Abstract—Marine Fishery Reserves (MFRs) are being adopted, in part, as a strategy to replenish depleted fish stocks and serve as a source for recruits to adjacent fisheries. By necessity, their design must consider the biological parameters of the species under consideration to ensure that the spawning stock is conserved while simultaneously providing propagules for dispersal. We describe how acoustic telemetry can be employed to design effective MFRs by elucidating important life-history parameters of the species under consideration, including home range, and ecological preferences, including habitat utilization. We then designed a reserve based on these parameters using data from two acoustic telemetry studies that examined two closely-linked subpopulations of queen conch (*Strombus gigas*) at Conch Reef in the Florida Keys. The union of the home ranges of the individual conch (aggregation home range: AgHR) within each subpopulation was used to construct a shape delineating the area within which a conch would be located with a high probability. Together with habitat utilization information acquired during both the spawning and non-spawning seasons, as well as landscape features (i.e., corridors), we designed a 66.5 ha MFR to conserve the conch population. Consideration was also given for further expansion of the population into suitable habitats.

Designing marine fishery reserves using passive acoustic telemetry

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Introduction

Passive acoustic telemetry has been used for many years by fisheries and wildlife biologists to elucidate a number of life-history parameters and to examine the ecological requirements of targeted populations (White and Garrott, 1990). The technology has evolved so that tags are now smaller and battery lives are longer, thus increasing the amount of data acquired and available to the manager or researcher. Coincident with the evolving technology has been the emergence of computer programs using geospatially referenced data (i.e., Geographic Information Systems or GIS). Taken together, these tools provide opportunities for understanding how populations behave and function within the resources available to them.

At the same time, the toolbox of strategies to conserve and manage fish stocks has expanded from traditional management schemes (e.g., limited-entry fisheries, quotas) to include the consideration of no-take marine fishery reserves (MFRs) (Bohnsack, 1994). A growing body of empirical evidence now suggests that in a variety of ways, the no-take approach may enhance commercial and recreational fishers' opportunities to target a population (Lubchenko et al., 2003). In particular, studies have suggested that more and larger individuals may become available to adjacent fisheries by "spillover" from the reserve via emigration (Roberts et al., 2001), the reproductive output of the population may be enhanced by the increased spawning biomass inside the reserve (Côté et al., 2001), and there may be a concomitant enhanced supply of propagules to downstream populations (Kramer and Chapman, 1999; Martel et al., 2000; Meyer et al., 2000; Lowe et al., 2003). However, other, less obvious benefits may also occur including increasing encounters between individuals due to the reduction of Allee effects (Stoner and Ray-Culp, 2000), increased fecundity (Bertelsen and Matthews, 2001), and enhanced or restored biodiversity via cascading trophic effects (Babcock et al., 1999). Furthermore, MFRs may provide opportunities to examine the effects of various fishing strategies in a controlled environment (Bohnsack, 1998). Despite these purported benefits, there are still many unanswered questions related to the optimal design (Boersma and Parrish, 1999), siting (Crowder et al., 2000), and connectivity within MFR networks (Warner and Cowen, 2002).

To design an effective MFR, knowledge of a variety of life-history parameters and ecological requirements of the population are required (Dugan and Davis, 1993). Because the size of an effective reserve will depend in part on the daily, seasonal, and ontogenetic movements of that species (Polacheck, 1990; Lowe et al., 2003), the evaluation of the home range (Kramer and Chapman, 1999), site fidelity (Lembo et al., 1999), and movements and migrations (Zeller et al., 2003) of individuals in the population is critical.

Habitat requirements must also be incorporated into an effective MFR design (Recksiek et al., 2001; Rodwell et al., 2003). Ideally, the high-quality habitats most preferred for forage, reproduction, and refuge will be conserved and protected not only for the existing individuals in the population, but also for providing additional resources as the population expands (Allison et al., 1998; Fogarty, 1999; Murray et al., 1999; Glazer and Kidney, 2004). Ecologically critical landscape features (e.g., corridors) must also be incorporated into the design to ensure that the reserve will protect the targeted population (Recksiek and Appeldoorn, 1998; Recksiek et al., 2001; Glazer and Kidney, 2004).

Despite the widespread recognition of these critical variables, the literature is depauparate with methods that provide guidance on how to incorporate a species' life-history and habitat requirements into an effective MFR design a priori (Recksiek and Appeldoorn, 1998). Rather, there are numerous examples of the evaluation of an MFR's function after it has been established (e.g., Meyer et al., 2000). Additionally, there are comprehensive papers that describe the theoretical considerations in marine reserve design, but few that provide practical guidelines (Botsford et al., 2003).

We present here an approach that links life-history parameters with habitat utilization of the targeted species to define the spatial extent of an optimally designed MFR. The design process incorporates data obtained from acoustic telemetry studies to delineate the area encompassed, the available habitat, and the habitat used by a population targeted for protection. Socioeconomic factors, as well as larval dispersal are beyond the scope of this paper and are therefore not considered in the design criteria. The method is applied to construct an MFR designed to protect a population of queen conch (*Strombus gigas*) in the Florida Keys.

Methods

Designing an MFR

We propose an MFR design process based on the distribution and ecological requirements of the population that is targeted for protection. The data on which the design will be based are acquired using acoustic telemetry.

Initially, two important considerations must be addressed. First, the manager must conclude that an MFR is an appropriate management tool to meet a specific objective based on a variety of social, economic, political, and scientific considerations. Upon embracing this strategy, the proportion of the population targeted for protection must be identified using many of these same criteria. In many cases, the entire population is targeted for conservation; in other cases, the population may be so dispersed that conservation of the entire population is impractical.

After these determinations are made, the design process is fairly straightforward (Fig. 1). First, the distribution of the population is identified in order to preliminarily determine the approximate location of the MFR. In heavily exploited or otherwise affected populations, historical information may be required. In any case, the high-quality habitats associated with reproduction, refuge, and forage should be considered.

In the next step, both the home ranges and the habitats used by individuals in the population are determined. Passive acoustic telemetry presents a versatile and relatively inexpensive method to locate tagged individuals, an important consideration in habitat-utilizations studies. Additionally, with a global positioning system receiver, the geospatial positions of each individual can be easily obtained for home range estimations.

Recognizing that the goal of these studies is to extend the results to a population that includes untagged individuals, an appropriate sample size is required. Ideally, this determination would be made with a power test; however that may be beyond the resources of the researcher or manager. Additionally, an adequate number of individuals must be resighted to ensure sufficient statistical power. However, the number of individuals tagged will also depend upon a variety of factors, including budgetary constraints. In any case, the acoustic tagging study should be conducted at a sufficient temporal scale to ensure that short-term (i.e., diurnal) and/or long-term (i.e., seasonal) movements are captured (Glazer et al., 2003). In our previous work, we determined that conch needed to be tracked for a minimum of eight months in order to ensure that seasonal differences in movements and habitat usage did not influence site fidelity and home range estimations (Glazer et al., 2003). These values may change depending on the species under examination.

The geospatial data acquired from the acoustic telemetry are used to examine how individuals behave in their environment. Computerized methods are making these analyses increasingly accessible within GIS (Hooge et al., 2001). In our process, the location data are used in two ways. First, site fidelity of the tagged individuals is examined. This is a critical step because our process for MFR design requires examination of home ranges, and meaningful home-range estimations require a high degree of site fidelity (Hooge et al., 2001). After site fidelity is validated, the second way the geospatial data are used is to estimate the home range of each tagged individual. We suggest using a probabilistic model (i.e., kernel method) because of its accuracy and robustness (Worton, 1989; Hooge et al., 2001).

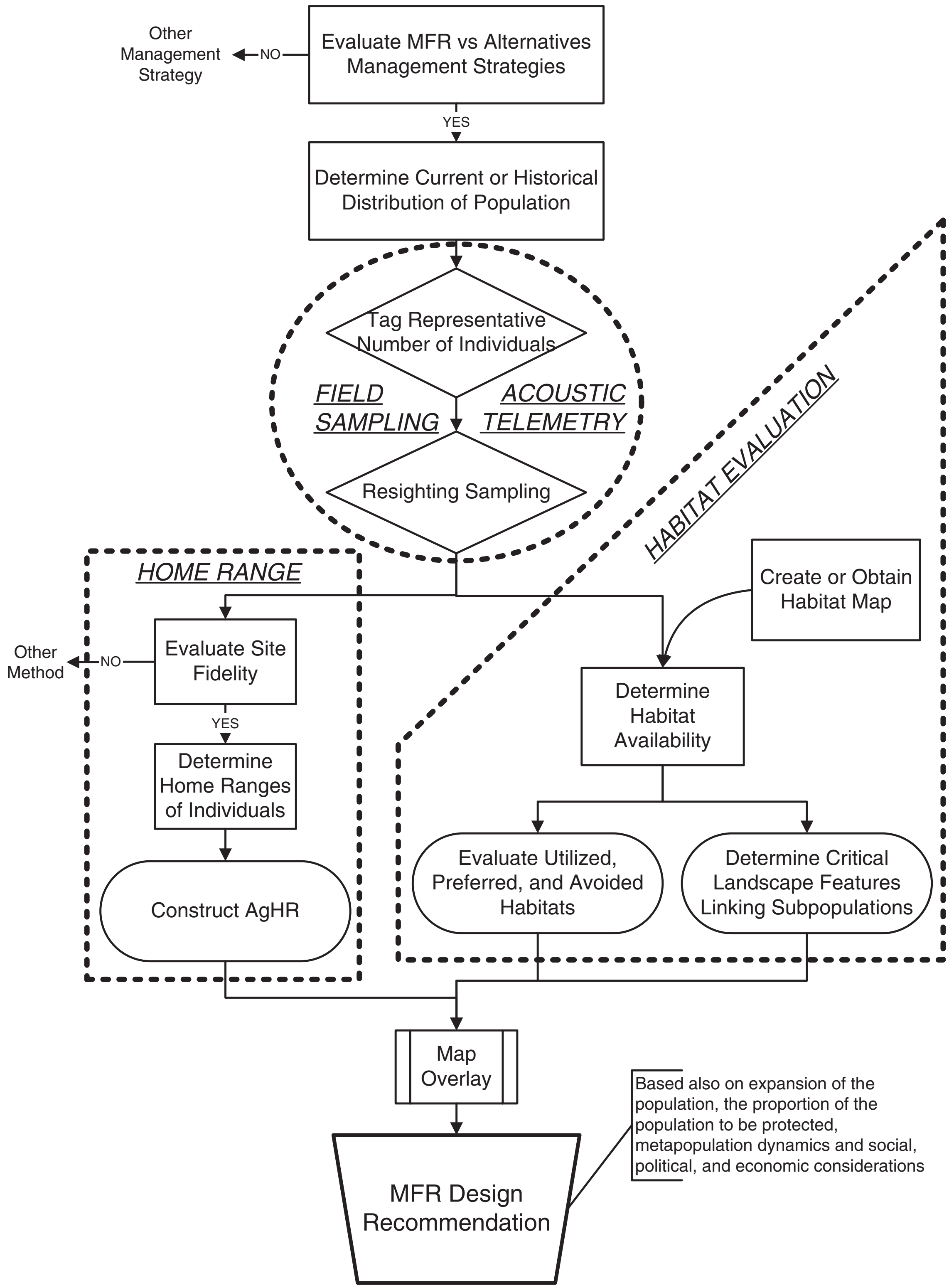

Figure 1

The process for designing a marine fishery reserve. Data acquired from acoustic telemetry studies are used to estimate home ranges of individuals and habitat utilization of the population.

The home range estimation can then be extended to the entire population. In 2003, we introduced a concept we called the aggregation home range (AgHR) to describe an area within which there is a 95% probability that the entire population of tagged individuals will be found (Glazer et al., 2003). The AgHR is represented as an irregular shape that describes the union of the polygons associated with the kernel home ranges of each tagged individual at the 95% probability level (Fig. 2). Given sufficient sample size, this shape approximates, with a high probability, the area occupied by the entire population.

Habitat-use studies provide additional data needed for designing an effective reserve. Because the size and shape of a home range is often dependant on habitat (Kramer and Chapman, 1999), the integration of these parameters into reserve design provides a powerful basis to define the spatial extent of the MFR. Data for these analyses are composed of two components: habitat availability and the habitats occupied by individuals in the population. These analyses then provide statistical representations of the habitats that are utilized, preferred, and avoided by the population (Neu et al., 1974).

Estimating the available habitat requires a map with a suitable spatial scale and appropriate habitat classifications for the targeted species. In many cases, habitat maps may already be available. Alternatively, they can be constructed, and a variety of methods exist to do so (White and Garrot, 1990).

Examining the habitats occupied by individuals requires an efficient method of locating individuals in what may be complex environments, and acoustic telemetry is, in many cases, ideal for this application (for a review, see Eristhee and Oxernford, 2001). The number of observations within each habitat is compared with the percent coverage of each habitat to provide a statistical representation of habitat utilization. Given a habitat map of the area with sufficient scale and resolution, habitats that should be conserved or which the population may colonize may be easily discerned.

Other habitat features should also be considered when designing an MFR. For example, corridors function to permit migration between patches of critical habitat—areas that are essential for reproduction and survival (White and Garrott, 1990). Corridors may also facilitate dispersal between habitat patches in fragmented landscapes (Berggren et al., 2002). If corridors are not protected, individuals may be susceptible to harvest when in transit or they may be unable to migrate into critical habitats (Simpson and Mapleston, 2002). Acoustic telemetry provides an efficient method to locate individuals that are in transit between habitat features and to identify those areas that must be conserved.

Further consideration must be given to habitats in cases where expansion of the population after protection is anticipated and desired. A population expands in one of two ways. First, the population may expand beyond its current boundaries as a result of density-dependent processes. In some cases, animals may even begin to use less desirable habitats (Rowley, 1994). Second, a corridor may be permeable and individuals may immigrate into previously unused adjacent habitats (Acosta, 1999). Both processes reinforce the need to identify corridors.

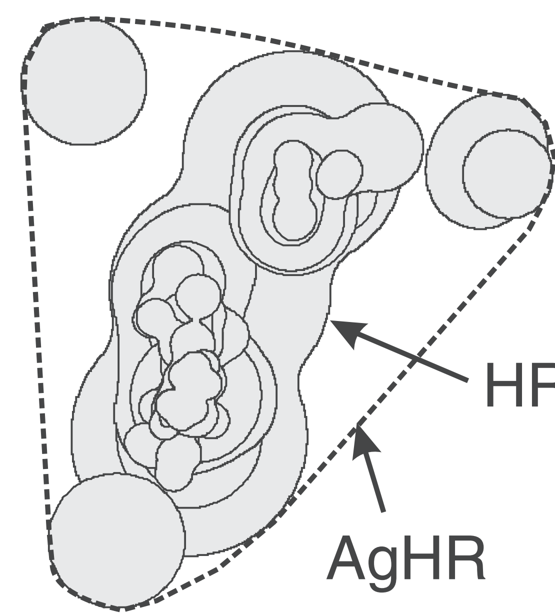

Figure 2

The aggregation home range (AgHR) describing the union of the 95% probability contours of the individual animals (HR). Data are from 23 queen conch (*Strombus gigas*) at French Reef in the Florida Keys (Glazer et al., 2003).

Once the AgHR and the important habitat features are identified, an overlay is constructed to visually interpret the results and to assist in the design of the MFR. This is easily accomplished within a GIS, where boundaries can be identified and manipulated.

An example

To construct an MFR, we used data from two studies of queen conch conducted in 1997 on a Florida Keys back reef (Glazer et al., 2003; Glazer and Kidney, 2004). In those studies, we tagged adult queen conch with acoustic transmitters (Sonotronics, Inc. Tuscon Arixona, USA; Fig. 3) at Conch Reef in the upper Florida Keys. Conch Reef is a shallow-water reef escarpment with two areas delineated for protection: a limited-use Sanctuary

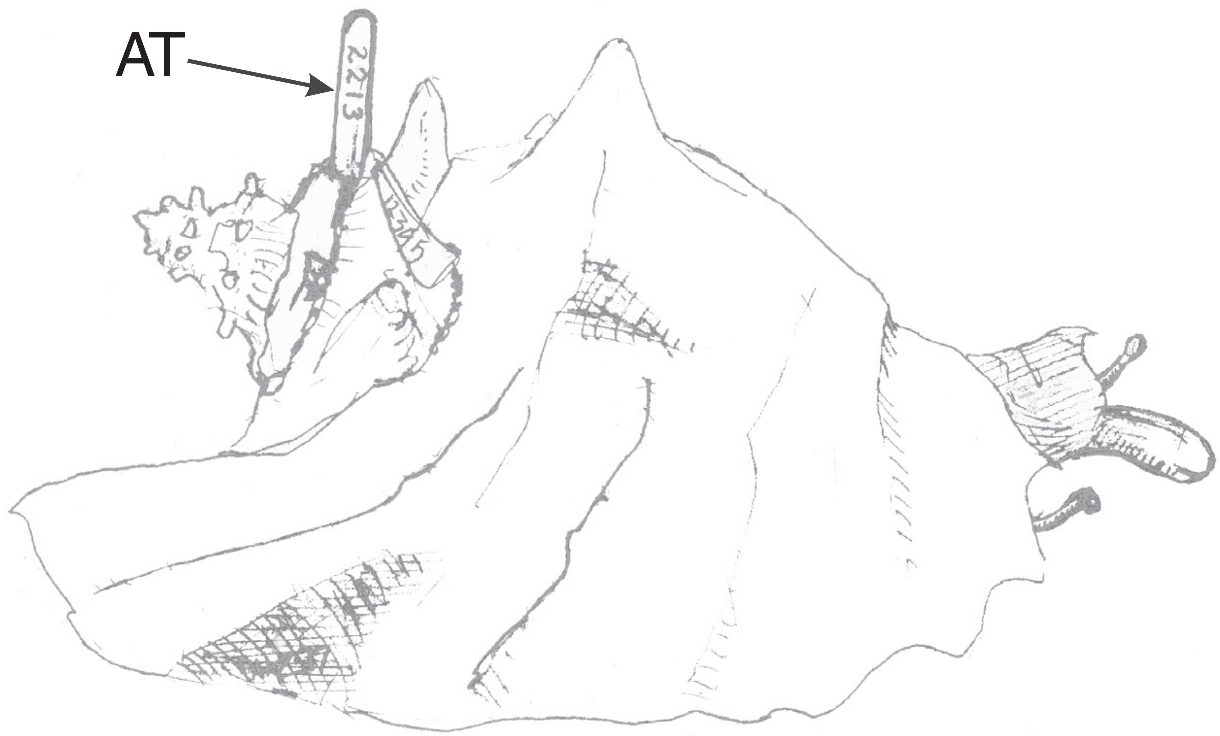

Figure 3

Passive acoustic transmitter (AT) attached to a queen conch (*Strombus gigas*) used in acoustic telemetry studies. A second tag, which was used to identify the conch if the acoustic tag was lost, is shown attached to the spire (for a further discussion, see Glazer et al., 2003).

Preservation Area (SPA) approximately 23.3 ha in area and a restricted access Research Reserve (RR) encompassing approximately 47.5 ha. The conch were located within two spatially distinct sub-populations (Fig. 4), but interchange was possible between them across a rubble field. We estimated that the total number of adult conch in both aggregations was approximately 345 individuals; therefore, about 11% of the population was tagged with acoustic transmitters. We conducted resighting sampling using hydro-acoustic receivers from a research vessel.

Using acoustic telemetry data (i.e., latitudes and longitudes), we determined the 95% probability contours for the home ranges for 21 conch (Glazer et al., 2003). These probabilities were graphically represented in a GIS.

We also examined the habitat requirements of the conch using acoustic telemetry data (Glazer and Kidney, 2004). These data were used in two ways. First we determined the available habitat to the population (Table 1) by constructing the minimum convex polygon of all observations of the 39 conch tagged with acoustic transmitters. Then we examined the habitat utilized and preferred by the conch by comparing the available habitat with the habitats occupied by the conch (Glazer and Kidney, 2004). Based on these analyses, we determined that the conch preferred coarse sand (Cs) and rubble/coarse sand (RbCs) substrates, especially during reproductive season (Table 1). At one site (C2), conch avoided rubble (Rb) relative to its availability; however, the rubble habitat served an important function. Two conch (5% of the tagged population) were observed moving from C1 to C2 across the shallow rubble ridge separating the two sites (Fig. 5). Additionally, observations of untagged conch on this rubble ridge suggest that this habitat serves as an important transit corridor.

These results were used to design an MFR for conch at this site. To design the reserve, we first constructed an AgHR at each subpopulation by drawing a smooth shape around the union of all the individual home range polygons (Fig. 5). We then used the answers from the following questions to further refine the design: 1) is there exchange between the two subpopulations (i.e., is there a migration corridor), 2) what habitats are critical

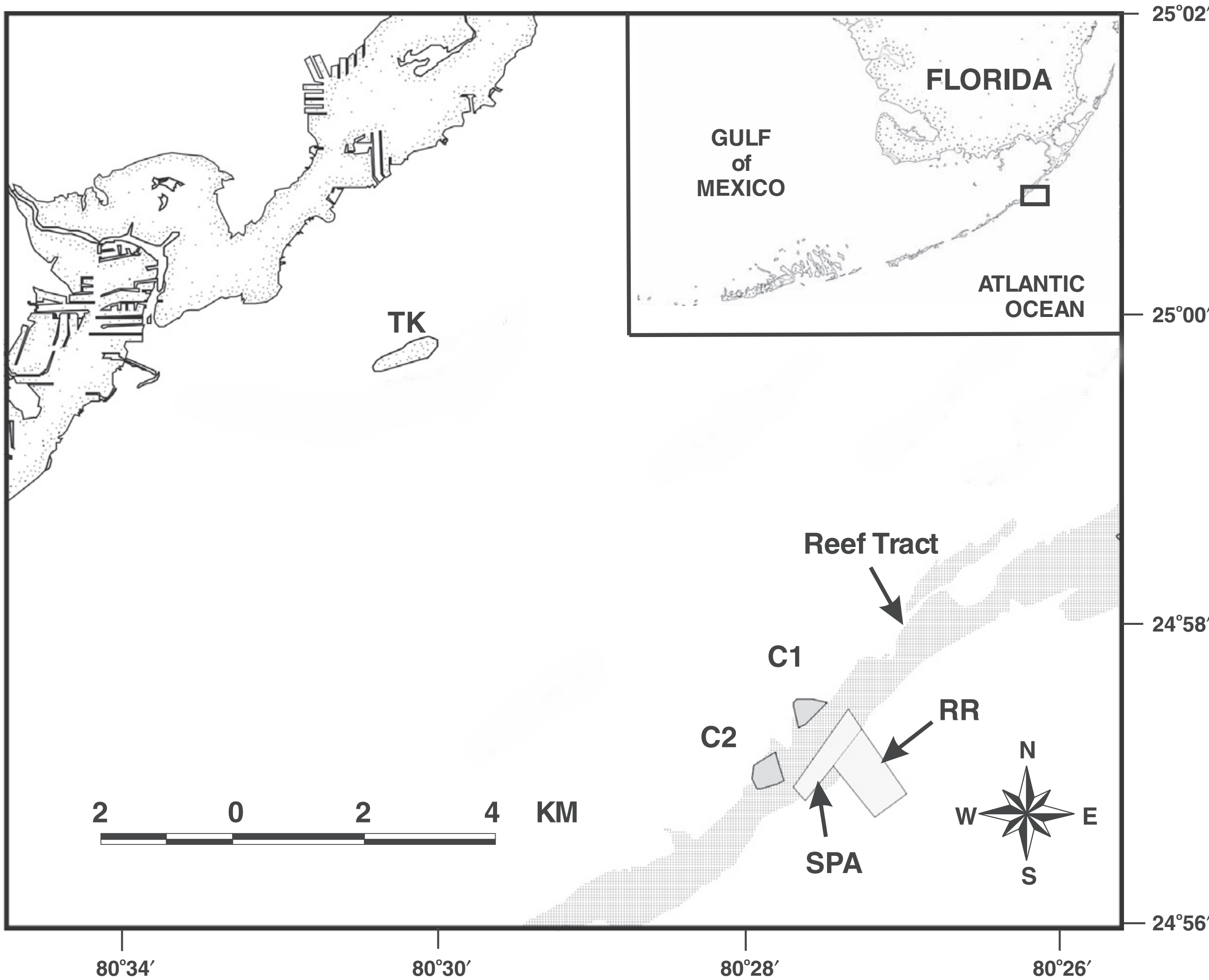

Figure 4

Sample sites for the queen conch (*Strombus gigas*) acoustic telemetry studies in the Florida Keys. All surveys were conducted at Conch Reef; C1 and C2 are subpopulations of queen conch. Two existing marine reserves are shown: a limited-use sanctuary preservation area (SPA) and a restricted-entry research reserve (RR). TK is Tavernier Key.

to conserve, 3) if expansion of the population were to occur in the future, what areas should be conserved relative to the preferred habitats, and 4) what is the simplest design for practical purposes (e.g., enforcement). Furthermore, we decided that this reserve should protect the entire population (i.e., both subpopulations).

The design we chose addressed each of these criteria. We selected a simple shape (i.e., a rectangle) that encompassed the following features: 1) the AgHRs of the two sub-aggregations, 2) the migration corridor between the two sub-aggregations, 3) habitats that were not avoided (except in the case of C2 where the rubble habitat represented the migration corridor), and 4) areas of adjacent habitats that were suitable (i.e., coarse sand, rubble/coarse sand, sparse seagrass/coarse sand, and rubble) but unoccupied and would allow for future expansion. For example, the majority of a deeper area of unoccupied course sand to the southeast of C1 was included in the MFR design (Fig. 5).

One other observation was considered when we designed our reserve. We observed two conch outside the boundaries of the AgHR at C2. We concluded that these animals represented "spillover," in a management context, from our proposed reserve design; therefore, an effective reserve would not need to encompass this location. The proposed reserve measures approximately 475 m x 1400 m and encompasses approximately 66.5 ha (Fig. 5).

Table 1

Habitat classification and utilization by queen conch tagged with acoustic transmitters at Conch Reef in the Florida Keys. The habitats were defined from high altitude photographs. Asterisks indicate habitats that were occupied by conch during the study. Those habitats that were preferred are indicated with a "P" and those that are avoided are indicated with an "A." N/A is not applicable; "—" indicates those habitats for which there was neither preference nor avoidance. Adapted from Glazer and Kidney (2004).

Code	Habitat	Preferred (P, subsite) or Avoided (A, subsite)	Spawning season—Preferred (P, subsite) or Avoided (A, subsite)
Rf	Reef—continuous barren carbonate substrate	N/A	N/A
Sd	Sand—particles pass through 2-mm sieve, but are retained on 0.5-mm sieve	N/A	N/A
Cs*	Coarse Sand—particles pass through 12-mm sieve, but are retained on 2-mm sieve	P,C2	P,C1
Rb*	Rubble—particles are retained on 12-mm sieve	A,C2	A,C2
RbCs*	Rubble/Coarse Sand—homogenous mix of Rb and Cs	P,C2	P,C2
SgsSd*	Mixed seagrass community (*Thalassia testudinum* and *Syringodium filiforme*), sparse with Sd substrate; seagrass blade density < 1200 • m^{-2} and canopy height < 15 cm	—	—
SgsCs	Mixed seagrass community (*T. testudinum* and *S. filiforme*), sparse with Cs substrate; seagrass blade density < 1200 • m^{-2} and canopy height < 15 cm	N/A	N/A
SgdSd*	Mixed seagrass community (*T. testudinum* and *S. filiforme*), dense with Sd substrate; seagrass blade density > 1200 • m^{-2} and canopy height > 15 cm	—	—
SgdCs*	Mixed seagrass community (*T. testudinum* and *S. filiforme*), dense with Cs substrate; seagrass blade density > 1200 • m^{-2} and canopy height > 15 cm	—	—

Discussion

Passive acoustic telemetry is a method commonly employed in a wide variety of aquatic studies (Zeller, 1998); as of 2003, there were over 320 articles referenced in the literature. In coral reef environments, it is becoming increasingly popular (Zeller, 1997; Eristhee et al., 2001; Beets et al., 2003). Perhaps one of the greatest strengths of this method is that it allows researchers to examine the habits of organisms under conditions that make other sampling strategies difficult. For example, occupied habitats may be examined during times when sampling is problematical (e.g., night: Meyer et al., 2000; Beets et al., 2003; Cartamil et al., 2003) and at sampling frequencies not practical using most other methods (Eristhee and Oxenford, 2001). Additionally, when hydrophones are deployed in situ, passive data collection becomes much simpler than on-site sampling (Lindholm and Auster, 2003) and provides a method to obtain large amounts of highly accurate data (Bolden, 2001). Furthermore, acoustic telemetry circumvents many of the problems associated with traditional mark-recapture technologies including sample size issues (Appeldoorn, 1997). For these reasons, acoustic telemetry has become a popular tool for conducting home range (Zeller, 1997; Eristhee and Oxenford, 2001; Parsons et al., 2003) and habitat preference (Lowe et al., 2003) studies.

In our case, the use of acoustic telemetry allowed us to increase our sample sizes by reducing the amount of labor needed to locate tagged individuals. Had we used traditional tag-recovery methods, it is likely that we would have had a significant reduction in recaptures. As a result, the home range estimations of each individual would likely have been much larger due to the increased variance associated with a reduction in sample size. Likewise, the habitat utilization estimations would probably have suffered from Type 2 errors from the increased variance associated with sample size reduction.

An additional benefit of passive acoustic telemetry is that it is fairly inexpensive. Nevertheless, there are trade-offs. In our studies, we used a single hydrophone deployed from a vessel. This required that at least one researcher was on the vessel for sampling. Using this approach, the up-front investment is fairly modest (approximately $1,500 U.S. for the receiver and hydrophone and $150 for each tag); however, a fairly significant investment in manpower and vessel use was required. On the other hand, labor can be reduced with a significantly greater investment in capital equipment, as in the case where the hydrophones are deployed in an array and the data are acquired passively (Bolden, 2001).

Despite the benefits attributed to acoustic telemetry for the examination of animal movements, the literature is devoid of papers that provide guidance for designing

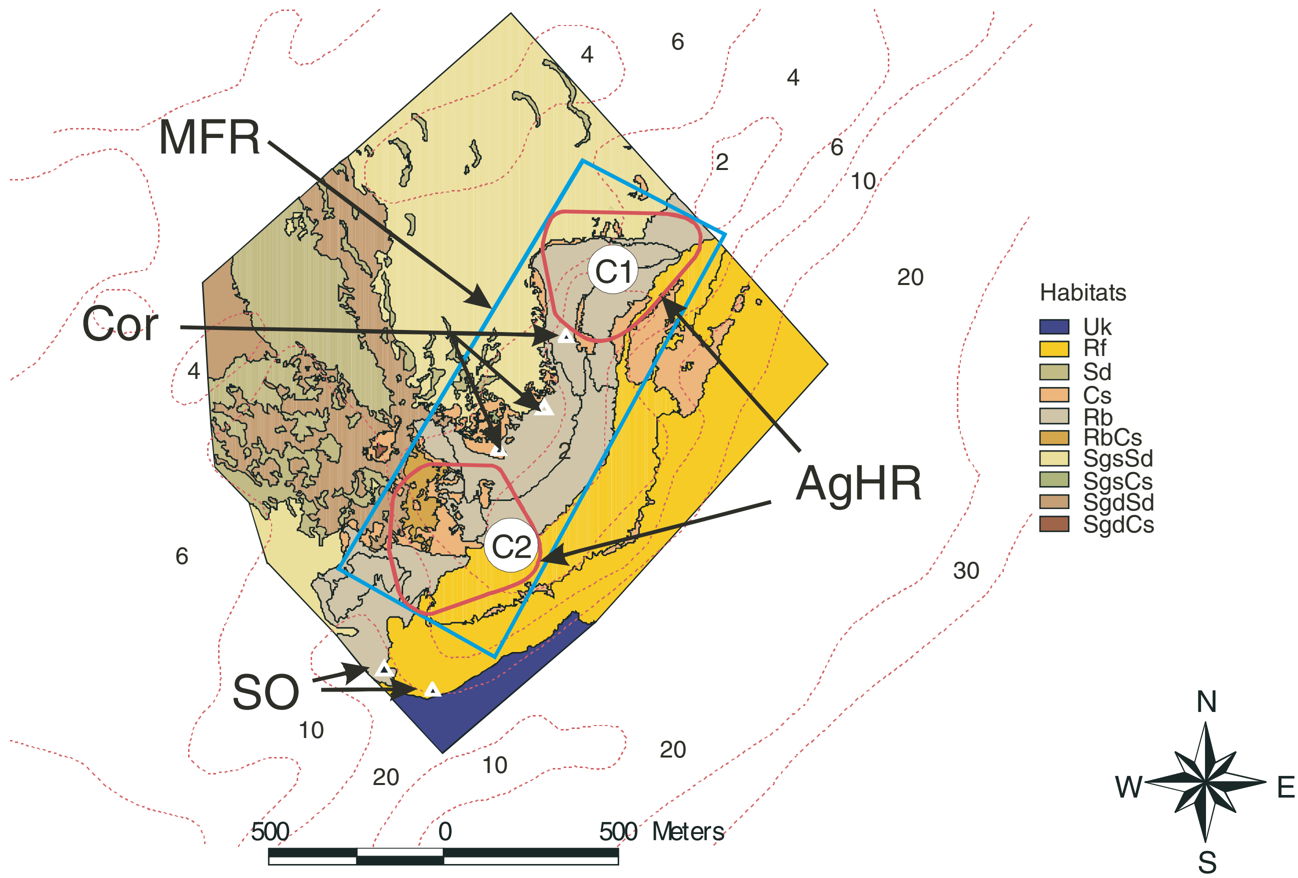

Figure 5

Habitat map derived from high-altitude photogrammetry. The proposed fishery reserve is indicated by MFR. The white triangles represent observations of queen conch (*Strombus gigas*) that are occupying a corridor (Cor) between C1 and C2 or "spillover" conch (SO) that have emigrated from the area defining the proposed reserve. The perimeters of the AgHRs of each sub-population are shown in red. Preferred, utilized, and avoided habitats are described in Table 1. Bathymetric contours (m) are shown for reference.

a reserve using data acquired from this method. In fact, we were only able to locate one paper that used empirical data of the movement of a population to design a reserve (Griffiths and Wilke, 2002) and, even in that study, movements were determined using traditional mark-recapture surveys. They described a method for estimating the minimum reserve size for temperate reef fishes in South Africa based on the radius of movements observed for a population of Sparids. They attached that radius to locations progressively further from the core of the population. In this way, they could predict the proportion of the population that would be protected and concluded that a minimum of three radii and a maximum of five radii would be sufficient to conserve the population.

In contrast to their method, we present a model based not on linear movements, but on the area occupied by individuals with probabilities assigned to that estimation. The use of spatially-explicit, probabilistic home-range models adds a level of security to the determination of what constitutes the area likely to be occupied by an existing or expanding population, especially given that a reserve may not function effectively if the size of the home range is underestimated (Stoner, 1997; Kramer and Chapman, 1999). Our approach has an added advantage in that it includes behavioral and ecological data in the design criteria. For example, by incorporating habitat utilization into the equation, one can make an informed estimation of what areas are likely to be colonized by an expanding population during their foraging and reproductive activities. This approach requires both an objective evaluation of the data and a subjective interpretation of the results.

In our study, we used a species that, in general, exhibits a high degree of site fidelity. However, not all marine animals exhibit this characteristic (i.e., they may be nomadic or highly migratory) and thus may lack fixed home ranges (Colton and Alevizon, 1983; White and Garrott, 1990). Our method may have limited applicability in these cases, especially as it relates to the incorporation of home range into the design of an MFR.

Additionally, queen conch move little and there is a relatively high probability of recapturing tagged individuals relative to more mobile species. For highly mobile species, recapture sitings may be limited due to emigration from the study site. However, probabilistic home range models account for this limitation in the estimation of the home ranges by assigning larger home ranges to individuals with fewer recaptures.

Acoustic telemetry studies may also provide other essential information for effective MFR design. Acosta (2002) studied carrying capacity within reserves in Belize using queen conch and spiny lobsters (*Panuluris argus*) tagged with acoustic transmitters. He predicted the maximum density for spiny lobsters and queen conch for a refuge in Belize by employing a recruitment/diffusion model and, at the end of his study, confirmed that densities of individuals had increased. Because an oft-cited benefit of reserve implementation is the predicted increase in the biomass of the targeted species as a reserve matures (Lubchenko et al., 2003), estimating carrying capacity may provide guidance on expected reproductive output from that reserve as well as functional changes within the ecosystem.

As population densities increase, other changes may occur. Habitat quality, a well-recognized variable that must be addressed for effective marine reserve design (Rowley, 1994; Appeldoorn, 1997; Acosta, 1999; Fogarty, 1999), may be affected. As expansion of the population occurs, less desirable habitats may become occupied in greater frequencies due to depensatory mechanisms (Fretwell and Lucas, 1970). We observed that an unoccupied habitat adjacent to an existing spawning aggregation at Looe Key in the Florida Keys was soon colonized after adult conch were transplanted into the existing aggregation. Additionally, this habitat was positively affected before long as spawning soon began to occur there (Glazer, personal observ.). For these reasons, what are seemingly poor habitats adjacent to an existing population should be carefully considered for inclusion in a reserve before being discounted.

Acoustic telemetry often provides an efficient mechanism to study the complexities associated with examining the movements of individuals and populations in fragmented landscapes (Beets et al., 2003). Because examining these movements is necessary for the conservation of critical habitats (Berggren et al., 2002), these data have now begun to be incorporated into designs of marine reserves (Christensen et al., 2003). However, the holistic approach that uses empirical observation to combine these features with areas occupied by populations is absent from the literature. The conservative approach is to include all habitats connecting distinct patches. This, of course, oversimplifies the question and may result in overprotection if isolated populations are not connected via corridors and are functioning as isolated metapopulations (Dethier et al., 2003). This may then have adverse economic, social, or enforcement consequences. For these reasons, it is essential to determine landscape features that must be conserved even though they are used infrequently. In our proposed reserve, we justified the inclusion of the rubble ridge between C1 and C2 because this feature served an important function as a migration corridor and, if not conserved, the two subpopulations may become isolated. It is unlikely that this area would have been identified as a critical feature without the use of acoustic telemetry given the rapid transit over the rubble ridge by the tagged individuals and the infrequent observations of untagged conch in the area.

When using our criteria to design an MFR, decisions must be founded on information obtained from appropriate temporal scales (Starr et al., 2002). Ontogeny and reproduction may require drastically different resources, and it is critical to design studies or use data that capture habitat requirements during different life stages. Shifts in habitat use during reproduction must be examined (Kramer and Chapman, 1999; Glazer et al., 2003). Because many fish species congregate to spawn, fishermen often target spawning aggregations. If a goal of the reserve is to enhance reproductive output, these aggregations should be identified and their conservation should be considered a high priority (Claro and Lindeman, 2003).

Despite the fairly straightforward approach we described, a good deal of subjectivity will ultimately be required when considering the dimensions of an effective MFR. In our example, we included areas outside of the existing AgHRs in our proposed MFR design to allow for future expansion of the population. We placed added emphasis on including course sand and rubble/coarse sand habitats because conch preferred them during both the reproductive and non-reproductive seasons. Areas of these habitats that were in close proximity to the subpopulations and to the corridor connecting them were included in our design to support increased reproduction in an expanding population. We also included a substantial amount of sparse seagrass/sand habitat that was not currently occupied, despite the fact that there was no preference or avoidance of that habitat (Glazer and Kidney, 2004), because we felt that these were areas that could be rapidly colonized.

It is critical that managers predefine the goals of a prospective MFR. Our approach may be perfectly suitable for enhancing biomass in the reserve and in adjacent fisheries via spillover, if the MFR is well designed. However, guaranteeing that the population is protected and that areas are available for future expansion are not enough to ensure that the reserve functions to meet all the predefined goals. For example, one goal of an MFR may be to provide propagules for dispersal to targeted locations. Therefore, consideration of oceanographic features is critical to ensure proper MFR function (Chiappone and Sullivan Sealey, 2000; Crowder et al., 2000), and the design criteria defined in this study may do little to ensure that this goal is achieved.

Managers must also evaluate the biological, logistical, and/or human resource constraints that may limit the scope of MFR design studies. For example, if the population in the targeted area is too small for telemetry studies, the project may need to be conducted in a different location with similar features. In these instances, home range and habitat utilization information may have to be obtained from the literature, and the researchers and/or managers should recognize that critical site-specific habitat features (e.g., corridors) would not be identified. In other cases, fiscal realities may limit the capacity to effectively evaluate MFR design parameters. In addition to scientific considerations, social, political, and economic factors must be evaluated when designing reserves. Thus, the spatially defined boundaries determined from home range and habitat preference studies are only a few of a suite of variables that must be considered to ensure that an MFR is appropriately designed.

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Literature cited

Acosta, C. A.
1999. Benthic dispersal of Caribbean spiny lobsters among insular habitats: implications for the conservation of exploited marine species. Conserv. Biol. 13:603–612.

2002. Spatially explicit dispersal dynamics and equilibrium population sizes in marine harvest refuges. ICES J. Mar. Sci. 59:458–468.

Allison, G. W., J. Lubchenko, and M. Carr.
1998. Marine reserves are necessary but not sufficient for conservation. Ecol. Appl. 8:79–92.

Appeldoorn, R. S.
1997. Dispersal rates of commercially important coral reef-fishes: what do tagging studies tell us about potential emigration from marine reserves? Proc. Gulf Caribb. Fish Inst. 49:54–63.

Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis.
1999. Changes in community structure in temperate marine reserves. Mar. Ecol. Prog. Ser. 189:125–134.

Beets, J., L. Muehlstein, K. Haught, and H. Schmitges.
2003. Habitat connectivity in coastal environments: patterns and movements of Caribbean coral reef fishes with emphasis on bluestripe grunt, *Heamulon sciurus*. *In* Caribbean marine protected areas: practical approaches to achieve economic and conservation goals (R. S. Appeldoorn, ed.), p. 29–42. Gulf Caribb. Res. 14(2).

Berggren, Å, B. Birath, and O. Kindvall.
2002. Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles of Roesel's bush-cricket (*Metrioptera roeseli*). Conserv. Biol. 16:1562–1569.

Bertelsen, R. D., and T. Matthews.
2001. Fecundity dynamics of female spiny lobster (*Panulirus argus*) in a south Florida fishery and Dry Tortugas National Park lobster sanctuary. Mar. Freshwater Res. 52:1559–1565.

Bohnsack, J. A.
1994. How marine fishery reserves can improve reef fisheries. Proc. Gulf Caribb. Fish. Inst. 43:217–241.
1998. Application of marine reserves to reef fisheries management. Aust. J. Ecol. 23:298–304.

Bolden, S. K.
2001. Nassau grouper (*Epinephalus striatus*, Pisces: Serranidae) movement in the Bahamas, as determined by ultrasonic telemetry. Ph.D. dissert., University of Miami, 172 p.

Boersma, P. D., and J. K. Parrish.
1999. Limiting abuse: marine protected areas, a limited solution. Ecol. Econ. 31:287–304.

Botsford, L. W., F. Micheli, and A. Hastings.
2003. Principles for the design of marine reserves. Ecol. Appl.13: S25–S31.

Cartamil, D. P., J. J. Vaudo, C. G. Lowe, B. M. Wetherbee, and K.N. Holland.
2003. Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for ecological interactions between sympatric elasmobranch species. Mar. Biol. 142:841–847.

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. Bull. Mar. Sci. 66:691–705.

Christensen, J. D., C. F. G. Jeffrey, C. Caldow, M. E. Monaco, M. S. Kendall, and R. S. Appeldoorn.
2003. Cross-shelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. *In* Caribbean marine protected areas: practical approaches to achieve economic and conservation goals (R. S. Appeldoorn, ed.), p. 9–27. Gulf Caribb. Res. 14(2).

Claro, R., and K. C. Lindeman.
2003. Spawning aggregation sites of snapper and grouper species (Lutjandae and Serranidae) on the insular shelf of Cuba. *In* Caribbean marine protected areas: practical approaches to achieve economic and conservation goals (R. S. Appeldoorn, ed.), p. 91–106. Gulf Caribb. Res. 14(2).

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

Côté, I. M., I. Mosqueira, and J. D. Reynolds.
2001. Effects of marine reserve characteristics on the protection of fish populations: a meta analysis. J. Fish Biol. 59:178–189.

Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy.
2000. Source-sink population dynamics and the problem of siting marine reserves. Bull. Mar. Sci. 66:799–820.

Dethier, M. N., K. McDonald, and R. R. Strathmann.
2003. Colonization and connectivity of habitat patches for coastal marine species distant from source populations. Conserv. Biol. 17:1024–1035.

Dugan, J. E., and G. E. Davis.
1993. Applications of marine refugia to coastal fisheries management. Can. J. Fish. Aquat. Sci. 50:2029–2042.

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

Eristhee, N., I. Popple, H. Oxenford, and W. Hunte.
2001. Methods and lessons learnt in the application of acoustic telemetry to coral reef fish movement studies. Proc. Gulf Caribb. Fish. Inst. 52:145–159.

Fogarty, M. J.
1999. Essential habitat, marine reserves and fishery management. Trends Ecol. Evol. 14:133–134.

Fretwell, S., and H. Lucas.
1970. On the territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Glazer, R. A., and J. A. Kidney.
2004. Habitat associations of adult queen conch in an unfished Florida Keys back-reef: applications to essential fish habitat. Bull. Mar. Sci. 75:205–224.

Glazer, R. A., G. A. Delgado, and J. A. Kidney.
2003. Estimating queen conch (*Strombus gigas*) home ranges using acoustic telemetry: implications for the design of marine fishery reserves. *In* Caribbean marine protected areas: practical approaches to achieve economic and conservation goals (R. S. Appeldoorn, ed.), p. 79–89. Gulf Caribb. Res. 14(2).

Griffiths, M. H., and C. G. Wilke.
2002. Long-term movement patterns of five temperate-reef fishes (Pisces: Sparidae): implications for marine reserves. Mar. Freshwater Res. 53:233–244.

Hooge, P. N., W. M. Eichenlaub, and E. K. Solomon.
2001. Using GIS to analyze animal movements in the marine environment. *In* Spatial processes and management of marine populations (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.), p. 37–51. University of Alaska Sea Grant, AK-SG-01-02, Fairbanks, Alaska.

Kramer, D. L., and M. R. Chapman.
1999. Implications of fish home range size and relocation for marine reserve function. Environ Biol. Fishes 55:65–79.

Lembo, G. I. A. Fleming, F. Økland, P. Carbonara, and M. T. Spedicato.
1999. Site fidelity of the dusky grouper *Epinephelus marginatus* (Lowe, 1834) studied by acoustic telemetry. Mar. Life 9:37–43.

Lindholm, J., and P. Auster.
2003. Site utilization by Atlantic cod (*Gadus morhua*) in offshore gravel habitat as determined by acoustic telemetry: implications for the design of marine protected areas. Mar. Sci. Tech. J. 37:27–34.

Lowe, C. G., D. T. Topping, D. P. Cartamil, and Y. P. Papastamatiou.
2003. Movement patterns, home range, and habitat utilization of adult kelp bass *Paralabrax clathratus* in a temperate no-take reserve. Mar. Ecol. Prog. Ser. 256:205–216.

Lubchenko, J., S. R. Palumbi, S. D. Gaines, and S. Andelman.
2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecol. Appl. 13:S3–S7.

Martell, S. J. D., C. J. Walters, and S. S. Wallace.
2000. The use of marine protected areas for conservation of lingcod (*Ophiodon elongatus*). Bull. Mar. Sci. 66:729–743.

Meyer, C. G., K. N. Holland, B. M. Wetherbee, and C. G. Love.
2000. Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. Environ. Biol. 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. Lubchenko, 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.

Neu, C. W., C. R. Byers, J. M. Peek, and V. Boy.
1974. A technique for analysis of utilization availability data. J. Wildl. Manage. 38:541–545.

Parsons, D. M., R. C. Babcock, R. K. S. Hankin, T. J. Willis, J. P. Aitken, R. K. O'Dor, and G. D. Jackson.
2003. Snapper *Pagrus auratus* (Sparidae) home range dynamics: acoustic tagging studies in a marine reserve. Mar. Ecol. Prog. Ser. 262:253–265.

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

Recksiek, C. W., and R. A. Appeldoorn.
1998. In pursuit of design criteria for marine fishery reserves. Proc. Gulf and Caribb. Fish Inst. 50:372–384.

Recksiek, C. W., B. R. Murphey, R. S. Appeldoorn, and K. C. Lindeman.
2001. Integrating fish fauna and habitat assessments: a fundamental step in fishery reserve design criteria. Proc. Gulf and Caribb. Fish Inst. 52:654–666.

Roberts, C. M., J. A. Bonsack, F. Gell, J. P. Hawkins, and R. Goodridge.
2001. Effects of marine reserves on adjacent fisheries. Science 294:1920–1923.

Rodwell, L. D., E. B. Barbier, C. M. Roberts, and T. R. McClanahan.
2003. The importance of habitat quality for marine reserve—fishery linkages. Can. J. Fish. Aquat. Sci. 60:171–181.

Rowley, R. J.
1994. Marine reserves in fisheries management. Aquatic Conserv.: Mar. Freshw. Ecosyst. 4:233–254.

Simpson, R. R., and A. J. Mapleston.
2002. Movements and habitat use of the endangered Australian freshwater Mary River cod, *Maccullochella peelii mariensis*. Environ. Biol. Fishes 65:401–410.

Starr, R. M., J. N. Heine, J. M. Felton, and G. M. Cailliet.
2002. Movement of the bocaccio (*Sebastes paucispinis*) and greenspotted rockfishes in a Montery submarine canyon: implications for the design of marine reserves. Fish. Bull. 100:324–337.

Stoner, A.W.
1997. The status of queen conch, *Strombus gigas*, research in the Caribbean. Mar. Fish. Rev. 59:14–22.

Stoner, A.W., and M. Ray-Culp.
2000. Evidence for Allee effects in an over-harvested marine gastropod: density-dependent mating and egg production. Mar. Ecol. Prog. Ser. 202:297–302.

Warner, R. R., and R. K. Cowen.
2002. Local retention of production in marine populations: evidence, mechanisms, and consequences. Bull. Mar. Sci. 70:245–249.

White, G. C., and R. A. Garrott.
1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, 383 p.

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

Zeller, D. C.
1997. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). Mar. Ecol. Prog. Ser. 154:65–77.
1998. Ultrasonic telemetry: its application for coral reef fisheries research. Fish. Bull. 97:1058–1065.

Zeller, D., S. L. Stoute, and G. R. Russ.
2003. Movements of reef fishes across marine reserve boundaries: effects of manipulating a density gradient. Mar. Ecol. Prog. Ser. 254:269–280.