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ESTIMATING QUEEN CONCH (*STROMBUS GIGAS*) HOME RANGES USING ACOUSTIC TELEMETRY: IMPLICATIONS FOR THE DESIGN OF MARINE FISHERY RESERVES

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ABSTRACT Marine reserves (MRs) may function as a vital tool in the conservation and management of marine resources if source populations are managed for the benefit of those downstream. Consequently, it is critical to evaluate the home range of marine animals to ensure that MRs are large enough to protect source populations. We used acoustic telemetry to study movements of adult queen conch (*Strombus gigas*) within aggregations at two sites in the Florida Keys from June 1997 through July 1998. A total of 68 conch were tagged and tracked for up to one year. Latitude and longitude of each conch were recorded biweekly and data used to estimate the minimum speed, degree of site fidelity, and home range of each animal. Conch showed significantly greater displacement/ time during the summer. There were no significant differences in movement rate, site fidelity, or size of home range between males and females. Mean home range was 5.98 ha. Based on estimated home ranges of the aggregations, the size and location of the existing reserves at these two sites were inadequate to protect the conch aggregations should the fishery reopen.

INTRODUCTION

The objective of marine reserves (MRs) is to "protect the structure, integrity, and stability of an ecosystem" (Appeldoorn 1998). MRs also function as a refuge from fishing pressure, allowing populations to be structured by natural mortality instead of by fishing mortality (Bohnsack 1993, Ingram and Patterson 2001, Jennings 2001). Numerous studies provide evidence that organisms within MRs are larger and/or more abundant than those outside of the refuges (Polunin and Roberts 1993, Roberts 1995, Russ and Alcala 1996, Stoner and Ray 1996, Chiappone and Sullivan Sealey 2000, Tewfik and Bene 2000). The resulting increase in abundance may result in a "spillover" via emigration from the MRs into adjacent areas (Keitt et al. 2001, Roberts et al. 2001a). In a metapopulation context (*sensu* Hanski 1998), the MR may also function as a "source" area by ensuring the protection of spawning stocks from harvest pressure and reducing the probability of Allee effects occurring. Thus, MRs may benefit fisheries outside of their borders in two ways: by enhancing abundance via emigration of adults and juveniles, and by increasing the larval supply to sink populations (Allison et al. 1998, Roberts et al. 2001a). Despite the benefits attributed to MRs, little has been published about determining their appropriate dimensions.

The queen conch, *Strombus gigas,* once supported significant commercial and recreational fisheries in south Florida. However, overharvesting and habitat loss led to the closure of the commercial fishery in 1976 followed by the closure of the recreational fishery in 1986. Despite the harvest moratorium, the population has not recovered to historical levels (Glazer and Berg 1994, Berg and Glazer 1995, Florida Fish and Wildlife Conservation Commission unpublished data). The lack of recovery has been attributed in part to diminished larval supply and recruitment resulting from small spawning aggregations (Stoner et al. 1997, Stoner and Ray-Culp 2000).

On July 1, 1997, the Florida Keys National Marine Sanctuary instituted a Zoning Action Plan that established a network of marine reserves (Figure 1) to protect sensitive marine resources from overuse and to separate conflicting visitor uses (US Department of Commerce 1996). These reserves, called Sanctuary Preservation Areas (SPAs) or Special Use Areas depending on their management goals, were implemented with consideration of the needs of sensitive habitats (e.g., reefs) and the socioeconomic impacts to fishers. They were implemented specifically to "enhance the reproductive capabilities of renewable resources [and] protect areas critical for sustaining and protecting important marine species." All consumptive harvesting is prohibited within the boundaries of these reserves.

Because Florida conch spawning aggregations are located in or close to the reserves (Florida Fish and Wildlife Conservation Commission unpublished data), the FKNMS has funded conch spawning aggregation
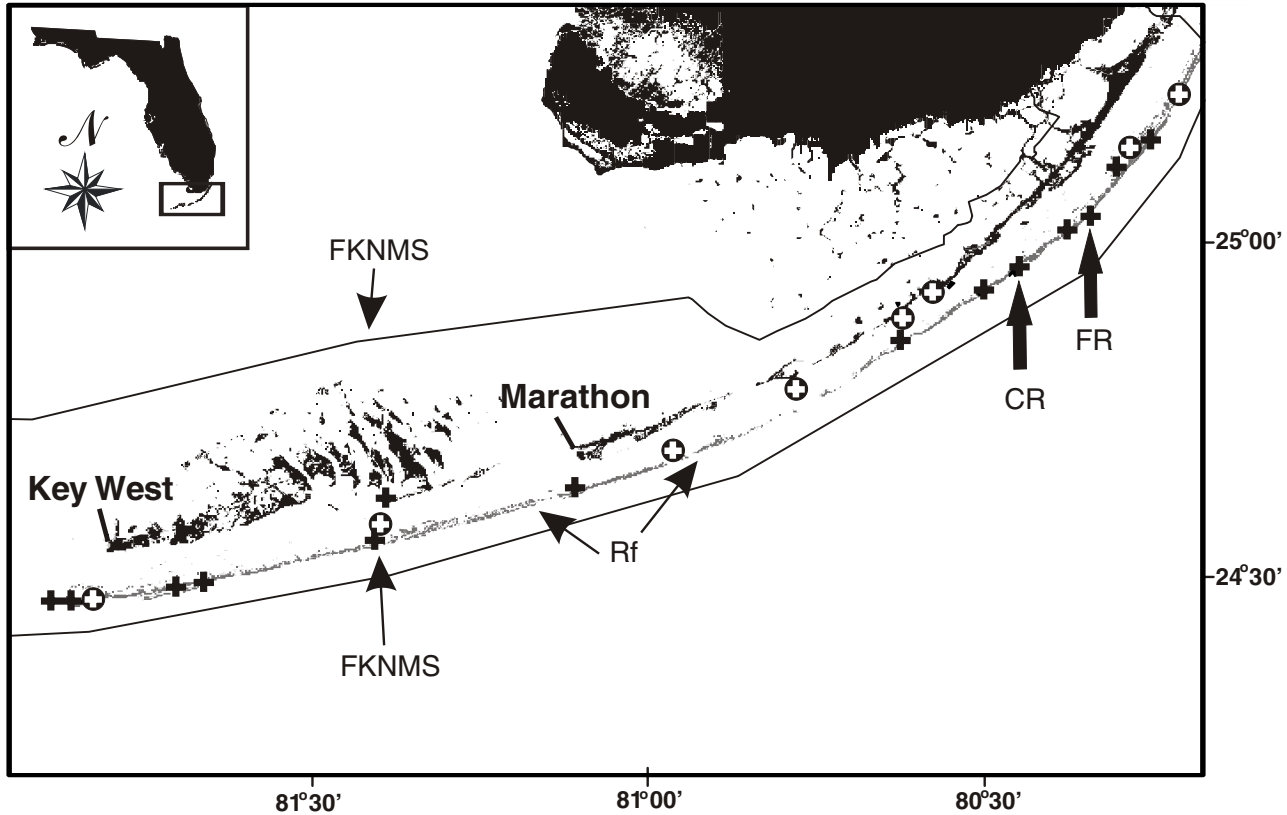
Figure 1. Sampling sites (Conch Reef: CR and French Reef: FR) for queen conch acoustic telemetry study in the Florida Keys National Marine Sanctuary (FKNMS). The locations of the no-take marine reserves (Sanctuary Preservation Areas [SPAs] and special use areas) are presented as crosses (conch aggregation present) or hollow crosses (few or no conch present). In most cases, the reserve is much smaller than depicted. The reef tract (Rf) is detailed to show the relationship of the reserves and the study sites with the reef.

surveys as part of its reserve monitoring study. However, because the reserves were established well after the closure of the conch fishery, they were not designed to address the biological or ecological requirements of queen conch and so may not adequately protect them if harvest is resumed. Yet, it is critical that the conch spawning stock is conserved because the estimated spawning stock throughout the 180 km Florida Keys archipelago was only about 18,000 individuals in 2000 (Florida Fish and Wildlife Conservation Commission unpublished data). In contrast, Stoner and Ray (1996) estimated that there were 208,000 adult conch in a 40 km long marine reserve in the Bahamas.

The size of a reserve needed to adequately protect a species will depend to a great extent on its daily, seasonal, and ontogenetic movements of that species (Polacheck 1990). Several recent studies have addressed the need to examine the movements and home ranges of animals to ensure that reserves function effectively (Kramer and Chapman 1999, Martel et al. 2000, Meyer et al. 2000). However, for home ranges to be calculated, the study organism must display a high degree of site fidelity (Spencer et al. 1990, Hooge et al. 2001). Not all marine animals exhibit high site fidelity (i.e., they may be nomadic or highly migratory) and thus may lack fixed home ranges (Colton and Alevizon 1983, White and Garrott 1990). For those species with high site fidelity, home range estimates can provide vital information for the design and placement of effective reserves (Kramer and Chapman 1999).

The purpose of our study was to estimate the home ranges of adult conch from two spawning aggregations in the Florida Keys. We also compared the sizes and locations of the existing reserves associated with these two aggregations with our estimated aggregation home ranges (AgHR) to determine if the existing reserves would adequately protect the aggregations from future exploitation should the fishery reopen.
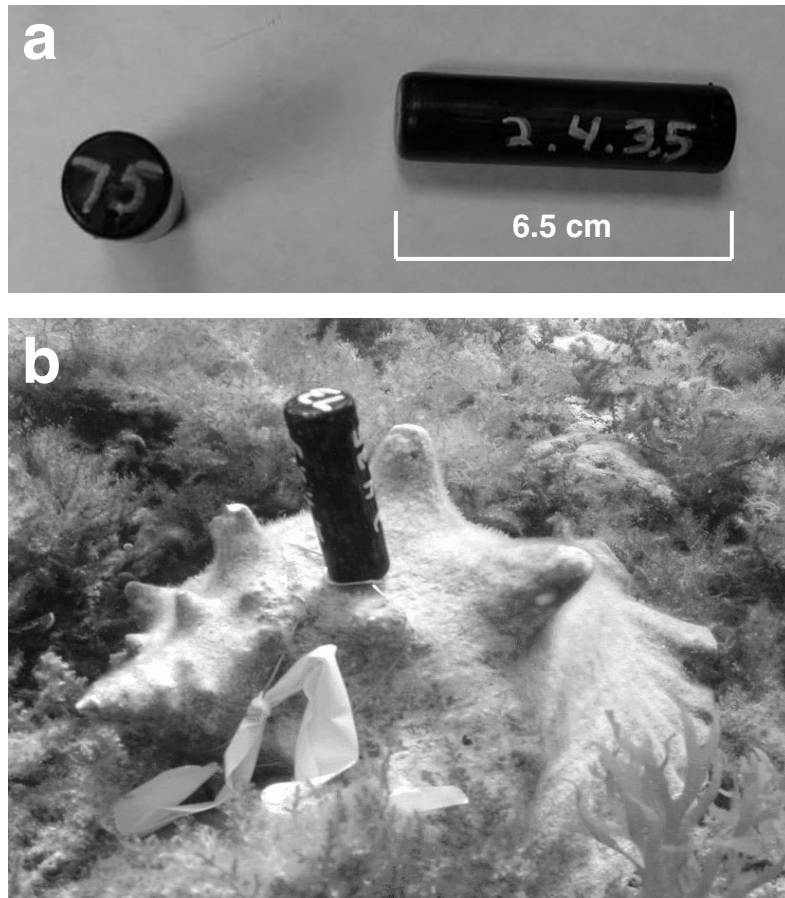
Figure 2. a) Acoustic transmitters used to track queen conch in this study. b) Acoustic transmitter with monel seizing wire attached to the spire of a conch.

METHODS

We used acoustic telemetry to study the movements of adult queen conch within spawning aggregations at two established marine reserves (Conch Reef SPA and French Reef SPA) in the Florida Keys (Figure 1). Queen conch at these two locations are normally found in the back-reef zone on coarse sand bottoms, rubble habitats, and surrounding seagrass patches. A total of 68 conch were tagged *in situ* with acoustic transmitters (Sonotronics, Tucson, Arizona, USA); however, we conducted analyses only on the 44 conch that were resighted more than three times because a minimum of four observations were required to calculate home ranges using the method described below. Acoustic transmitters were attached with monel wire to the spire of each conch (Figure 2). Sex was determined for each conch at the time of tagging by examining external sex organs. Each transmitter emitted a unique pulse and/or frequency, which allowed us to track individual animals. Conch were tracked on a biweekly basis or as weather permitted over a period of one year (June 1997 through July 1998) in order to determine the maximum extent of each individual's home range. An eight-channel Global Positioning System GPS receiver was used to determine the latitude and longitude of each conch during monitoring. In most cases, the GPS was differentially corrected, resulting in positions accurate to within 5 m; however, in some instances, the differential receiver failed, thus, reducing the accuracy to a maximum of 100 m. Only positions from individuals that were directly observed were used in the analyses. These data were analyzed in a Geographic Information System (ArcView 3.1, ESRI, USA) using the Animal Movement Analysis Extension (Hooge et al. 2001). This application utilizes spatially explicit data to determine parameters related to each animal's movements, including minimum movement rate, degree of site fidelity, and home range.

Minimum movement rate (meters·day^{-1}, hereafter referred to as speed) was calculated based upon the linear

distance between consecutive location points and the number of days between consecutive sightings. Because the time interval between observations was often extensive, the actual distance traversed may be grossly underestimated. Thus, estimations of speed are useful for relative comparisons only. We used the Mann-Whitney U test to compare the ranks of the mean speed of conch by sex and by site. The Kruskal-Wallis test was used to examine differences in the ranks of the mean speed among seasons.

Site fidelity is defined as "the tendency of an animal either to return to an area previously occupied or to remain within the same area for an extended period of time" (White and Garrott 1990). Site fidelity was determined for each conch by using a Monte Carlo simulation (with 120 random walk iterations) developed by Spencer et al. (1990) and Hooge et al. (2001) in which the actual movement of the conch was compared with the simulation results. The simulation calculated distances between successive locations; these positions were then randomly chosen without replacement until none remained. Taken in sequence, these locations generated the random movement paths. An animal would be considered to have a high degree of site fidelity if its actual movements were more constrained than the simulated ones. We used Spearman's rho statistic to determine if the number of observations influenced the degree of site fidelity. We also used Spearman's rho statistic to examine if the number of days a conch was tracked influenced the degree of site fidelity. This has important implications for marine reserve design because organisms that undergo seasonal migrations may be judged to lack site fidelity if they are not tracked long enough. This, in turn, may influence the estimations of home ranges.

The home range for each individual was calculated by using the probabilistic kernel model (Worton 1989). This model is preferred over the traditional minimum convex polygon method because it is less sensitive to small sample sizes (Worton 1989, Hooge et al. 2001). Additionally, most animals do not use the area within their home range equally; a species will utilize different resources according to its needs during that stage of its life history. Probability contours were generated from the density of observations within an area. The 95% location probability contour was defined as the animal's home range, and the 50% contour was identified as the core area of activity where the animal spends most of its time (Hooge et al. 2001). We used the Mann-Whitney U test to compare the conch home ranges and core areas by sex and by site. Kruskal-Wallis tests were used to determine if tracking time influenced the home-range and core-area estimates. We also used the Mann-Whitney U test to compare home ranges and core areas for conch that exhibited high site fidelity and those that had low site fidelity.

In order to determine if the existing reserves would be effective for conch should the fishery reopen, we calculated the union of all the individual home ranges (i.e., the full extent of the 95% probability contours) to estimate the AgHR for each site. The reserve design at each site was evaluated by overlaying the area occupied by the AgHR with the existing reserve boundaries.

RESULTS

Movements

There was no statistically significant difference in ranks of the mean speed of conch between the two sexes (Table 1; U = 183, Z = –1.38, P = 0.169) or between conch inhabiting the two sites (Table 1; U = 188, Z = –1.25, P = 0.209). However, there was a statistically significant difference in the ranks of the mean speed of conch among the four seasons of the year (χ^2 = 27.01, df = 3, P < 0.001); conch moved at a greater mean speed during the summer (Table 1).

Site Fidelity

Conch were tracked an average of 245 days, from a minimum of 109 days to a maximum of 368 days (Table 2). There was no difference in the degree of site fidelity

TABLE 1

Mean speed (meters·day^{-1} ± one standard error) by sex, site, and season of queen conch tagged with acoustic transmitters. Because of the time interval between observations, mean speed may greatly underestimate the actual distance traversed. Thus, speed should be viewed for relative comparisons only.

Category	N	Mean Speed
Sex		
female	23	2.16 ± 0.21
male	21	2.57 ± 0.24
Site		
Conch	21	2.05 ± 0.14
French	23	2.64 ± 0.27
Season		
winter	29	2.10 ± 0.21
spring	26	1.92 ± 0.25
summer	24	4.17 ± 0.41
fall	33	2.32 ± 0.20

TABLE 2

Data by site and sex of individual queen conch tracked using acoustic telemetry. N represents the number of times a conch was resighted. Days are total number of tracking days. Mean Speed is in meters·day^{-1}. Site Fidelity represents the percentage of Monte Carlo simulations that were less constrained than the observed movements. Home Range and Core Area (the 95% and 50% location probability contours, respectively, from the kernel model) are in hectares.

| Site	Sex	Tag #	N	Days	Mean Speed	Site Fidelity	Home Range (95%)	Core Area (50%)
Conch	female	5000	15	340	2.20	.88	3.06	0.51
		5008	10	202	1.92	.64	2.24	0.37
		5010	15	280	2.61	.45	5.89	1.60
		5014	13	335	1.94	.98	1.96	0.36
		5019	10	299	2.28	.93	3.18	0.52
		5022	12	202	1.54	.66	0.85	0.18
		5025	9	148	3.53	.40	4.61	0.76
		5102	8	179	1.66	.64	2.45	0.41
		5107	4	179	1.15	.99	3.02	0.63
		5122	7	144	1.41	.24	1.69	0.30
		11997	10	240	1.25	.97	3.17	0.81
		12404	15	348	2.33	.88	3.06	0.51
	male	5005	14	302	2.91	.86	3.88	0.66
		5016	10	237	2.30	.88	3.23	0.65
		5023	12	246	2.75	.31	7.42	0.99
		5118	9	198	1.39	.64	1.12	0.12
		5119	9	199	1.19	.08	2.56	0.51
		6178	10	199	2.31	.11	6.72	0.99
		6180	9	198	2.75	.79	5.02	0.94
		6184	9	179	1.75	.51	2.29	0.33
		6196	9	198	1.80	.42	1.97	0.56
French	female	5052	12	348	0.97	.68	1.03	0.15
		5053	16	348	1.36	.99	0.63	0.08
		5054	12	347	3.48	.90	8.05	0.94
		5055	11	235	1.83	.77	1.67	0.55
		5059	17	368	2.29	.79	5.01	0.69
		5063	11	325	1.88	.99	2.11	0.37
		5064	15	348	1.41	.94	1.07	0.08
		5066	15	368	2.67	.97	5.04	0.54
		5073	13	347	5.54	.66	27.54	7.74
		6103	8	192	2.64	.79	5.04	1.07
		6122	8	192	1.83	.25	3.00	0.64
	male	5051	6	109	2.17	.64	1.92	0.59
		5056	12	276	4.77	.83	6.27	1.26
		5061	13	348	1.01	.95	0.50	0.08
		5071	7	151	3.48	.99	1.88	0.55
		5072	8	294	2.16	.99	4.00	0.63
		6102	8	186	2.32	.40	3.09	0.64
		6106	8	187	1.81	.66	2.04	0.25
		6108	5	186	2.23	.99	16.21	4.48
		6112	7	192	3.70	.63	17.72	3.21
		6113	4	191	5.37	.99	59.61	12.37
		6114	5	186	2.06	.50	5.24	0.97
		6116	8	192	3.80	.10	15.28	2.89
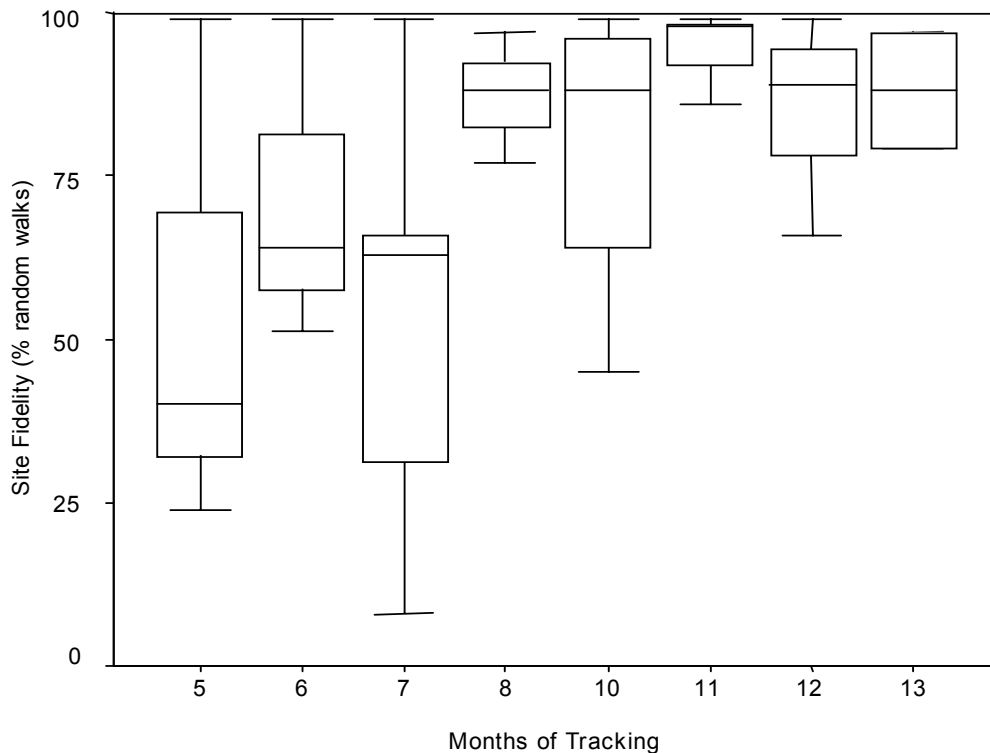
Figure 3. The influence of tracking time (months) on the site fidelity (percentage of simulated random walks that were less constrained than the observed movements) of tagged queen conch (*N=44*). The box represents the interquartile range, which contains 50% of the values. The horizontal line bisecting the box indicates the median. The whiskers are lines that extend to the highest and lowest values, excluding outliers.

between the sexes (U = 188.5, Z = –1.25, P = 0.212). The number of observations did not affect the degree of site fidelity (rho = 0.181, *N* = 44, P = 0.241). However, there was a significant positive correlation between the number of tracking days and the degree of site fidelity (rho = 0.374, *N* = 44, P = 0.012). Conch tracked less than eight months had significantly lower site fidelity than conch tracked more than eight months (Figure 3; U = 93, Z = –3.48, P = 0.001). Based on this, we classified those conch whose actual movements were more constrained than at least 60% of the Monte Carlo random walk simulations as having high site fidelity. Thirty-two of the 44 conch (72.7%) exhibited high site fidelity (Table 2).

Home Range and Core Area

Home ranges varied from a minimum of 0.50 ha to a maximum of 59.61 ha (Table 2); the mean home-range size was 5.98 ha (s.e. = 1.47 ha). Core areas ranged from 0.08 ha to 12.37 ha (Table 2); the mean core area size was 1.22 ha (s.e. = 0.33 ha).

There were no statistically significant differences in home-range size (U = 182, Z = –1.40, P = 0.162) and core-areas size (U = 170, Z = –1.68, P = 0.093) between

males and females (Table 3). Additionally, there were no significant differences in home-range size (U = 210, Z = –0.740, P = 0.459) and core-area size (U = 196, Z = –.07, P = 0.285) of conch between the two sites (Table 3). Tracking time did not influence the estimates of the sizes of home range (χ^2 = 8.41, df = 7, P = 0.298) or core area (χ^2 = 7.77, df = 7, P = 0.354) (Figure 4).

Home-range size and core-area size were not significantly different between conch that showed high site fidelity and those that did not (Table 3; home range: U = 153, Z = –1.03, P = 0.304; core area: U = 145, Z = -1.24, P = 0.215). As a result, we included the home ranges of conch that did not exhibit high site fidelity along with those that did in order to provide better spatial coverage for the AgHR estimates. The AgHR at French Reef was estimated to be 72.9 ha, whereas the AgHR of the aggregation at Conch Reef was calculated to be 22.5 ha (Figure 5).

DISCUSSION

Estimating the spatial patterns of resource usage by wildlife populations is critical for developing effective management strategies (White and Garrott 1990). In this

TABLE 3

Mean home-range and core-area sizes (hectares ± one standard error) of queen conch tagged with acoustic transmitters by sex, site, and site fidelity. High site fidelity indicates that the individual's observed movements were more constrained than 60% of the simulated random walks. Low site fidelity indicates that the individual's observed movements were less constrained than 60% of the simulated random walks.

Category	N	Home Range	Core Area
Sex			
female	23	4.15 ± 1.13	0.86 ± 0.32
male	21	8.00 ± 2.80	1.60 ± 0.59
Site			
Conch	21	3.30 ± 0.38	0.61 ± 0.07
French	23	8.43 ± 2.72	1.77 ± 0.61
Site Fidelity			
high	32	6.36 ± 1.99	1.32 ± 0.45
low	12	4.98 ± 1.09	0.93 ± 0.21

study, we estimated the AgHR of two adult conch aggregations and found that the current reserves at the two study sites are inadequate to protect conch should the fishery reopen in the future. The AgHR at French Reef was estimated to be 72.9 ha, but the SPA is only 37 ha; additionally, most of the aggregation is located outside the SPA (Figure 5). At Conch Reef, the size of the SPA (95 ha) is adequate to protect the conch (22.5 ha AgHR). However, none of the aggregation is located within the boundaries of the SPA (Figure 5). It should be noted that these reserves were not designed with conch in mind when they were established because the species was already fully protected from harvest.

If the conch fishery is reopened, the size and location of existing reserves must be reexamined. Some are probably too small to adequately protect existing spawning aggregations of conch, and most aggregations in the Florida Keys are located outside of the boundaries of existing reserves (Florida Fish and Wildlife Conservation Commission unpublished data). Therefore, if the conch fishery reopens with only the current reserves in place, the goals of maintaining ecosystem health and enhancing fisheries (at least relative to queen conch) would not be achieved.

Our results also show that conch moved at a greater mean speed during the summer (the height of the reproductive season) than during the rest of the year. This greater speed may be due to the increased metabolic activity associated with warmer waters and increased

movement related to reproductive activities (i.e., males searching for mates and females moving to the appropriate habitat to lay their egg masses). Several studies have reported that adult conch move to a different habitat during the reproductive season, but return to their feeding grounds after mating and spawning (Hesse 1979, Stoner and Sandt 1992).

These seasonal migrations may also explain the positive correlation we found between site fidelity and the number of days a conch was tracked. In general, the more time a conch was tracked, the higher its site fidelity. We believe this to be an artifact of the conch's seasonal patterns of movements and the fact that we were unable to track all animals for an entire year, both of which may have profound implications for home-range estimations. For example, if a conch was tracked from June to January and moved off its spawning grounds during that time, it would be described as having relatively low site fidelity. However, if tracking had continued throughout the year and the conch had returned to its spawning grounds, it would have been described as having high site fidelity. Therefore, we suggest that site fidelity studies must address seasonal variability in movements or else results may underestimate site fidelity and, therefore, home-range. Nevertheless, there were no statistically significant differences in home-range and core-area estimations between conch that exhibited high and low site fidelity. This might be expected if conch in general don't migrate very far from their feeding grounds during the breeding season (Stoner and Sandt 1992).

Appeldoorn (1995) stated that intensive fishing pressure might invoke depensatory mechanisms as densities are reduced, limiting the ability of conch to locate mates (i.e., Allee effects) and increasing the chance of recruitment failure. Stoner and Ray-Culp (2000) suggested that the slow recovery in Florida may be a result of Allee effects due to low encounter rates between males and females in low-density aggregations. In addition to density, the reproductive output of the aggregation will also depend upon overall abundance. Since abundance is a function of density and area, it is critical that reserves be adequately sized and properly located so that spawning aggregations can be protected from exploitation. At our study sites, densities were high (French Reef: 540 conch · ha⁻¹; Conch Reef: 290 conch · ha⁻¹; Florida Fish and Wildlife Conservation Commission unpublished data); yet, the modest spatial extent of the aggregations resulted in low estimates of overall abundance (French Reef: 995 conch; Conch Reef: 345 conch). Most other conch aggregations in Florida also have high densities and low overall abundance. Aggregations sharing these
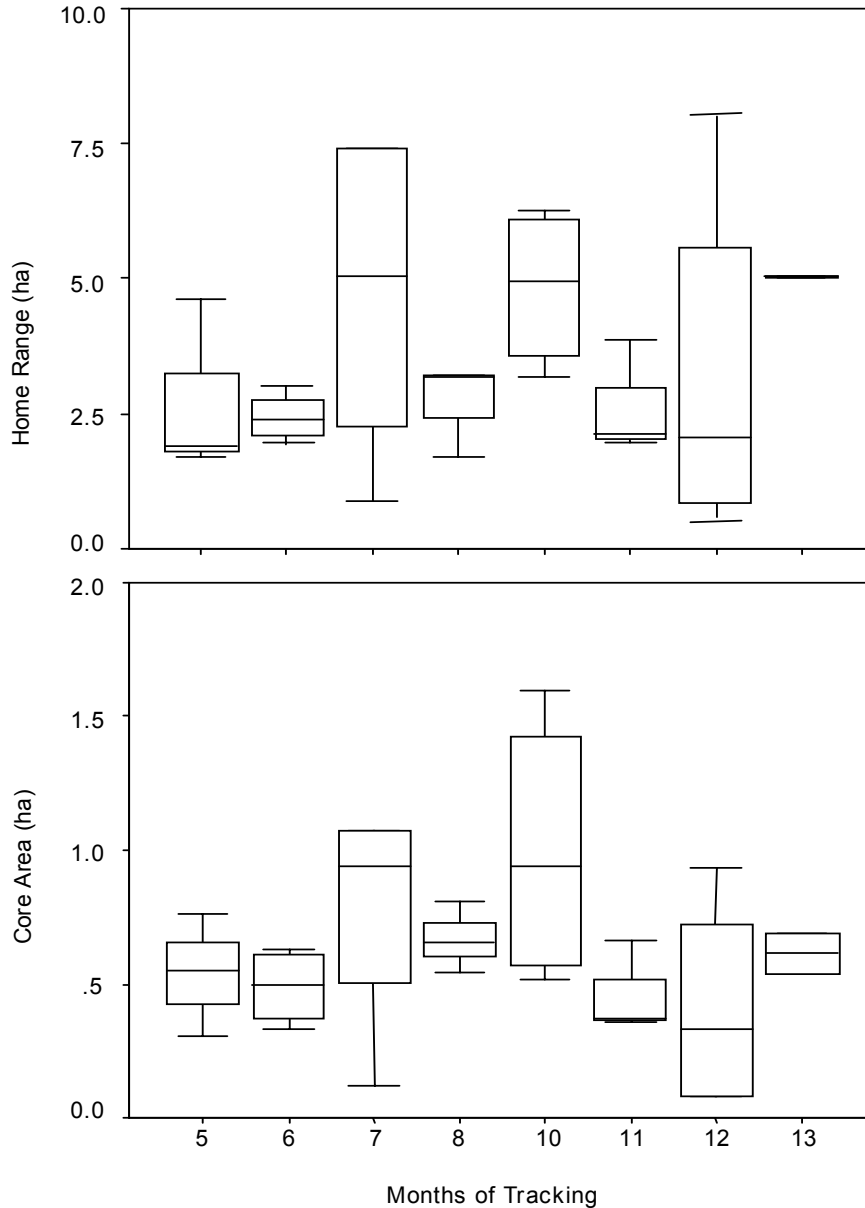
Figure 4. The influence of tracking time (months) on the estimates of home range and core area of tagged queen conch (N=44). The box represents the interquartile range, which contains 50 % of the values. The horizontal line bisecting the box indicates the median. The whiskers are lines that extend to the highest and lowest values, excluding outliers.

characteristics are highly susceptible to overharvest if not managed carefully.

Stoner (1997) suggested that conch fishery reserves must be designed in the context of metapopulation dynamics. He also suggested that the success of the conch population in the Exuma Cays Land and Sea Park in the Bahamas was due, in part, to the park's large size. Lauck et al. (1998) stated that marine reserves need to be large enough to protect the resource in the event of overfishing and that spawning areas should be protected so that they may act as "sources." However, several researchers have

posited that a network of marine reserves can sustain ecosystem function and protect exploited species better than one large reserve can (Murray et al. 1999, Roberts et al. 2001b). In Florida, where conch are highly aggregated at many discrete locations, one large reserve may not be sufficient in a reopened fishery and a network of marine reserves is probably more suitable.

Clearly, information in addition to home ranges must be considered for effective design of fishery reserves. Defining the appropriate size and location of a reserve depends on essential information about the habi-
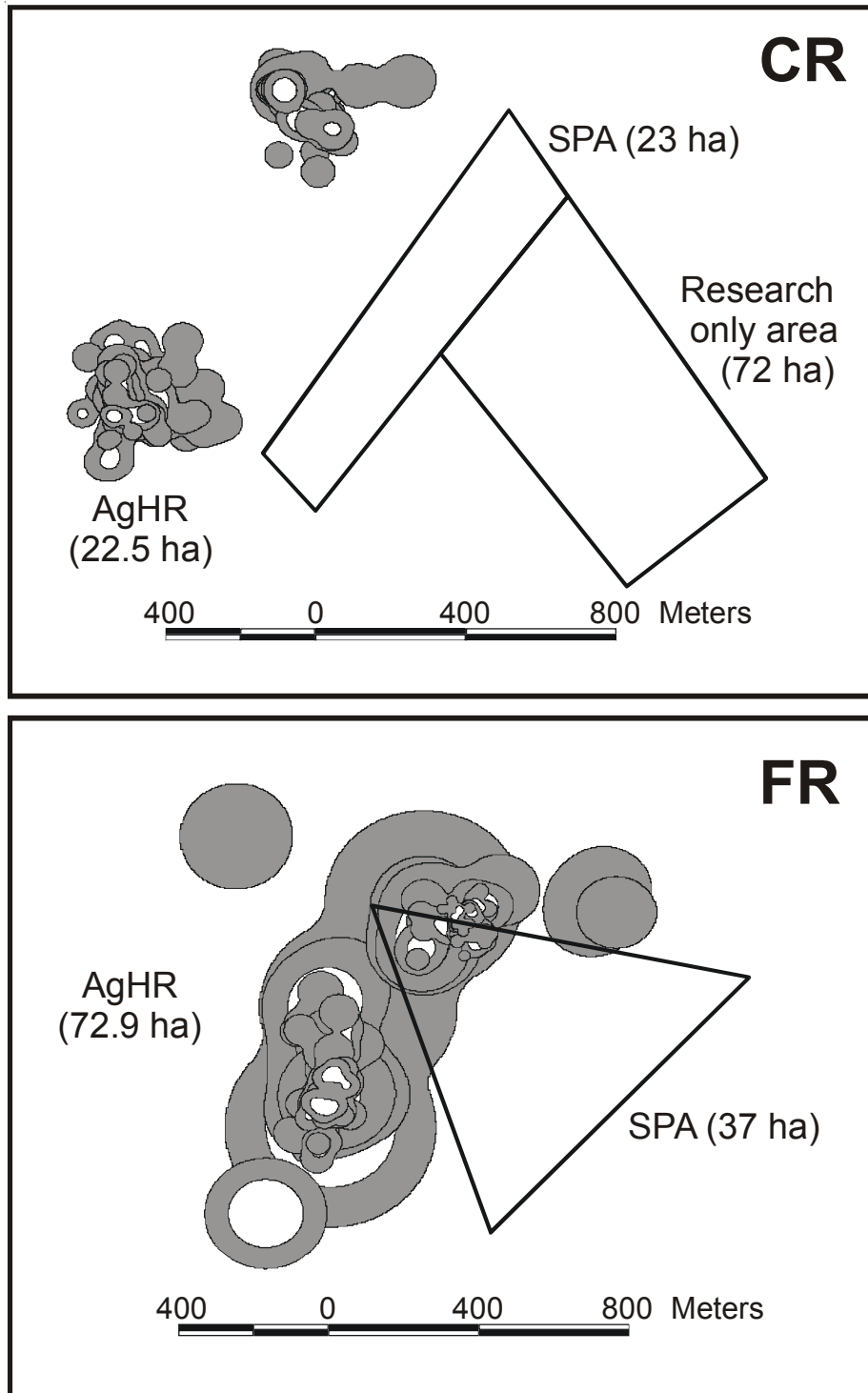
Figure 5. Home ranges and core areas of the individual queen conch at Conch Reef SPA (CR: N=21) and French Reef SPA (FR: N=23). The gray polygons represent the home ranges (95% location probability contours) of individual conch. The white polygons represent the core areas (50% location probability contours) of individual conch. Not all core areas are represented because of overlapping home ranges. In addition, not all 95% contours depicted have associated core areas because the overall 95% contour for an individual may consist of more than one contour due to widely separate observations. The aggregation home range (AgHR) was based on the union of all the individual home ranges.

tat requirements and dispersal capabilities of a species (Fogarty 1999). Home-range information must be linked with habitat requirements and availability as well as with migration corridors and hydrodynamic patterns to ensure effective placement and design of a reserve (for reviews see Allison et al. 1998, Murray et al. 1999).

ACKNOWLEDGMENTS

LITERATURE CITED

Allison, G.W., J. Lubchenco, and M.H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8:S79–S92.

Appeldoorn, R.S. 1995. Potential depensatory mechanisms operating on reproductive output in gonochoristic molluscs, with particular reference to strombid gastropods. ICES Marine Science Symposia 199:13–18.

Appeldoorn, R.S. 1998. Ecological goals for marine fishery reserve design: workshop summary. Proceedings of the Gulf and Caribbean Fisheries Institute 50:294–303.

Berg, C.J., Jr. and R.A. Glazer. 1995. Stock assessment of a large marine gastropod (*Strombus gigas*) using randomized and stratified towed-diver censusing. ICES Marine Science Sympsoium 199:247–258.

Bohnsack, J.A. 1993. Marine reserves: they enhance fisheries, reduce conflicts, and protect resources. Oceanus Fall:63–71.

Chiappone, M. and K.M. Sullivan Sealey. 2000. Marine reserve design criteria and measures of success: lessons learned from the Exuma Cays Land and Sea Park, Bahamas. Bulletin of Marine Science 66:691–705.

Colton, D.E. and W.S. Alevizon. 1983. Movement patterns of bonefish, *Albula vulpes*, in Bahamian waters. Fishery Bulletin, US 81:148–154.

Fogarty, M.J. 1999. Essential habitat, marine reserves, and fishery management. Trends in Ecology and Evolution 14:133–134.

Glazer, R.A. and C.J. Berg, Jr. 1994. Queen conch research in Florida: an overview. In: R.S. Appeldoorn and B. Rodriguez, eds. Queen Conch Biology, Fisheries, and Mariculture. Fundación Cientifica Los Roques, Caracas, Venezuela, p. 79–95.

Hanski, I. 1998. Metapopulation dynamics. Nature 396:41–49.

Hesse, K.O. 1979. Movement and migration of the queen conch, *Strombus gigas*, in the Turks and Caicos Islands. Bulletin of Marine Science 29:303–311.

Hooge, P.N., W.M. Eichenlaub, and E.K. Solomon. 2001. Using GIS to analyze animal movements in the marine environment. In: G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, and D. Witherell, eds. Spatial Processes and Management of Marine Populations. University of Alaska Sea Grant, AK-SG-01-02, Fairbanks, AK, USA, p. 37–51.

Ingram, G.W. and W.F. Patterson, III. 2001. Movement patterns of red snapper (*Lutjanus campechanus*), greater amberjack (*Seriola dumerili*), and gray triggerfish (*Balistes capriscus*) in the Gulf of Mexico and the utility of marine reserves as management tools. Proceedings of the Gulf and Caribbean Fisheries Institute 52:686–699.

Jennings, S. 2001. Patterns and prediction of population recovery in marine reserves. Reviews in Fish Biology and Fisheries 10:209–231.

Keitt, T.H., M.A. Lewis, and R.D. Holt. 2001. Allee effects, invasion pinning, and species' borders. American Naturalist 157:203–216.

Kramer, D.L. and M.R. Chapman. 1999. Implications of fish home range size and relocation for marine reserve function. Environmental Biology of Fishes 55:65–78.

Lauck, T., C.W. Clark, M. Mangel, and G.R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications 8:S72–S78.

Martel, S.J.D., C.J. Walters, and S.S. Wallace. 2000. The use of marine protected areas for conservation of lingcod (*Ophiodon elongatus*). Bulletin of Marine Science 66:729–743.

Meyer, C.G., K.N. Holland, B.M. Wetherbee, and C.G. Lowe. 2000. Movement patterns, habitat utilization, home range size, and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. Environmental Biology of Fishes 59:235–242.

Murray, S.N., R.F. Ambrose, J.A. Bohnsack, L.W. Botsford, M.H. Carr, G.E. Davis, P.K. Dayton, D. Gotshall, M.A. Hixon, J. Lubchenco, M. Mangel, A. MacCall, D.A. McArdle, J.C. Ogden, J. Roughgarden, R.M. Starr, M.J. Tegner, and M.M. Yoklavich. 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. Fisheries 24:11–24.

Polacheck, T. 1990. Year around closed areas as a management tool. Natural Resource Modeling 4:327–354.

Polunin, N.V.C. and C.M. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series 100:167–176.

Roberts, C.M. 1995. Rapid build-up of fish biomass in a Caribbean marine reserve. Conservation Biology 9:815–826.

Roberts, C.M., J.A. Bohnsack, F. Gell, J.P. Hawkins, and R. Goodridge. 2001a. Effects of marine reserves on adjacent fisheries. Science 294:1920–923.

Roberts, C.M., B. Halpern, S.R. Palumbi, and R.R. Warner. 2001b. Designing marine reserve networks: why small, isolated protected areas are not enough. Conservation Biology in Practice 2:10–17.

Russ, G.R. and A.C. Alcala. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Marine Ecology Progress Series 132:1–9.

Spencer, S.R., G.N. Cameron, and R.K. Swihart. 1990. Operationally defining home range: Temporal dependence exhibited by hispid cotton rats. Ecology 71:1817–1822.

Stoner, A.W. 1997. The status of queen conch, *Strombus gigas*, research in the Caribbean. Marine Fisheries Review 59:14–22.

Stoner, A.W. and M. Ray. 1996. Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production. Fishery Bulletin, US 94:551–565.

Stoner, A.W. and M. Ray-Culp. 2000. Evidence for allee effects in an over-harvested marine gastropod: density-dependent mating and egg production. Marine Ecology Progress Series 202:297–302.

Stoner, A.W. and V.J. Sandt. 1992. Population structure, seasonal movements, and feeding of queen conch, *Strombus gigas*, in deep-water habitats of the Bahamas. Bulletin of Marine Science 51:287–300.

Stoner, A.W., N. Mehta, and T.N. Lee. 1997. Recruitment of *Strombus* veligers to the Florida Keys reef tract: relation to hydrographic events. Journal of Shellfish Research 16:19–29.

Tewfik, A. and C. Bene. 2000. Densities and age structure of fished versus protected populations of queen conch (*Strombus gigas* L.) in the Turks and Caicos Islands. Proceedings of the Gulf and Caribbean Fisheries Institute 51:60–79.

US Department of Commerce. 1996. Florida Keys National Marine Sanctuary Final Management Plan/Environmental Impact Statement (FMP/EIS), Volume I. National Oceanic and Atmospheric Administration, Sanctuaries and Reserves Division. 319 p.

White, G.C. and R.A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego, CA,USA.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168.