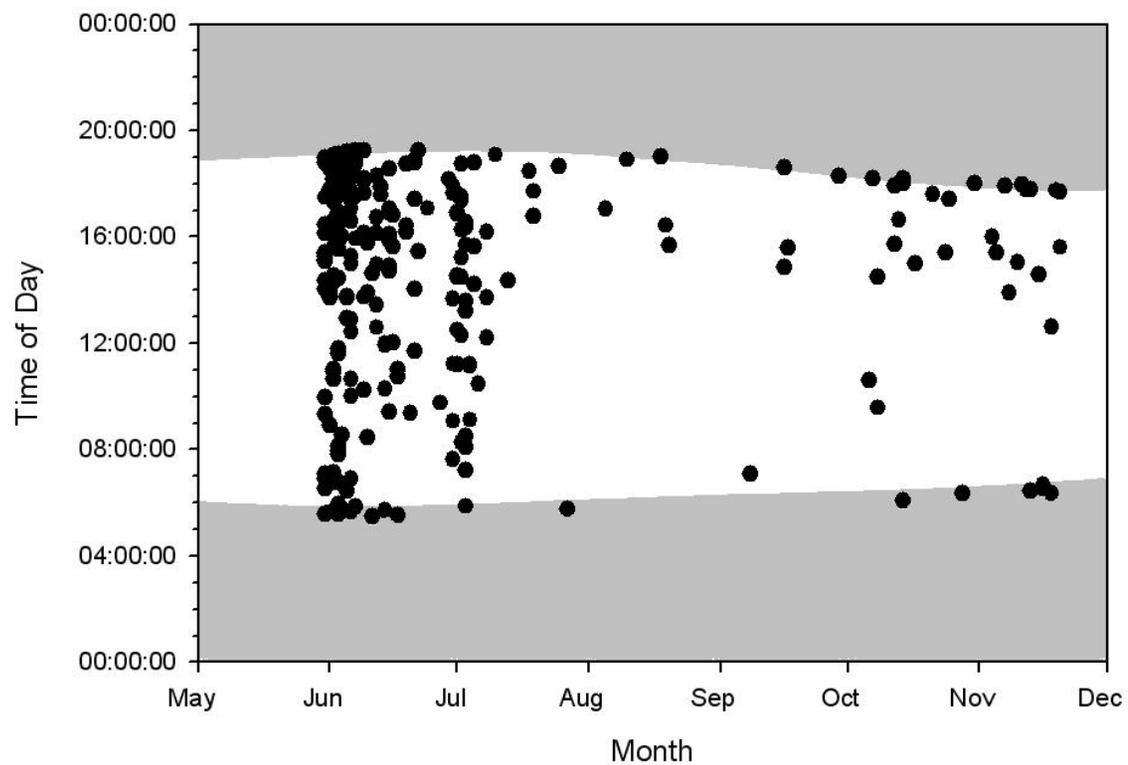


Figure 4.7. Recorded transmissions for all receivers for WW-Y throughout the day and over the course of the receiver deployment period in black dots. Gray areas indicate times after sunset and prior to sunrise for Hawai'i during this time period.

Daytime Movement of *Scarus rubroviolaceus* (WW-W)

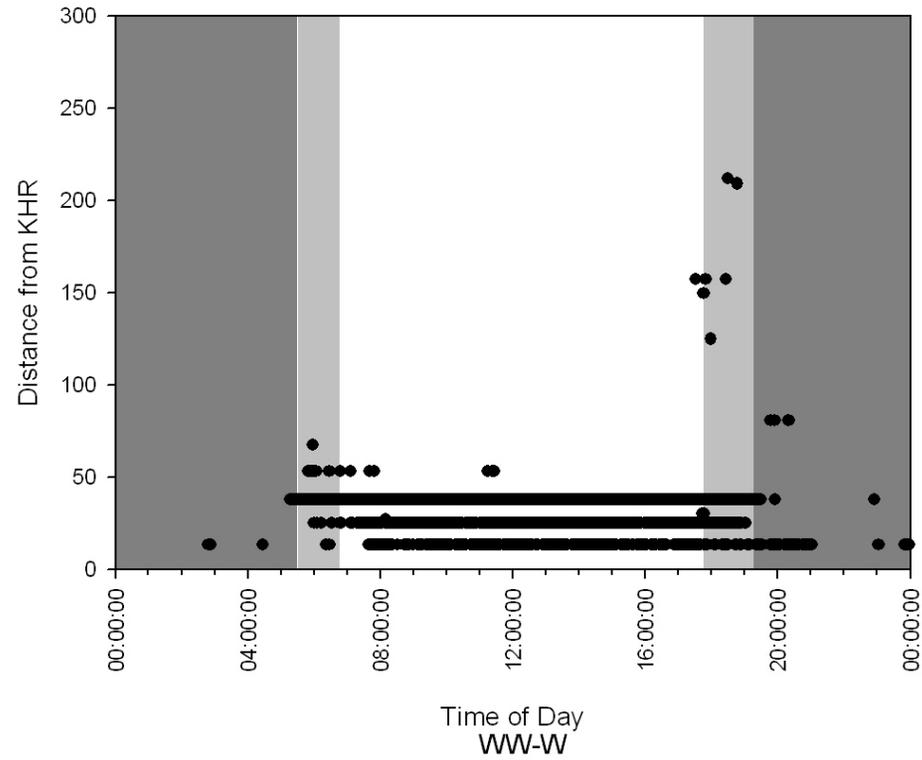


Figure 4.8. Examples of daytime movement: high activity (greater movement away from home range) during the late evening, which is the most common pattern. Detection range for receivers approximately 40m. Light gray illustrates the range of sunrise or sunset over the course of the study, and dark gray illustrates the night-time duration.

Site Fidelity over Time (Ch-F)

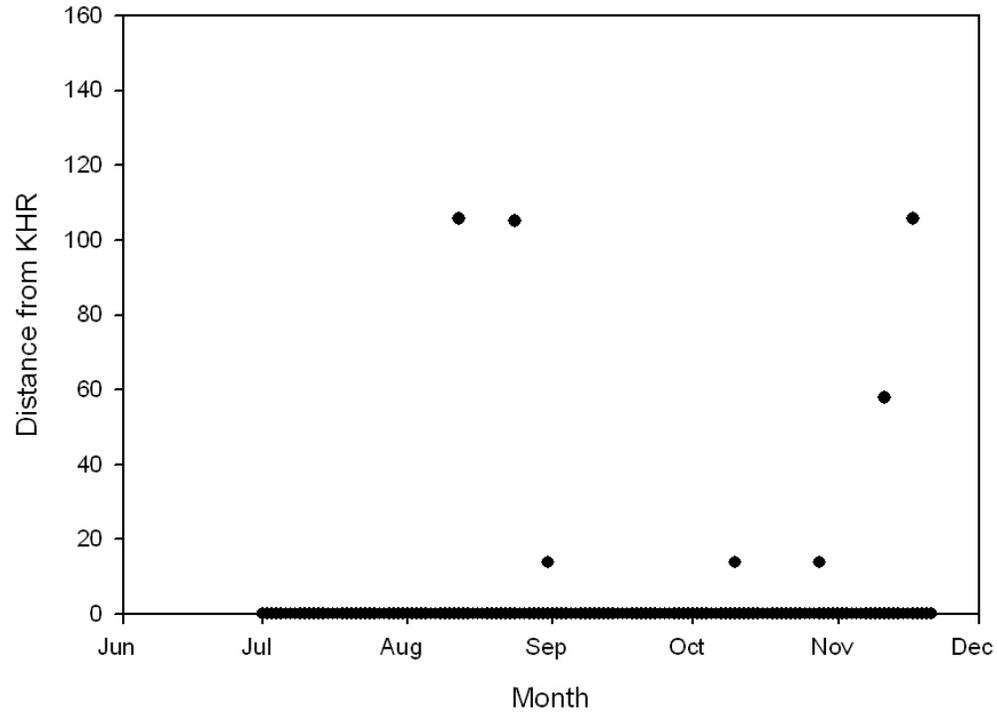


Figure 4.9. Evidence of site fidelity over the course of several months for one individual. Detection range of the receiver approximately 40m. A few long forays are evident, as well as consistent and frequent transmissions to a receiver within the home range.

Long-term Shift in Location of an IP *S. rubroviolaceus* (WW-W)

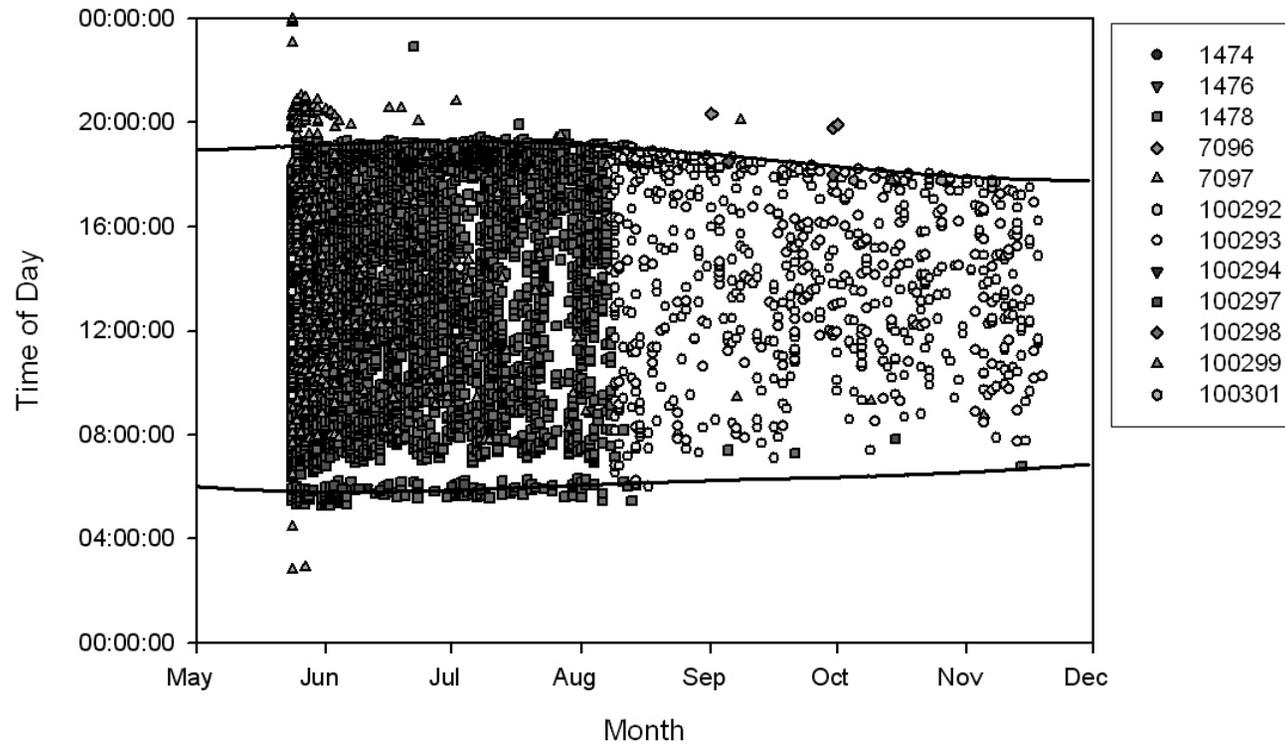


Figure 4.10. Observed shift from deeper receivers (7097 and 1478) to shallower receiver (100293) later in the year. Symbols represent individual receivers with detections of this individual.

CHAPTER 5

SUMMARY AND CONCLUSIONS

Summary

To better understand the biology and ecology of large protogynous hermaphrodites and consider the needs for effective management of these species, this dissertation posed three questions: (I) What is the present status of parrotfish communities in Hawai'i, and what anthropogenic factors are influencing these communities? (Chapter 2); (II) How do life history characteristics shape the response of *S. rubroviolaceus* to anthropogenic stressors, and how can fisheries managers use this information to more effectively manage stocks of this species? (Chapter 3); (III) What are the movement and social patterns for *S. rubroviolaceus*, how do they affect population and distribution dynamics, and how do they inform management decisions? (Chapter 4).

I. The study addressing the first question was conducted on the island of Oahu and provided valuable information, not only to establish a baseline status of parrotfish communities for this area, but also to provide better insight into habitat associations for these species. Scarid communities in this heavily fished region are dominated by smaller species and smaller individuals within all species. Specific habitat characteristics such as rugosity, substrate diversity, and percent live coral cover were positively correlated with scarid numerical abundance. Scarids, however, were patchily distributed and were often absent from preferable

habitats, suggesting that intense fishing pressure may be an important factor preventing these fish from fully exploiting available habitats. This research is the first thorough, broad-scale study of scarid community structure in Hawai'i, and provides important information that has management and conservation implications for parrotfish in Hawai'i and throughout tropical coral reef ecosystems.

II. The study addressing the second question was also conducted on the island of Oahu and provided the first in-depth reproductive analysis of *Scarus rubrovioalceus*, a large-bodied and valuable species in parrotfish fisheries. Fifty percent of the population of this species become reproductively mature at 34 cm FL, which is larger than the current minimum size limit for harvest in Hawai'i. These fish are also fairly long-lived; the oldest fish collected was 22 years old. It is evident that protecting a relatively few large females may be more beneficial to the future of populations of large hermaphrodites than protecting more, smaller individuals. The observed predominance of initial phase (IP) males as a reproductive strategy may not only be a response to intense fishing pressure, but it may also influence the population's future response to fishing pressure. It is apparent that on Oahu intense fishing activity is not only depleting fish numbers, but also, because these fish are large protogynous hermaphrodites, it is also altering the socio-sexual structure and population dynamics of this species.

III. The third question was addressed in the final study, which was conducted on the Kona Coast of Hawai'i Island. Site fidelity and sizes of home range were explored by studying 21 marked, free ranging individuals. All

individuals showed strong diurnal activity patterns, and site fidelity was prominent over the course of several months. Home range size was significantly influenced by depth, but the interaction between home range size and fish size was inconsistent. While some home ranges were held for at least nine months, home range borders were somewhat dynamic. Occasional long forays from the home range were observed in many individuals. This information is vital for understanding the effectiveness of marine reserves for protecting adult spawning stocks and the potential for spillover of adults grown to maturity in reserves. Following up on this study can lead to understanding spatial population dynamics related to fish size, depth of home range, reproductive behavior, and sleeping sites of this large, dominant coral reef herbivore.

Conclusions

Worldwide population declines in coral reef fisheries call for a reassessment of management strategies (Munro 1996). One of the primary issues hindering conservation and sustainability of these fisheries is that management strategies are seldom specifically designed for the unique life histories, complex socio-sexual systems, and population dynamics associated with hermaphroditism (Russ 1991). Little biological information is available for many exploited reef species, and much of our knowledge on the dynamics of hermaphroditism and its implications in social and population dynamics is based on smaller, unfishery species. The present studies have presented information on previously unstudied species and have provided data on a large-bodied, hermaphroditic fishery species,

which will deepen our insight on reproductive, social and population dynamics of these exploited species.

While the present study (Chapter 2) demonstrated clear associations between parrotfish communities and habitat characteristics, studies conducted elsewhere have not found conclusive relationships (Hart et al. 1996, Ohman & Rajasuriya 1998, Gust 2002). Knowledge of habitat associations (or lack thereof) is critical for effective management, particularly if ecosystem-based management techniques are employed. MPAs will only be effective for protecting spawning stocks if they contain habitat favorable to the species of interest. The study detailed in Chapter 2 also demonstrates the importance of having baseline population-level information on exploited species. No true baseline information existed for these species prior to this study, so densities of species were difficult to gauge.

The importance of basic biological information for species across geographical ranges was illustrated in Chapter 3. A minimum size limit for catch of Hawaiian parrotfish was established without reproductive data available on these species in Hawai'i. At the time, the only data for *Scarus rubroviolaceus* was a study conducted in the Seychelles (Grandcourt 2002). While the minimum size limit chosen for Hawaiian parrotfish might have seemed adequate based on the Seychelles study, the life history characteristics documented in our study were markedly different from those of Seychelles, probably affected by differences in annual mean sea surface temperatures at these widely separated latitudes. *S. rubroviolaceus* in Hawai'i reach a larger size, mature later, reach a greater age,

and grow more slowly than their Seychelles conspecifics. Life history characteristics should be determined for each independent fishery location to develop effective management.

Further research is still needed to understand the dynamics of sex change and sex determination in protogynous hermaphrodites, particularly large-bodied and diandric species. The present study emphasizes the importance of large females in the population to maintain high levels of egg production. Loss of terminal phase (TP) males in protogynous hermaphrodite populations elsewhere has led researchers to believe that sperm limitation or male limitation may also occur where size-selective fisheries target the largest individuals (Hawkins & Roberts 2003, Alonzo & Mangel 2004). However, most of these studies are based on the assumption of low levels of IP males and treat all IP individuals as female. The very high occurrence of IP males in this study (Chapter 3), relative to that found in the less-exploited Seychelles (Grandcourt 2002), suggests that IP male dynamics should not be ignored. The IP male strategy may be, in part, an adaptive response to high mortality rates, and may reduce the overall fishery effect of sperm or male limitation. However, since this is the first known suggestion of high IP male numbers resulting from size-selective fishing pressure, the consequences of this alternative male tactic are unknown.

Because of the extraordinarily complex life history dynamics illustrated in Chapter 3, and our current inability to effectively model these dynamics, effective management strategies for protogynous hermaphrodites may need to move from species-based tactics towards ecosystem-based strategies (i.e. MPAs). For MPAs

to be effective, knowledge of habitat requirements (Chapter 2) and movement patterns (Chapter 4) are necessary. *S. rubrovioalceus*, like many coral reef species, is site attached and has discrete home ranges. Managers can use the home range estimates presented here to quantify the expected number of parrotfish that may be maintained within an MPA of a given size. However, management decisions should take note that long distance forays, sleeping site locations, and reproductive activity may require protection of an area much larger than the home ranges themselves. Water depth and phase (IP or TP) are also important determinants of home range size.

In conclusion, the future of coral reef fisheries depends on our ability to effectively manage these fisheries, and our management decisions can only be as effective as the depth of our understanding of these systems. Management of protogynous hermaphroditic fishes, with their complex physiology, behavior and population dynamics, is challenging. It is clear that one of the most critical avenues of research for these fishes is in basic life history, which has been largely neglected for most species. Once we have a firm understanding of the dynamics of sex determination and sex change in protogynous hermaphrodites, we can then appreciate how these dynamics apply at social and population levels.

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