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MARINE RESERVE DESIGN CRITERIA AND MEASURES OF SUCCESS: LESSONS LEARNED FROM THE EXUMA CAYS LAND AND SEA PARK, BAHAMAS

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ABSTRACT

Among the many potential benefits of no-take marine reserves, three important postulated effects are (1) to supply biomass of harvestable individuals to fished areas through emigration; (2) to increase spawning-stock biomass, which subsequently magnifies larval recruitment; and (3) to restore more natural size-frequency distributions of the protected populations, specifically to enhance the larger size classes, which may affect sex ratios and reproductive output. The Exuma Cays Land and Sea Park (ECLSP), covering 442 km^2 in the central Bahamas, was established in 1958 and closed to fishing in 1986, making it one of the first and largest marine reserves or 'no-take' zones in the western Atlantic. The ECLSP is ideally situated between small-scale developments in the northern and southern Exuma Cays and encompasses a diversity of contiguous shallow-water habitats from the Great Bahama Bank to the eastern platform margin in Exuma Sound. Scientific investigations during the past decade have compared queen conch, spiny lobster, and grouper resources in the ECLSP to those in adjacent fished areas and have demonstrated greater species diversity, density, biomass, potential reproductive output, and larval densities for these species. The lack of historical data limits determination of whether closure to fishing has resulted in increases in these attributes over time, but available data strongly support the contention that the ECLSP has significantly greater spawning-stock biomass of various organisms because of protection from fishing. Although evidence is strong that the ECLSP is an important source of larvae to adjacent areas in the Exuma Sound ecosystem, few data show adult emigration to fished areas. Some target species outside the reserve may have declined, and because the ECLSP probably depends on larval transport from upcurrent areas, awareness is growing that this reserve will not be successful in isolation. Experiences in the ECLSP suggest that marine reserves will be most successful if they contain contiguous habitats from bank to deeper shelf (>30 m) environments, minimize threats such as coastal development, and provide protection of unique features such as spawning aggregations.

Global awareness has grown that marine fisheries are in decline and have been greatly mismanaged in all parts of the world. This pattern largely reflects a burgeoning human population with inherent needs for food and income and the increased economic value of fisheries products (Jennings and Polunin, 1996). In tropical coastal ecosystems, fisheries differ from most other natural resources (Christy, 1997). First, they exploit an extremely heterogeneous range of species and therefore provide an exceptionally wide range of products. Second, complex biological and physical processes, many of which remain poorly studied, control the natural limits to the supply of fishery organisms. Third, the resources are very mobile, because of the complex life cycles of most marine fishes and invertebrates. Determining potential yields is difficult because of the paucity of data for many species, complex biological interactions, and logistical constraints like limited enforcement capacity. Finally, property rights are usually poorly defined, resulting in open access, too much fishing effort, and often overcapitalization (Roberts and Polunin, 1991; Waters, 1991).

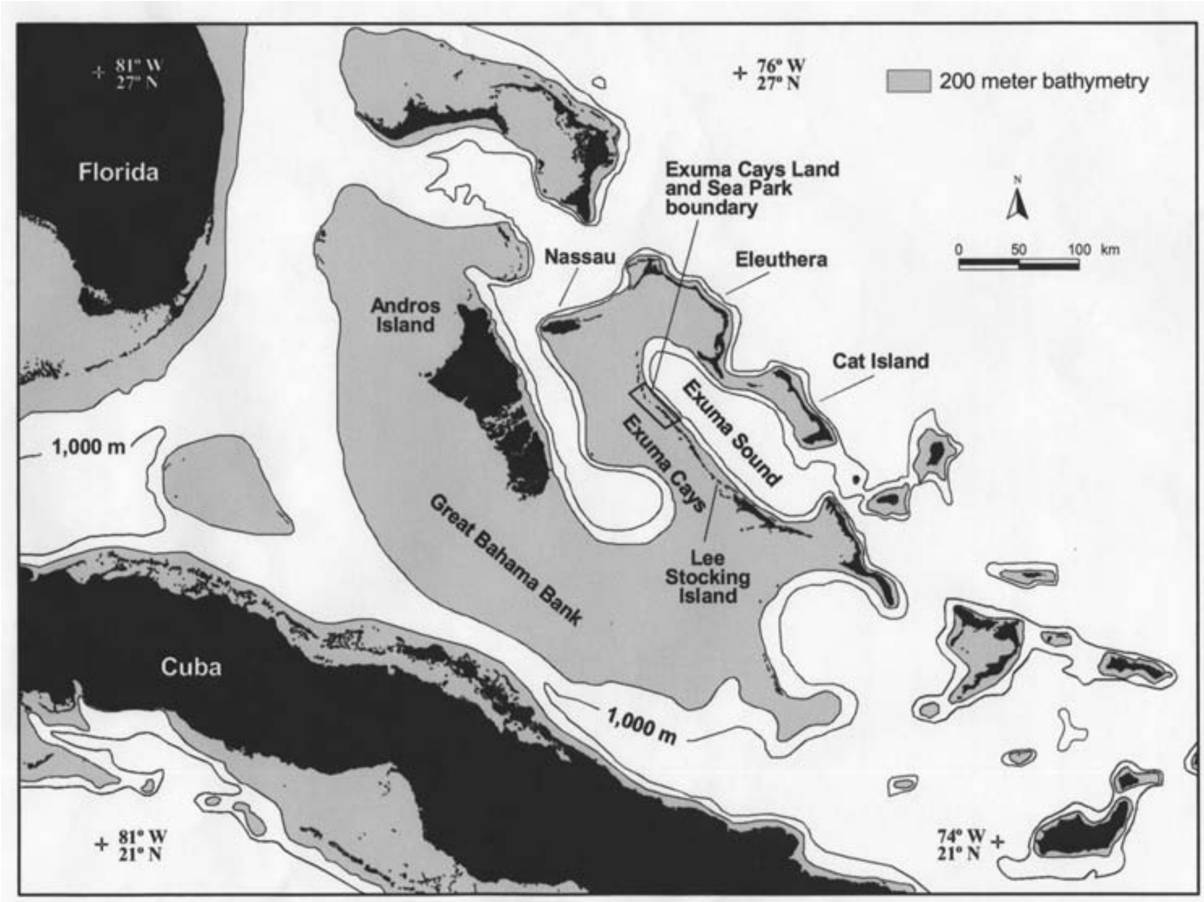

Figure 1. Location of the Exuma Cays Land and Sea Park, a marine reserve closed to fishing since 1986, in the central Bahamas.

One proposed management option is the establishment of no-take marine reserves, sometimes called marine fishery reserves or harvest refugia (Plan Development Team, 1990). Several reviews of the benefits and design of marine reserves are available (Roberts and Polunin, 1991; Dugan and Davis, 1993; Rowley, 1994). Here, we discuss the goals and successes of the Exuma Cays Land and Sea Park (ECLSP), a large marine reserve in the central Bahamas closed to all forms of fishing since 1986, by synthesizing previous scientific investigations of important fishery species and discussing the lessons learned and implications for marine reserve design. The configuration of the park and its dramatic differences in fishery resources from fished areas can help managers define goals and evaluate the relative impact of closure to fishing. Previously published results for groupers (Sluka et al., 1996a,b, 1997) and queen conch (Stoner and Ray, 1996) are summarized to illustrate differences between the ECLSP and fished areas in species composition, abundance, and size distribution. The criteria for designing single reserves and reserve networks are discussed and illustrate the importance of protecting contiguous habitats used by different life stages, protecting spawning-stock biomass to facilitate larval transport, and linking marine reserves by physical transport processes.

Study Area

The Exuma Cays comprise about 40 main islands and many smaller islets and rocks extending 200 km along the eastern edge of the Great Bahama Bank (Fig. 1). They are bordered by Exuma Sound to the east, a semienclosed deep basin (>1000 m) 250 km long and 50–90 km wide, and by the Great Bahama Bank (mean depth of 3 m) to the west (Fig. 2). Near-surface flow in Exuma Sound can be characterized as primarily wind-driven (Stoner et al., 1994), but mesoscale eddy fields are superimposed on the northwestward drift (Colin, 1995) and dominant large-scale gyres extend to depths of 200 m (Lipcius et al., 1997). Except near tidal inlets, tidal oscillations are a minor perturbation to the wind-driven circulation. The platform shelf along the islands bordering Exuma Sound is narrow (generally <2 km wide), and water exchange between the sound and the Great Bahama Bank occurs through numerous tidal inlets (ranging from <100 m to >2 km wide) between the islands.

The Exuma Cays Land and Sea Park (ECLSP) was established by the government of the Bahamas in 1958, under the National Trust Act, to preserve the natural heritage of the Bahamas (Fig. 2). The following year, the Bahamas National Trust, a nongovernmental organization, was created by an Act of Parliament and charged with the administrative responsibility for the national park system. The ECLSP encompasses a 35-km–long section of the northern Exuma Cays and covers 442 km^2 (Fig. 2). Although most islands are owned by the Bahamas government or the trust, some are privately owned or leased. Initially, limited fishing was allowed in the park, but by the 1980s, fishing pressure in the park had apparently increased, and the trust changed the park bylaws in 1986 to close the entire area to all forms of fishing. A park warden has been on site since 1989. Presently one warden is assisted by a volunteer support fleet and the Bahamian Defense Force. The ECLSP is subjected to some level of poaching, as reflected, for example, in the decrease in abundance and biomass of Nassau grouper with increasing distance from the ranger station (Warderick Wells, west of site W1 in Fig. 2; Sluka et al., 1996b, 1997).

Review of Research on Important Fishery Species

Grouper Assemblages.—Groupers of the family Serranidae are important top-level predators in coral reef ecosystems worldwide. Many grouper species exhibit slow growth to a large size, late age of first reproduction, and sex reversal (protogynous hermaphroditism); in addition, some species aggregate to spawn (Manooch, 1987; Shapiro, 1987; Sadovy and Colin, 1995). Conventional management of grouper fisheries (catch or effort) has largely failed to prevent stock declines, probably because of both lack of biological knowledge and socioeconomic factors such as enforcement capacity (Sadovy, 1994). Protection of groupers in no-take marine reserves may reverse the effects of fishing, for example changing species composition and increasing densities and sizes of target species (Russ, 1985; Roberts and Polunin, 1991).

Artisanal and commercial fishing for groupers in the Bahamas is primarily aimed at Nassau grouper (*Epinephelus striatus*); this species is the third most important commercial fishery (behind spiny lobster and queen conch) and the most important finfish species in the Bahamas. Most landings are fish caught in spawning aggregations during December–February at several locations such as Andros, Cat Island, and Long Island (Sadovy, in press). Although only 2% of the roughly 362 mt of annual catch (worth over $1.7 million) originates from the Exuma Cays, this figure does not include individuals caught for local consumption (V. Deleveaux, Bahamas Department of Fisheries, pers. comm.). In the Exuma Cays, spear guns, traps, and hook and line are used to fish for grouper.

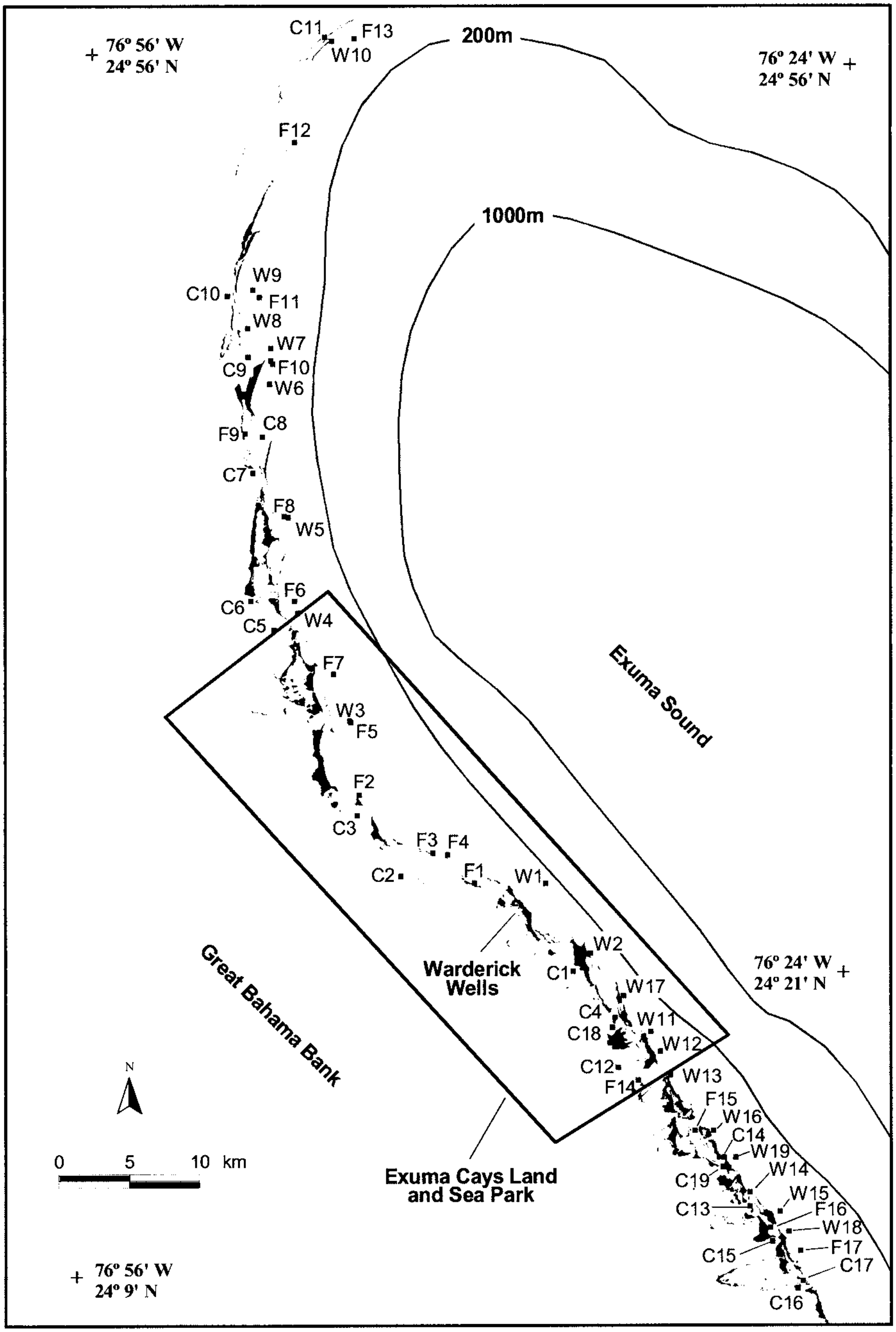

Figure 2. Reef and hard-bottom sites surveyed for benthic community structure and grouper density and size within and outside the Exuma Cays Land and Sea Park, a no-take marine reserve, during 1995 (see Sluka et al., 1996b). Hard-bottom types: C = channel reef, W = windward hard bottom, and F = fringing reef.

Sluka et al. (1996a,b, 1997) conducted visual transect surveys (20 m × 5 m; total transects = 550) at 55 sites along 90 km of the Exuma Cays during 1995 to quantify differences in grouper species composition, density, and biomass among three types of hard-bottom habitat inside and outside of the ECLSP: channel reefs (2–11 m depth), fringing reefs (1–20 m), and windward hard bottom (4–12 m) (Fig. 2). These habitat types constitute the majority of shallow-water (<30 m) hard-bottom area in the Exuma Cays and represent variations in benthic community structure (e.g., coral coverage), environmental setting (e.g., current regime), and topographic complexity (Sluka et al., 1996b).

Sluka et al. (1996b) identified eight species of groupers in the Exuma Cays (Fig. 3) and found that the frequency distributions (G-test, $\chi^2_{0.05,18} = 28.9$, $P < 0.001$) and densities (number of individuals 100 m^{-2}) of species inside the ECLSP differed significantly from those outside. Nontarget, smaller grouper species such as graysby (*Epinephelus cruentatus*), coney (*E. fulvus*), and red hind (*E. guttatus*) comprised 80% of the groupers observed (n = 318) north of the ECLSP and 88% of those (n = 268) observed south of it (Fig. 3, top). Nassau grouper represented a greater percentage of the individuals recorded within the ECLSP (23.5%) than north (13.5%) or south (9.0%) of it. Nontarget species were significantly less abundant within the ECLSP than outside it. For example, graysby were most abundant north of the ECLSP ($P < 0.05$; F-test), whereas coney were most abundant south of the park ($P < 0.001$; F-test; Fig. 3, bottom). The mean density of Nassau grouper was nearly twice as high within the ECLSP as in adjacent fished areas ($P < 0.01$; F-test; Fig. 4, top), but habitat types did not differ significantly ($P > 0.05$; F-test).

Mean biomass (g 100 m^{-2}) of graysby, coney, red hind, Nassau grouper, and tiger grouper inside the ECLSP all differed significantly ($P < 0.05$; F-test) from those outside (Sluka et al., 1996b). Graysby biomass was greater north of the ECLSP, whereas coney biomass was greater south of the reserve. Mean Nassau grouper biomass was three times greater within the ECLSP ($P < 0.001$; F-test), whereas mean biomass north and south of the reserve differed little (Fig. 4, middle). Mean Nassau grouper biomass did not differ statistically among the hard-bottom habitat types ($P > 0.05$; F-test). Estimates of Nassau grouper fecundity showed that the number of eggs potentially produced within the ECLSP (8.61×10^6 eggs ha^{-1}) was 6–6.4 times greater than those produced north (1.43×10^6) and south (1.35×10^6) of the reserve (Sluka et al., 1997). This result is not surprising given the significant differences in Nassau grouper size distributions between the ECLSP and fished areas (G-test, $\chi^2_{0.05,7} = 14.1$, $P < 0.05$; Fig. 4, bottom). Thirty-five percent of the individuals inside the park were larger than 50 cm TL and thus likely to be sexually mature (Sadovy and Colin, 1995), whereas 8% of the groupers observed south of the ECLSP and 14% of those observed south of it were estimated to be sexually mature.

CONCH.—Queen conch (*Strombus gigas*) is the second most important fishery in the Bahamas and has supported local fisheries dating back to the Lucayan Indians (Stoner, 1997a). Queen conch stocks have been depleted in some areas of the Bahamas, especially near New Providence and Grand Bahama Island. The largest known conch fisheries near the ECLSP are in northern Exuma Sound, in relatively shallow waters both on the Great Bahama Bank and on the narrow shelf bordering Exuma Sound (Stoner, 1997a). Fishing for queen conch in the Exuma Cays is restricted primarily to free diving, but there is some use of hookah (compressor) systems. A conch may be taken only if it has a well-formed lip (i.e., is at least 3.5–4 yrs old).

LARVAL ABUNDANCE AND DISTRIBUTION.—Stoner and O'Connell (1994) and Stoner and Ray (1996) sampled for larval queen conch veligers at 13 stations from off Warderick

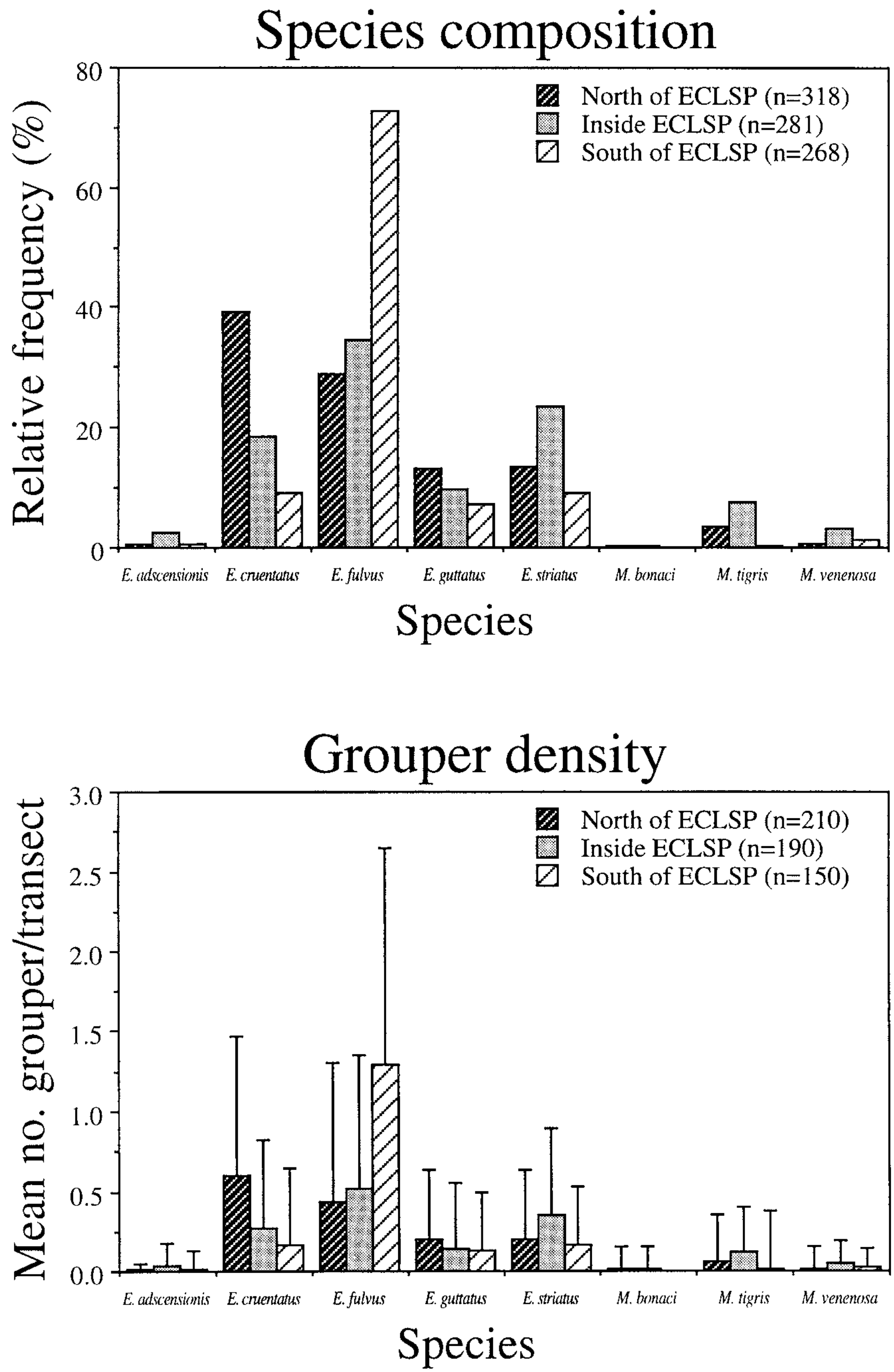

Figure 3. Relative frequency distribution (top, n = numbers of groupers surveyed) and mean density (number of ind 100 m^{-2}) of grouper species (bottom, n = number of 20-m × 5-m transects) north of, within, and south of the Exuma Cays Land and Sea Park, a no-take marine reserve. Error bars represent one standard deviation. Data from Sluka et al. (1996b).

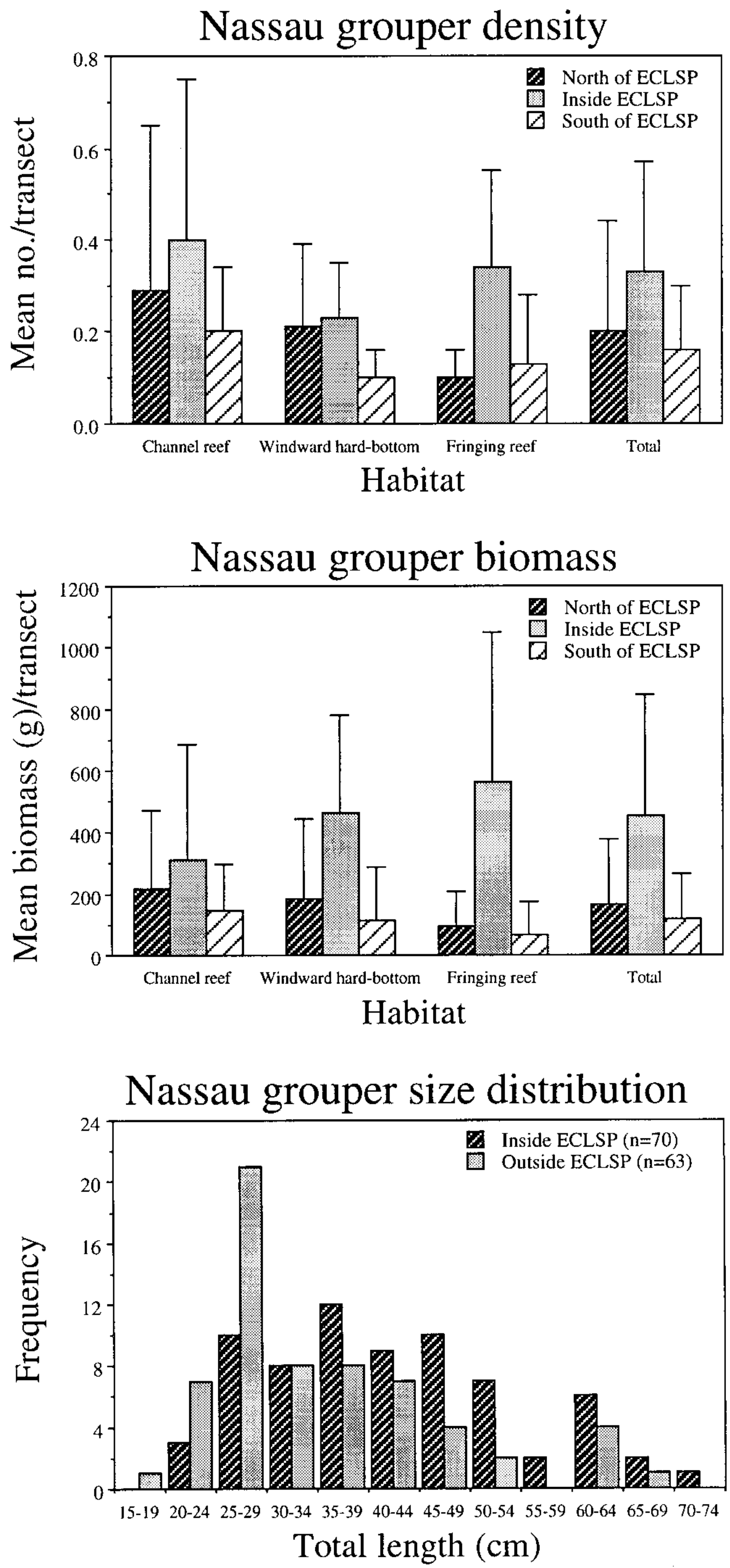

Figure 4. Mean density (number of ind 100 m^{-2}; top), biomass (g 100 m^{-2}; middle), and size-frequency distribution (n = number of individuals sampled; bottom) of Nassau grouper (*Epinephelus striatus*) in hard-bottom habitats within and outside the Exuma Cays Land and Sea Park, a no-take marine reserve. Error bars represent 1 SD. Data from Sluka et al. (1996b).

Wells (in the central ECLSP near the ranger station) to off western Eleuthera Island and from Lee Stocking Island to Cat Island from inshore (4–5 m depth) to the shelf edge (25 m) during 1993–1994 (Stoner and O'Connell, 1994; Stoner and Ray, 1996). Veliger densities recorded varied over time, but the two stations in the ECLSP had consistently higher densities than those in fished areas. Mean larval densities were greatest (173.5–197.9 larvae m^{-3}) in the ECLSP and decreased (30.2–45.7 larvae m^{-3}) across the Exuma Sound approaching western Eleuthera Island. Larval concentrations were much lower (8.03–13.5 larvae m^{-3}) off Lee Stocking Island, a fished area, and decreased further along a transect eastward across Exuma Sound to Cat Island. Most of the veligers in the ECLSP were either <0.5 mm, that is, recently hatched from benthic eggs, or >1.0 mm, most of which were probably competent to metamorphose. Comparatively few late-stage larvae were found in the southern Exuma Sound near Lee Stocking Island, indicating larval advection from south to north and/or low larval production and retention in the southern Exuma Cays.

Densities of queen conch veligers in the ECLSP were apparently the highest ever recorded in the wider Caribbean (Stoner and Ray, 1996). This pattern may explain the very large populations of conch in the ECLSP and the very small populations near Cat Island, potentially reflecting a direct relationship between larval supply to nursery habitats (a function of the number of females copulating and laying eggs) and the population size of juvenile queen conch (Stoner et al., 1992). A surface current carries larvae with relative consistency along the Exuma Cays to the northwest at approximately 5–10 cm s^{-1} (0.1–0.2 kts). The large numbers of late-stage larvae, which are 2–3 wks old, probably have their source somewhere in the southern Exuma Cays, whereas early-stage larvae in the ECLSP are probably derived from eggs produced in the reserve. Analysis of shell middens indicates that the eastern Exuma Sound (near Cat Island) probably never had an important conch fishery, corroborating the present-day low abundance of conch in that area and reflecting the advection of larvae from east to west in the Exuma Sound (Stoner, 1997a). Whether the high abundance of larvae in the park is related to a large local spawning stock is not known. The ECLSP does seem to be an important source of conch larvae for adjacent fished areas in the northern Exuma Cays.

ADULT DISTRIBUTION AND ABUNDANCE.—Comparisons of adult queen-conch density estimates in the ECLSP with those at Lee Stocking Island indicated greater densities ($P < 0.001$; F-test) in the ECLSP in both bank and shelf habitats (Fig. 5). Most adult conch in the fished area (>87%) were found in depths greater than 10 m, whereas only 39% of the adult conch in the ECLSP were in depths greater than 10 m (Stoner and Ray, 1996). These differences may not be due solely to differences in fishing pressure, because conch numbers may increase as a result of the accumulation of larvae from south to north along the Exuma Cays, but naturally occurring high numbers of conch in the ECLSP make its location valuable, and the ECLSP is probably exporting large numbers of larvae to the northern Exuma Cays.

MEASURES OF SUCCESS FOR MARINE RESERVES

Several studies have demonstrated the many potential benefits of no-take marine reserves for fishery resources (reviewed by Dugan and Davis, 1993; Rowley, 1994). Two of these have received greater attention: local emigration of large juveniles and adults to

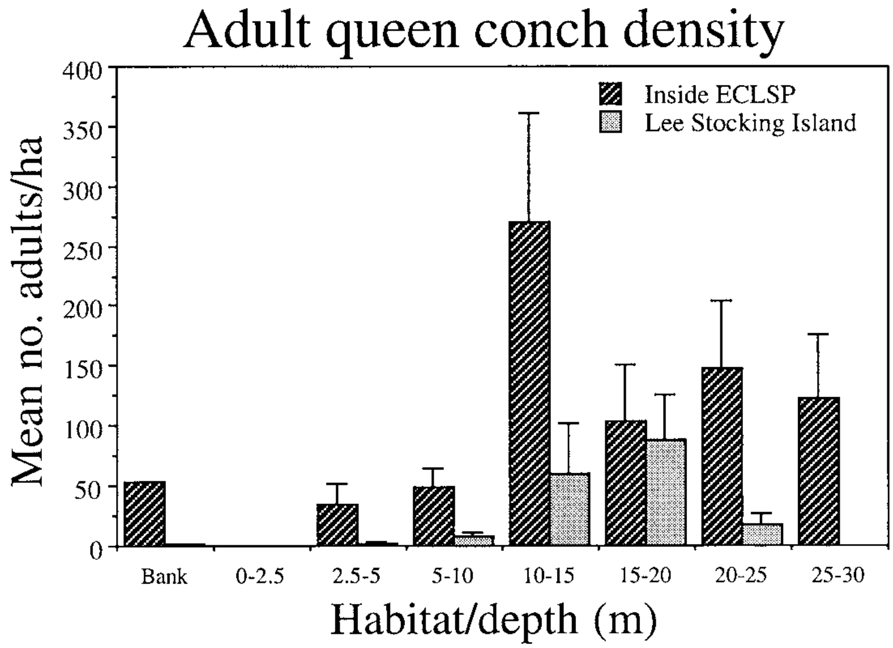

Figure 5. Mean density (number of individuals/ha) of adult queen conch (*Strombus gigas*) in a fished area (Lee Stocking Island) and a no-take marine reserve (Exuma Cays Land and Sea Park) from bank to shelf (0–30 m depth) habitats. Error bars represent 1 SE. Data from Stoner and Ray (1996).

adjacent fished areas and the enhancement of broad-scale or regional fisheries by means of larval export as a result of conservation of spawning-stock biomass (Rowley, 1994).

Emigration of large juveniles and adults from marine reserves to fished areas is related to the ability of fished species to reach greater densities and larger sizes in the reserve and to the movement patterns of individuals across reserve boundaries (Rowley, 1994). Studies of queen conch, spiny lobster, and Nassau grouper in the ECLSP have found greater adult densities and sizes than in fished areas in the region (see Table 1 and references). These patterns are the most common and direct responses of fishery target species to protection from fishing, but other, more complex responses can affect other species and trophic levels (Roberts and Polunin, 1991; Dugan and Davis, 1993). For example, nontarget grouper species were less abundant and comprised a smaller proportion of the total groupers observed in the ECLSP than in fished areas. This pattern potentially reflects differences in competition or predation release between reserve and fished areas. Unfortunately, the studies conducted in the ECLSP, like many other investigations of marine reserves, have been hampered by a lack of replication either in time or in space. For example, we have no historical data on the status of fishery-target species from the park's creation in 1958 to its closure to fishing in 1986. Even the earliest studies were not initiated until after 1990, so it is difficult to gauge whether the significant differences in density and size of target species within the ECLSP reflect (1) greater fishing pressure adjacent to the reserve since closure, (2) preservation of the status quo as of the closure, and/or (3) an increase in density and biomass after closure. Monitoring can help resolve this issue to some extent, but one of the important considerations for future Bahamian marine reserves is to collect baseline information before closure.

Few data support enhancement of fishers' catch by emigration of adults from marine reserves to fished areas (Roberts and Polunin, 1991; Dugan and Davis, 1993). The extent of emigration of large juvenile and adult fishery organisms from the ECLSP has not been

Table 1. Benefits of the Exuma Cays Land and Sea Park (ECLSP), a no-take marine reserve, for fishery target species. Data from Sluka et al. (1996b), Stoner and Ray (1996), and Lipcius et al. (1997).

Target	Variable	Comparison
Reef and hard-bottom habitats	Topographic complexity	ECLSP = N. Exumas > S. Exumas
	Species composition	ECLSP representative of central Bahamas
	Benthic coverage	ECLSP most similar to N. Exumas
Queen conch (*Strombus gigas*)	Adult distribution/density	ECLSP > Lee Stocking Island
	Larval (veliger) density	ECLSP > S. Exumas and areas east of Exuma Sound
Spiny lobster (*Panulirus argus*)	Adult density	ECLSP > Eleuthera, Lee Stocking Island, Cat Island
	Juvenile density	ECLSP > Cat Island, Lee Stocking Island > Eleuthera
	Postlarval settlement	Cat Island > Eleuthera > Lee Stocking Island > ECLSP
Groupers (Serranidae)	Species composition	Relative abundance of nontarget species greater in adjacent fished areas
	Density	Significantly greater densities of larger grouper species in ECLSP
	Size distribution	Greater mean size/proportion of larger size classes for target species in ECLSP
	Biomass	Greater mean biomass of target species in ECLSP
	Potential egg production	4.5–7 times greater by Nassau grouper in the ECLSP

documented. For large reef fishes such as Nassau grouper, no tagging data are available to reveal the extent of movement across reserve boundaries. In analyzing spatial patterns of Nassau grouper density, Sluka et al. (1997) found that densities at sites within 5 km of the ECLSP boundaries were more similar to those in the reserve than were those of areas further away. This pattern may be due to emigration but may also reflect greater fishing pressure farther north (closer to Nassau) and south (small fishing villages) of the ECLSP. Some emigration is plausible on the basis of the known movements of fishes such as groupers (Plan Development Team, 1990), but emigration is likely to be local, as opposed to regional enhancement of fisheries through larval transport. Emigration will also be a function of the displacement of fishers and the potential increases in fishing effort near reserve boundaries, both of which remain to be quantified for the ECLSP.

The degree to which larval production and settlement are increased by marine reserves is even more difficult to test because individual planktonic larvae cannot be tracked. Moreover, complex factors such as transport process and settlement affect the success of larval recruitment (Lipcius and Cobb, 1993). Larval enhancement is likely if adequate spawning-stock biomass is conserved within the marine reserve(s), if larvae are transported to an area where they can recruit to a fishery, if an increase in larvae leads to an increase in the number of larvae that settle, and if larval settlement is the limiting factor for the fishery rather than habitat availability. High larval densities in the Exuma Cays, particularly within the ECLSP, appear to be directly associated with the high abundance of spawning stocks such as queen conch (Stoner and Ray, 1996) and Nassau grouper (Sluka et al., 1996b). The relative importance of this pattern for Nassau grouper, however, depends on the presence of spawning aggregations within the reserve's boundaries. Only anecdotal evidence is available that Nassau grouper form spawning aggregations in the ECLSP (R. Darville, ECLSP warden, pers. comm.).

Available data suggest that the ECLSP is an important source of larvae for other areas in the Exuma Sound ecosystem (Lipcius et al., 1997). For queen conch, the high densities of larvae exported from the ECLSP probably represent a significant recruitment source for the northern Exuma Cays. An along-shore drift of about 1.5–3 km d^{-1} and a mesoscale gyre in the northern Exuma Sound can carry conch larvae produced in the ECLSP to nurseries in the northern Exuma Cays and eastward across Exuma Sound to southern Eleuthera Island. Reports from fishers and from the Bahamas Department of Fisheries indicate that the numbers of juvenile conch have increased in these areas over the last 10 yrs, the time period during which fishing has been prohibited in the ECLSP. For Nassau grouper, protection from fishing has probably resulted in preservation of highly fecund individuals or an increase in size leading to greater reproductive output. On the basis of surface circulation in Exuma Sound (Colin, 1995) and studies of postsettlement preferences of Nassau grouper (Eggleston, 1995), it is likely that grouper larvae produced within the ECLSP have a high probability of settling in the northern Exuma Cays (e.g., like queen conch), but no data exist to reveal the degree to which this pattern has benefited Nassau grouper recruitment and density outside of the ECLSP. The question of whether an increase in larvae arriving at an area leads to an increase in the number of larvae that settle underlies the difficulty of determining stock-recruitment relationships; doing so also requires a greater understanding of the relative importance of larval and habitat availability. For example, settlement and nursery areas may be the limiting factor for spiny lobster in the Exuma Cays (Herrnkind and Lipcius, 1986), whereas queen conch may be primarily limited by larval supply to nursery areas (Stoner et al., 1994).

Implications for Marine Reserve Design

The ECLSP provides a learning tool for assessing design criteria for future reserves in the Bahamas. Marine reserves should be large enough to retain a large portion of protected individuals long enough for the effects of protection (on, e.g., density, size, fecundity) to be realized (Rowley, 1994). The appropriate size for a marine reserve is easier to determine if the movement patterns of the species chosen for protection and the fishing pressure in adjacent areas are known. The success of the ECLSP in protecting spawning stocks of species such as queen conch and Nassau grouper and, in turn, producing potentially high numbers of larvae is probably a function of its large size, but it probably depends on a supply of larvae from spawning populations elsewhere (Stoner and Ray, 1996; Sluka et al., 1996b). In the case of queen conch, the ECLSP is clearly large enough to protect a significant reproductive stock in relatively undisturbed habitats (Stoner, 1997b), where physical transport features concentrate competent larvae and export them to down-current nurseries and fishing grounds (Stoner and Ray, 1996). Because of current patterns in Exuma Sound, however, the ECLSP is probably not large enough to hold a self-sustaining conch population.

The shape of marine reserves can influence the movement of organisms across boundaries and is primarily a function of the perimeter-to-area ratio of the protected area (Roberts and Polunin, 1991). The type and spatial extent of habitat bordering the reserve will influence emigration, e.g., whether the reserve is within a larger patch of similar habitat or borders very dissimilar areas. The shape of the reserve will also influence larval recruitment, dependent on the intersection of the reserve area with prevailing currents. In the case of queen conch in the Exuma Cays, late-stage queen-conch larvae arriving in the central area of the ECLSP must originate from areas well to the south as a result of physical transport processes (Stoner and Ray, 1996). The abundance of recruits probably contributes to high densities of juveniles and adults observed in the ECLSP.

Effective marine reserve location depends critically on proximity to fishery activities, habitats encompassed, and effective enforcement capacity (Rowley, 1994). Because many marine invertebrate and fish species produce planktonic larvae, marine reserves should ideally be located such that their larval production is exported to both suitable habitats and fished areas. The ECLSP appears to serve this function for queen conch and probably for Nassau grouper. Spiny-lobster larvae produced in the ECLSP, however, are probably delivered to 'sink' areas with lower-quality nursery habitats, such as Cat Island (Lipcius et al., 1997). By virtue of its large size (roughly 35 km long × 13 km wide), the ECLSP harbors a diversity of contiguous habitats, from the shallow Great Bahama Bank to the deep waters (> 30 m) bordering Exuma Sound that are representative of the central Bahamas (Chiappone et al., 1997a,b). These contiguous habitats are critical for various life stages of fishery target organisms (Sandt and Stoner, 1993). For example, shallow bank habitats with algal and seagrass patches and patch reefs are important nursery areas for juveniles, whereas shelf hard-bottom habitats are important for adults (Herrnkind and Lipcius, 1986; Eggleston, 1995).

Enforcement and outreach programs are perhaps the most important considerations in marine reserve design and implementation, because even relatively moderate levels of poaching can quickly deplete the gains achieved by closure (Roberts and Polunin, 1991). In the ECLSP, spatial patterns of large grouper density and biomass clearly indicate a decrease with increasing distance from the park ranger station, indicating that pervasive poaching may occur (Sluka et al., 1996b). The whole of ECLSP is not functionally protected from poaching, because of the logistical constraints of patrolling a very large reserve with few personnel (R. Darville, ECLSP ranger, pers. comm.).

Species considerations in marine reserve design are important because those species most likely to show dramatic responses to protection are probably those with limited movement and age/size distributions that have been lowered by fishing pressure (Rowley, 1994). Species like Nassau grouper have long life spans and high site fidelity (Plan Development Team, 1990). An important reserve design criterion for such species is to include spawning aggregations within reserve boundaries. Anecdotal information suggests the presence of a Nassau grouper spawning aggregation in the ECLSP (R. Darville, ECLSP warden, pers. comm.), and protection of such aggregations is critically important to maintenance of the larval production potential for regional fisheries. At least 20% of the known Nassau grouper spawning aggregations in the western Atlantic are thought to have disappeared (Sadovy, in press), and the need is pressing to include at least some of the remaining ones in marine reserves (Sadovy, 1994).

In conclusion, several important summary points can be made about the ECLSP as a marine reserve and the applicability of lessons about marine reserve design criteria learned in the Bahamas:

- Marine reserves like the ECLSP play a role beyond mere protection of fishery target species. They afford many other economically and ecologically valuable services and provide an opportunity to study marine ecosystems in the absence of fishing pressure. Marine reserves should be viewed holistically as one component of coastal-zone or ecosystem management. The increasing importance of marine reserves like the ECLSP in providing the sustainable yield of products, maintenance of biodiversity, and protection from the effects of pollution and habitat degradation is paramount in the management of larger marine ecosystems.
- Because of the potential fishery value of exported larvae, a better understanding of the strategic locations of reserves and of the general oceanographic conditions within the dispersal range of larvae is necessary (Roberts, 1997). The ECLSP may enhance fishery populations of grouper and queen conch in down-current areas through larval transport, but this may not be the case for spiny lobster.
- Marine reserves need to incorporate design features that protect habitats required by different life stages of organisms. Reserve designs that consider ontogenetic requirements of the target species and strategic locations for larval production, import, export, and metapopulation dynamics will optimize fishery and conservation benefits for marine vertebrate and invertebrate species with pelagic larvae.
- The ECLSP cannot effectively function in isolation given the apparent increased fishing effort outside it. The ECLSP probably depends, in part, on larval transport from other areas. Marine reserve networks that are linked by oceanographic processes are essential in the larger Exuma Sound ecosystem. These networks must be replicated in space and time and should be representative of the diverse habitats and environmental settings in the larger ecosystem (Ballantine, 1997). Marine reserve networks can buffer the effects of local extinctions in other reserves and additionally buffer the entire system (reserves and fished areas) from local recruitment failures (Rowley, 1994). Networks also allow for scientific replication (multiple types of one habitat) and representation (to protect habitats used by multiple life stages, from nursery to reproduction).
- Marine reserves are likely to be a very effective conservation measure in the Exuma Cays because of the difficulty of collecting fishery-dependent data and enforcing relatively complex catch and effort regulations.
- The ECLSP is not wholly protected from fishing because of poaching and the logistical constraints of patrolling a large reserve with limited staff. Greater enforcement capacity is required and, at the same time, a more directed effort at community education and outreach to raise awareness of existing regulations and to gain support for preserving the natural heritage of this important large marine ecosystem.

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