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# Home range and movement patterns of the Redlip Parrotfish (*Scarus rubroviolaceus*) in Hawaii

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**Abstract** The activity and movement of the Redlip Parrotfish, *Scarus rubroviolaceus,* near Wawaloli reef, Hawaii (19°43′06″N, 156°03′11″W), was investigated with active and passive tracking techniques from April through November 2007. Site fidelity was determined and home range sizes were measured for 21 individuals. All individuals showed strong diurnal activity patterns and relatively stable home ranges. Terminal phase individuals had larger home range areas than initial phase fish, and home range size increased with depth. Occasional long forays from the home range were observed in many individuals. Forays often occurred in crepuscular hours and may represent migrations to/from nocturnal sheltering sites. Findings from this study underscore the importance of depth and nighttime shelter migrations as design considerations for effective marine protected areas (MPA) for large parrotfishes.

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## Introduction

Passive and active tracking studies in marine ecosystems have become increasingly important to address demographic, behavioral, and management questions (Heupel et al. 2006; Righton and Mills 2006). The combination of both active and passive tracking permits a comprehensive analysis of animal movement and behavior, including detailed, but short-duration observations, as well as long-term, large-scale, continuous monitoring (Bolden 2001; Afonso et al. 2008a). Analyses of animal home range and movement patterns have provided valuable information on the effectiveness of marine reserves and may be used to estimate spillover of individuals into fishery areas (Kramer and Chapman 1999; Eristhee and Oxenford 2001; Kaunda-Arara and Rose 2004b; Afonso et al. 2008a; Williams et al. 2009; Meyer et al. 2010). 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 and Buckman 1973; Jones 2005; Righton and Mills 2006; Afonso et al. 2008a; Claisse et al. 2011). As such, spatially based management techniques, like MPAs, are frequently sought as potential management tools.

Parrotfish (Labridae, formerly Scaridae; see Westneat and Alfaro 2005), particularly larger bodied species, are economically valuable in fisheries and tourism (Smith 1993; Page 1998; McClanahan et al. 1999). Despite this, relatively little information is available on their movement and spatial activity patterns, particularly for larger parrotfish species that are a major component of some tropical

fisheries. Most studies investigating territoriality or home range in parrotfish have been conducted on Caribbean species, have had a strict sociobiology focus, have primarily investigated smaller, less vagile species, and/or have included relatively small sample sizes (Table 1).

Parrotfish can have complex social structures, which can strongly influence population density and dynamics (Alevizon and Landmeier 1984; Colin and Bell 1991; van Rooij et al. 1996; Kuwamura et al. 2009). Most are sequential protogynous hermaphrodites and exhibit two color phases: initial phase (IP) fish which are primarily females but may include a small proportion of males, and terminal phase (TP) fish which are all males. Parrotfish often spawn throughout the year, and some species may undergo migrations to specific spawning sites (Thresher 1984). TP males are typically territorial, with one male defending a territory against other males and maintaining a harem of females within that territory (Thresher 1984). However, other social dynamics may occur for some species, and the complexity of social dynamics exhibited by parrotfishes is likely underrepresented in the literature (Clifton 1989; Clifton 1991; Muñoz and Warner 2004; Afonso et al. 2008a).

*Scarus rubroviolaceus* Bleeker is a large parrotfish species found throughout the Indo-Pacific, which serves an important ecological function as a bioeroder (Ong 2007; Ong and Holland 2010). Few studies have investigated *S. rubroviolaceus*, despite its prominence in recreational, artisanal, and commercial fisheries in Hawaii and throughout its broad Indo-Pacific distribution (Clements and Bellwood 1988; Connell et al. 1998; Page 1998; Jennings et al. 1999; McClanahan et al. 1999; Grandcourt 2002; Ong 2007). Information on the movement and behavior of this species is essential to fisheries management and conservation efforts, particularly if spatial protection measures are implemented. The aim of this study was to describe the home ranges and movement patterns of *S. rubroviolaceus* on a typical coastal reef tract along the western coast of Hawaii Island using both active and passive tracking techniques. Further, the influence of phase (i.e., TP, IP), body length, and depth on home range area are investigated. This study provides basic information for understanding social patterns, distribution, and population dynamics of this species, and it provides a basis for effective management strategies for this large parrotfish and other similar, valuable fisheries species.

## Materials and methods

### Study site

This study was conducted on the 6.81 ha Wawaloli reef tract on the western coast of Hawaii Island, chosen because

of minimal fishing influence (pers. obs.). The Wawaloli 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, and high cover of live coral aggregations (particularly *Pocillopora meandrina*, *Montipora capitata*, *Porites compressa*, and *Porites lobata*) (Ortiz and Tissot 2008). The bulk of the study was conducted on the reef slope, and the habitat was fairly consistent across the study area.

### Characterization of parrotfish assemblage at Wawaloli

Numerical abundance and biomass estimates were obtained using underwater visual censuses. Six replicate belt transect censuses (100 m × 5 m) were conducted following the method of Howard et al. (2009). Starting points for transects were randomly selected from available latitude and longitude coordinates within the Wawaloli study area with the Animal Movement extension to ArcView 3.2 (Hooge and Eichenlaub 1997). For each starting point, habitat maps and bathymetry were used to determine transect orientation, so that each belt would maintain a relatively constant depth and survey a contiguous habitat type. Depths of transects ranged from 5 to 17 m. Species, number, and estimated total length (cm) were recorded, and biomass estimates for each species were obtained by a length–weight conversion based on allometric growth: $W = aL^b$, where $w$ = weight (g), $L$ = length (cm), and $a$ and $b$ are allometric growth constants obtained empirically from Howard (2008).

### Movement observations

Movement and behavior of *S. rubroviolaceus* was observed using multiple techniques. Night surveys were conducted in conjunction with tagging events to provide anecdotal information pertinent to sheltering locations. Daytime active tracking by snorkelers was used to investigate fine-scale movement patterns of all observed externally t-bar tagged fish; this technique permitted home range analyses of those individuals with robust observations. A subset of externally t-bar tagged individuals was also implanted with acoustic transmitters ("acoustically tagged") to permit passive acoustic tracking. Passive acoustic tracking provides a temporally and spatially more expansive, though coarser-scale, coverage of movement patterns than can be acquired by visual active tracking of externally tagged individuals alone. Many individual fish were observed using multiple techniques, though some fish were exclusively observed with only one technique. For example, some fish that were both externally t-bar tagged and acoustically tagged were not observed by snorkelers during

**Table 1** Summary of parrotfish movement and territory studies and methodology employed

| Location | Species | Study | Total length (cm)[a] | Sample size | Observation period (h) | N observations per individual | Method of territory estimate | Territory size estimate (m$^2$) |
|---|---|---|---|---|---|---|---|---|
| Mediterranean | *Sparisoma cretense* | de Girolamo et al. (1999) | 50.0 | 7 | 0.33–2 | 6–12 | Aggr. Observ. Map | 189–587 |
| | | Afonso et al. (2008b) | 50.0 | 12 | 24 and 45 | 2+ | MCP | 7,000–103,600 |
| | | | | | | | KUD | 2,300–191,000 |
| Caribbean/ West Atlantic | *Scarus iseri* | Ogden and Buckman (1973) | 35.0 | Unspecified | 0.67 | Unspecified | Not identified | 12 |
| | | Mumby and Wabnitz (2002) | | 25 | 0.33 | 1 | Map 1 min. intervals | 41–120 |
| | *Sparisoma aurofrenatum* | Mumby and Wabnitz (2002) | 28.0 | 25 | 0.33 | 1 | Map 1 min. intervals | 82–319 |
| | | Muñoz and Motta (2000) | | 10 | Unspecified | Unspecified | Aggr. Observ. Size | 240 ± 137.4 |
| | *Sparisoma chrysopterum* | Mumby and Wabnitz (2002) | 46.0 | 17 | 0.33 | 1 | Map 1 min. intervals | 170–324 |
| | | Muñoz and Motta (2000) | | 7 | Unspecified | Unspecified | Direction movement | 4,371.5 ± 5869.5 |
| | *Sparisoma rubripinne* | Mumby and Wabnitz (2002) | 47.8 | 17 | 0.33 | 1 | Map 1 min. intervals | 168–1,400 |
| | *Sparisoma viride* | Mumby and Wabnitz (2002) | 64.0 | 27 | 0.33 | 1 | Map 1 min. intervals | 91–289 |
| | *Sparisoma radians* | Marconato and Shapiro (1996) | 20.0 | 22 | 0.5–1 | 1 | Aggr. Observ. Size | Unspecified |
| | *Scarus taeniopterus* | Dubin (1981) | 35.0 | 22 | Unspecified | Unspecified | Not specified | 120–500 |
| | *Scarus rubroviolaceus* | Ong (2007) | 70.0 | 5 | 1– 4 | 17–22 h/fish | MCP | 2,635 ± 2,183 |
| Hawaii | *Chlorurus bleekeri* | Bellwood (1985) | 49.0 | 4 | Unspecified | 50 + or > 10 h/ fish | Map of locations | 300–500+ |
| Great Barrier Reef | *Chlorurus microrhinos* | Welsh and Bellwood (2012a) | 70.0 | 7 | 13 | 44–62.75 h/fish | MCP | 5,430–13,070 |
| | | | | | | | KUD | 4,830–12,869 |
| | *Chlorurus gibbus* (now *C. microrhinos*) | Bellwood (1985) | 70.0 | 1 | Unspecified | 50 + or > 10 h/ fish | Map of locations | 1,000+ |
| | *Chlorurus japanensis* | Bellwood (1985) | 31.0 | 1 | Unspecified | 50 + or > 10 h/ fish | Map of locations | 500+ |
| | *Scarus flavipectoralis* | Bellwood (1985) | 40.0 | 1 | Unspecified | 50 + or > 10 h/ fish | Map of locations | 100+ |
| | *Scarus frenatus* | Bellwood (1985) | 47.0 | 11 | Unspecified | 50 + or > 10 h/ fish | Map of locations | 180–1,800+ |
| | *Scarus niger* | Bellwood (1985) | 40.0 | 1 | Unspecified | 50 + or > 10 h/ fish | Map of locations | 250 |
| | *Scarus oviceps* | Bellwood (1985) | 35.0 | 4 | Unspecified | 50 + or > 10 h/fish | Map of locations | 300 |
| | *Scarus rivulatus* | Welsh and Bellwood (2012b) | 40.0 | 18 | Passively assessed | 7,818–50,558 passive acoustic detections | Passive acoustic receivers– maximum possible home range size | 4,290–43,030 |
| | *Scarus rubroviolaceus* | Bellwood (1985) | 70.0 | 6 | Unspecified | 50 + or > 10 h/fish | Map of locations | 500–700 |

[a] Maximum size estimates (Total Length) and valid binomial name obtained from fishbase.org (Froese and Pauly 2012). Aggr. Observ. Map = Hand drawn map of aggressive interactions with neighbors, Aggr. Observ. Size = Largest length and width based on observation of aggression, Direction movement = Largest length and width based on observation of change in direction of movement, *KUD* Kernel Utilization Distribution, Map 1 min. intervals = Hand drawn map of locations at 1 min interval, Map of locations = Hand drawn map of locations, *MCP* Minimum Convex Polygon

daytime active tracking, but were observed by stationary passive acoustic receivers. Likewise, some individuals with both t-bar and acoustic tags were identified by snorkelers but never detected on receivers. The combination of both active and passive tracking techniques, therefore, provides a more comprehensive assessment of movement patterns and a broader sampling of individuals than would be obtained using only one tracking technique.

### Night surveys and tagging

During April and May 2007, SCUBA divers conducted haphazard sweeps of the Wawaloli area at night to identify nocturnal shelter locations of *S. rubroviolaceus* and to capture fish for t-bar and acoustic tagging. A GPS unit at the surface, attached to a float, was towed by a diver in order to record the capture location of tagged fish as well as the location of resighted, previously t-bar tagged fish during nighttime resting behavior.

Divers captured resting parrotfish at night with hand nets. For each captured fish, color phase was recorded and fork length (FL) was measured to the nearest millimeter. Each individual was externally tagged with a unique color/location combination of t-bar tags (Floy Tag, Seattle, WA) and then released at its capture location. No juvenile phase fish were tagged.

A subset of tagged fish was also implanted with acoustic transmitters (Table 2). Captured fish were raised slowly from depth to minimize barotrauma. 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 × 7 mm diameter) was implanted, using standard field surgical procedures (Meyer and Holland 2005). Incisions were sealed with Vetbond tissue adhesive, and fish were allowed to recover in an onboard recovery tank. Once the fish was active and appeared to be successfully recovered from surgery, it was slowly returned to depth and returned to the capture site.

### Daytime active tracking by snorkelers

Active visual tracking of t-bar tagged individuals was conducted during daylight hours by a snorkeler with a towed GPS unit from April through August 2007. Fish location was recorded every 5 s, 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 parrotfish behavior. Pilot studies tracking focal individuals for periods longer than 1 h indicated that forays of fish were of short duration, and thus, tracking periods of 20 min were amply representative of an individual's short-term movement patterns. Afterward, attempts were made to maintain individual tracks for at least 20 min. A track was ended after 20 min or if visual contact could not be maintained, even if lost temporarily. In order to adequately characterize longer-term movement patterns, fish used in analyses included those tracked multiple times, regularly (often daily) throughout the study period, and with different tracks occurring throughout daylight hours.

### Site fidelity and home range analysis

The Animal Movement Analysis Extension (AMAE) for ArcView 3.2 was used for geospatial analysis of data resulting from active visual tracking data (Hooge and Eichenlaub 1997). Only individuals meeting minimum sample size thresholds were included in the site fidelity and home range analyses (Righton and Mills 2006). Minimum sample size was determined using techniques described in Odum and Kuenzler (1955) where bootstrapped subsamples of location data points from individuals, here we used 100 replicates, were used to develop home range estimates. Minimum sample size was determined as the number of data points required for the observation-area curve to reach an asymptote: the point where mean home range size changed 1 % or less as data points are added in 5-point intervals.

Site fidelity tests were used within the AMAE program to determine whether total individual fish movement, combining the complement of tracking events for each individual, was significantly different from random Monte Carlo walks. Only those fish showing site fidelity were used in home range analyses (Powell 2000).

Various estimates of home range area were calculated and will be referred to as follows: (1) 95 % Kernel Home Range (95 % KHR) contour area (home range area, m²), (2) 50 % Kernel Home Range (50 % KHR) contour area (core area, m²), and (3) Minimum Convex Polygon (MCP) area (m²). KHR provides probability contours, showing the

**Table 2** Size and phase (initial phase, IP/terminal phase, TP) of conventional and acoustically tagged *Scarus rubroviolaceus* at Wawaloli

| 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 |

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 and Oxenford 2001; Rechisky and Wetherbee 2003; Righton and Mills 2006). We define the core utilization area as that part of an individual's home range that is particularly important and most heavily utilized (Powell 2000). We use a 50 % probability contour to quantify the core area for each individual (Jones 2005; Righton and Mills 2006). We implemented KHR using Least Squares Cross Validation (LSCV) to determine the smoothing factor, as this is generally considered a robust and descriptive home range analysis (Seaman and Powell 1996; Powell 2000; Righton and Mills 2006). Because of their prevalence in tracking literature, we also present Minimum Convex Polygons (MCP) to allow 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 (Powell 2000).

To assess the stability of home ranges, temporal variation in KHR area for individuals was examined based on subsets of location points corresponding to month or to time of day, determined a priori (morning: sunrise to 11:00, midday: 11:01–15:00, and late afternoon: 15:01 to sunset). Only fish with enough data points to satisfy minimum sample size requirements for each of the temporal stratifications were assessed. Tests of the null hypothesis, that home range remained unchanged during the study period, were assessed with a paired $t$ test and repeated measures ANOVA. Both tests were two-tailed and a type-I alpha level of 0.05 was used to reject the null hypothesis.

### Statistical analyses

Model selection via AICc (Burnham and Anderson 2002) was used to investigate the influence of (1) phase, (2) body length, and (3) home range depth on home range area. AICc, the second-order bias corrected Akaike's Information Criterion, includes an additional term to correct for bias related to small sample size ($n$) that becomes negligible when n is large. Akaike weights ($w_i$) were calculated to assess the relative likelihood of each model in the candidate model set and were interpreted as a weight of evidence in favor of the hypothesis represented by a model (Akaike 1973; Burnham and Anderson 2002; Anderson 2008). Since body size and phase clearly co-varied in our sample with TP fish being larger than IP fish (IP: mean size 39.0 cm FL, 95 % CI 34.6–43.5; TP: mean size 48.9 cm FL, 95 % CI 45.2–52.5), we created a new variable "*standardized* FL" by standardizing FL relative to the mean FL of each phase (i.e., the new variable is the residuals from a one-way ANOVA of

**Table 3** Model selection results for the model set investigating the effect of mean home range depth (Depth), fork length standardized to the mean of each Phase (*standardized* FL) and Phase on log home range area

| Model | AICc | ΔAICc | $w_i$ | Np |
|---|---|---|---|---|
| Phase + depth | 3.3 | 0.0 | 0.48 | 4 |
| Phase * depth | 6.1 | 2.8 | 0.12 | 5 |
| Phase + depth + *standardized* FL | 6.3 | 3.0 | 0.11 | 5 |
| Phase | 6.5 | 3.1 | 0.10 | 3 |
| Phase * *standardized* FL + depth | 6.5 | 3.2 | 0.10 | 6 |
| Phase * depth + *standardized* FL | 9.4 | 6.1 | 0.02 | 6 |
| Phase + *standardized* FL | 9.5 | 6.2 | 0.02 | 4 |
| Depth | 9.7 | 6.4 | 0.02 | 3 |
| Phase*standardized* FL | 10.2 | 6.9 | 0.02 | 5 |
| *standard* FL | 11.3 | 8.0 | 0.01 | 3 |
| Depth + *standardized* FL | 12.8 | 9.5 | 0.00 | 4 |
| Depth * *standardized* FL | 15.5 | 12.2 | 0.00 | 5 |

Models were ranked according to the difference in AICc (ΔAICc). A ΔAICc of greater than 2 can be interpreted as equivalent to a significant difference. Akaike weights ($w_i$) are interpreted as a weight of evidence in favor of the hypothesis represented by the model. Np: number of estimated parameters estimated for each model
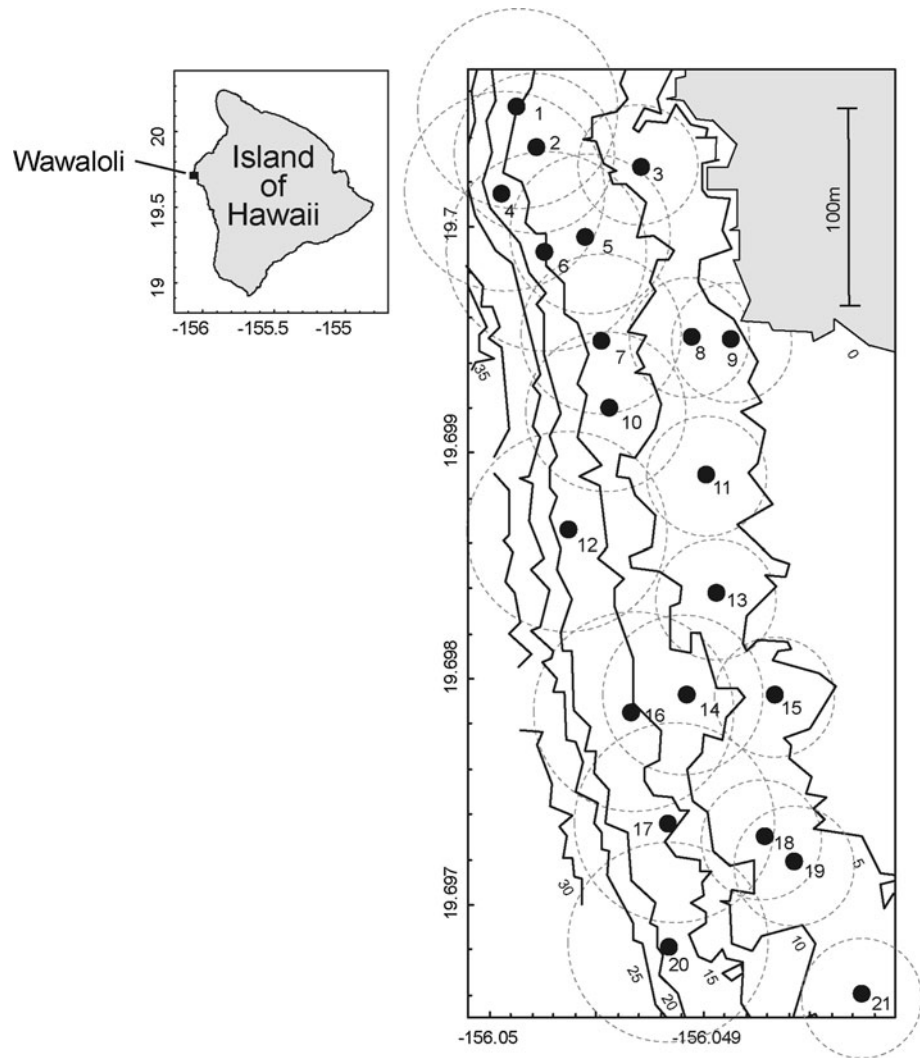
differences in FL between phases, see Graham 1997). This removes the co-linearity between the two variables and permits us to evaluate the effect of body size relative to others fish in the same phase. The candidate model set contained all combinations of the single, additive, and one-way interaction effects of "Phase" (categorical), "*standardized* FL" (linear), and core home range area "Depth" (linear) on home range area (Table 3). Models were fitted by minimizing the sum of squares. AICc values and model-averaged parameter estimates were calculated using the "AICcmodavg" package in R (R_Development_Core_Team 2009). Home range area and average depth of core area were $\log_{10}$ transformed to meet model assumptions.

### Passive acoustic tracking

Prior to acoustic transmitter implantation, 21 Vemco VR1, VR2, and VR2 W acoustic receivers were range tested. For details on the range testing methodology and discussion of factors influencing detection range, see Claisse et al. (2011). Receivers had a depth-specific maximum detection range (15–20 m deep: 50 m range, 10–15 m: 40 m range, 5–10 m deep: 30 m range).

The array of receivers was deployed from April through December 2007 in the Wawaloli study area (Fig. 1). Receivers were secured to the substrate and suspended 2–3 m above the bottom with a float to increase the effective detection range in the complex boulder and coral reef environment. Based on the assessed detection ranges, receivers were located to maximize coverage of the entire

depth range, length and breadth of the study site; however, specific locations were sometimes dependent on the availability of secure attachment points for the receivers.

Spatial patterns, such as straight-line minimum or maximum distance travelled, were analyzed using AMAE 2.0 for ArcView 3.2 (Hooge and Eichenlaub 1997). Statistical software (Minitab 13) was used to investigate temporal patterns, such as circadian detection frequency and location, and seasonal changes in location of detection. Passive tracking data were also compared to other movement data for those individuals whose movement was assessed by daytime active tracking or nighttime survey techniques.

## Results

### Characterization of parrotfish assemblage at Wawaloli

At Wawaloli, parrotfish density was $140 \pm 41$ fish ha$^{-1}$ and mean biomass was $93.6 \pm 23.9$ kg ha$^{-1}$. The density

of *S. rubroviolaceus* was $106.7 \pm 32.5$ fish ha$^{-1}$. There were $727 \pm 221$ *S. rubroviolaceus* in the study area, with a biomass of $555.0 \pm 149.1$ kg.

### Movement observations

#### Night surveys and tagging

Forty-one fish were tagged with t-bar tags; fish size ranged from 29 to 61 cm FL (Table 2). Of these, 17 fish were also implanted with acoustic tags. While all fish captured were t-bar tagged, attempts were made to distribute acoustic tags evenly for IP and TP fish and across captured size spectra.

Over the course of 13 nocturnal surveys (19.32 h), 11 of the original 41 tagged fish were resighted. Home range data collected during daytime active tracking by snorkelers were collected for 7 of these 11 resighted fish, and of these, 3 were resighted within their daytime home ranges. Three of the 11 resightings were fish for which we have no daytime active or passive acoustic tracking data. One fish

without tracking data was resighted at night next to the area where it was tagged, while the other two ranged 44–308 m away from the original tagging location.

While many fish were observed taking refuge at night within or near their daytime home ranges (as defined using daytime active tracking by snorkelers), nighttime refuge locations varied, and most fish did not consistently use the same refuge. Nine of the 12 TP (75 %) and 4 of 8 IP (50 %) used in home range analyses were t-bar tagged within their daytime home range. The remaining fish were t-bar tagged in locations that ranged from 1 to 116 m from their daytime home range.

### Daytime active tracking by snorkelers

Thirty of the 41 (73 %) t-bar tagged *S. rubroviolaceus* were resighted by snorkelers during daytime active tracking between April and August 2007. A total of 1,370 tracking sessions were conducted, with a total track time of 9,903 min and 242,270 location fixes for all fish. Because of the large number of location data points for each individual fish and the inability of the software to handle the volume of points, the active tracking data were reduced to 60-s time intervals for analysis (One individual was reduced to 90-s time intervals because of an extremely large number of location data points). Seventeen individuals with the largest number of location points (>200 after the aforementioned reduction) were used to determine the minimum allowable sample size for home range and site fidelity analyses. 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). 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 exhibited site fidelity.

The 20 fish exhibiting site fidelity with adequate sample size were used in home range analyses (Table 4). Kernel home ranges and MCPs for all fish used in analyses are reported in Fig. 2, Table 4, and Online Resource 1. Large TP male territories tended to encompass one to a few IP home ranges.

Individual home range locations were relatively stable throughout the study period, although there were some daily changes in home range shape over the course of the study. Adequate sample sizes (>74 location points) were available for each of the morning (dawn to 11 am), midday (11:01 a.m. to 3 p.m.), and afternoon (3:01 pm to dusk) time strata to create temporally based KHR for 14 fish. Similarly, 10 individuals had large enough sample sizes in

each of 2 months to assess any temporal changes on a monthly scale within the study period. There were no apparent patterns in these temporal changes, and KHR areas were not substantially different among subsets of points relating to daytime periods (repeated measures ANOVA, $F_{(2,13)} = 2.385$, $p = 0.112$) or months (Paired $t$ test, $t_9 = 0.248$, $p = 0.278$). One TP individual disappeared from our surveys part-way through our study. Afterward, a neighboring TP male expanded his territory by 11.9 %, to include much of the area formerly occupied by the missing TP male (Online Resource 2a,b).

*Scarus rubroviolaceus* home range area increased with depth and TP fish had larger home ranges than IP fish. Model selection provided the most support for the ANCOVA style model that contained the additive effects of phase and depth, which explained 43 % of the variation
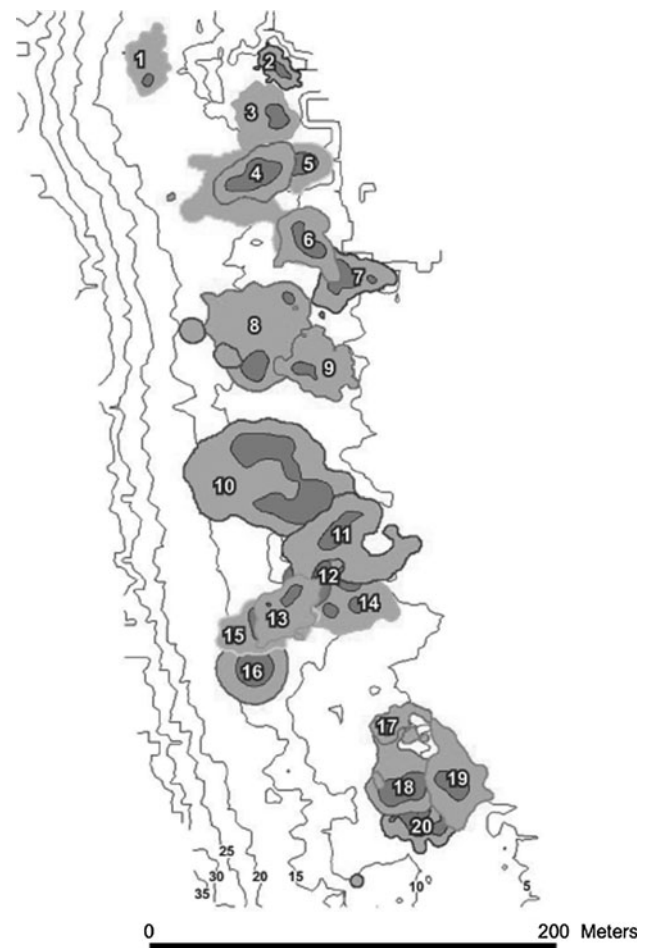


**Fig. 2** Kernel home range estimates for 20 fish with adequate location sample sizes to support analyses. *Dark gray* illustrates the core use area (50 % probability in the Kernel Home Range estimate), and *light gray* represents the total home range estimated (95 % probability contour). Individual home ranges can be cross-referenced by number in Table 4 and Online Resource Figure 1. Bathymetry is displayed behind home ranges by solid black lines at 5 m increments

**Table 4** Snorkeling based daytime active tracking of 20 *Scarus rubroviolaceus* individuals used in Wawaloli home range estimates

| Fish | Home range ID no. | Phase | FL (cm) | No. of tracking events | Span of active tracking (days) | Sample size (# fixes at 60 or 90 s interval) | MCP area (m²) | Kernel 95 % area (m²) | Kernel 50 % area (m²) | Avg. core depth (m) | Deepest part of 95 % KHR (m) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ny[a] | 14 | IP | 29.0 | 79 | 54 | 590 | 8,253 | 1,066 | 162 | 8 | 12 |
| WW-Wa | 13 | IP | 36.0 | 80 | 53 | 508 | 1,783 | 733 | 66 | 12 | 14 |
| Wa | 1 | IP | 37.5 | 61 | 45 | 574 | 1,252 | 479 | 24 | 13 | 13 |
| GG-P | 4 | IP | 39.0 | 75 | 78 | 415 | 6,147 | 783 | 246 | 9 | 14 |
| GG-G | 20 | IP | 40.0 | 14 | 56 | 84 | 653 | 759 | 243 | 8 | 10 |
| GG-TB | 3 | IP | 41.0 | 74 | 85 | 438 | 2,160 | 701 | 94 | 7 | 11 |
| YY-Wa | 16 | IP | 42.0 | 21 | 22 | 239 | 7,008 | 909 | 250 | 15 | 17 |
| ChCh-Fa | 2 | IP | 48.0 | 64 | 47 | 445 | 492 | 256 | 47 | 5 | 5 |
| F-Fa | 15 | TP | 39.0 | 36 | 49 | 269 | 2,971 | 1,072 | 123 | 14 | 16 |
| P–P | 17 | TP | 42.0 | 7 | 13 | 88 | 439 | 343 | 40 | 6 | 7 |
| Y-G | 5 | TP | 44.0 | 78 | 78 | 408 | 7,008 | 2,391 | 179 | 8 | 14 |
| B-R | 12 | TP | 45.0 | 3 | 22 | 75 | 1,178 | 1,500 | 112 | 9 | 16 |
| R | 9 | TP | 46.0 | 77 | 107 | 563 | 3,395 | 843 | 59 | 6 | 7 |
| Y-Ya | 18 | TP | 48.0 | 80 | 53 | 803 | 11,256 | 1,094 | 273 | 7.5 | 9 |
| R-R | 11 | TP | 49.0 | 86 | 85 | 431 | 3,902 | 1,646 | 180 | 7.5 | 13 |
| G-P | 10 | TP | 50.5 | 51 | 85 | 548 | 10,259 | 3,700 | 946 | 10 | 17 |
| Ch-Fa | 7 | TP | 51.0 | 77 | 51 | 463 | 3,196 | 713 | 161 | 5 | 7 |
| R/RRR | 19 | TP | 53.0 | 80 | 80 | 330 | 4,642 | 995 | 150 | 6 | 8 |
| F-Ch | 6 | TP | 58.0 | 34 | 53 | 321 | 3,873 | 711 | 137 | 5 | 7 |
| P-G | 8 | TP | 61.0 | 81 | 90 | 417 | 3,030 | 1,982 | 166 | 8 | 13 |

Identification numbers correspond to numbers shown in Fig. 2 and Online Resource 1

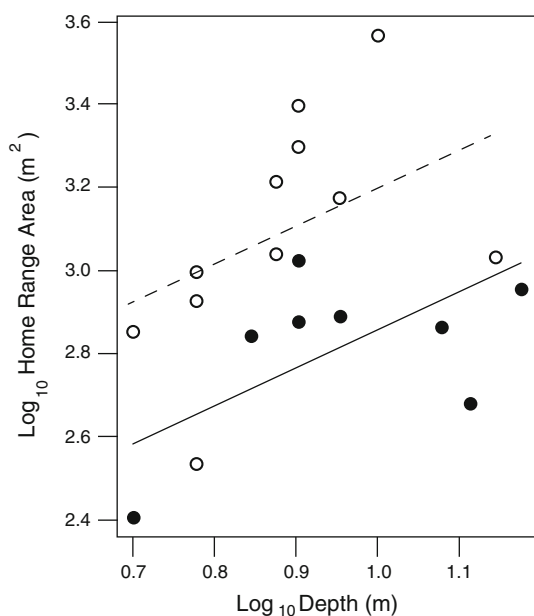[a] Individuals included in both active and passive tracking studies



**Fig. 3** Relationship between $\log_{10}$ home range area and $\log_{10}$ mean depth of the home range area for *Scarus rubroviolaceus* initial phase (IP, *filled circles*; *solid line*) and terminal phase (TP, *open circles*; *dotted line*) fish, based on the highest ranked model (Table 3)

in $\log_{10}$ home range area (Table 3; Fig. 3). It received 48 % of the total $w_i$ and had a 2.8 AICc difference between it and the second ranked model. AICc difference greater than 2 can be interpreted as a significant difference in a hypothesis testing framework. Back-transforming from the $\text{Log}_{10}$ scale, mean size of an IP fish home range is 382 m² and 1,043 m² at 5 m and 15 m depth, respectively. Meanwhile, mean size of a TP fish home range is 834 m² and 2,279 m² at 5 and 15 m depth, respectively. While there was some model selection uncertainty with the top five ranked models receiving 10 % or greater of the $w_i$ (Table 3), all of these models contain the effect of phase, and 4 out of the 5 contain the additive or interactive effects of phase and depth. Some of this uncertainty is likely due to the small sample size ($n = 8$ IP fish and 12 TP fish), and therefore, single fish have a relatively large influence on the results. The positive effect of depth on home range area in IP fish is primarily due to a single shallow IP individual with a very small home range. Contrarily, this effect in TP fish would have been much larger, but it was diminished by the deepest TP fish having a relatively small home range (Fig. 3). When we produce model-averaged parameter estimates and 95 % CI's, which accounts for this model

selection uncertainty (Burnham and Anderson 2002), the same results were still clear (Model-averaged Phase parameter estimate, 95 % CI: 0.33, 0.11–0.55; Model-averaged Depth parameter estimate, 95 % CI: 0.93, 0.18–1.69). Finally, even though *standardized* FL was included in the third ranked model in the set (Table 3), it had no effect on home range size (modeled-averaged parameter estimate, 95 % CI: 0.00, −0.02 to 0.03).

*Passive acoustic tracking*

Fourteen of 17 fish internally tagged with acoustic transmitters were detected on stationary passive acoustic receivers (Table 5). All fish were detected primarily during the day (Fig. 4). Overall, of the 17,755 detection events, 84.2 % occurred in daytime hours (approximately 0700–1800), 1.8 % occurred in crepuscular hours (approximately 0530–0700 and 1800–2000), and 14.0 % occurred in nighttime hours (approximately 2000–0530). One individual was detected continually throughout day and night over the course of several days, but this probably occurred because the receiver was located immediately adjacent to the fish's nighttime resting area. When this fish is excluded from the dataset, 94.5 % occurred in daytime hours, 2.1 % occurred in crepuscular hours, and 3.4 % occurred in nighttime hours. Among the few nighttime detections that occurred, none involved individuals detected on multiple receivers over the course of an evening, which indicates limited nocturnal activity.

Eight fish used in home range analyses were also acoustically tagged. For these individuals, 50.0 % of the acoustic detections were within the individual's home range and 99.5 % of the detections were on a receiver within 50 m of the 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 in some individuals (Table 5). Movement activity away from the fish's home range tended to occur in crepuscular hours (Fig. 5). An individual's long forays often were not in the same direction and occurred both parallel and perpendicular to the reef slope. Large females seemed to make more and longer forays than TP males or small females (Table 5), although there were too few individuals to warrant statistical analysis.

As with active tracking analyses, passive tracking data suggest that *S. rubroviolaceus* movement patterns were relatively stable throughout this study. Fish did not show any detectable shift in receiver detection other than two IP fish. These individuals had a large number of detections throughout the study, and there was a shift in the predominant receiver receiving the signals. Both fish shifted

from (a) having most detections by receivers that were slightly deeper but close to their home range during summer months (May through August) to (b) having most detections by 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 (Online Resource 3).

## Discussion

The present study provides critical information for parrotfish fishery management in Hawaii. Traditional fisheries management techniques, such as minimum size limitations of catch based on size at maturity, may be deficient, particularly with sexually labile species (Birkeland and Dayton 2005; Choat and Robertson 2002). Fishing intensity has been correlated with decreased mean size and decreased number of terminal phase males for some scarine species (Hawkins and Roberts 2003). The high degree of site fidelity seen in *S. rubroviolaceus*, however, makes them a good candidate for management through Marine Protected Areas (MPAs); though, conscious and deliberate MPA design would be required.

This study, along with others (Ong 2007; Meyer et al. 2010; Welsh and Bellwood 2012a), highlights the influence of specific physical habitat qualities on movement patterns of large parrotfishes, and MPA strategies must include this information when considering protective capabilities and spillover. Fish in enclosed bays (Ong 2007, Meyer et al. 2010) may exhibit very different movement patterns than those on open coastlines (the present study). Long forays observed at Wawaloli in the late evening may well be attempts to find appropriate nighttime shelter sites as is seen in other parrotfish species (Dubin and Baker 1982). *S. rubroviolaceus* along the Wawaloli coastline shelter up to 116 m away (and potentially further) from their daytime home range, while similar sized parrotfish in the enclosed Pioneer Bay, Great Barrier Reef, have been found to shelter within 24 m of their home ranges (Welsh and Bellwood 2012a). Meyer et al. (2010) also identified obvious diel habitat shifts for parrotfishes in Hawaii, indicating requirements for different daytime and nighttime habitats. If parrotfish are fished at night while sheltering, 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 and Dayton 2005;

**Table 5** Passive acoustic tracking of 17 *Scarus rubroviolaceus* at Wawaloli

| Fish | FL (cm) | Phase | Date acoustic tagged released | Last recorded transmission | Total days passively tracked | Total transmissions detected | No. of receivers visited | % of detected transmissions on receivers > 50 m away from KHR | Max. distance detected from KHR or initial tagging location (m)[a] |
|------|---------|-------|------|------|------|------|------|------|------|
| Ny–a | 29.0 | IP | 5/24/2007 | 11/20/2007 | 180 | 363 | 4 | 0 % | 46 |
| WW-Wa | 36.0 | IP | 5/23/2007 | 11/19/2007 | 180 | 6,500 | 12 | 0.49 % | 212 |
| W–a | 37.5 | IP | 5/30/2007 | 11/18/2007 | 172 | 82 | 1 | 0 % | 3 |
| YY-Y | 39.0 | IP | 5/23/2007 | 5/26/2007 | 3 | 2 | 2 | n/a | 71 |
| YY-Wa | 42.0 | IP | 5/30/2007 | 11/7/2007 | 161 | 44 | 8 | 25.00 % | 229 |
| WW-Y | 43.0 | IP | 5/30/2007 | 11/20/2007 | 174 | 293 | 3 | n/a | 166 |
| FF-F | 47.0 | IP | 5/23/2007 | 11/5/2007 | 166 | 26 | 10 | n/a | 223 |
| ChCh-Fa | 48.0 | IP | 5/29/2007 | 11/11/2007 | 184 | 42 | 7 | 97.62 % | 310 |
| F-Fa | 39.0 | TP | 5/23/2007 | 11/19/2007 | 180 | 4,897 | 5 | 0.08 % | 208 |
| W-W | 39.0 | TP | 5/23/2007 | n/a | 0 | 0 | 0 | n/a | n/a |
| P-Ny-P | 43.5 | TP | 5/24/2007 | 6/4/2007 | 11 | 41 | 10 | n/a | 362 |
| W-Y | 45.0 | TP | 5/24/2007 | 11/7/2007 | 167 | 2 | 1 | n/a | 65 |
| Y-W | 45.0 | TP | 5/24/2007 | n/a | 0 | 0 | 0 | n/a | n/a |
| Y-Ya | 48.0 | TP | 5/24/2007 | 9/15/2007 | 129 | 325 | 2 | 0 % | 3 |
| Ch-Fa | 51.0 | TP | 5/29/2007 | 11/21/2007 | 194 | 5,138 | 5 | 0.08 % | 106 |
| W-F | 52.0 | TP | 5/31/2007 | 6/15/2007[b] | 15 | 4 | 2 | n/a | 144 |
| F-Ch | 58.0 | TP | 5/29/2007 | n/a | 0 | 0 | 0 | n/a | n/a |

Note that only 8 individuals are present in both the snorkeler-based active tracking portion of the project (Table 4) and were detected using passive acoustic receivers

[a] Individuals included in both active and passive tracking studies

[b] The active tracking portion of this study observed this fish for more than 1 month after the last detection recorded
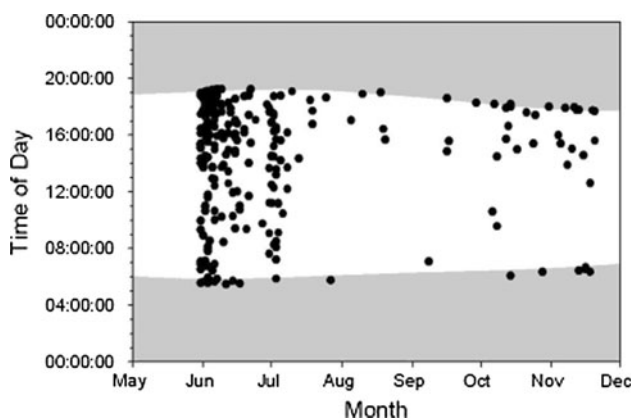


**Fig. 4** Diel pattern of detections for one representative acoustically tagged individual (WW-Y, no home range estimated, Table 5). *Gray areas* indicate times after sunset and prior to sunrise. The attenuation of detections over time is indicative of battery power reduction over time

Howard 2008), protecting home ranges and sleeping sites for these females may be particularly important.

In scarines, movements beyond the home range typically occur near dawn and are related to spawning migrations away from the reef (Bellwood 1995a; Bellwood 1995b; Ong 2007; Afonso et al. 2008a). While the presence of spawning migrations could not be refuted by the present study, there was no evidence to support it, and long-distance movements in this study occurred near dawn and dusk, with no apparent spawning activity at dusk. Long forays by individual fish often were not in the same direction and thus not indicative of a repetitive migration pattern expected in sequential spawning fish. While anecdotal, potential differences in distance and frequency of long forays between large IP individuals and smaller IP or TP fish may be an important behavioral pattern and further investigation would be useful. Among many other potential reasons, such a pattern could be due to limitations in adequate nighttime sheltering crevices for larger bodied individuals. Competition for sheltering sites with nearby TP fish could force large-bodied IP fish to shelter further from their home range.

Parrotfish reproductive behavior can show tremendous intra- and inter-specific variability (Thresher 1984; Muñoz and Warner 2004; Afonso et al. 2008b), and little reproductive information is available on *S. rubroviolaceus*. Ong (2007) interpreted repeated absences of *S. rubroviolaceus* from its home range in Hanauma Bay, Oahu, for a period near dawn as reproductive migrations out of the bay. In the present study, only 2 fish (1 each of IP and TP) seemed to exhibit a pattern such as Ong described: consistently

**Fig. 5** Passive detection distances from nearest margin of Kernel Home Range estimates for 8 acoustically tagged fish for which home range estimates are also available (Tables 4, 5). *Boxes* represent quartiles with thick *black line* as median, whiskers include the 95th percentile of points. Crepuscular hours during this study are presented in the 05:00–07:00 and 17:30–20:00 bins
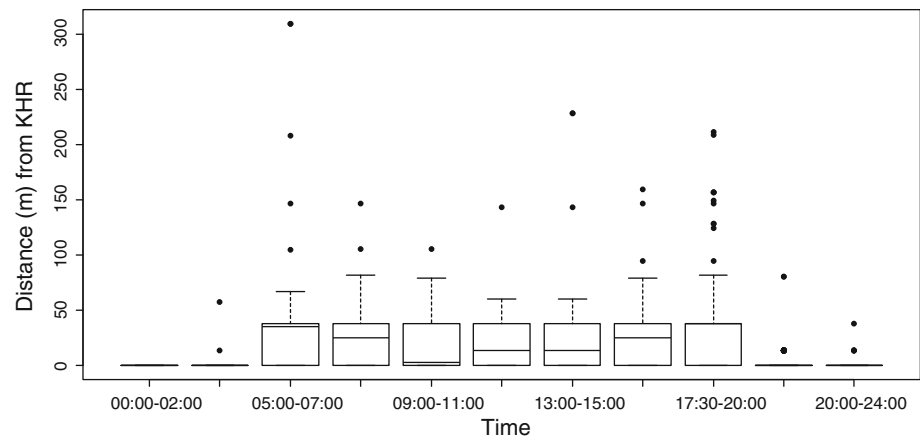
detected on receivers adjacent to their home ranges, except for frequent absences for 30–90 min time periods, close to dawn. While fish could potentially be traveling at dawn to spawn in very deep waters, our data cannot confirm this. Spawning by some TP males was observed within their territories, in the morning, during the present study. Therefore, mass spawning migrations for this species at this site seem unlikely. Since large harems were not present in TP territories and some IP individual home ranges did not overlap with any TP individuals, females may spawn with males during their migration from their sheltering site to their daytime home range. Reproductive behavior of these fish in open coastal reef systems, compared to Ong's study in a small enclosed bay, warrants further exploration.

Local topography and social structure may also be an important consideration in MPA design. Our study suggests that water depth may be a key factor influencing home range size and thus impacting social structure and carrying capacity within an area. For *S. rubroviolaceus* in Wawaloli, home range size was related to the fish's phase and depth of home range, but not to its body length. Length-home range size relationships have frequently been demonstrated in reef fish, including parrotfish species, in a number of studies (Zeller 1997; Mumby and Wabnitz 2002; Jones 2005). However, Afonso et al. (2008b) did not find a relationship between home range size and body length, nor home range size and sex in a temperate, functionally gonochoristic parrotfish. While we did not find a pattern of fish length influencing home range area after we standardized for phase (i.e., within each phase, we did not see a positive effect of size on home range), behavioral influences could be confounding. As seen in other studies, most TP fish appeared to be territorial, with aggressive behavior (chasing and flashing) toward other TP individuals in bordering home ranges (Robertson 1972; Choat and Robertson 1975; de Girolamo et al. 1999; Afonso et al. 2008a). Larger IP fish would also show aggressive behavior toward smaller individuals, but this behavior did not

exclude other individuals from sharing their home range, and IPs with overlapping home ranges would often feed together (Clifton 1989; Clifton 1990). If TP individuals are maintaining a territory that includes a harem of females, then home range size may be more a function of the number of females within a male's harem and combined size of the haremic females' home ranges than the size of the TP male. Some of the smallest TP home ranges had no females overlapping in their home ranges during the study period.

Long-term (spanning months), discrete, and consistent home ranges or territories seem to be the norm for *S. rubroviolaceus*, although borders may be somewhat dynamic and influenced by local social conditions. In this study, this was evident in the TP fish that expanded its home range after a neighboring TP fish disappeared from the area, and the two IP fish that shifted positions relative to nearby acoustic receivers between summer and fall/winter months. This suggests future investigations 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. Site fidelity is a prerequisite for territoriality, since territoriality is the behavioral defense of a spatial resource (Powell 2000). However, one TP male in our study did not exhibit site fidelity and therefore could not have had a defined territory.

*Scarus rubroviolaceus* is a large parrotfish and may be exhibiting greater mobility than most previously studied parrotfish 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 also underrepresented in most movement studies because resightings or recaptures are limited to a small reef area (Kaunda-Arara and Rose 2004a).

Movement patterns described here suggest additional measures may be necessary to complement even

well-designed MPAs in Hawaii. Because many coral reef fishes, including parrotfish, are particularly vulnerable to spearfishing at night while they are sheltering, the success of MPAs for parrotfish management in Hawaii would be greatly enhanced if nighttime spearfishing with SCUBA were prohibited, as it has been in American Samoa, Queensland (Great Barrier Reef, Australia), Palau, Fiji, French Polynesia, the Seychelles, and elsewhere in the tropics. Other management measures, in addition to MPAs, may also be important for parrotfish species that form roving schools, utilize large portions of the reef, and may not be contained within a protected area (Welsh and Bellwood 2012b).

## References

Afonso P, Fontes J, Holland KN, Santos RS (2008a) Social status determines behaviour and habitat usage in a temperate parrotfish: implications for marine reserve design. Mar Ecol Prog Ser 359:215–227

Afonso P, Morato T, Santos RS (2008b) Spatial patterns in reproductive traits of the temperate parrotfish *Sparisoma cretense*. Fish Res 90:92–99

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petran BN, Csaki F (eds) Proceedings of the 2nd international symposium on information theory. Akademiai Kiadi, Budapest, pp 267–281

Alevizon W, Landmeier D (1984) Variability in the population structures of four western Atlantic parrotfishes. Environ Biol Fish 10:149–158

Anderson DR (2008) Model based inferences in the life sciences: A primer on evidence. Springer Science + Business Media, LLC., New York

Bardach JE (1958) On the movements of certain Bermuda reef fishes. Ecology 39:139–146

Bellwood DR (1985) The functional morphology, systematics and behavioural ecology of parrotfishes (Family Scaridae). Dissertation. James Cook University North Queensland, Australia

Bellwood DR (1995a) Carbonate transport and intrareefal patterns of bioerosion and sediment release by parrotfishes (family Scaridae) on the Great Barrier Reef. Mar Ecol Prog Ser 117:127–136

Bellwood DR (1995b) Direct estimate of bioerosion in two parrotfish species, *Chlorurus gibbus* and *C. sordidus* on the Great Barrier Reef, Australia. Mar Biol 121:419–429

Birkeland C, Dayton PK (2005) The importance in fishery management of leaving the big ones. Trends Ecol Evol 20:356–358

Bolden SK (2001) Using ultrasonic telemetry to determine home range of a coral-reef fish. In: Silbert JR, Nielsen JL (eds) Electronic tagging and tracking in marine fisheries: proceedings of the symposium on tagging and tracking marine fish with electronic devices. Kluwer Academic Publishers, Honolulu, pp 167–188

Burnham KP, Anderson DR (2002) Model selection and multimodel inference, a practical information-theoretic approach. Springer Science + Business Media, LLC., New York

Choat JH, Robertson DR (1975) Protogynous hermaphroditism in fishes of the family Scaridae. In: Reinboth R (ed) Intersexuality in the animal kingdom. Springer, Heidelberg, pp 263–283

Choat JH, Robertson DR (2002) Age-based studies on coral reef fishes. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic, San Diego, pp 57–80

Claisse JT, Clark TB, Schumacher BD, McTee SA, Bushnell ME, Callan CK, Laidley CW, Parrish JD (2011) Conventional tagging and acoustic telemetry of a small surgeonfish, *Zebrasoma flavescens*, in a structurally complex coral reef environment. Environ Biol Fish 91:185–201

Clements KD, Bellwood DR (1988) A comparison of the feeding mechanisms of two herbivorous labroid fishes, the temperate *Odax pullus* and the tropical *Scarus rubroviolaceus*. Aust J Mar Fresh Res 39:87–107

Clifton KE (1989) Territory sharing by the Caribbean striped parrotfish, *Scarus iserti*: patterns of resource abundance, group size and behaviour. Anim Behav 37:90–103

Clifton KE (1990) The cost and benefits of territory sharing for the Caribbean coral reef fish, *Scarus iserti*. Behav Ecol Sociobiol 26:139–147

Clifton KE (1991) Subordinate group members act as food-finders within striped parrotfish communities. J Exp Mar Biol and Ecol 145:141–148

Colin PL, Bell LJ (1991) Aspects of the spawning of labrid and scarid fishes (Pisces:Labroidei) at Enewetak Atoll, Marshall Islands with notes on other families. Environ Biol Fish 31:229–260

Connell SD, Samoilys MA, Smith MPL, Leqata J (1998) Comparison of abundance of coral-reef fish: catch and effort surveys vs. visual census. Aust Ecol 23:579–586

de Girolamo M, Scaggiante M, Rasotto MB (1999) Social organization and sexual pattern in the Mediterranean parrotfish *Sparisoma cretense* (Teleostei: Scaridae). Mar Biol 135:353–360

Dubin RE (1981) Pair spawning in the princess parrotfish, *Scarus taeniopterus*. Copeia 1981:475–477

Dubin RE, Baker JD (1982) Two types of cover seeking behavior at sunset by the princess parrotfish *Scarus taeniopterus*, at Barbados, West Indies. Bull Mar Sci 32:572–583

Eristhee N, Oxenford HA (2001) Home range size and use of space by Bermuda chub *Kyphosus sectatrix* (L.) in two marine reserves in the Soufriere Marine Management Area, St. Lucia, West Indes. J Fish Biol 59:129–151

Froese R, Pauly D (eds) (2012) FishBase. http://www.fishbase.org, version (08/2012). Accessed 2 Aug 2012

Graham MH (1997) Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey Peninsula, central California, USA. J Exp Marine Biol and Ecol 218:127–149

Grandcourt EM (2002) Demographic characteristics of a selection of exploited reef fish from the Seychelles: preliminary study. Mar Freshw Res 53:123–130

Hawkins JP, Roberts CM (2003) Effects of fishing on sex-changing Caribbean parrotfishes. Biol Conserv 115(213–22):6

Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar Freshw Res 57:1–13

Hooge PN, Eichenlaub B (1997) Animal movement extension to arcview. In: Office ASC-BS (ed). U.S. Geological Survey, Anchorage, AK

Howard KG (2008) Community structure, life history, and movement patterns of parrotfishes: large protogynous fishery species. Dissertation. University of Hawaii-Manoa, Honolulu

Howard KG, Schumacher BD, Parrish JD (2009) Community structure and habitat associations of parrotfishes on Oahu, Hawaii. Environ Biol Fish 85:175–186

Jennings S, Reynolds JD, Polunin NVC (1999) Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. Conserv Biol 13:1466–1475

Jones KMM (2005) Home range areas and activity centers in six species of Caribbean wrasse (Labridae). J Fish Biol 66:150–166

Kaunda-Arara B, Rose GA (2004a) Long-distance movements of coral reef fishes. Coral Reefs 23:410–412

Kaunda-Arara B, Rose GA (2004b) Out-migrations of tagged fishes from marine reef national parks to fisheries in coastal Kenya. Environ Biol Fish 70:363–372

Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. Environ Biol Fish 55:65–79

Kuwamura T, Sagawa T, Suzuki S (2009) Interspecific variation in spawning time and male mating tactics of the parrotfishes on a fringing coral reef at Iriomote Island, Okinawa. Ichthyol Res 56:354–362

Marconato A, Shapiro DY (1996) Sperm allocation, sperm production and fertilization rates in the bucktooth parrotfish. Anim Behav 52:971–980

McClanahan TR, Muthiga NA, Kamukuru AT, Machano H, Kiambo RW (1999) The effects of marine parks and fishing on coral reefs of northern Tanzania. Biol Conserv 89:161–182

Meyer CG, Holland KN (2005) Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. Environ Biol Fish 73:201–210

Meyer CG, Papastamatiou YP, Clark TB (2010) Differential movement patterns and site fidelity among trophic groups of reef fishes in a Hawaiian marine protected area. Mar Biol 157:1499–1511

Mumby PJ, Wabnitz CCC (2002) Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. Environ Biol Fishes 63:265–279

Muñoz RC, Motta PJ (2000) Interspecific aggression between two parrotfishes (*Sparisoma*, Scaridae) in the Florida Keys. Copeia 674–683

Muñoz RC, Warner RR (2004) Testing a new version of the size-advantage hypothesis for sex change: sperm competition and size-skew effects in the bucktooth parrotfish, *Sparisoma radians*. Behav Ecol 15:129–136

Odum EP, Kuenzler EJ (1955) Measurement of territory and home range size in birds. Auk 72:128–137

Ogden JC, Buckman NS (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54:589–596

Ong L (2007) The ecological importance of parrotfish as bioeroders and sediment producers and their conservation within small marine protected areas. Dissertation. University of Hawaii-Manoa, Honolulu

Ong L, Holland KN (2010) Bioerosion of coral reefs by two Hawaiian parrotfishes: species, size differences and fishery implications. Mar Biol 157:1313–1323

Ortiz DM, Tissot BN (2008) Ontogenetic patterns of habitat use by reef-fish in a Marine Protected Area network: a multi-scaled remote sensing and in situ approach. Mar Ecol Prog Ser 365:217–232

Page M (1998) The biology, community structure, growth and artisanal catch of parrotfishes of American Samoa. Department of Marine & Wildlife Resources, American Samoa

Powell RA (2000) Animal home ranges and territories and home range estimators. In: Boitani L, Fuller TK (eds) Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, pp 65–110

R_Development_Core_Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rechisky EL, Wetherbee BM (2003) Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environ Biol Fish 68:113–128

Righton D, Mills C (2006) Application of GIS to investigate the use of space in coral reef fish: a comparison of territorial behavior in two Red Sea butterflyfishes. Int J Geogr Inf Sci 20:215–232

Robertson DR (1972) Social control of sex reversal in a coral-reef fish. Science 177:1007–1009

Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085

Seaman DE, Millspaugh JJ, Kernohan BJ, Burndige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. J Wild Manag 63:739–747

Smith MK (1993) An ecological perspective on inshore fisheries in the main Hawaiian Islands (Fisheries of Hawaii and US-associated Pacific Islands). Mar Fish Rev 55:31–46

Thresher RE (1984) Reproduction in reef fishes. TFH Publications, Neptune City, pp 399

van Rooij JM, Kroon FJ, Videler JJ (1996) The social and mating system of the herbivorous reef fish Sparisoma viride: one-male versus multi-male groups. Environ Biol Fishes 47:353–378

Welsh JQ, Bellwood DR (2012a) Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. Coral Reefs 31:55–65

Welsh JQ, Bellwood DR (2012b) How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*. Coral Reefs 31:99–1003. doi:10.1007/s00338-012-0922-z

Westneat MW, Alfaro ME (2005) Phylogenetic relationships and evolutionary history of the reef fish family Labridae. Mol Phylogenet Evol 36:370–390

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

Zeller DC (1997) Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). Mar Ecol Prog Ser 154:65–77

Zeller DC (1998) Spawning aggregations: patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. Mar Ecol Prog Ser 162:253–263