Acoustically monitoring coral reef fishes to determine short-term spatial and temporal movement and habitat utilization patterns

By

Wessley Brandon Merten

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Approved by:

Richard S. Appeldoorn, Ph.D. Chairperson, Graduate Committee	Date
Paul M. Yoshioka, Ph.D. Member, Graduate Committee	Date
Edgardo Ojeda, Ph.D. Member, Graduate Committee	Date
Mónica Alfaro, Ph.D. Representative of Graduate Studies	Date
Nilda E. Aponte, Ph.D. Director of the Department	Date

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Abstract

The spatial and temporal movement and habitat utilization patterns of coral reef fishes were quantified using acoustic telemetry on 16 coral reef fish taken from 9 species across 5 families. Fish were caught in traps and surgically implanted with coded-acoustic transmitters and released back into the water by divers. The study site in La Parguera, Puerto Rico included 12 acoustic receivers set in an array from nearshore mangrove habitats to midshelf fringing reef zones. Samples were monitored from 1 to 63 days with total detections ranging from 1 to 43,182. Only two fish, both *Ocyurus chrysurus*, were recorded to have moved outside of the release site to contiguous receivers. The maximum distance traveled by *O. chrysurus* was approximately 7 km during a 30-hr period, with the furthest displacement from the release site being 1.2 km. Temporal movement patterns were observed to vary among species. The temporal pattern of recordings suggest that some species were engaging in crepuscular and nighttime feeding while others were seeking shelter during the same period. To more accurately quantify fine-scaled spatial and temporal movement patterns future studies should focus on determining *a priori* receiver-transmitter detection ranges and effective receiver-receiver overlap.

Resumen

Los movimientos espacio-temporales y los patrones de utilización de hábitat en peces de arrecifes de coral fueron cuantificados utilizando telemetría acústica sobre 16 individuos de 9 especies, provenientes de 5 familias de peces. Los peces fueron capturados con nasas y por medio de cirugía se le implantaron trasmisores acústicos codificados, para luego ser liberados al agua por buzos. El área de estudio en La Parguera, Puerto Rico incluye 12 receptores acústicos, los cuales fueron colocados a manera de red, desde los hábitats de manglar costeros hasta las zonas de arrecifes de franja, sobre la plataforma insular. Las muestras fueron monitoreadas de 1 a 63 días para un total de detecciones que variaron desde 1 a 43,182. En sólo dos peces, ambos *Ocyurus Chrysurus,* se registró movimiento fuera de los sitios de liberación, hacia los receptores contiguos. La mayor distancia recorrida por *O. chrysurus* fue aproximadamente 7 km en un período de 30 días, y el desplazamiento más lejano del lugar de liberación fue de 1.2 km. Se observó que los patrones de movimientos temporales variaron entre especies. Los registros de los movimientos temporales obtenidos sugieren que algunas especies realizaron incursiones de alimentación crepuscular y nocturna mientras que otras, durante el mismo período, iban en busca de refugio. Para una cuantificación más precisa de los patrones de movimientos espaciales y temporales, los estudios futuros deben enfocarse en la determinación *a priori* de los intervalos de detección del receptor/emisor y en el solapamiento efectivo entre receptor-receptor.

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My academic background evolved from a youthful lad with an infatuation with the ocean, to a directed student focused on marine science field research, particularly in the realm of fisheries, and raising awareness about environmental issues including protecting and conserving precious natural resources. The guidance and advice of many mentors, friends, and family have led me to these academic pursuits, including this milestone, and have allowed me to build a firm background and acquire confidence in coordinating and orchestrating research projects.

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The fieldwork to this thesis was rigorous, and wouldn't have been accomplished without the support of my lab partners and the workers of the school. Therefore, I would like to thank my lab partner Stephanie Williams who endured endless hours in the field always with a smile, and Dr. Francisco Pagán, Michael Nemeth, and Michelle Schärer for their collaboration when needed, and Anthony Marshak for his guidance on how to navigate the reefs and what to do when you're stranded. In addition, I would like to thank Marcos Rosado for eagerly helping me

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1.0 INTRODUCTION

A healthy ecosystem has a sustained diversity of interacting species that provide resources and services that humans benefit from directly, or indirectly. To manage these resources and services properly it is necessary to maintain the integrity of the ecosystem in the face of natural and human induced stressors (Costanza et al. 1997). A substantial percentage of the world's marine food webs, fisheries, and coral reefs have been destroyed or altered due to human induced stressors (Pauly et al. 1998; Jackson et al. 2001; Worm et al. 2006; Stone 2007). The use of marine protected areas (MPAs) to minimize human stressors, and slow habitat alterations, has been proposed as one way to maintain ecosystem viability within the context of ecosystem-based management (EBM) (Almany et al. 2007).

A healthy functioning ecosystem has a continued renewal of biomass, and sufficient export and import of nutrients to and from nearby habitats. A "no-take" marine protected area (MPA) is thought to be a critical component of EBM, and therefore the size of the MPA is important. The size should allow the communities within it, and outside of it, to be sustained through an adequate nutrient and biomass flow to and from the MPA (Schärer et al. 2006; Almany et al. 2007). Within an ecosystem based management context, quantifying information on the range of movement, habitat utilization and connectivity patterns of key economic and ecological species is necessary to define "essential fish habitat (EFH)" and to establish the proper MPA size, location, and boundaries that will ensure a sustained, healthy, and functionally viable ecosystem (Clark et al. 2005; Ault et al. 2005; Heupel et al. 2006; Friedlander et al. 2007; Friedlander & Monaco 2007; Meyer et al. 2007).

Connectivity and differential habitat utilization by tropical fishes have been studied at different spatial and temporal scales in coral reef ecosystems (Ogden & Buckman 1973; Holland et al. 1993; Holland et al. 1995; Tulevech and Recksiek 1994; Appeldoorn 1997; Dahlgren & Eggleston 2000; Chapman & Kramer 2000; Ogden & Quinn 2002; Beets et al. 2003; Christensen et al. 2003; Lindholm et al. 2003; Nagelkaken & van de Velde 2003; Zeller et al. 2003; Meyer & Holland 2005; Humston et al. 2005; Semmens et al. 2005; Lindholm et al. 2005; Lindholm et al. 2006; Aguilar-Perera & Appeldoorn 2007; Meyer et al. 2007; Pittman et al. 2007), and this connectivity among habitats supports important ecological functions. For instance, on-reef excretion of organic matter by fish that feed off-reef is important for coral (Meyer et al. 1983; Meyer & Schultz 1985). Mechanisms of organic matter transport (vectors, pathways, and distances) need to be quantified if ecologically important habitat connections are to be maintained. Studies of habitat connectivity between patch reefs, mangroves, seagrass beds, and rocky shores indicate that patch reefs have significantly higher densities of fish, greater biomass, and more observed species when the reefs were in close proximity to mangroves, seagrass beds, and rocky shores (Appeldoorn et al. 2003; Pittman et al. 2007).

Reef habitat connectivity through the movement of fishes occurs at small and large scales. Ontogenetic migrations, the progressive movement of fish life stages from a given habitat to another represents the longer and larger scale of migration (Aguilar-Perera & Appeldoorn 2007). Changes in length frequency distributions and abundances of important coral reef fishes, such as grunts and snappers, across deep and shallow fore-reefs, patch reefs, and slopes gives evidence of ontogenetic shifts from shallower to deeper sites (Appeldoorn et al. 1997; Dahlgren & Eggleston 2000; Nagelkaken & van de Velde 2003; Appeldoorn et al. 2003). This movement across different habitats represents a significant transfer of productivity within the ecosystem, which for the most part remains unstudied. A notable exception is the work of Deegan (1993), who quantified exportation of productivity and energy between Gulf of Mexico estuarine and

coastal marine ecosystems through the ontogenetic migrations of menhaden from juvenile estuarine habitats to adult non-estuarine habitats.

A second mechanism of fish migration important for connecting habitats is through feeding migrations, which occur on shorter spatial and temporal scales. Many species display diel migrations seeking refuge and shelter in reefs during the day but moving over extensive areas of sand, coral rubble, and seagrass habitat to forage at night (Meyer et al. 2007). Such feeding migrations have been demonstrated in many studies (Ogden & Buckman 1973; Holland et al. 1993; Tulevech and Recksiek 1994; Nagelkerken et al. 2000; Chapman & Kramer 2000; Eristhee and Oxenford 2001; Beets et al. 2003; Lindholm et al. 2003; Meyer et al. 2007; Friedlander & Monaco 2007) with movements ranging from 100 to 5,000 m (Beets et al. 2003; Lindholm et al. 2005; Meyer et al. 2007).

Tulevech and Recksiek (1994) tracked adult white grunts (*Haemulon plumieri)* in Puerto Rico and Florida, where regular nocturnal and crepuscular movements of 130-560 m between reef and seagrass habitats were observed. Additional observations suggest that the timing and frequency of off-reef migrations between adult and juvenile fish differed, with juveniles displaying more frequent and regular movements than adults. Juveniles school over reefs during the day then migrate to seagrass beds at night to forage, crossing the seagrass-reef boundary multiple times (Boumeester 2005). Kendall et al. (2003) found the distribution of juvenile French grunts (*Haemulon flavolineatum)* to be positively correlated with hard bottom habitats being proximal (within 100 m) to soft bottom habitats, but there was no correlation found for adults. However, in a similar approach Appeldoorn et al. (2003) found correlations of grunt and snapper biomass with surrounding feeding habitats up to 1000 m from patch reef areas. Quantifying the distance of habitat utilization will strengthen these correlations.

Acoustic tagging studies in St. John U.S.V.I. show that lane snapper (*Lutjanus synagris*) and blue-striped grunt (*Haemulon sciurus*) displayed diel feeding migrations ranging between 300 to 700 m from protective reef habitats during day-time hours to foraging in seagrass beds at night (Friedlander & Monaco 2007). Daily crepuscular movements of white goat fish (*Mulloidichthys flavolineatus)* in Hawaii were similar but more consistently quantified to 600 m (Holland et al. 1993). Grey snapper (*Lutjanus griseus)* movement in Everglades National Park, Florida, has been inferred to occur between mangrove habitats, seagrass beds, and reef areas but the distance moved is unknown (Thayer et al. 1987). Territories of *Acanthurus coeruleus* were estimated to be quite small, varying between 76 m^2 on reef crest to 273 m^2 on uncolonized pavement (Semmens et al. 2005). Chapman and Kramer (2000) recaptured *Sparisoma viride* 40 m from release sites. These values relate with home range estimates of 200-800 m^2 found in this species in Bonaire (Rooij et al. 1996). Red hind (*Epinephelus guttatus*) and coney (*Cephalopholis fulva*) (Beets et al. 2003) rarely move outside their home reef site (<100 m), and Zeller et al. (1998) observed the same with coral trout (*Plectropomus maculatus)* (<220 m). Lindholm et al. (2005) tagged yellowtail snappers (*Ocyurus chrysurus*), which displayed lengthier movements (> 4 km) crossing multiple habitat boundaries (reef-seagrass, reef-sediment, sediment-seagrass). Eristhee and Oxenford (2001) showed a home range of Bermuda chub (*Kyphosus sectatrix*) to be between 30-39,000 m^2 (~97-111 m radius). Drastically larger home ranges exist among species like giant trevally (*Caranx ignobilis*), whose daily movements typically range less than 5,000 m, but underwent longer infrequent 19,000 m excursions lasting a few days (Meyer et al. 2007).

Determining species home range and habitat boundary crossings are necessary for calculating inter-habitat transfer rates. Clark et al. (2005) investigated these on a seascape scale

off of La Parguera, PR, by setting gillnets at habitat boundaries to catch fish during small scale feeding migrations. Examination of gut contents and direction of movement relative to the habitat boundary allowed calculation of inter-habitat transfer rates. While the direction and amount of nutrient transportation and utilization of different habitats were observed, there was no quantification of how far the nutrients were being transported between habitats and the exact timing of the crossings (Clark et al. 2005). Thus, the quantity and direction of transport could be estimated but the range of transport (i.e., the spatial scale), and timing (i.e., the temporal scale) remains unknown.

The primary objective of this study was to quantify the movement of selected coral reef fishes relative to feeding migrations. This included estimation of the distance moved, temporal patterns of movement, and potentially pathways used and habitat boundaries traversed. This information can then be used in defining the distance organic material is transferred across the seascape via feeding migrations, and guide managers to decide what area, and type of habitats should be included in the establishment of marine protected areas.

2.0 MATERIALS AND METHODS

2.1 Study Site:

The principal approach used in this study was acoustic tracking. The study area (Figure 1) was located off La Parguera, Puerto Rico, and constitutes a sub-area studied by Clark et al. (2005). Selected dominant families (e.g. Lutjanidae, Haemulidae, and Acanthuridae) from that study (Clark et al. 2005) were targeted in this study. Different species within the following families were sampled to represent different trophic levels: Acanthuridae and Scaridae (herbivores), Haemulidae and Epinephelidae (invertebrate feeders), and Lutjanidae (piscivors).

The scale of the study was restricted to a swath of area (~ 5.2 sq. km) from Laguna Monsio Jose, including the seagrass and mangrove lined coastline, through the inner shelf reef habitats of Collado, La Raya, La India, and Atrevesado, to San Cristobal a middle shelf fringing reef (Figure 1). The chosen area was based on the locations gillnets were frequently placed in the study of Clark et al. (2005). This area provides a representation of a variety of habitats, i.e. mangrove shoreline and cays, seagrass beds, coral reefs, and unconsolidated sediment tracks, and associated habitat boundaries including mangrove-seagrass, mangrove-unconsolidated sediment, reef-seagrass, seagrass-unconsolidated sediment, and mangrove-unconsolidated boundaries.

A 21-ft open deck center-console equipped boat with a 115 hp outboard engine was used in the study. Fish were caught in traps (3/8" rebar WxLxH = 1 x 1 x 0.3 m, metal mesh size = 2.5 cm). The gear was set at shallow (< 10 m) locations from the inner shelf reef line to the middle shelf reef line. Free-diving was used to check for a catch, and scuba was employed to retrieve the trap. An occupied trap was hoisted by a diver and clipped to a stern line hanging off the boat. Fish were poured into a 20 gal tub of seawater aerated by a live-bait pump; fish not used for tagging were identified, counted, and released.

2.2 Surgical Procedure:

Chosen fish (>20 cm) were placed in a covered bin clipped to the side of the boat. A bucket (5 gal) was filled with seawater (4 gal) and anesthetic (1 g) (Tricaine-S Methanesulfonate and baking soda (sodium bicarbonate)). Both surgical gear and transmitters were disinfected (24 hrs) before use in NOLVASAN solution diluted (~30:70) with mineral-free water. The fish to be tagged was put into the bucket until calm and the time it took was recorded (mean = 3.4,

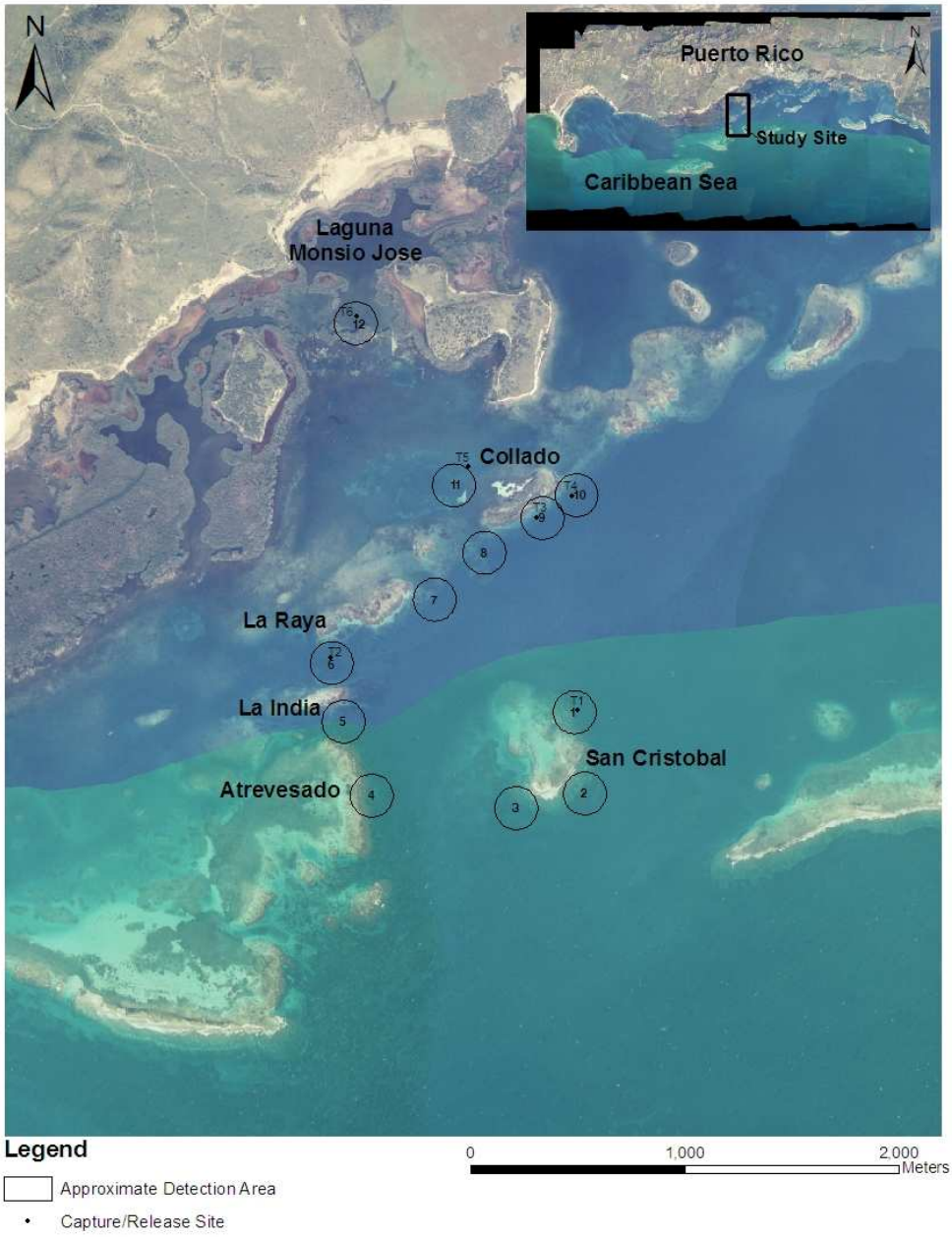

Figure 1. Aerial photo of the study site. The inset displays the southwest portion of the coast of Puerto Rico with the study site outlined by a box. The nominal detection area (100 m radius) is applied to each of the 12 receivers numbered. The capture/release site is indicated by a point and labeled by trap number (T#).

SD = 1.08 min). When calm, the fish was placed on thin layers of foam in a cooler with seawater (~3-4 gal) and a medium dosage (~.5 g) of anesthetic just before surgery began.

Scales were removed using a scalpel, and a 1-1.5 cm incision was made, anterior to posterior, behind the pelvic fin girdle. For scarids, more time was required to remove their rigid scales, and for acanthurids the incision was made laterally behind the pectoral fins and cut downwards toward the pelvic girdle. To allow easier access to the incision site the pectoral fins

were moved to the side by use of clothes pins. The transmitter, covered with a creamy antibiotic (Polysporin Bacitracin Zinc Polymyxin B Sulfate), was then inserted. Two different sutures were used (Monosof 5-0 nylon polyamide) 45cm 3/8 cutting 19mm USS DG sutures, and (Surgipro 3-0 polypropylene 75cm 1/2 taper 26mm v-20). The incision was closed with a series of 4-5 'surgeon's knots' depending on the size and position of the incision. Then, the area was blotted with a rag and skin glue (3M New Skin Liquid Bandage Hydroxyquinoline 1% First Aid Antiseptic) was lightly dabbed on the area. The time of the procedure was recorded (mean = 11.6 min. SD = 2.16 min.). Following the procedure, the fish was placed back in the aerated boat-based recovery bin until revived and recovered.

Before a fish was released, it was placed in the submerged bin on the side of the boat and allowed to acclimate to the surroundings. It was then released by slowly turning the bin on its side. The fish swam out under its own power and down to the bottom allowing the diver to follow and record its movements and behavior. The fish was observed until it was no longer visible. Another method used was to swim the fish down to the bottom using a fisherman's mesh bag with locking mechanism.

2.3 Acoustic Methods:

Transmitters used were V7-2L-R04K's (VEMCO Ltd., Nova Scotia), which acoustically transmitted a unique identification code. Two types of receivers were used. The primary were Vemco VR2's, an underwater, multi-channel acoustic receiver that can identify VEMCO coded transmitters by code, date, and time. Preliminary field tests unveiled the maximum range of detection between receiver and transmitter to be approximately 250 m. Therefore, the twelve VR2's were set in an array with respect to this theoretical detection radius. This arrangement is designed to pick-up movements along or through geomorphologic corridors or bottlenecks over a period of three months.

Receiver moorings were constructed of stainless steel cable (5 m of 3/8") with a cinderblock on one end and a subsurface float on the other. The cable was wrapped through the cinderblock into a loop and clamps (2.25-in) were adhered. Additional clamps were used above and below the subsurface float to reduce slippage. The top clamp was situated above a pvc pipe (0.5-in) that was used to reduce friction between the buoy and the top clamp. A cable tie was positioned (2 m) above the block indicating the location the receiver was to be fixed. The receivers were fixed at this spot by using two industrial sized cable ties, and three large cable ties. A brass chain (12-in) was strung through the lower attachment hole and locked with a small brass lock. Mooring blocks were placed in holes in the reef, among gorgonians, or buried in sediment to reduce the chance of movement.

Using VEMCO User Environment software (VUE), VR2 data were uploaded onto a computer three times during the study period: (5/9/08, 6/20/08, and 8/12/08). The data saved included the receiver configuration (code map, clock initialization, receiver serial number, deployment location, etc.) and the tag detection information (transmitter code, date, and time).

The second type of receiver used was a boat-based hydrophone. This was used to make periodic observations of additional information on presence/absence, small scale movements, and temporal habitat use of the fish.

To depict temporal patterns the quantitative movement data from each tagged fish were organized into graphs depicting daily movements for a selected period (3 days). This was done to focus on their short-term movement patterns. These graphs showed detection patterns per tagged species at detected receivers. The percentage of total detections by time of day was

summarized between three time periods: daytime (800-1530), crepuscular (400-730 and 1600-1930), nighttime (2000-330).

3.0 RESULTS

Over the course of four months, acoustic data were collected from 16 fish, which included nine species sampled from five families (Table 1). Sizes ranged from 20 to 31 cm FL (mean = 24.2 cm, SD = 3.4 cm) and 275 to 1200 g (mean = 581.8 g, SD = 278.1 g). Detections were obtained from twelve receivers. The number of detections ranged from 1 to 43,182 (mean = 4703, SD = 10337.9) spanning periods from 1 to 63 days. To focus on finer scaled temporal patterns, data are included here over a three-day period (Table 2). The proportion of detections by time varied between samples when defined by time periods: daytime (800-1530), crepuscular (400-730 and 1600-1930), and nighttime (2000-330).

Distances Moved

Of the 16 individuals, 14 were detected only within one station's detection radius. Of these, additional position fixes were obtained for four individuals. *Acanthurus bahianus* 1 was recaptured 27 m east from Station 1. While in the trap the fish was not being detected by the receiver. For *Epinephelus guttatus* 8 two confirmed positions were determined. The first came on June 9, six days after release, when the fish was observed visually under a ledge about 14 m from the receiver; no detections were recorded at this time. The second occurrence, an active position fix, was obtained on June 30 at 1009 triangulated to be 30 m northeast of Station 1. This occurred at a time when no detections were recorded with the passive receiver. Detections from the passive receiver were last recorded 144 hours before this fix on June 24 at 1323, and 38 hours after this fix on July 2 at 0049. *Lutjanus griseus* 13 was detected four times using the boat-based hydrophone with distances from station 12 ranging from ~15 to 250 m. Similarly, no detections were recorded in the passive receiver at the time of these fixes.

Lastly, *Lutjanus synagris* 10 was recaptured on June 19 in a trap set 97 m east-northeast of its release site at Station 11. No detections were made after 1947 on June 18 until the fish was re-released the next morning near the station.

Two of the three yellowtail snappers were recorded to have moved between stations (maximum = 1200 m). *Ocyurus chrysurus* 14 was detected at 6 different stations: 9, 10, 8, 7, 6, and 4 (Figure 2, left). Movement began at 0100 on March 29 after being stationary for 10 hours after release within Station 9's detection range. The fish first moved west from Station 9 to Station 8 (311 m, all distances are receiver to receiver) then back east to Station 9 in the 0130 interval and continued further east to Station 10 (197 m), then back west to Station 9. At 0200 it was detected back at Station 10. From 0230 until the 0630 interval, the fish was undetected. Then, during the 0700 interval the fish was again detected at Station 10 and proceeded west through Station 9, and last detected at Station 7 (632 m); it was not detected at Station 8. This represented a nominal movement of 632 m within a ½ hour. No further detections occurred for 10 hours until 1700, when it was detected at Station 4, 1197 m from the release site. Total nominal movement at this point was 3042 m. At 2000 the fish was again detected moving back to the east, being observed first at Station 7 and moving to Station 8 and eventually to Station 9 at 2030. Later that evening at 0030 the fish was detected again at Station 10, 840 m from station 7. Within nearly 23.5 hours this fish moved a nominal 3882m (3.8 km). Movements continued from 0100 to 0200 when the fish again swam west to Station 8 and Station 7, then back east to

Table 1. Family and species tagging information: capture and release site, date released, receiver fixes, total detections, and days recorded (an * indicates those fish tagged with old transmitters). Also reported for selected three-day periods (see text) are percent time present and percent time by period: day (0800-1530), crepuscular (0400-0730 and 1600-1930), night (2000-0330).

Family	Species	Fish Num	Size (cm)	Weight (gm)	Capture/ Release Site	Date of Release	Station Fixes	Total Detections	Days Recorded	% Present (3-day)	% Time Period (3-day)		
											Crepuscular	Day	Night
Acanthuridae													
	Acanthurus bahianus	1	20	550	T1	5/24	1	1970	7	62	22	22	18
	Acanthurus bahianus	2	21	650	T2	5/24	6	426	63	34	11	22	1
Scaridae													
	Sparisoma aurofrenatum	3	22	350	T2	4/1	6	649	20*	73	26	28	19
	Sparisoma viride	4	28	910	T3	6/11	9	11095	63	70	24	34	12
Haemulidae													
	Haemulon plumieri	5	28	500	T3	3/29	9	1433	6*	95	32	32	31
	Haemulon sciurus	6	26	475	T2	4/1	6	935	5*	73	27	30	16
	Haemulon sciurus	7	22	425	T5	7/3	11	118	31	17	2	15	0
Serranidae													
	Epinephelus guttatus	8	25	375	T1	6/4	1	1014	40	19	4	6	9
Lutjanidae													
	Lutjanus synagris	9	31	1200	T6	5/24	12	4357	18	33	13	20	0
	Lutjanus synagris	10	26	625	T5	6/12	11	5548	63	62	27	25	10
	Lutjanus synagris	11	20	300	T1	6/3	1	1	1	1	100	0	0
	Lutjanus griseus	12	22	475	T6	3/29	12	4223	11*	80	29	33	18
	Lutjanus griseus	13	21	350	T6	5/24	12	43182	29	76	27	33	16
	Ocyurus chrysurus	14	21	275	T3	3/28	10, 9, 8, 7, 6, 4	215	3*	25	9	3	14
	Ocyurus chrysurus	15	29	1200	T4	4/25	10, 9, 8, 7	80	1*	25	10	13	2
	Ocyurus chrysurus	16	26	650	T1	5/23	1	5	56	1	0	100	0

station 10 (509 m, total = 830 m). From the 0200 to 0300 intervals the fish fluctuated between receivers (Station 10 and 9) until the 0330 interval where it was detected traveling the entire Collado corridor from Station 10, west to Station 9, Station 8, and finally Station 7 (805 m). Two hours later the fish was detected at Station 6, another 560 m to the west. The last transmission was logged during the 1200 interval on March 30, still at Station 6. The nominal distance traveled during the 36 hour period from 0100, March 29 to 1200, March 30 was 7.4 km taken from station to station.

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2		10	10_9
2:30			10_9
3			10_8
3:30			10 9 8 7
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16	9		
16:30	9		
17	9	4	
17:30	9		
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19	9		
19:30	9		
20	9	7_8	
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17:30	10
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21	8_7
21:30	
22	
22:30	
23	
23:30	

Figure 2. Detection histories for *Ocyurus chrysurus*. Left: *O. chrysurus* 14 from March 28-30. Right: *O. chrysurus* 15 on April 25. The number in the first column is the beginning of each 30-min. time interval, with the shaded blocks representing the crepuscular periods. The other columns represent individual days. Black indicates continuous, dark grey represents > 10, and light grey represents < 10 detections during each time interval. Numbers within each block indicate the station(s) where detection occurred during that interval.

Ocyurus chrysurus 15 was released at Station 10 and later detected at Stations 9, 8, and 7 (Figure 2, right). Movement began after being stationary for 5.5 hours. The fish was found to the west (Station 9) at 1800, a nominal distance of 197 m. Three hours later it was next detected

at Station 8 and moving to Station 7, a distance of 632 m from station 10. No further detections were recorded.

Temporal Patterns

The two yellowtail snappers for which sustained detection records were obtained showed similar temporal patterns of movement. After release there was an initial period of inactivity as the fish stayed near their respective passive receivers. Detected movements all occurred during nocturnal and crepuscular periods (Figure 2). In fact, with the exception of the periods immediately following release, only one period of daytime detection was observed. The third yellowtail snapper was tagged at Station 1(San Cristobal) and was lost within an hour after release.

Three *Lutjanus synagris* were tagged, but *L. synagris* 11 released at Station 1 (San Cristobal) was lost immediately after tagging. Figure 3 shows the temporal detection patterns for

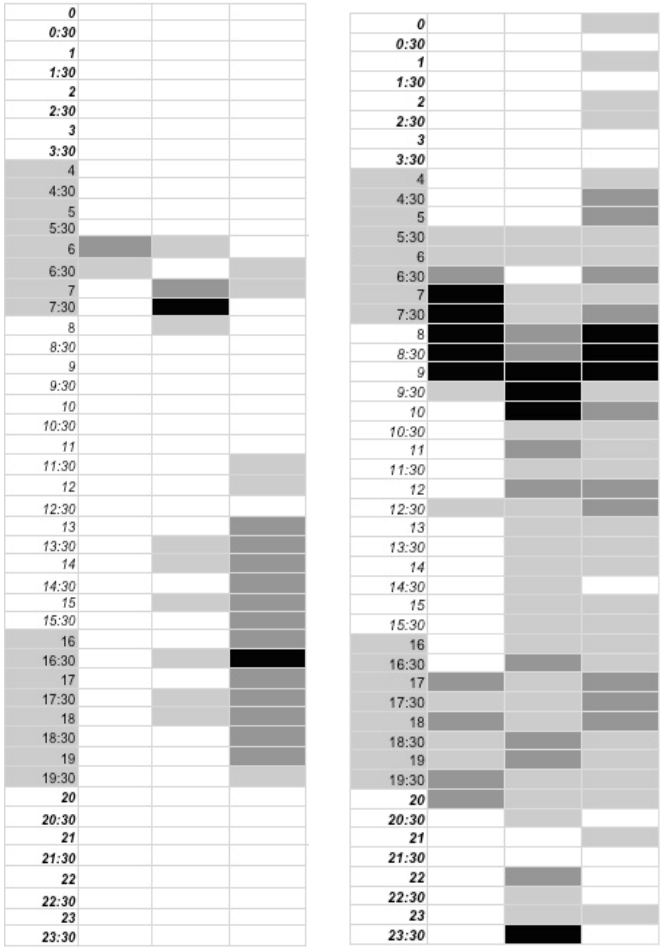

Figure 3. Detection histories for *Lutjanus synagris*. Left: *L. synagris* 9 from May 24-26 detected at station 12. Right: *L. synagris* 10 from June 12-14 detected at station 11. The number in the first column is the beginning of each 30-min. time interval, with the shaded blocks representing the crepuscular periods. The other columns represent individual days. Black indicates continuous, dark grey represents > 10, and light grey represents < 10 detections during each time interval.

the other two fish. For the period May 23-26, a day after being released *L. synagris* 9 (left) was detected most during crepuscular periods and in late afternoon. It was never detected at night.

Two *Lutjanus griseus* were tagged, both at Station 12. The proportion of time spent within the detection field of that station was similar for both, as was their behavior (Figure 5). High encounter rates were recorded when the fish were detected. Both fish were detected throughout daytime periods. At times each fish went undetected throughout the night. On these occasions detections would be lost immediately after the crepuscular period and would not occur again until the late morning crepuscular period.

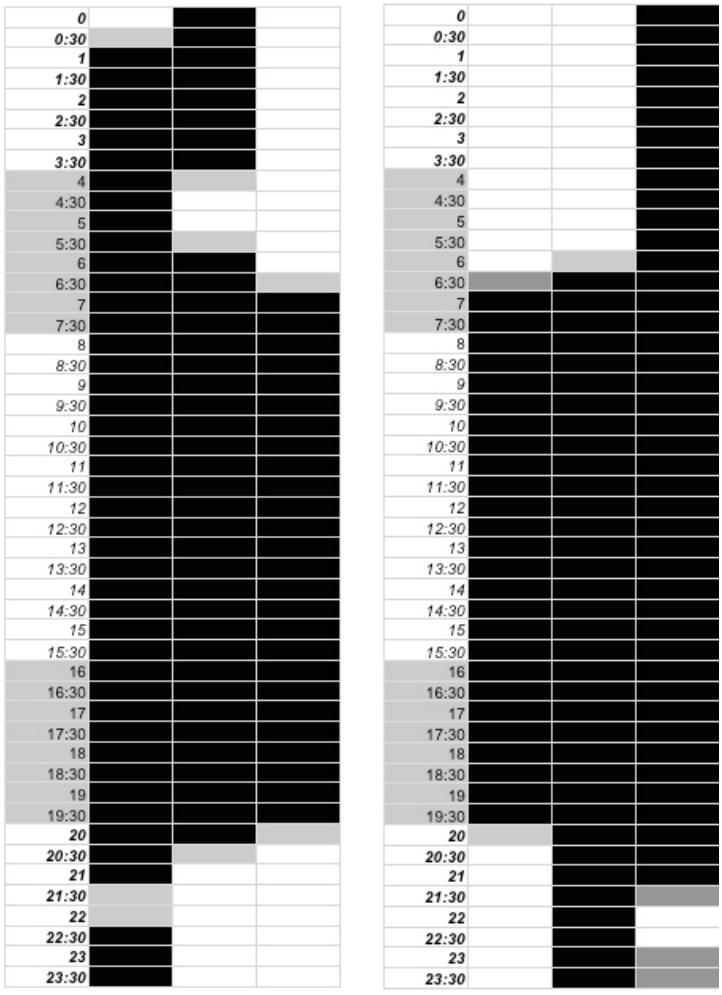

Figure 4. Detection histories for *Lutjanus griseus*. Left: *L. griseus* 12 from March 29-31 detected at Station 12. Right: *L. griseus* 13 from May 24-26 detected at Station 12. The number in the first column is the beginning of each 30-min. time interval, with the shaded blocks representing the crepuscular periods. The other columns represent individual days. Black indicates continuous, dark grey represents > 10, and light grey represents < 10 detections during each time interval.

Two *Acanthurus bahianus* were tagged, which showed similar temporal patterns (Figure 5). Starting one day after tagging, both fish had a greater frequency of detection during the day extending into the evening crepuscular period, yet detection frequency was variable between time periods. *A. bahianus* 1 had more detections over all and was detected during much of the night, while *A. bahianus* 2 was not observed at night.

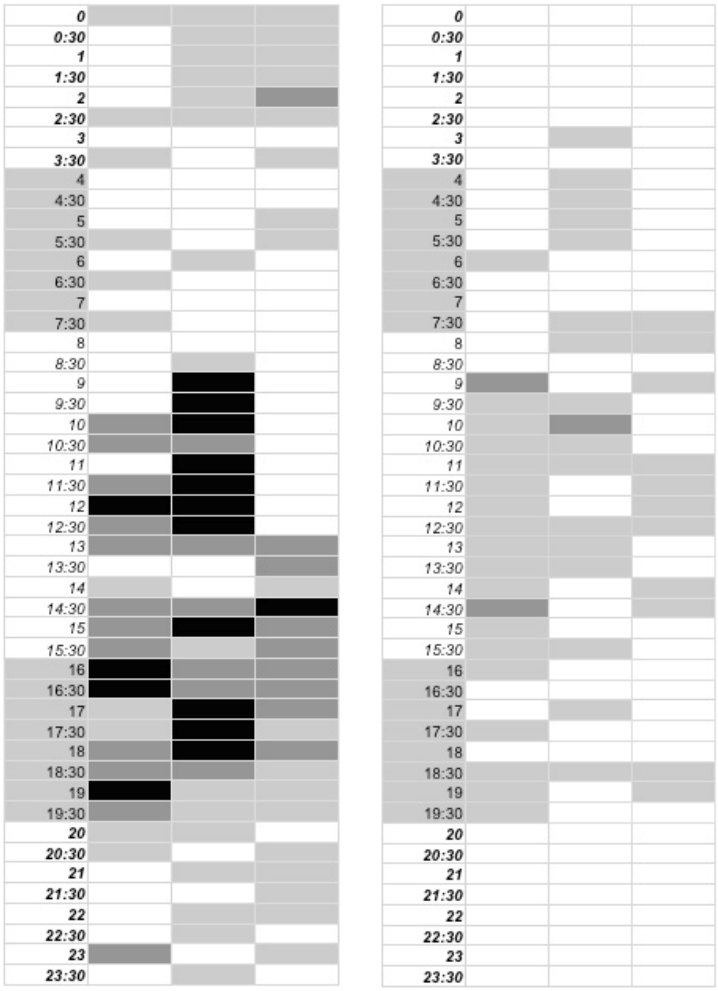

Figure 5. Detection histories for *Acanthurus bahianus*. Left: Detection data of *A. bahianus* 1 from May 24-26. Detected at station 1. Right: *A. bahianus* 2 from May 24-26. Detected at station 6. The number in the first column is the beginning of each 30-min. time interval, with the shaded blocks representing the crepuscular periods. The other columns represent individual days. Black indicates continuous, dark grey represents > 10, and light grey represents < 10 detections during each time interval.

Two scarids were tagged, *Sparisoma aurofrenatum* 3 and *S. viride* 4, with both records beginning the day after tagging (Figure 6). Although the total time detected for both fish was nearly equal, there were obvious differences in their temporal patterns. High rates of detection for *S. aurofrenatum* 3 were frequent but sporadic and were recorded through all time periods, while for *S.viride* 4 frequent high rates of detection were recorded consistently during the day, extending into the crepuscular periods but never during the night.

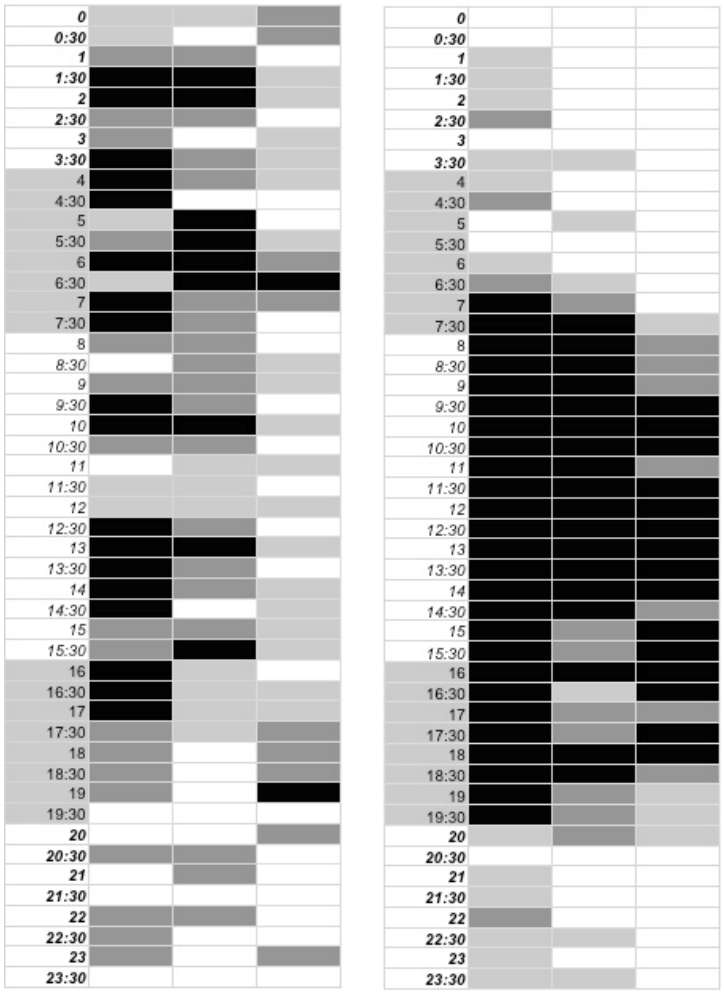

Figure 6. Detection histories for two species of *Sparisoma*. Left: *S. aurofrenatum* 3 from April 1-3 detected at Station 6. Right: *S. viride* 4 from June 11-13 detected at Station 9. The number in the first column is the beginning of each 30-min. time interval, with the shaded blocks representing the crepuscular periods. The other columns represent individual days. Black indicates continuous, dark grey represents > 10, and light grey represents < 10 detections during each time interval.

Figure 7 shows detection histories of two *Haemulon sciurus.* Starting the day after tagging, *H. sciurus* 6 was commonly recorded with varying intensity throughout all monitoring periods, with higher detection rates more frequently observed from the end of dawn through into the evening crepuscular period. In contrast, the best three-day record for *H. sciurus* 7 began 24 days after tagging. Still, this fish was detected only to a limited extent. Nevertheless, the basic pattern is similar in that detections began toward the end of dawn and extended into the day. The fish was never detected during dusk or night.

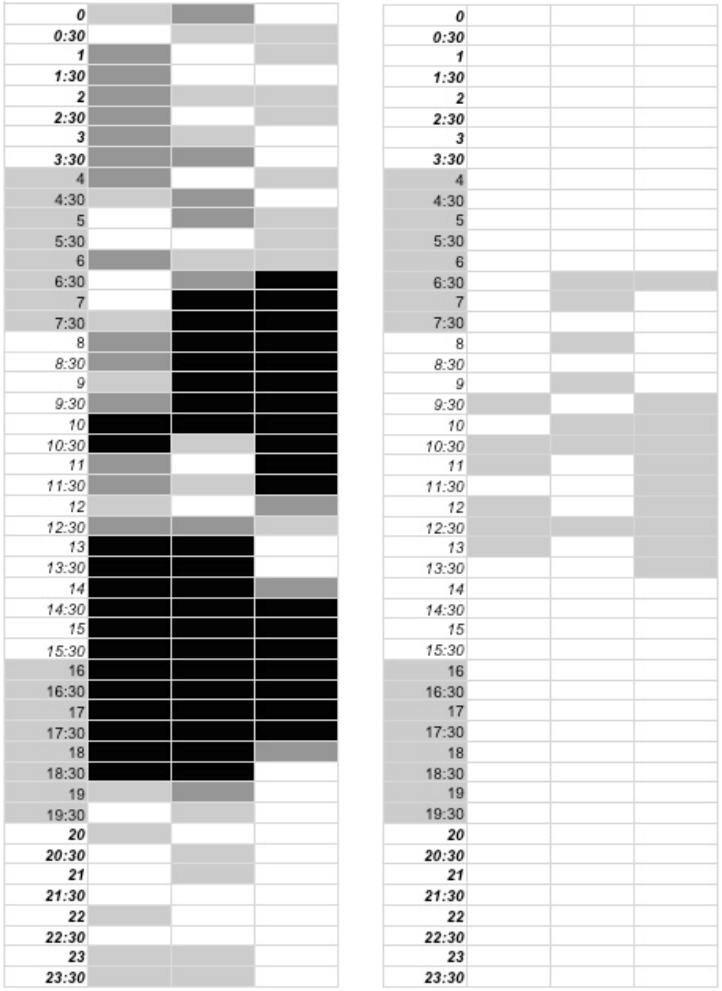

Figure 7. Detection histories for *Haemulon sciurus*. Left: *H. sciurus* 6 from April 1-3 detected at Station 6. Right: *H. sciurus* 7 from June 3-5 detected at Station 11. The number in the first column is the beginning of each 30-min. time interval, with the shaded blocks representing the crepuscular periods. The other columns represent individual days. Black indicates continuous, dark grey represents > 10, and light grey represents < 10 detections during each time interval.

The last haemulid sampled was *H. plumieri* 5. Figure 10 conveys the detection history beginning one day after release. The fish was detected nearly uniformly throughout the period (day (32%), crepuscular (32%), and night (31%)), and high rates of detection were consistently recorded throughout all the time periods, with a slight decline during the last night.

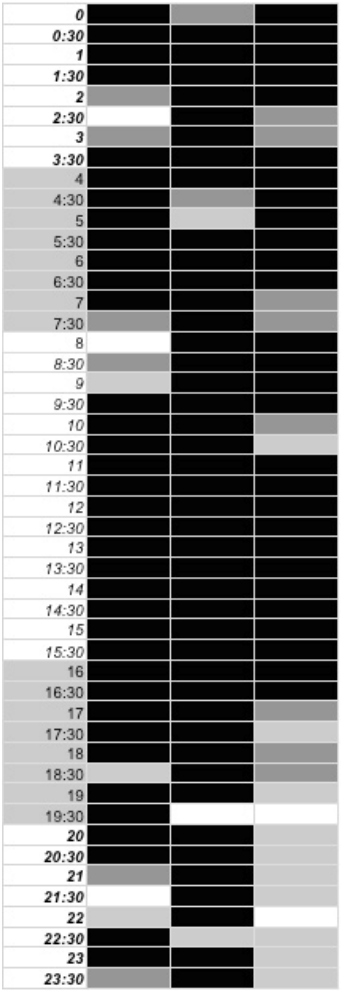

Figure 8. Detection history for *Haemulon plumieri* 5 from March 29-31 detected at Station 9. The number in the first column is the beginning of each 30-min. time interval, with the shaded blocks representing the crepuscular periods. The other columns represent individual days. Black indicates continuous, dark grey represents > 10, and light grey represents < 10 detections during each time interval.

The last species tagged was *Epinephelus guttatus* 8 (Figure 9). Low detection rates occurred throughout the period, which began the day after tagging. Periods when detections occurred appeared to be aggregated, but randomly distributed. On the second day the fish was only detected once and went un-detected for 34.5 hours until the next morning when the detections resumed.

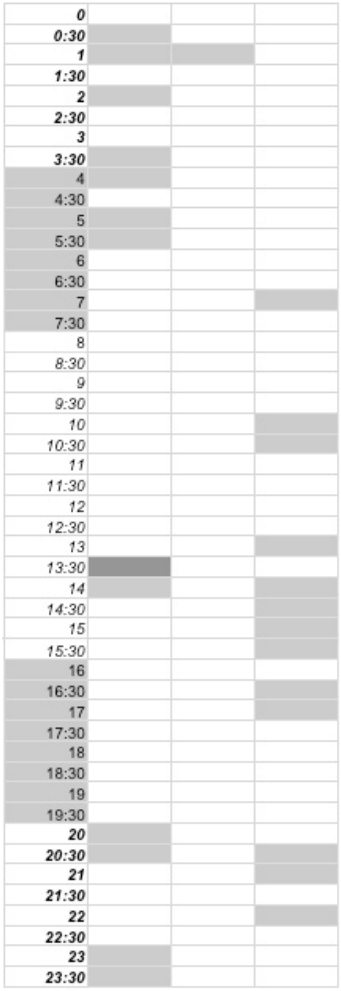

Figure 9. Detection history for *Epinephelus guttatus* 9 from June 4-6 detected at Station 1. The number in the first column is the beginning of each 30-min. time interval, with the shaded blocks representing the crepuscular periods. The other columns represent individual days. Black indicates continuous, dark grey represents > 10, and light grey represents < 10 detections during each time interval.

4.0 DISCUSSION

The 16 coral reef fishes acoustically tagged in this study were sampled to gain a broad picture of the temporal and spatial movement patterns of reef fishes. Interpretation of the results relies on the assumption that tagging does not affect behavior and, in this study, and that the range of detection can be reasonably approximated, as this will affect estimates of potential distances moved and behavior patterns.

Each fish was monitored by a diver following its release, and abnormal behaviors were never witnessed. Typically, each fish quickly swam into a hole or reef recess. To compensate for this, in most cases the first day of each detection record was eliminated in the analysis. Exceptions were all three *O. chrysurus*, and *L. synagris* 11, which otherwise did not display 3-day records of detection. For *O. chrysurus* 14 and 15 the period of inactivity immediately after release probably reflects a period of recovery, and this time period was discounted when assessing movement behavior. *Ocyurus chrysurus* 16 and *L. synagris* 11 were both released at

Station 1 (San Cristobal) and detected only a few times before going absent. The former was observed swimming down into a hole, which would have limited initial detections. The latter, oddly, had four detections on the first day and was not detected again until 54 days later (July 16). In contrast, sight of *L. synagris* 11 was lost prior to it reaching the bottom, so its fate is unknown.

Differential detection range, between locations and studies, is one of the most important problems affecting acoustic studies (Heupel et al. 2006). Many factors, including the power and frequency of tags, and the acoustic environment (e.g., rugosity, surf, depth, wind and waves, bubbles and habitat type) can affect detection range (Domeier 2005). The *in situ* pre-study used V7 transmitters that had been stored for 940 days, but otherwise was run under optimal conditions in a sheltered lagoon, with a resulting detection range of approximately 250 m. Nevertheless, location fixes (boat-based hydrophone or traps) clearly showed that detection range was often much lower. This was also evident from the movement of the yellowtail snappers, a species occurring relatively up in the water column, as no simultaneous detections occurred between receivers where significant receiver-receiver overlap was theoretically present (Figure 1). A similar problem was evident in the results of another study conducted in the U.S. Virgin Islands (Friedlander & Monaco 2007). The movement of *O. chyrsurus* 14 consecutively across four contiguous receivers (805 m) in a half-hour period on March 30 was used to estimate detection range more accurately. Assuming a straight line motion at a constant speed, the timing of detections at each receiver puts limits on the range of detection, which in this cased was estimated at 100 m. While this and five other fish were tagged with similarly old tags, the pre-study suggests that low battery life was not the major problem affecting detection range, at least in the short term. One of these (*S. aurofrenatum* 3) was detected for 20 days. Additionally, all three fish for which separate fixes where made had new tags. Thus, it is much more likely that bottom topography and habitat type were responsible for low detection ranges. For example, *A. bahianus* 1 was recaptured along the lateral slope of San Cristobal, which although was only 27 m away from the station, the station was located further up the slope with shallow, rugose coral habitat in between. *Epinephelus guttatus* 8 twice went undetected in the same area, once when tracked with the boat-based hydrophone, and once when observed while diving. In the latter case the fish was located under a ledge that clearly would have blocked signal reception. In addition, *Lutjanus griseus* 13 was tracked on four occasions with the boat-based hydrophone in a calm bay consisting of a mix of unconsolidated sediment and seagrass habitats surrounded by a mangrove shoreline. Unfortunately, the passive receiver in the area was stolen before we could upload those potential data from it and compare them to the active tracking position fixes acquired. Lastly, *L. synagris* 10 was found in a trap set into seagrass, as was the passive receiver due to the shallow depth of the bay. Seagrass, particularly with their air-filled spaces, can easily interfere with sound transmission.

From the results it can be seen that the timing of movements varies among species. Yet, the majority of the 16 individuals monitored were recorded more often during daytime than during the crepuscular or nocturnal periods. The lower detection rates during the latter periods suggests that these fish may be migrating out of range to forage in adjacent habitats or shelter, which disrupts transmission, to avoid predation. Of the species monitored in this study, adult *Haemulon sciurus, H. plumieri* and *Lutjanus synagris*, have been observed in acoustic and observational studies to exhibit daily feeding migrations from daytime refuge habitats to adjacent feeding habitats during crepuscular and night time periods (Tulevech & Recksiek 1994; Beets et al. 2003; Friedlander & Monaco 2007). In the present study, the bluestriped grunts (*Haemulon*

sciurus 6 & 7) showed noticeable diel presence/absence periodicity, and the same pattern was observed for lane snappers (*Lutjanus synagris* 9 & 10). This pattern suggests that feeding migrations were occurring, and that these were on a scale greater than the range of detection. In contrast, *H. plumieri* was detected fairly consistently, so it is not clear if that individual was undergoing significant feeding migrations or not. The gray snapper, *L. griseus,* also undergoes feeding migrations, dispersing from daytime refuge areas just before sunset to feed at night (Claro & Lindeman 2008). Data from the present study suggest that the migration distance is variable, as on some nights the fish were not detected while on others they were detected frequently throughout the nocturnal period.

Sheltering in undetectable locations during crepuscular and nighttime periods to avoid predation can also result in diel patterns with more frequent detection during daytime periods. *Acanthurus bahianus*, *Sparisoma viride*, and *Sparisoma aurofrenatum* are known to utilize a home area during the day but seek shelter during crepuscular and nighttime periods (Semmens et al. 2005; Chapman & Kramer 2000; Lindholm et al. 2006). In the present study, the observed pattern of lower detection during crepuscular and nighttime periods for these species is thus most likely explained by sheltering behavior.

Unlike the species above, *Epinephelus guttatus* was detected only intermittently with no evidence of periodicity. The reduced detection frequency is probably related to its behavior of sheltering in crevices (Randall 1967), as was observed for the individual in this study. Beets et al. (2003) tracked five red hind and found none of them to leave reef habitat. They found more activity during the day, but only one individual moved more than 100 m.

The two yellowtail snappers were the only fish recorded to move across receivers. These movements were recorded only during nocturnal and crepuscular periods. Movements up to approximately 7 km for total distance traveled and 1.2 km displacement were recorded for *O. chrysurus* 14 as it followed the inner fore-reef shelf break from Collado west towards La Raya and then south to Atrevesado, the furthest recorded site; *O. chrysurus* 15 was only recorded to moved approximately 600 m along the same corridor before its signal was lost. The long time periods when the fish went undetected coupled with their wide range of movement prevents precluding from these data that there were no significant movements during the day. However, Lindholm et al. (2005) conducted a similar study in the Florida Keys, observing the movements of nine *O. chrysurus* along the outer forereef tract. In their study, most fish made limited movements between two stations approximately 500 m apart, and these occurred predominately during crepuscular or nocturnal periods. Fish were fairly continuously detected, suggesting that little time was spent away from the reef tract, and that fish were thus using the forereef as a migration corridor. On rare occasions fish were found to move up to 4 km, but with no receivers in between the timing and pattern of this movement is ill-defined. They also found more detections during the day, which they attributed to variations in behavior. During the day fish were observed by divers to be up in the water column in direct line of sight with the receivers. At night fish occurred more solitary near the reef, where topographical interference with reception was more likely. These observations are all consistent with the limited observations in the present study. The greater number of receivers along the reef tract allowed for greater resolution on the timing of movements and total distance move along the reef tract. Fish up in the water may have remained nearby, but out of the ~100-m range of detection. The use of old tags in these fish may have contributed to the latter.

Movements across habitat boundaries during daily feeding migrations has been demonstrated for many coral reef fishes (Ogden & Buckman 1973; Holland et al. 1993, 1995;

Tulevech and Recksiek 1994; Holland et al. 1995; Meyer et al. 2000; Dahlgren & Eggleston 2000; Chapman & Kramer 2000; Ogden & Quinn 2002; Beets et al. 2003; Lindholm et al. 2003; Nagelkaken & van de Velde 2003; Clark et al. 2005; Semmens et al. 2005; Lindholm et al. 2005; Meyer et al. 2007), yet few studies have quantified the amount of organic matter transferred via these migrations. In La Parguera, Clark et al. (2005) used gillnets set at habitat boundaries and gut-content analysis to study cross-habitat transport of organic material during diel feeding migrations. They caught 8 of the 9 species tagged in the present study, of which five were represented by only a few individuals, suggesting little cross-habitat movement (Table 2). The case of yellowtail snapper is interesting in that this species showed the greatest degree of movement in the present study. On the one hand, its vulnerability to gill nets may be low, particularly during the day if they are up in the water column. On the other hand, if their movement was indeed constrained to follow the reef contour, they would not have encountered a habitat boundary as defined by Clark et al. (2005).

Table 2. Species found migrating across habitat boundaries in data (unpublished) from study of Clark et al. (2005) in La Parguera, PR: Number of individuals caught, percent of total, shelf strata where found and habitat boundary and direction of movement (the latter two shown in decreasing order). The shelf strata are (inshore to offshore) Lagoon (L), Outer Lagoon (OL), and Bank Shelf (B). Habitats are Reef (R), Seagrass (S), Unconsolidated (U), and Mangrove (M).

Species	Num	%	Shelf Strata	Habitat Boundary + Direction
Acanthurus bahianus	2	0.27	OL	R→S
Sparisoma aurofrenatum	3	0.40	OL, L	S→R
Sparisoma viride	2	0.27	L, B	R→S
Haemulon plumieri	21	2.80	OL > L, B	R→S > S→R > U→S > S→U
Haemulon sciurus	51	6.79	L > OL > B	U→S > R→S > S→R > All others
Epinephelus guttatus	0	0.00	-	-
Lutjanus synagris	6	0.80	OL	U→S > R→S, S→R
Lutjanus griseus	74	9.85	L > OL, B	S→U > R→S, U→M, S→R > all others
Ocyurus chrysurus	3	0.40	OL, B	R→S, S→R

In contrast, three species *H. plumieri* (2.8%), *H. sciurus* (6.8%) and *L. griseus* (9.9%) were caught with some frequency by Clark et al. (2005) (Table 2). For *H. plumieri* most individuals were caught at the reef-seagrass habitat boundary. The tagging record in the present study showed little indication of diel migration, at least of any distance. However, there are small patches of seagrass off the forereef of Collado (Station 9) that would still be within range of the receiver, so these may be utilized by white grunt residing on the forereef. Individually, these patches would not meet the 1 acre minimum mapping unit to be included in the NOS habitat map used by Clark et al. (2005). For *H. sciurus*, Clark et al. (2005) found the greatest degree of food transport from unconsolidated sediments to seagrass, with the reef-seagrass interface being of secondary importance. One of the tagged blue-striped grunts in the present study occurred predominately near Station 6 located in a pass between two reefs and connecting shallow seagrass and sand with deeper forereef habitats. This fish could have easily resided on

reef and migrated to a variety of habitats to feed without needing to move much beyond the range of detection. The other individual was only rarely detected at Station 11, which is located in shallow seagrass suggesting either it moved into seagrass during the day to feed, or that it was detected at greater range when further up in the water column while residing in backreef mangroves of Collado. Both tagged individuals of *L. griseus* were near Station 12, located in seagrass near mangroves and were initially caught in a trap set in seagrass. Given that gray snapper in that area reside in the mangroves, it can be assumed that feeding migrations cross the mangrove-seagrass boundary. Indeed, Clark et al. (2005) caught one gray snapper at the mangrove-seagrass interface 189 m from Station 12. There are also patches of unconsolidated sediment within that mangrove lagoon, and Clark et al. (2005) found the greatest food transport for gray snapper to occur from unconsolidated to seagrass, with unconsolidated to mangrove being of second importance. The tagging data from each of these species suggests that, regardless of the habitat boundaries crossed, the distances that organic matter is transported are low, on the order of 100-200 m, and that for other species the distance is potentially much less than this (with the exception of *Ocyurus chrysurus*).

Temporal and spatial movement data can provide insight into connectivity between habitats, migratory corridors, and pathways utilized by the fish. Uncovering these connections can lead to defining 'essential fish habitat' on a seascape scale and allow managers to determine the potential impacts of habitat alterations or potential interventions, including the potential for marine reserves to meet biological and social goals. The data from this study, although limited in numbers of species and individuals, is valuable in developing an emerging sense of dynamics at the seascape level, particularly in providing information key to verifying inferences made based on species distribution patterns.

The results of this study also point to additional studies or modifications in approach that will lead to more detailed and valuable information. For example, increasing species replicates and receiver coverage to deduce a more accurate representation of small scale movement behaviors of coral reef fishes should yield additional insight in habitats utilized and the timing and magnitude of movements. In addition, this should include investigation of differences in movement patterns by sampling and replicating fish of all sizes. One key outcome is the knowledge that receiver detection ranges are dependent on behavior and that the types, arrangement and locations of habitat, with the result that detection range for any receiver can vary markedly in different directions. It is also reasonable to expect that the reception of transmitters may be adversely affected in shallow areas affected by high wind and wave conditions because of the introduction of bubbles and air in the water column. If investigation of the detection variability around each receiver had been known in the present study, instead of mapping detection range to a single receiver in an open bay, the spatial arrangement of the 12 receivers and the spatial scale of the study would have been quite different. For the use of passive receivers to reach their full potential, it will be necessary for future studies to map detection ranges in detail, taking into account expected fish behavior.

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