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TOWARDS SUSTAINABLE MULTISPECIES FISHERIES IN THE FLORIDA, USA, CORAL REEF ECOSYSTEM

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ABSTRACT

Southern Florida coral reefs generated an estimated 71,000 jobs and US$6 billion in economic activity in 2001. These ecosystem goods and services, however, are threatened by increased exploitation and environmental changes from a rapidly growing regional human population. To address these threats, we adopted an ecosystem-based perspective and developed a systems science analysis framework over the last decade to better assess and improve sustainable multispecies reef fisheries in the Florida Keys. Here we describe our progress and provide three example applications. We first built upon traditional catch and effort stock assessment methodologies by collecting spatially-explicit, fishery-independent data covering all reef fishes and reef habitats in the Keys. An optimized sampling strategy and a new length-based assessment framework provided synoptic spatial estimates of species abundance and size structures. Models were developed that encompassed the complex biological dynamics of fish stocks and a broad range of environmental and human impacts, including fisheries, non-target species, predator-prey interactions, species movements, ontogenetic changes in habitat associations, and physical processes. We show that the snapper-grouper fishery in the Florida Keys is experiencing overfishing and that stocks are overfished relative to established benchmarks for resource sustainability. Spatially explicit models demonstrated the potential effectiveness of no-take marine reserves to support sustainable fisheries, and were employed to objectively evaluate marine reserve boundary options in the Dry Tortugas. We show the importance of considering physical coupling and regional water quality changes resulting from Everglades restoration. A fishery systems science framework improves understanding of impacts from fishery extraction, ecosystem alterations, and natural oceanographic variability on the dynamics of exploited fish stocks.

Coral reefs in southeastern Florida and the Florida Keys provide the ecological foundation for vital fisheries and a tourism-based economy that generated an estimated 71,000 jobs and US$6 billion of economic activity in 2001 (Johns et al., 2001). They also contributed to the designation of Florida as the "fishing capital of the world" by the state legislature (FWC, 2003). Coral reef ecosystem goods and services, however, extend beyond fishing to include a range of educational, scientific, aesthetic, and other recreational uses, such as snorkeling, SCUBA diving, and tourism.

The Florida Keys reef ecosystem is considered one of the nation's most significant, yet most stressed marine resources (U.S. Department of Commerce, 1996) and is managed by Florida, the National Oceanic and Atmospheric Administration (NOAA), and the National Park Service. Reef fisheries target the "snapper-grouper complex," which consists of 73 species of mostly groupers and snappers, but also grunts, jacks, porgies, and hogfish. The fishery has been intensively exploited over the past 75 yrs, during which the local human population has grown exponentially and generated concerns over sustainable fishery productivity. Many reef species are extremely sensitive to exploitation (Coleman et al., 2000; Musick et al., 2000), and coastal development subjects coral reefs to a suite of other stressors that can cumulatively impact reef fish populations by degrading water quality and damaging nursery

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and adult habitats (Bohnsack and Ault, 1996; Lindeman et al., 2000; Jackson et al., 2001; Porter and Porter, 2001).

Traditional single-species assessment methods have proven conceptually and analytically inadequate for developing reliable multispecies assessments and models to address complex coral reef issues (Bohnsack and Ault, 1996; Bohnsack, 1998). For these reasons, we embarked on a research program in the early-1990s to begin to address the full range of issues for managing coral reef fisheries in the Florida Keys. The goal was to use an ecosystem-based perspective that integrates biological, oceanographic, habitat, and human dynamic factors to better manage sustainable multispecies reef fisheries. Here we describe our progress in developing and applying a fishery systems science framework to address assessment and modeling needs for managing the coral reef fishery in the Florida Keys. We provide three example applications of our research approach to explore inter-related management issues involving fishery exploitation, marine reserve design and utility, and potential impacts of the Everglades restoration on reef fish dynamics and productivity.

Fishery Systems Science

Fishery systems science (FSS), a topic of theoretical and practical interest (cf., Rothschild, 1971, 1973; Walters, 1986; Ault, 1996; Rothschild et al., 1996), defines an analytical framework with two principal goals: (1) to improve the understanding of the impacts of fishery extractions, ecosystem alterations, and natural oceanographic variability on the dynamics of exploited fish stocks; and (2) to use this knowledge to recommend modifications of human activities to ensure long-term sustainable use of fishery resources. In principle, sustainable exploited populations need sufficient reproductive capacity in terms of the biomass of spawning adults to replenish themselves into the indefinite future. The FSS framework (Fig. 1) has two "primary" elements, the coral reef ecosystem and the interacting human-fishery sector, and three "derived" elements: data acquisition, model building, and resource risk assessment. Data acquired from biotic and abiotic components of the coral reef ecosystem and the human-fishery sector are used to construct mathematical and statistical models that reflect the complexity and uncertainty of real ecosystem processes and their interactions with the human-fishery sector. Models of perceived reality are then employed to assess the risks to fish stock sustainability under current and anticipated future conditions of fishing intensity, water management practices, and other environmental conditions. Knowledge and insights gained are provided to managers and policymakers, who in turn implement regulations to modulate human impacts on the ecosystem to ensure fishery sustainability. The key difference between our FSS approach and simpler decision theory approaches is our assumption that more complex models are necessary to adequately describe and manage complex natural ecosystems.

The elements of the analysis framework (data acquisition, modeling, and risk assessment) are ubiquitous to most real-life fishery science applications (Fig. 1). The centerpiece of the analysis process is an integrated suite of mathematical models that couple ecosystem dynamics and human impacts (Ault et al., 1998, 1999b, 2003a; Wang et al., 2003). This suite of models evolved from cohort-structured models of fish population dynamics impacted by fishing and is rooted in fundamental fishery science concepts pioneered by Baranov (1918), Russell (1931), Thompson and Bell

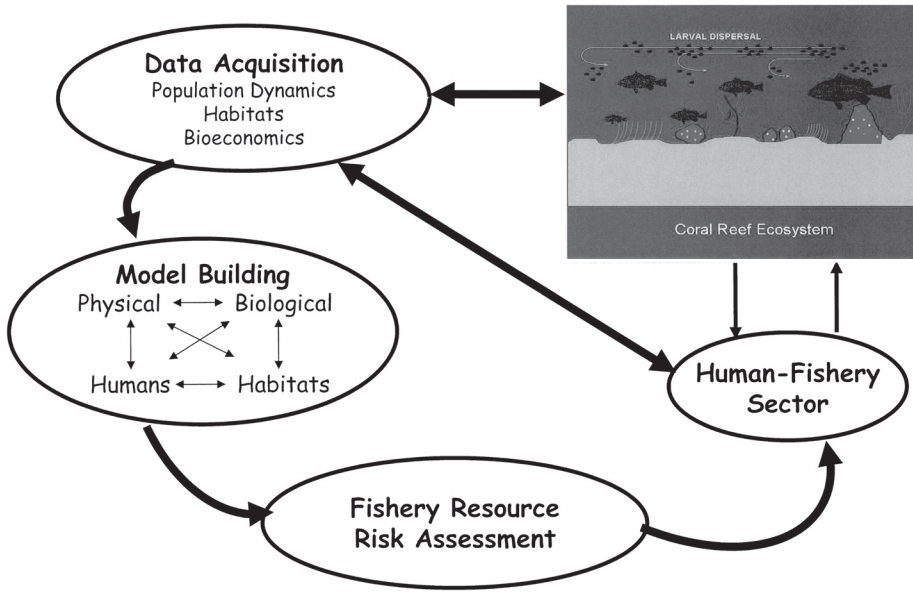


Figure 1. Overview of the components in a systems science approach to multispecies fishery management in coral reef ecosystems.

(1934), and Beverton and Holt (1957). Age-structured stock production models integrate a series of mathematical functions that explicitly represent population processes of recruitment, growth, reproduction, and mortality from natural causes and fishing (Table 1) to describe the dynamics of abundance or biomass of a cohort (i.e., a group of individuals born at the same time) over its lifespan, or the entire population of cohorts over time. Age-structured models are currently used to assess dynamic fishing impacts on a target population (e.g., Quinn and Deriso, 1999; Haddon, 2001).

The demographic modeling framework is analogous to an engineering "control system" (Wagner, 1975; Sterman, 2000), in which a fish population is viewed as a biomass production facility and population dynamic processes are the machinery that governs the capacity to produce biomass. Resource managers achieve sustainability goals by manipulating two control variables: size-age of capture and fishing mortality rate. Traditionally, size-age of capture is controlled by minimum size limits or gear restrictions (e.g., mesh size, trap escape vents, hook size, seasonal and spatial closures), while mortality rates are controlled by fishing effort restrictions through quotas, bag limits, limited entry, and time and spatial closures.

Fishing impacts are normally evaluated as tradeoffs between yields (in biomass) extracted by the fishery relative to the biomass of spawners remaining in the sea that are required to ensure sustained production. This concept is illustrated in Figure 2 using two widely used fishery management benchmarks: yield-per-recruit (YPR) and spawning potential ratio (SPR). YPR is the expected lifetime yield of a cohort scaled to annual recruitment of newborns for a given combination of fishing mortality rate and minimum capture age or size. SPR is the expected lifetime spawning biomass of a cohort for a given combination of fishing mortality and age of capture scaled to the unexploited lifetime spawning biomass. In the U.S. south Atlantic, the federal mini-

Table 1. Comparison of population-dynamic and environmental forcing features among structured assessment models used in analyses of sustainable multispecies fisheries in the Florida U.S. coral reef ecosystem.

Data-model-analysis feature	Fishery-dependent stock assessment	Fishery-independent stock assessment	MPA design and utility	Everglades restoration
Data period	1983–2002	1979–2003	1999–2002	1994–2003
Minimum mapping unit (i.e., spatial resolution)	600 km^2	0.04 km^2	0.04–1.0 km^2	0.25 km^2
Growth model	*Length-age:* von Bertalanffy growth function (VBGF) *Weight-length:* power function (PF)	*Length-age:* VBGF *Weight-length:* PF	*Length-age:* VBGF *Weight-length:* PF	*Shrimp (prey)* Length-age: molt-process model Weight-length: power funcion *Fish (predator)* Bioenergetic growth model
Mortality estimation				
Primary data source	Discrete dynamic estimates from fishery-dependent commercial & recreational fleets (e.g., trip tickets, MRFSS, headboats).	Pooled dynamic estimates from fishery-independent, diver visual survey (i.e., RVC).	Fishery-independent, diver visual survey	Fishery-independent; *Bay habitats:* trawl survey *Reef habitats:* diver visual survey
Secondary source			Fishery-dependent, recreational fleet	Fishery-dependent, recreational & commercial fleets
Uncertainty	50% CV	15% CV		
Natural mortality	Lifespan estimator	Lifespan estimator	Lifespan estimator	*Shrimp prey:* lifespan estimator *Fish predator:* base rate–lifespan estimator; modulated by bioenergetic growth
Total mortality	Average length, stock synthesis, VPA & surplus production	Average length	Average length	*Shrimp prey:* catch curve *Fish predator:* average length
Recruitment dynamics	Yes	No	Spatially-averaged	Biophysical dependent
Movement models	None	None, but data spatially-structured	Cellular automata	*Shrimp prey:* cellular automata model *Fish predator:* advection-diffusion-taxis model
Predator-prey interactions	None	None	None	Generalized functional response dependent on spatial arrangement of prey-predator (Cosner et al., 1999)
Environmental forcing functions	None	None	Benthic habitats	Benthic habitats, water temperature, salinity, tides, currents, mass transport
Management control variables	Fishing mortality (F), capture age-length (L)	Fishing mortality (F), capture age-length (L)	Fishing mortality (F), capture age-length (L), spatial closures	*Shrimp prey & fish predator:* F, capture age-L, spatial closures *Habitat:* freshwater flow regimes
Management benchmarks	Yield-per-recruit (YPR), spawning potential ratio (SPR)	YPR-SPR, F/F_{msy}, B/B_{msy}	YPR-SPR, AHP analysis of fishing & non-fishing impacts	YPR-SPR, Spatial growth potential
Primary references	Ault et al., 2003b, 2005	Ault et al., 1998, 2003b, 2005	Meester et al., 2001, 2004 Ault et al., 2000	Ault et al., 1999b, 2003a Wang et al., 2003

mum standard is 40% SPR for Goliath grouper, *Epinephelus itajara* (Lichtenstein, 1822), and 30% SPR for other reef fish stocks (NOAA Fisheries, 2002). These values are derived from density-dependent stock-recruitment theory where the number of recruits to a population is expected to be approximately the same at or above the minimum SPR threshold. As shown for hogfish, *Lachnolaimus maximus* (Walbaum, 1792), the maximum YPR value at which SPR is at or above the 30% threshold denotes the level of exploitation expected to produce "maximum sustainable yield" (MSY) (Fig. 2).

Our program builds upon this control system approach by employing several basic principles of systems science to strengthen the connections and flow of information among the elements in Figure 1. From a number of theoretical approaches for applying systems science techniques to fisheries issues that have been proffered (c.f., Rothschild, 1971, 1973; Walters, 1986; Ault, 1996; Rothschild et al., 1996), we derived three operational tenets to guide our program. The first tenet is to use the desired analysis endpoints to assist in the design of the scientific investigation. We first identify specific human and environmental impacts to be evaluated, the most efficient control variables for mitigating those impacts, and the metrics needed to evaluate

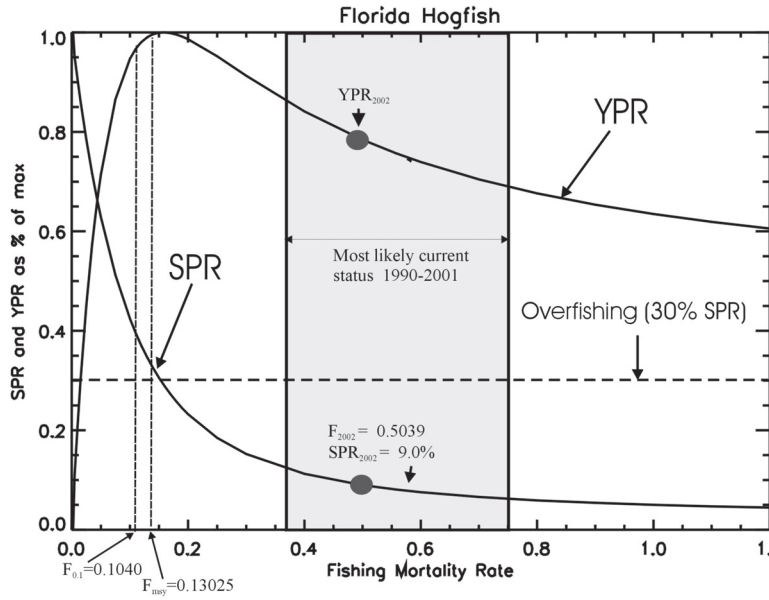


Figure 2. Two principal fisheries management benchmarks for hogfish (*Lachnolaimus maximus*): yield-per-recruit (YPR as a % of maximum) and spawning potential ratio (SPR as a % of maximum) with respect to fishing mortality rate. The shaded area represents the most likely fishery status from 1990–2001.

risks to fishery sustainability from the impacts. Next we develop the modeling framework and population dynamic functions necessary for analyzing the combination of impacts, control variables, and management benchmarks (Ault and Fox, 1989; Ault and Ehrhardt, 1991; Ehrhardt and Ault, 1992; Ault et al., 1998, 1999b, 2003b). Finally, we develop data acquisition procedures to obtain the necessary data with sufficient precision to parameterize the demographic models (Bohnsack and Bannerot, 1986; Bohnsack et al., 1999; Ault et al., 1999a, 2001, 2002). Design of the scientific process thus begins at the question to be addressed and systematically proceeds in reverse fashion through all of the steps necessary to conduct the analysis.

The second tenet is to employ iterative learning to improve accuracy and precision of all facets of the scientific process. A familiar application of this concept is in statistical model-building. In regression modeling, for example, the procedure of model identification —parameter estimation— diagnostic checking and validation is repeated until a model is obtained that provides a satisfactory fit to the data and meets assumptions regarding the error probability distribution. A key step in the iterative process is the use of objective performance criteria to determine whether a satisfactory outcome has been achieved based on statistical measures or whether further investigation is required. The ultimate goal is to build a mathematical ecosystem-impact model that accurately and precisely reflects reality and that can be independently validated.

The third tenet is to maximize information content at minimum cost. While the second tenet focuses on iterative learning and information accuracy (i.e., ensuring that our perception matches reality), the third tenet focuses on precision and the cost of obtaining information. An example is statistical experimental design in which increased precision is associated with increasing sample sizes (i.e., costs). However, a

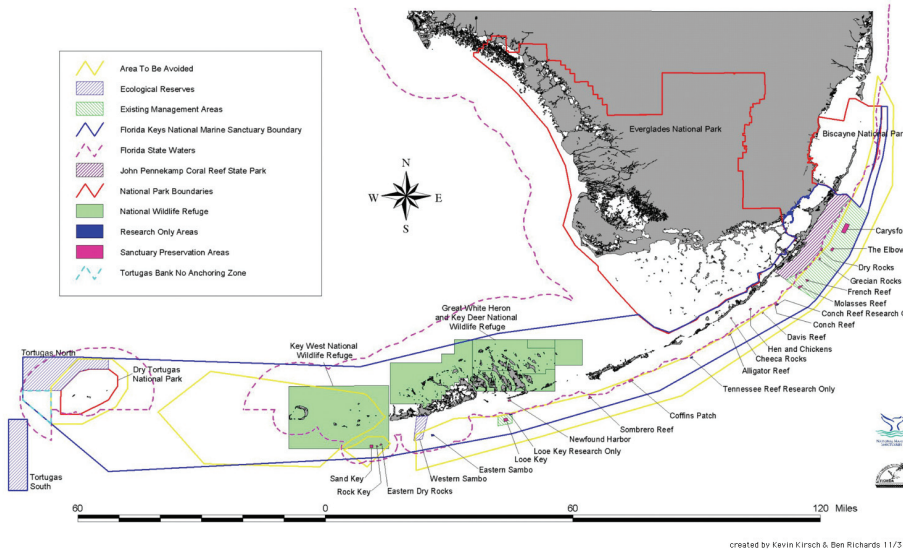


Figure 3. Configuration of coral reef areas managed in the Florida Keys by the Florida Keys National Marine Sanctuary, National Park Service, National Wildlife Refuge, and State of Florida.

point of diminishing returns is eventually reached where the additional benefits of increased precision are not justified by the escalating costs. By objectively identifying these cost-benefit tradeoffs, we can maximize the value obtained from limited monetary resources to achieve our ultimate goal of developing accurate, precise, and cost-effective information and models within a scientific analysis framework for fisheries assessment and management.

The Florida Keys Coral Reef Ecosystem

The Florida Keys coral reef extends 400 km southwest along an island archipelago from Key Biscayne near Miami to the Dry Tortugas region west of Key West (Fig. 3). The reef ecosystem is managed by different government agencies with specific spatial jurisdictions. Fisheries are managed by the Florida Fish and Wildlife Conservation Commission and two federal fishery management councils (U.S. South Atlantic and Gulf of Mexico). Fishing regulations can also apply in the Florida Keys National Marine Sanctuary (FKNMS) under NOAA (Department of Commerce); in three national parks (Biscayne, Everglades, Dry Tortugas) and four National Fish and Wildlife Refuges (Department of Interior); and in John Pennekamp Coral Reef State Park (Florida Department of Environmental Protection).

Unique topographic and oceanographic conditions (Fig. 4) help sustain the highly productive Florida Keys coral reef ecosystem. The coastal marine environment exhibits relatively little topographic variation, although the sea floor abruptly plummets to depths of 1500 m or more several kilometers seaward of the barrier reef tract (Fig. 4A). Oceanographic dynamics are influenced by the Loop Current in the southeastern Gulf of Mexico which merges with the Florida Current near the Dry Tortugas and then flows parallel to the barrier reef through the Straits of Florida towards Miami (Fig. 4B). This unique geophysical setting promotes dynamic oceanographic conditions comprised of intricate recirculating gyres and surface currents

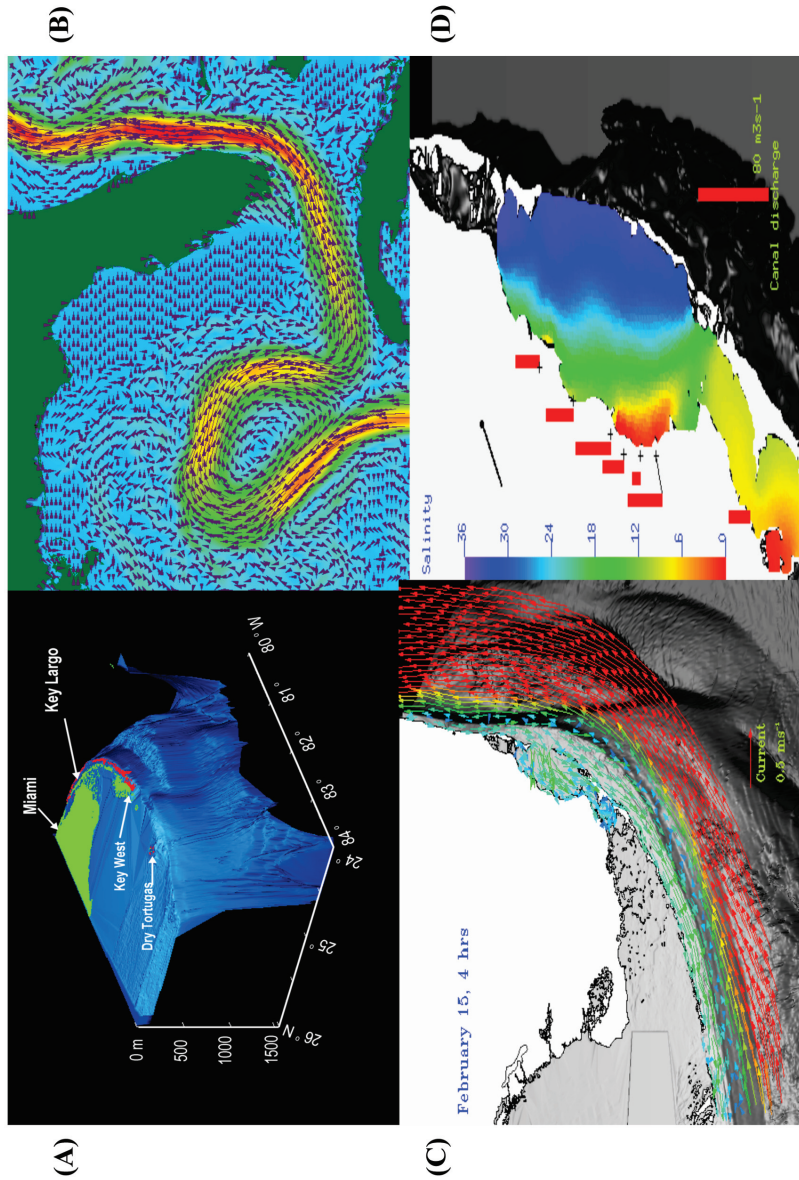


Figure 4. Topography and physical oceanography of southern Florida and the Florida Keys: (A) 3-D map showing the relationship between terrestrial and marine topography from the Everglades through the coral reef ecosystem (barrier coral reef is red); (B) surface currents in the northern Caribbean, Gulf of Mexico, and Straits of Florida; (C) surface currents from offshore (Straits of Florida) to inshore (Biscayne Bay) in the coral reef ecosystem; (D) Biscayne Bay salinity dynamics showing canal discharge points as histograms on the western shoreline.

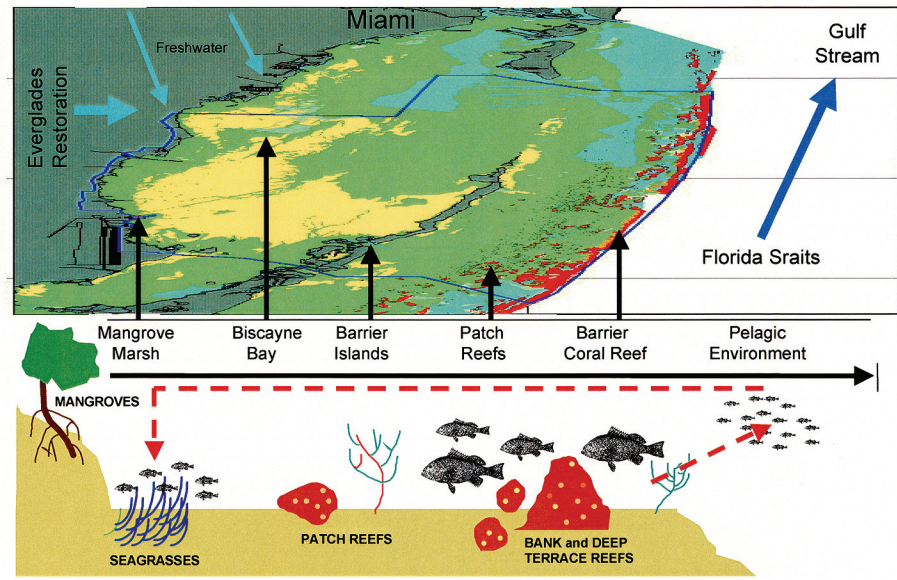


Figure 5. Relationship of life history and ontogeny of the snapper-grouper complex to cross-shelf habitats and oceanographic processes.

with some of the highest current speeds in the world (Stommel, 1976; Olson, 2001, 2002). The seaward edge of the barrier reef tract is usually subjected to open tidal exchange from the Florida Straits with its warm, clear, low nutrient waters conducive to coral reef development. These conditions are periodically interspersed with pulses of nutrient-rich waters from locally intense upwelling events along certain deep reef margins where some of the most luxuriant coral habitats are found (e.g., Miller et al., 2001; Olson, 2001, 2002; Ault et al., 2002).

The Florida Keys have a subtropical maritime climate with moderate temperatures and two seasons: the summer wet season (May–October), marked by numerous convective thunderstorms, and the winter dry season (November–April) which features infrequent, fast-moving, dry cold fronts. Water circulation in coastal bays (Fig. 4C) is primarily influenced by tides and wind (Wang et al., 2003). During the wet season, fairly sharp salinity gradients exist in coastal bays (Fig. 4D) in which near-freshwater conditions found along the coastal shoreline progressively change to near-oceanic conditions at the barrier islands.

Benthic habitats exhibit a distinct cross-shelf pattern (Fig. 5). Fringing mangrove habitats occur on the land-sea edge of coastal bays and around barrier islands. Coastal bays have three main benthic habitat types: seagrass beds, bare unconsolidated substrates, and oolitic limestone hardbottoms populated with sponges and octocorals. Seaward of the barrier islands, benthic habitat types include stony coral patch reefs and barrier reefs, sponge-gorgonian covered hardbottoms, seagrass beds, and carbonate sands.

The Florida Keys have more than 500 fish species, including 389 that are reef-associated (Stark, 1968), and thousands of invertebrates, including corals, sponges, shrimps, crabs, and lobsters. Species in the snapper-grouper complex utilize a mosaic of cross-shelf habitats and oceanographic features over their life spans (Ault and Luo,

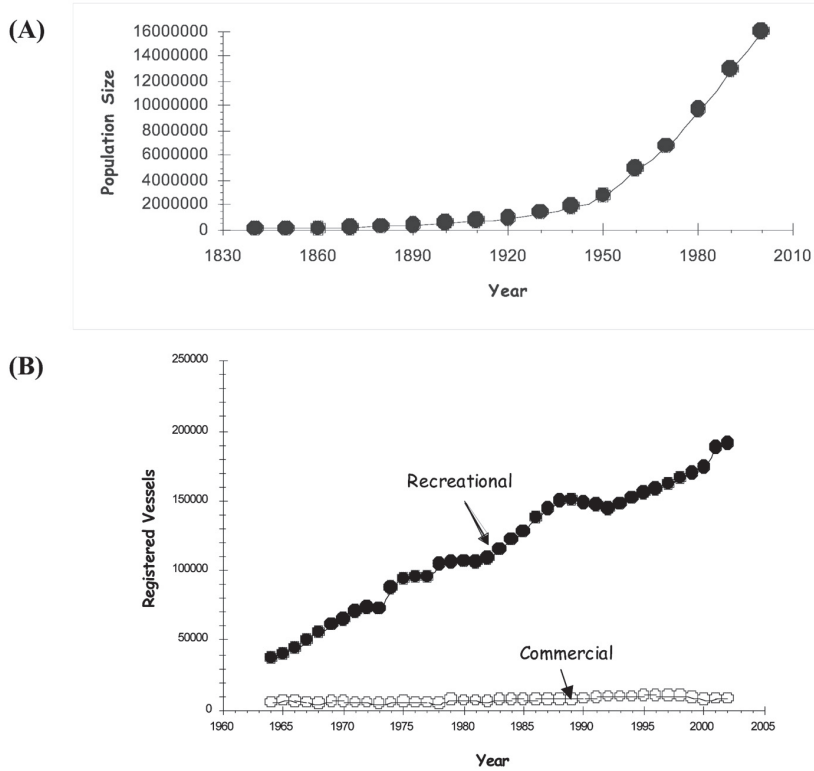


Figure 6. Human population growth and vessel registrations in Florida. (A) Florida's population from 1840–2000. (B) Growth of commercial and recreational fleets in southern Florida (Palm Beach, Broward, Miami-Dade, Monroe, and Collier Counties) from 1964–2002. Source: Florida Statistical Abstracts (2002).

1998; Lindeman et al., 2000). Most adults spawn on the barrier reefs and sometimes form large spawning aggregations (Domeier and Colin, 1997). The Dry Tortugas region, in particular, contains numerous known spawning aggregation sites (Schmidt et al., 1999). Pelagic eggs and developing larvae are transported from spawning sites along the barrier reef tract by a combination of seasonal wind-driven currents and unique animal behaviors to eventually settle as early juveniles in a variety of inshore benthic habitats (Lee et al., 1994; Ault et al., 1999b). Some of the most important nursery habitats are located in the coastal bays and near barrier islands (Lindeman et al., 2000; Ault et al., 2001). As individuals develop from juveniles to adults, ontogenetic habitat utilization patterns generally shift from coastal bays to offshore reef environments.

The Human–Fishery Sector

Coral reefs in the Florida Keys are impacted by fishing and indirectly by habitat degradation from other human activities including coastal development, altered freshwater flow, and changes in water quality from pollution, sedimentation, and excess nutrients (CERP 1999; Cowie-Haskell and Delaney, 2003). Human impacts have grown as a result of Florida's tenfold population growth from 1.5 million people

in 1930 to 16 million in 2000 (Fig. 6A). In 2000, over 5 million residents, nearly a third of Florida's population, lived in the five southern counties adjacent to coral reefs (Palm Beach, Broward, Miami-Dade, Monroe, and Collier). In addition, over three million tourists visit the Keys annually (Leeworthy and Vanasse, 1999).

Precise data on coral reef fishing effort trends do not exist, but are reflected by state-wide fishing statistics and numbers of registered boats. In 2001, for example, an estimated 6.7 million recreational fishers took 28.9 million marine fishing trips in Florida and caught 171.6 million fish, of which 89.5 million (52%) were released or discarded (U.S. Department of Commerce, 2002). From 1964–2002 the number of registered recreational boats in southern Florida grew by more than 500%, while the number of commercial vessels grew at a much lower rate, about 150% (Fig. 6B). Many of these vessels are used for fishing and for non-extractive activities, such as sailing, sightseeing, transportation, snorkeling, and SCUBA diving. Increased fishing fleet size has been accompanied by a number of technological advances that have been estimated to have quadrupled average fishing power (Mace, 1997), i.e., the proportion of stock removed per unit of fishing effort (Gulland, 1983). These advances include improvements in fishing tackle, hydroacoustics (depth sounders and fish finders), navigation (charts and global positioning systems), communication, and inexpensive, efficient, and more reliable vessel and propulsion unit designs (Bohnsack and Ault, 1996; Ault et al., 1997, 1998). These fishing trends have thus become an obvious concern to the fishery sustainability and persistence of the coral reef ecosystem.

Fisheries in southern Florida are complex (Bannerot, 1990; Chiappone and Sluka, 1996). Adult reef fishes are caught for food and sport around bridges and on offshore patch and barrier reefs. Commercial and sport fisheries also target spiny lobster, marine aquarium fishes and invertebrates, inshore and offshore. Pink shrimp, a principal prey item of the snapper-grouper complex, are intensively exploited. Offshore, a substantial commercial food fishery targets adult pink shrimp inhabiting softbottoms near coral reefs. In coastal bays and near barrier islands, juvenile pink shrimp are commercially targeted as live bait for the recreational fishery. Both food and sport fisheries target pre-spawning subadult pink shrimp as they emigrate from coastal bay nursery grounds to offshore spawning grounds. Inshore, sport fisheries pursue highly prized game fishes, including spotted seatrout, sheepshead, black and red drum, snook, tarpon, bonefish, and permit, while commercial fisheries primarily target sponges and crabs. Offshore of the deep margin of the barrier reef, commercial and sport fisheries capture an assortment of species including amberjack, king and spanish mackerel, barracuda, sharks and small bait fishes (e.g., Exocoetidae, Mullidae, Carangidae, Clupeidae, and Engraulidae). Farther offshore (seaward of the 40 m isobath), commercial and sport fisheries catch dolphinfish, tunas, and swordfish, and sport fishers target sailfish, wahoo, and white and blue marlin.

The principal factors influencing the dynamics and sustainability of snapper-grouper populations are illustrated in Figure 7. Besides exploitation, other factors can affect reef fish populations including: (1) fishery removal of key prey (e.g., shrimps, baitfish) and predators (e.g., barracuda, sharks), (2) alterations to benthic habitats (e.g., loss of mangroves and seagrasses to shoreline development, channel dredging, and ship groundings), and (3) alterations to water quality (e.g., pollution, nutrification, and turbidity), quantity, and timing of freshwater inflows. Other environmental issues facing the Keys include coral declines from diseases and bleaching, invasion of exotic species, shifts to algal dominance, and damage from contact by anchors,

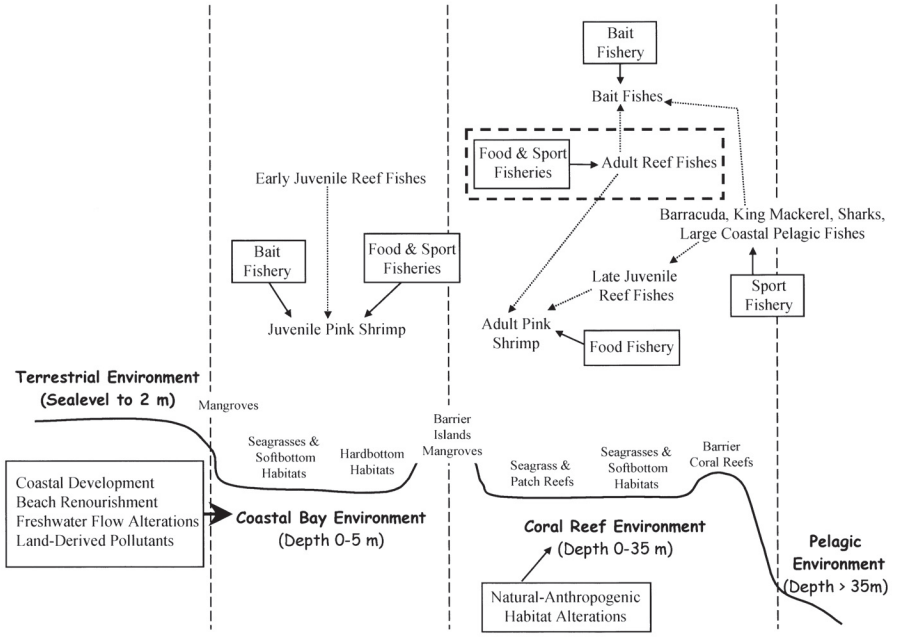


Figure 7. Conceptual diagram of reef ecosystem and fishery processes that influence sustainability of exploited reef fishes. Principal biotic components and human impacts (boxes and solid arrows) are shown distributed over cross-shelf habitats of the Florida Keys. Dotted arrows denote predator-prey relationships. The dashed box denotes components and impacts that are the traditional focus of fishery science and management.

grounded vessels, divers, snorkelers, and fishing gear. In addition, hurricanes have a 16% annual probability of striking the Keys (Neumann, 1987) and damaging habitat. Looking at the full spectrum of impacts suggests that achieving sustainable reef fisheries will likely entail substantially more analysis of inter-related factors than simply assessing fishing mortality rates for a few snapper and grouper species (Bohnsack and Ault 1996; Ault et al., 1999b; Lindeman et al., 2000).

Fishery Systems Science Applications

Below we show applications of our FSS framework to coral reef ecosystem management in the Florida Keys. We assess: (1) fishery exploitation, (2) marine reserve design and utility, and (3) potential impacts of Everglades restoration on reef fish community dynamics.

Fishery Exploitation.—Although Native Americans fished for groupers and snappers on the reefs long before the arrival of European settlers (Oppel and Meisel, 1871), reef fishing in southern Florida began in earnest in the 1920s. Despite the long and storied history of the fishery and some early recommendations for integrated information systems (Broadhead, 1952), fishery monitoring programs for individual snapper-grouper species only began in the early 1980s following growing public conflicts and sharp declines in catches (Bohnsack et al., 1994; Bohnsack and Ault, 1996; Harper et al., 2000). To mitigate these declines, the South Atlantic Fishery Management Council in 1983 and the Florida Marine Fishery Commission in 1984 began

establishing minimum size, season, and bag limit restrictions on a number of reef species and prohibiting certain fishing gears (e.g., spears, power heads, fish traps, roller trawls, etc.) in specific areas (Bohnsack et al., 1994). Fisheries were closed and remain closed for Nassau grouper, *Epinephelus striatus* (Bloch, 1792); Goliath grouper; queen conch, *Strombus gigas* Linnaeus, 1758; and stony corals (Bohnsack et al., 1994).

While there was great interest in building traditional fishery stock assessment models to evaluate the effects of exploitation, this process was impaired by a dearth of age-size structured fishery-dependent statistics. Existing data were greatly weighted towards a few grouper and snapper species, but comparatively light for the full range of exploited species, which includes 18 groupers, 14 snappers, 14 grunts, and several other species. To address this lack of data, a fishery-independent reef fish visual census (RVC) program was established in 1979 to assess species presence, abundance, and sizes for the entire reef fish community (Bohnsack and Bannerot, 1986; Bohnsack et al., 1999). These surveys obtained data on over 250 reef fish species, including both pre-exploited and exploited sizes of target populations, as well as non-exploited species. Because the initial surveys had limited spatial coverage, they needed to be expanded to reflect stock-wide dynamics and responses to exploitation. We therefore developed an expanded fishery-independent monitoring and assessment approach to directly assess population trends over time. The principal goal of the RVC survey was refined to generate efficient statistical estimates of reef fish species abundance and biomass by size to assess mature stock condition and recruitment in the Florida Keys reef ecosystem. We incorporated specific knowledge of species' ontogenetic habitat use in the sampling survey design to reduce estimated variance and bias in a cost-effective way (Ault et al., 2002). These improvements in statistical survey design reduced the RVC survey error for target species from about 50% CV in the early 1990s to about 10%–20% CV in 2001.

A key aspect of our efforts was the use of fishery-independent data to calculate the average size of fish in the exploited phase for each stock (Ault et al., 1998). This stock assessment indicator quantifies the condition of an exploited population (Table 1), and since it is strongly correlated with population numbers and biomass, can be effectively used to estimate total instantaneous mortality rates (Ault and Ehrhardt 1991; Ehrhardt and Ault, 1992; Fig. 8). Next, we estimated a suite of population-dynamic parameters from a comprehensive review and statistical analysis of population dynamics data for snapper-grouper species from a number of local and regional databases (e.g., Claro et al., 2001). Fishery independent mortality estimates from a length-based analysis were calibrated with a length dependent on age-structured simulation model (Ault et al., 1998) and corroborated with mortality estimates obtained from fishery-dependent size data (Fig. 8A). We then combined population-dynamic parameters with estimates of fishery mortality and used a length-based cohort structured simulation model to evaluate exploitation impacts on the stock relative to a number of reliable management benchmarks for sustainability (i.e., YPR and SPR). We cross-validated our conclusions with fishery-dependent data and age-structured stock synthesis (Methot, 1990; Quinn and Deriso, 1999) and non-equilibrium surplus production models (Prager, 1994). We applied the model to the 35 reef fish species (groupers, snappers, grunts, barracuda, and hogfish) for which there were sufficient survey data and population parameter estimates. Results showed that 65% of the 35 assessed exploited reef fish stocks were below the then existing federal

standards for sustainability (Ault et al., 1998). In fact, the observed high fishery exploitation levels had been occurring for most snapper-grouper stocks since the late 1970s, precipitating a condition known as "serial overfishing" in which the fishery first depletes more valuable species (usually large, long-lived grouper and snapper) and then progressively switches to less valuable species (Ault et al., 1997, 1998, 2001, 2002). Updated estimates of SPR for 34 species for the period 2000–2002 are given in Figure 9.

Later, we applied new, more conservative precautionary control rule benchmarks for fishery sustainability (Restrepo and Powers, 1999) to our data based on minimum stock size and maximum fishing mortality thresholds (Ault et al., 2005). The analysis estimated that exploitation levels were 2–10 times higher than the fishing mortality rate required to achieve MSY (Fig. 10), and showed that most of the large, desirable, and economically valuable groupers and snappers in the Florida Keys have been depleted. The result of intensive fishing is that few large, mature fish remain on the reef to reproduce. Despite the availability of fishery-independent data for stock assessments, the status of many species remains unknown because requisite population dynamics parameter estimates are lacking for much of the reef fish community, particularly non-target species.

Our research has also shown a gradient of fishing impacts in the Florida Keys that runs from a high in the north near human population centers in Miami and Key Largo (Harper et al., 2000; Ault et al., 2001), and decreases to the southwest in the Dry Tortugas region, except for local peaks around Marathon and Key West (Ault et al., 2002). Despite isolated areas of lower exploitation, however, overall the evidence suggests that existing traditional management controls on the Keys reef fishery are insufficient to ensure long-term sustainability.

Marine Protected Area Design and Utility.—Observations of declining fishery resources and habitats in the Keys caused some management entities to seek alternative methods for mitigating human impacts (Culhane, 2002; Cowie-Haskell and Delaney, 2003; Brock and Culhane, 2004; Bohnsack et al., 2004). In particular, a broad interest developed among managers, scientists, and many stakeholders in exploring the potential utility of using "no-take" marine protected areas (MPAs) to rebuild depleted fish stocks, conserve marine biodiversity, and reduce conflicts among different resource users; e.g., hook-and-line fishers and scuba divers (Bohnsack and Ault, 1996; U.S. Department of Commerce, 1996; Bohnsack, 1998; Roberts et al., 2001; Halpern and Warner, 2002). In this effort, we have pursued three lines of research to: (1) extend the fisheries demographic model to specific places to examine the potential of using areal fishing closures as an additional management control variable, (2) apply this model to assist design of reserves that reduce fishing impacts on snapper-grouper stocks, and (3) design empirical studies to track reserve performance after implementation. Below we highlight some of our progress on the first two lines of research.

A spatial demographic model was formulated in an optimization-simulation framework to take into account heterogeneous distributions of both fishes and fishers, fish movements, and the spatial redistribution of fishing mortality after reserve implementation (Meester, 2000; Meester et al., 2001, 2004; Table 1). The Keys coral reef environment (> 11,000 km^2) was divided into 1 km^2 spatial units and each unit was assigned a reef habitat category based on a combination of cross-shelf position (e.g., nearshore, offshore), coral reef structure (e.g., patch and barrier reefs),

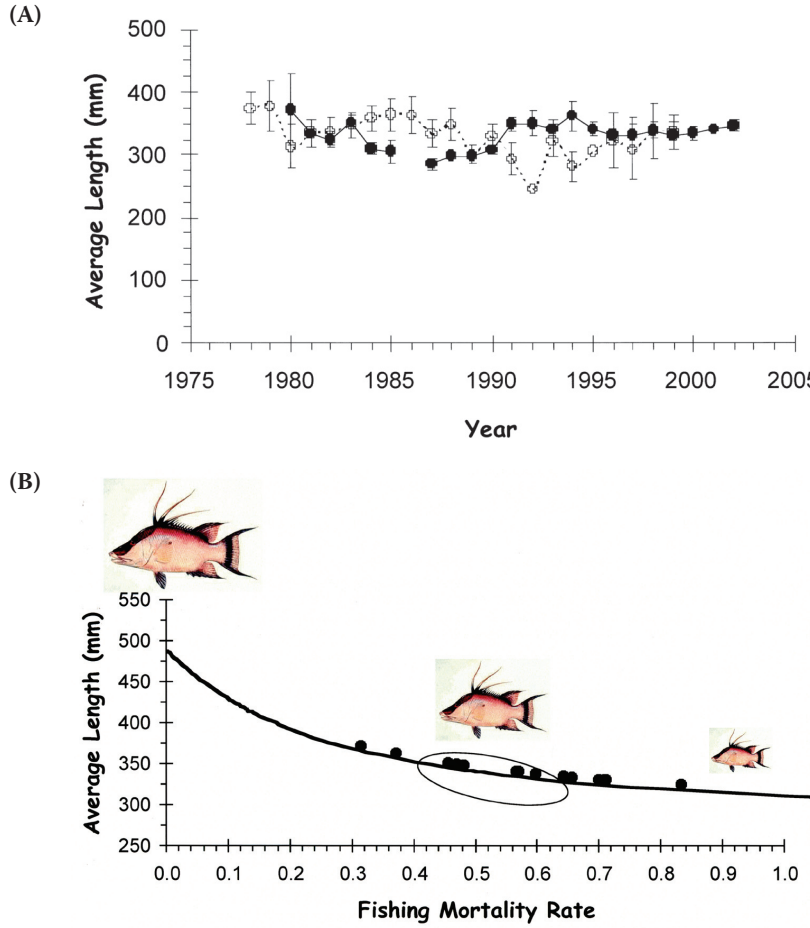


Figure 8. (A) Comparisons of estimates of average length of hogfish in the exploited phase from fishery-independent reef fish visual (RVC) census diver surveys (solid points) and fishery-dependent headboat surveys (open circles) for 1978–2002. (B) Theoretical relationship (solid line) between average length of exploited phase and fishing mortality rate, and observed point estimates (solid circles) for hogfish for 1990–2002.

and depth. For key species in the analyses, abundance of size-age cohorts was proportionally distributed among spatial units according to habitat-specific densities estimated from RVC surveys. Cohort movement among spatial units was modeled according to several different scenarios of snapper-grouper site fidelity over a cohort's lifespan, ranging from strong (no movement among spatial units) to moderate (home range movement patterns) to weak (meandering, random movement pattern). This approach enabled us to evaluate a range of movement patterns given the lack of data on fine-scale movement of snapper-grouper species (Ault et al., 2000). Prior to simulated reserve implementation, the spatial pattern of fishing effort was distributed in proportion to spatial density estimates of a given fish stock, under the assumption that fishers know the spatial patterns of fish abundance. We also assumed conservatively that reserve implementation did not eliminate fishing effort, but rather displaced it from protected to non-protected spatial units. Thus, after implementation, the overall stockwide nominal fishing effort remained the same, but the fishing

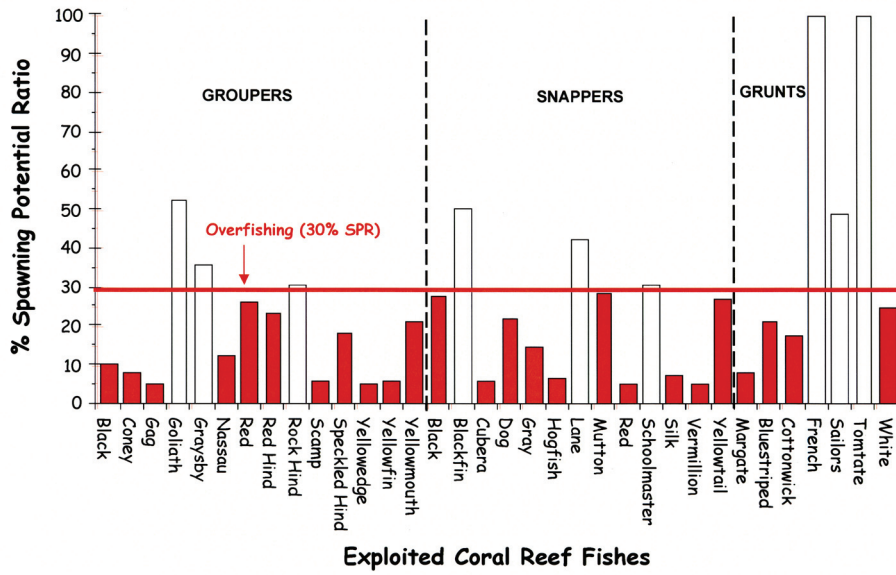


Figure 9. Spawning potential ratio (SPR) analysis for 34 exploited species in the snapper-grouper complex from the Florida Keys for the period 2000–2002. Dark bars indicate overfished stocks and open bars indicate stocks that are above the 30% SPR standard.

mortality rate dropped to zero inside reserves and increased to higher levels outside the reserves.

A series of computer simulation experiments were conducted to elucidate the attributes of reserve design that are most influential in the spatial control of fishing impacts (Ault et al., 2000; Meester, 2000; Meester et al., 2001, 2004). These experiments entailed tracking sustainability metrics (e.g., SPR) over a 20-yr period for a suite of snapper, grouper, and grunt species after implementation of spatial closures of varying sizes, numbers, locations, etc. The main finding was that the effect of reserve implementation on stock sustainability was highly dependent upon the location of closures in relation to a species' habitat use pattern. For example, reserves placed in highly productive habitats, determined by high associated resource abundance, increased SPR over time due to the displacement of fishing effort to less productive habitats. Conversely, reserves placed in less productive habitats displaced fishing effort to more productive habitats, resulting in decreased SPR over time. Fish movement patterns also influenced reserve effectiveness. Designs that maximized the time spent inside the reserve boundaries by exploited size cohorts were the most effective in enhancing sustainability. Thus, an effective reserve for a species with home range movement needs to be of sufficient size and location that the home range of a proportion of the population is fully contained within the reserve borders.

In the 1990s, the National Park Service (NPS) and FKNMS began formulating management plans for the Tortugas region that included marine reserves. We applied our spatial demographic model to predict effects of spatial closures as part of an evaluation of proposed management options for mitigating visitor impacts on natural resources in Dry Tortugas National Park (DTNP) (Ault et al., 2000; Meester et al., 2001; Culhane, 2002). The Tortugas region possesses a number of key attributes that made it an ideal location for establishing marine reserves, including extensive and

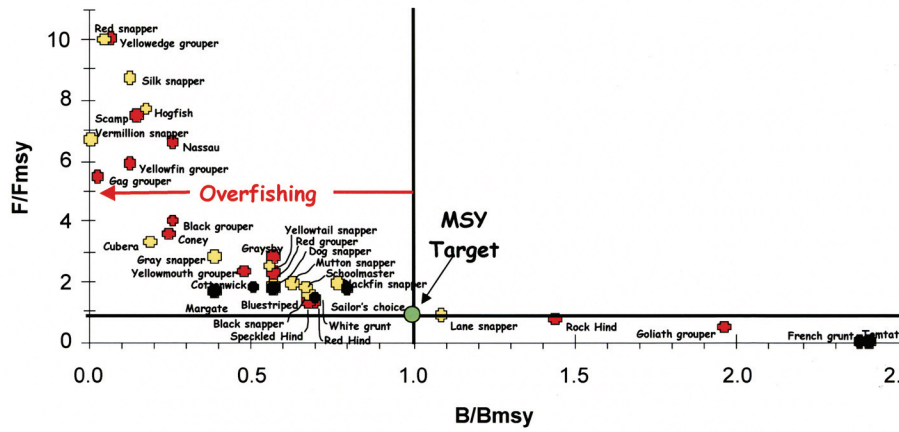


Figure 10. Estimates of the new "precautionary rule" federal criteria for the sustainability of fisheries for 34 species from the Florida Keys snapper-grouper complex. Fisheries above the F/F_{msy} level of 1.0 are considered "overfished."

luxuriant coral reef habitats (Miller et al., 2001), numerous known snapper-grouper spawning sites (Schmidt et al., 1999), and oceanographic conditions conducive for both local retention and export of larvae to other areas in the Keys ecosystem (Lee et al., 1994; Wang et al., 2003; Fig. 4B). A variety of alternative plans were developed for DTNP; some without and some with reserves of differing configurations.

We first conducted spatially intensive fishery-independent diver surveys to characterize and map the benthic habitats (Fig. 11A) and reef fish populations (Fig. 11B) in the Tortugas (Ault et al., 2002; Franklin et al., 2003). Data for 20 snapper-grouper species were then used to parameterize the spatial demographic model for DTNP and to help finalize the design of reserves in FKNMS waters. Simulations were run over 20-yr time horizons to compare the effects of various spatial closure scenarios, including: the status quo (no spatial closures and no changes to existing fishing regulations), and design scenarios C (Fig. 11C) and D (Fig. 11D) that differed in boundary configurations. Key findings for the majority of cases (19 species) were: (1) the status quo scenario resulted in sustainability metrics decreasing to levels below federal benchmarks (i.e., existing levels of fishing mortality on snapper-grouper populations in DTNP were not sustainable); (2) implementation of reserve design C or D resulted in sustainability metrics increasing over time; and, (3) the two reserve designs performed similarly for most grouper species, but design C (Fig. 11C) outperformed design D (Fig. 11D) for most snapper and grunt species.

Simulation results were also incorporated into a more comprehensive "ecosystem analysis" of DTNP alternative management plans addressing a range of human visitor stressors, including fishing, boating, diving, and camping on park natural resources listed in Table 2. A variety of metrics (i.e., management benchmarks) were taken into consideration for evaluating visitor effects on the various resource features, including some of the sustainability metrics from the spatial simulation analyses. Each alternative plan included a number of control measures designed to mitigate the various types of visitor impacts; e.g., daily limits on number of visitors, establishment of reserves, permit system to limit daily vessel use in ecologically sensitive habitats, etc. To analyze the complex combination of control variables simultaneously, we developed an analytic hierarchy process (AHP) model to evaluate each management

plan with respect to its likely effects on the suite of management benchmarks. AHP models are management science tools used to break down complex decision analysis problems into a set of component parts (Saaty, 1986; Saaty and Vargas, 1994). Parts were arranged in a hierarchical order in which the ecosystem components in Table 2 were the first level, and resource features were the second level. The parts of each level were assigned numerical weighting factors based on their relative importance determined by consensus of park managers, and these values were then synthesized into a single, composite weighted score. Quantitative and qualitative data can be combined into this single objective framework (Saaty, 1990). For our application, resource assessment information culled from research studies in the Tortugas region, including our fishery-independent surveys and simulation results, were utilized to weight potential visitor stressors according to their likely impacts on each important resource feature. Resulting AHP scores provided a quantified relative scale of the level of detrimental human impacts on park natural resources expected to result from implementation of various management plans. The highest scores (i.e., the highest levels of detrimental impacts) were associated with plans that did not contain additional controls on fishing, and had minimal controls on human visitation to the park. Plans with the lowest scores included spatial no-take zones and daily limits on visitation. Partially on the basis of this analysis, reserve design 1 was subsequently chosen by the NPS as the preferred management alternative and is set to be implemented in the near future (Culhane, 2002; Brock and Culhane, 2004).

Impacts of Everglades Restoration.—The third application focuses on the potential effects of habitat alteration on reef fishery sustainability resulting from planned Everglades restoration activities. From the late 1940–1960s, the Army Corps of Engineers and the South Florida Water Management District constructed an elaborate network of canals that drained wetlands for agriculture and human habitation, reduced seasonal flooding in urban areas, and provided freshwater for human use. This water management system was a major factor in promoting regional human population growth (Fig. 6). The canal network also detrimentally impacted the Everglades and coastal marine ecosystems by altering the distribution of freshwater within the watershed and the quantity, quality, timing, and spatial locations of freshwater discharges to coastal bays. The Comprehensive Everglades Restoration Plan (CERP, 1999) is a 30-yr project aimed at correcting some of these adverse environmental effects and restoring the terrestrial everglades ecosystem while meeting the anticipated human water needs for the next 50 yrs.

To better understand how some of these proposed changes might affect coastal bay nursery habitats and reef fishery sustainability, we developed a spatial demographic model that explicitly linked population dynamic processes of growth, survivorship, recruitment, and spatial movements to key biotic and abiotic habitat features (Ault and Olson, 1996; Ault et al., 1999b, 2003a; Cosner et al., 1999; Wang et al., 2003; Table 1). The spatial biophysical model tracks multiple cohorts of a fish species (predator) and shrimp species (prey) through time and space. A bioenergetics model was used to describe growth and its influence on mortality and reproductive rates of the fish predator. We modeled prey consumption rates as a function of animal weight, water temperature, salinity, and prey abundance. Modeled respiration rates were functions of weight, temperature, salinity, and average swimming speed. A finite-element hydrodynamic model for Biscayne Bay (Wang, 1978; Wang et al., 1988, 2003) was used to simulate salinity and water currents over a fine-scale spatial

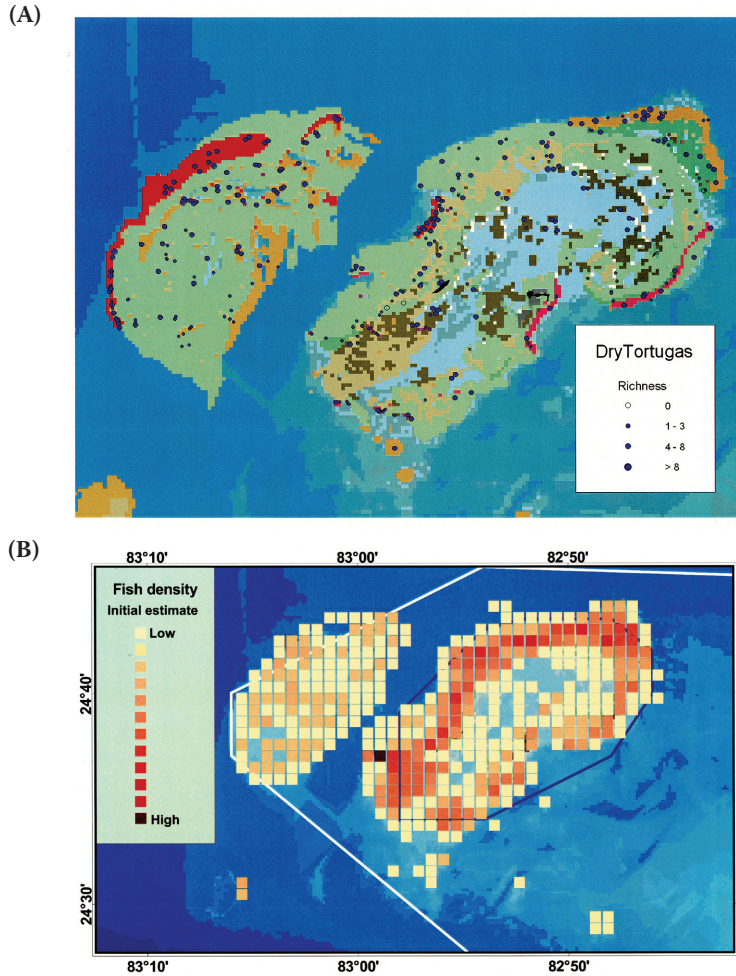
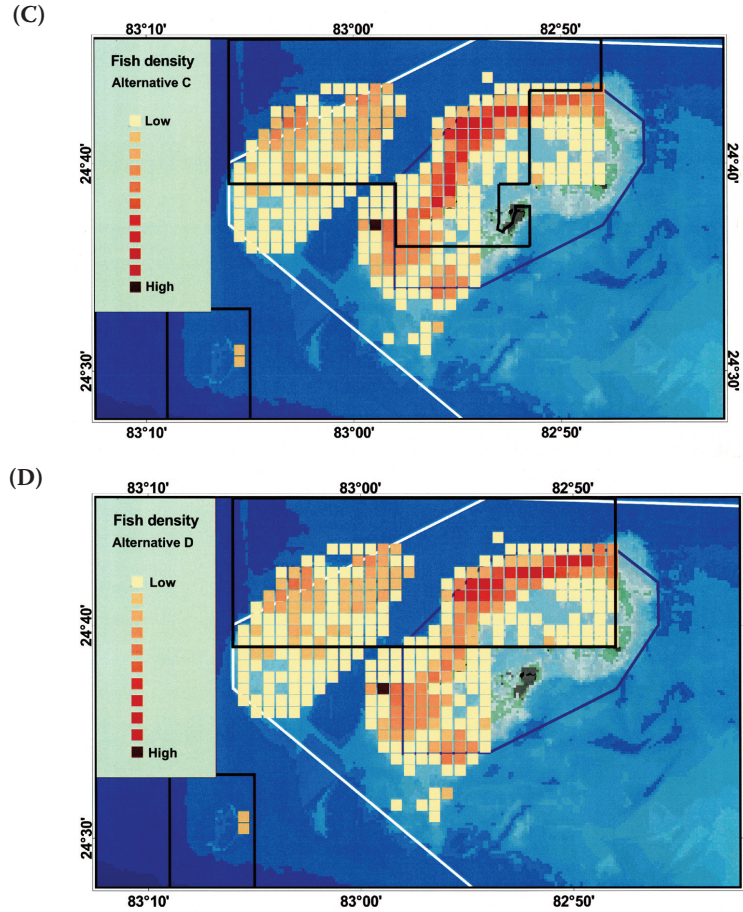


Figure 11. Example of spatial simulation-optimization analysis of marine protected area designs for Dry Tortugas National Park. (A) Benthic habitat map and 1999/2000 visual survey sites showing observed snapper-grouper diversity by site. (B) Initial spatial abundance estimates for black grouper (*Mycteroperca bonaci*) used in the outset of 20-yr MPA design efficacy simulations. *(Opposite page)* (C–D) Black grouper spatial abundance estimates at the end of 20-yr simulations for MPA designs: (C) alternative C (i.e., preferred scenario), and (D) alternative D.

grid in response to wind, tides, and freshwater inflows from canal discharges. A temperature-dependent function was used to model shrimp (prey) growth and shrimp movements were modeled as a function of benthic habitat. The bioenergetics model was used to compute the "spatial growth rate potential" (a spatial index of resource productivity) of the fish predator for each spatial grid cell. Predator movements were based on a search of environment-habitat features that maximized spatial growth rate potential. Natural mortality was dynamically influenced by spatial growth rate potential. Spatial patterns of shrimp and fish recruitment were estimated from larval transport and settlement models that utilized the Biscayne Bay hydrodynamic model (Wang et al., 2003).



Spatial predator-prey model parameters and initial conditions were developed from a number of field and laboratory studies (Ault et al., 1999b). Fishery-independent trawl surveys conducted seasonally in Biscayne Bay (Ault et al., 1999a) provided the primary biological data for setting the initial conditions of spatial abundance for fish and shrimp and were also used to empirically validate model simulation results.

We evaluated two alternative water management scenarios proposed under CERP (Ault et al., 2003a). The "95Base" scenario reflects environmental and human water uses under actual 1995 regional human population and socioeconomic conditions. The "D13R" scenario considers operation changes in water management and water uses for population size projected to occur in 2050 (see www.sfwmd.gov). We found that the highest growth rate potential for juvenile fish (predator) occurred on the bay's midwestern side in both water management scenarios due to the combination of available seagrass beds, high shrimp (prey) densities, and favorable salinities (Fig. 12). In comparing the two scenarios, greater freshwater inputs under D13R resulted in higher daily spatial growth rate potentials than 95Base. D13R also resulted in greater overall population biomass for the fish predator over time compared to 95Base (Fig. 13). Exploitation of the fish (predator) reduced the observed differences in abundance. The implication for snapper-grouper species that utilize coastal bay environments as nursery grounds is that alterations to freshwater inflows may in-

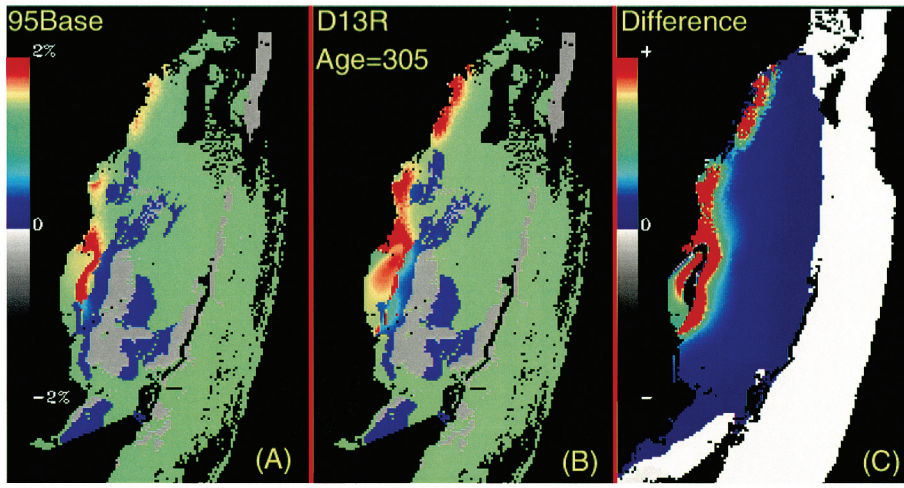


Figure 12. Modeled spatial growth potential or "habitat quality" for the predator (fish) in typical scenario runs of water management strategies (A) 95Base, (B) D13R, as well as (C) the difference between scenarios expressed as D13R–95Base. [Modified from Ault et al., 2003a]

fluence sustainability by changing the abundance of age classes recruiting to the exploited phase of the stock. Depending on which particular water management scenario is selected under the plan for Everglades restoration (and there are more under consideration than the two described here), sustainability could likely be enhanced or jeopardized.

Discussion

Our FSS approach has advanced the understanding of the risks associated with human impacts on the sustainability of the snapper-grouper fishery in the Florida Keys coral reef ecosystem. Two key factors of this approach were to: (1) expand assessment capabilities beyond typical fishery catch and effort data to include fishery-independent data, non-targeted species, species interactions, physical coupling, and ontogenic changes in habitat associations; and, (2) apply systems science principles to improve the information flow in the fisheries analysis process.

A major research finding was that the snapper-grouper complex is experiencing overfishing under current levels of exploitation and that stocks are overfished relative to established sustainable benchmarks (Fig. 10). Calculated current fishing mortality rates are 2–10 times that required to achieve MSY and chronic overfishing has occurred in the Florida Keys for more than two decades. We arrived at these conclusions using new NOAA control rule benchmarks and a length-based assessment with data obtained from fishery-independent surveys that provided spatially synoptic estimates of species abundance and length. Iterative analysis of fish and habitat associations after each survey led to improved accuracy and precision of population estimates while maintaining relatively constant sampling costs. We cross-validated our conclusions with fishery-dependent data and age-structured stock synthesis and surplus production models.

We also spatially extended our length-age structured demographic modeling framework to show the potential of marine reserves to reverse overfishing in the

Table 2. (A) Example of an analytical hierarchy process (AHP) model circumscribing the decision-making process to achieve the management goal of defining a preferred alternative for marine protected area design configuration in the Dry Tortugas, Florida. (B) List of possible stressors acting on the resources in the AHP model.

(A) Ecosystem Component	Resource feature	Management benchmarks	(B) Stressors
Fishery	Exploited reef fishes (snapper-grouper complex) Exploited macroinvertebrates (lobsters, shrimp, etc.) Reef herbivores (damselfish, parrotfish, surgeonfish) Sharks Exploited pelagics (mackerels, dolphinfish, etc.) Baitfish Exceptional fishery resources Endangered/threatened species	Spawning stock biomass (reproductive capacity) Average size in exploited phase Eggs – stock fecundity Yields Catch-per-unit effort Limit control Diversity Spawning aggregations	Private motor boats, commercial vessels, sailboats propeller damage fuel leakage anchoring sewage noise Moorings establishment use Seaplanes Snorkeling/SCUBA Swimming Facilities construction Artificial lighting Hiking Camping Picnicking Wildlife watching Photography
Benthic Habitats	Coral reefs (hard corals, octocorals, sponges) Hardbottoms Seagrasses Sand Islands Exceptional habitat resources	Diversity Percent cover Abundance Fish diversity Fish abundance and size structure	
Wildlife	Frigate birds Sooty and noddy terns Migratory birds Green and loggerhead turtles Exceptional wildlife resources Endangered/threatened resources	Nesting sites Breeding pairs Abundance Resilience	
Marine Environment	Environmental setting Fishing opportunities Encounters with others Natural soundscape Natural lighting Education and Interpretation Safety Water quality	Reef fish and pelagic status Number of visitors Distribution of human users Activities of boats, planes, and humans Water quality indices	

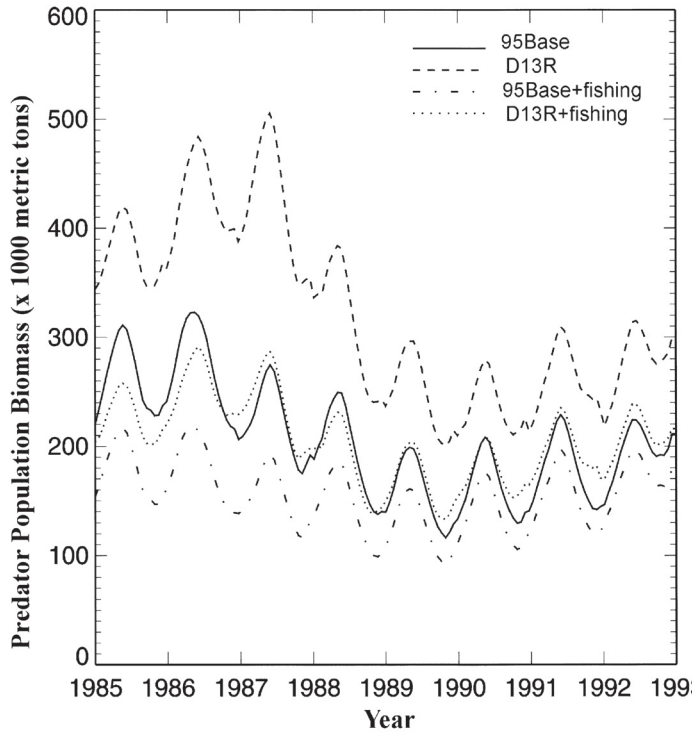


Figure 13. Coastal bay to coral reef spatial simulation model outputs for biomass of the predator (fish) for the period 1985–1993 using 95Base and D13R scenarios with and without exploitation. [Modified from Ault et al., 2003a]

Florida Keys. We developed spatially structured predictive models that consider reef fish abundance, reef habitat, and fishing effort, and we added fish movement as an important dynamic process. Our simulations and the environmental impact index derived from AHP decision models were used to evaluate alternative designs and to select final boundaries for implementing new marine reserves in the Dry Tortugas. In light of the severe overfishing problems in the Florida Keys, the process of reserve design and implementation by FKNMS and NPS represents a precautionary and proactive marine resource management measure. Additionally, both agencies are implementing monitoring programs to track reserve performance.

Lastly, we showed that coupled biophysical models were effective for understanding resource risks associated with exploitation and non-fishing impacts, such as habitat alterations in coastal bay nursery habitats. Innovative features of these models were the incorporation of bioenergetics to link growth, survivorship, and movement of predator and prey species, as well as to environmental features such as hydrodynamics, water quality, and benthic habitat. A unique aspect of this modeling was the development of a new sustainability metric, "spatial growth rate potential," as a measure of the productive capacity of habitats. The down side of this approach is that it requires precise spatial data, many parameter estimates, explicit links to physical models, and is computationally expensive to implement.

Compared to decision theory based on relatively simple models with few parameters (e.g., Hilborn and Walters, 1992), our systems science framework attempts to

better model reality and predict management results using more complex models that capture a wider breadth of factors. We believe that this approach is preferable because it is ecosystem-based in considering the many diverse and important physiological, ecological, physical, oceanographic, and human processes. While we have made significant advances, spatial multi-cohort structured demographic modeling is at an early stage of development. More theoretical and empirical work is needed to better understand and model fish movements, predator-prey interactions, and spatial dynamics of fishing fleets. These models will require high resolution, spatially-explicit, co-occurrent biological and physical data for both animal populations and environmental forcing features that can only be obtained from fishery-independent sampling surveys. More reality checks are needed to cross-validate statistical estimates, and to test robustness and reliability of model parameters and predictions, and model validity at all stages of analysis. True validation will require comparing model-predicted future ecosystem responses to management changes in human impacts with those that actually occur.

Future Prospects for Sustainable Fisheries

An immediate priority is to reduce fishing mortality rates in the Florida coral reef ecosystem to levels that ensure long-term fishery sustainability and productivity. Whether stocks decline from fishing or detrimental environmental changes, the appropriate fishery policy choice is the same: reduce fishing pressure (Rosenberg, 2003). We believe that traditional approaches of simply adjusting minimum size limits and establishing seasons, gear restrictions, quotas and bag limits alone are unlikely to be effective at reducing fishing pressure because multispecies reef fish fisheries are especially vulnerable to continued bycatch release mortality, technological improvements in fishing, ecosystem alterations, and growing demands for participation, especially by the recreational sector. Even if fishing mortality was reduced to zero throughout the Keys, the life history characteristics of species in the snapper-grouper complex indicate that recovery may take over 10 yrs for most snapper species and more than 20 yrs for most grouper species. Our spatial demographic models show the potential value of coupling traditional control measures with spatial closures in this effort to ensure fishery sustainability.

Any management actions to control fishing mortality must anticipate future regional human population growth and exploitation demands. The systems science framework shows that any gains achieved towards rebuilding depleted reef fish stocks through effort reductions could easily be lost due to other factors affecting sustainability such as habitat degradation and exploitation of prey and predator species. Habitat alterations, including loss and degradation of seagrass and mangroves (e.g., Porter and Porter, 2001) and reef-building corals (e.g., Gardner et al., 2003), have occurred throughout the Keys from a variety of anthropogenic and natural impacts and have likely reduced the productive capacity of the ecosystem for sustaining snapper-grouper populations. Also, fisheries on prey resources, notably pink shrimp and baitfishes, may be reducing reef fish food supply and thus impeding stock rebuilding.

The challenge to achieving long-term reef fish sustainability requires new scientific approaches and management measures commensurate with the rising complexity of human-ecosystem interactions. Our nascent development of a FSS framework

has shown some progress that we believe is an important step towards meeting this challenge.

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Literature Cited

Ault, J. S. 1996. A fishery management system approach for Gulf of Mexico living resources. Pages 106–111 *in* P. J. Rubec and J. O'Hop, eds. GIS applications for fisheries and coastal resources management. Gulf States Marine Fisheries Commission 43, Ocean Springs.

_____ and N. M. Ehrhardt. 1991. Correction to the Beverton and Holt Z-estimator for truncated catch length-frequency distributions. ICLARM Fishbyte 9: 37–39.

_____ and W. W. Fox, Jr. 1989. FINMAN: simulated decision analysis with multiple objectives. Pages 166–179 *in* E. F. Edwards and B. A. Megrey, eds. Mathematical analysis of fish stock dynamics. Am. Fish. Soc. Symp. 6, Bethesda.

_____ and J. Luo. 1998. Coastal bays to coral reefs: systems use of scientific data visualization in reef fishery management. International Council for the Exploration of the Seas. ICES C. M. 1998/S: 3. Estoril, 16 p.

_____ and D.B. Olson. 1996. A multicohort stock production model. Trans. Am. Fish. Soc. 125: 343–363.

_____, J. A. Bohnsack, and G. A. Meester. 1997. Florida Keys National Marine Sanctuary: retrospective (1979–1995) assessment of reef fish and the case for protected marine areas. Pages 385–395 *in* D. A. Hancock, D. C. Smith, A. Grant, and J. P. Beumer, eds. Developing and sustaining world fisheries resources: the state of science and management. 2nd World Fisheries Congress Proceedings. CSIRO Publishing, Collingwood.

_____, _____, and _____. 1998. A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys. Fish. B-NOAA 96: 395–414.

_____, J. Luo, and J. D. Wang. 2003a. A spatial ecosystem model to assess spotted seatrout population risks from exploitation and environmental changes. Pages 267–296 *in* S.A. Bortone ed. Biology of spotted seatrout. CRC Press, Boca Raton.

_____, S. G. Smith, and J. A. Bohnsack. 2005. Evaluation of average length as an indicator of exploitation status for the Florida coral reef fish community. ICES J. Mar. Sci. 61.

_____, _____, G. A. Diaz, and E. Franklin. 2003b. Florida hogfish fishery stock assessment. Rpt. to Flor. Fish and Wildlife Cons. Com. 67 p., figs., tables.

_____, G. A. Diaz, S. G. Smith., J. Luo, and J. E. Serafy. 1999a. An efficient sampling survey design to estimate pink shrimp population abundance in Biscayne Bay, Florida. North Am. J. Fish. Manage. 19: 696–712.

_____, G. A. Meester, J. Luo, S. G. Smith, and K. C. Lindeman. 2000. Natural resources affected environment. Dry Tortugas National Park Gen. Manage. Plan. National Park Service. Denver. 250 p.

_____, S. G. Smith, G. A. Meester, J. Luo, and J. A. Bohnsack. 2001. Site characterization for Biscayne National Park: assessment of fisheries and habitats. NOAA Tech. Memo. NMFS-SEFSC-468. 185 p.

_____, S. G. Smith, J. Luo, G. A. Meester, J. A. Bohnsack, and S.L. Miller. 2002. Baseline multispecies coral reef fish stock assessment for the Dry Tortugas. NOAA Tech. Memo. NMFS-SEFSC-487. 117 p.

_____, J. Luo, S. G. Smith, J. E. Serafy, J. D. Wang, R. Humston, and G. A. Diaz. 1999b. A spatial dynamic multistock production model. Can. J. Fish. Aquat. Sci. 56 S1: 4–25.

Bannerot, S. P. 1990. Fisheries biology. Pages 246–265 *in* Fish communities and fisheries biology. Synthesis of available biological, geological, chemical, socioeconomic, and cultural resource information for the South Florida area. Rpt. for Minerals Manage. Ser., U.S. Dept. Interior, Continental Shelf Associates, Inc. Jupiter. 657 p.

Baranov, T. L. 1918. On the question of the biological basis of fisheries. Nauchn. Issled. Ikhtiologicheskii Inst. Izv. 1: 81–128.

Beverton, R. J. H. and S. J. Holt. 1957. On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food. Fishery Investigations (UK), series II, vol. XIX. Lowestoft. 533 p.

Bohnsack, J. 1998. Application of marine reserves to reef fisheries management. Aust. J. Ecol. 23: 298–304.

_____ and J. S. Ault. 1996. Management strategies to conserve marine biodiversity. Oceanography 9: 73–82.

_____ and S. P. Bannerot. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. U.S. Dept. Commer., NOAA Tech. Rep. NMFS 41. 15 p.

_____, Ault, J. S., and B. Causey. 2004. Why have no-take marine protected areas? Amer. Fish. Soc. Symp. 42: 185–193.

_____, D. E. Harper, and D. B. McClellan. 1994. Fisheries trends from Monroe County, Florida. Bull. Mar. Sci. 54: 982–1018.

_____, D. B. McClellan, D. E. Harper, G. S. Davenport, G. J. Konoval, A. M. Eklund, J. P. Contillo, S. K. Bolden, P. C. Fischel, G. S. Sandorff, and others. 1999. Baseline data for evaluating reef populations in the Florida Keys. NOAA Tech. Memo. NMFS-SEFSC-427. 52 p.

Broadhead, G. 1952. Information system needed for sustaining Florida fisheries. Proc. Gulf Caribbean Fish. Inst. 2: 55–62.

Brock, R. J. and B. F. Culhane. 2004. The no-take research natural area of Dry Tortugas National Park (Florida): wishful thinking or responsible planning? Amer. Fish. Soc. Symp. 42: 67–74.

CERP (Comprehensive Everglades Restoration Plan). 1999. Central and southern Florida project, comprehensive review study, final integrated feasibility report and programmatic environmental impact statement. U.S. Army Corps of Engineers and South Florida Water Manage. District, West Palm Beach (http://www.evergladesplan.org/about/rest_plan.cfm).

Chiappone, M. and R. Sluka. 1996. Fishes and fisheries. Site characterization for the Florida Keys National Marine Sanctuary and environs. Nature Conservancy. The Preserver, Zenda, WI. 6: 149 p.

Claro, R., K. C. Lindeman, and L. R. Parenti. 2001. Ecology of the marine fishes of Cuba. Smithsonian Institution Press, Washington. 253 p.

Coleman, F. C., C. C. Koenig, G. R. Huntsman, J. A. Musick, A. M. Eklund, J. C. McGovern, R. W. Chapman, G. R. Sedberry, and C. B. Grimes. 2000. Long-lived reef fishes: the grouper-snapper complex. Fisheries 25: 14–21.

Cosner, C., D. L. DeAngelis, J. S. Ault, and D.B. Olson. 1999. Effects of spatial grouping on the functional response of predators. Theor. Popul. Biol. 56: 65–75.

Cowie-Haskell, B. D. and J. M. Delaney. 2003. Integrating science into the design of the Tortugas ecological reserve. Mar. Technol. Soc. J. 37: 1–14.

Culhane, B. 2002. A new era for marine resource protection at Dry Tortugas and the Florida Keys. Pages 30–32 *in* J. Selleck, ed. Natural resource year in review—2001. U.S. Dept. Interior, Natl. Park Serv., Lakewood.

Domeier, M. L. and P. L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. Bull. Mar. Sci. 60: 698–726.

Ehrhardt, N. M. and J. S. Ault. 1992. Analysis of two length-based mortality models applied to bounded catch length frequencies. Trans. Amer. Fish. Soc. 121: 115–122.

Florida Statistical Abstracts. 2002. University of Florida, Gainesville. 846 p.

Franklin, E. C., J. S. Ault, S. G. Smith, J. Luo, G. A. Meester, G. A. Diaz, M. Chiappone, D. W. Swanson, S. L. Miller, and J. A. Bohnsack. 2003. Benthic habitat mapping in the Tortugas region, Florida. Mar. Geod. 26: 19–34.

FWC. 2003. Fishing capital of the world. Florida Fish and Wildlife Conservation Commission, Tallahassee. <http://www.floridaconservation.org>

Gardner, T. A., I. M. Cote, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. Science 301: 958–960.

Gulland, J. A. 1983. Fish stock assessment: a manual of basic methods. FAO/Wiley Series on Food and Agriculture. 1: 223 p.

Haddon, M. 2001. Modeling and quantitative methods in fisheries. Chapman and Hall/CRC Press, Boca Raton. 406 p.

Halpern, B. S. and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecol. Lett. 5: 361–366.

Harper, D. E., J. A. Bohnsack, and B. R. Lockwood. 2000. Recreational fisheries in Biscayne National Park, Florida, 1976–1991. Mar. Fish. Rev. 62: 8–26.

Hilborn, R. and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York. 570 p.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–638.

Johns, G. M., V. R. Leeworthy, F. W. Bell, and M. A. Bonn. 2001. Socioeconomic study of reefs in southeast Florida: Final Report. Hazen and Sawyer Environmental Engineers and Scientists, New York. 349 p.

Lee, T. N., M. E. Clarke, E. Williams, A. F. Szmant, and T. Berger. 1994. Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. Bull. Mar. Sci. 54: 621–646.

Leeworthy, V. R. and P. Vanasse. 1999. Economic contribution of recreating visitors to the Florida Keys/Key West: Updates for years 1996–1997 and 1997–1998. NOAA, Silver Spring. 20 p.

Lindeman, K. C., R. Pugliese, G. T. Waugh, and J. S. Ault. 2000. Developmental pathways within a multispecies reef fishery: management applications for essential fish habitats and protected areas. Bull. Mar. Sci. 66: 929–956.

Mace, P. 1997. Developing and sustaining world fishery resources: state of science and management. Pages 1–20 *in* D. A. Hancock, D. C. Smith, A. Grant, and J. P. Beumer, eds. Developing and sustaining world fisheries resources: the state of science and management. Proc. 2nd World Fishery Congress, Brisbane.

Meester, G. A. 2000. A mathematical programming and simulation-based approach to determining critical factors in the design of effective marine reserve plans for coral reef fishes. PhD Diss., University of Miami, Coral Gables. 309 p.

_____, J. S. Ault, S. G. Smith, and A. Mehrotra. 2001. An integrated simulation modeling and operations research approach to spatial management decision making. Sarsia 86: 543–558.

_____, A. Mehrotra, J. S. Ault, and E. Baker. 2004. Designing marine reserves for fishery management. Manage. Sci. 50: 1031–1043.

Methot, R.D. 1990. Synthesis model: an adaptive framework for analysis of diverse stock assessment data. Inter. North Pac. Fish. Comm. Bull. 50: 259–277.

Miller, S. L., M. Chiappone, D. W. Swanson, J. S. Ault, S. G. Smith, G. A. Meester, J. Luo, E. C. Franklin, J. A. Bohnsack, D. E. Harper, and D.B. McCllelan. 2001. An extensive deep reef terrace on the Tortugas Bank, Florida Keys National Marine Sanctuary. Coral Reefs 20: 299–300.

Musick, J. A., M. M. Harbin, S. A. Berkeley, G. H. Burgess, A. M. Eklund. L. Findley, R. G. Gilmore, J. T. Golden, D. S. Ha, G. R. Huntsman, J. C. McGovern, S. J. Parker, S. G. Poss, E. Sala, T. W. Schmidt, G. R. Sedberry, H. Weeks, and S. G. Wright. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). Fisheries 25: 6–30.

Neumann, C. J. 1987. The National Hurricane Center Risk Analysis Program (HURISK). NOAA Tech. Memo., NWS-NHC-38. 56 p.

NOAA Fisheries. 2002. The status of U.S. Fisheries: 2002 report to congress. 111 p.

Olson, D. B. 2001. Biophysical dynamics of western transition zones: a preliminary synthesis. Fish. Ocean. 10: 133–150.

_____. 2002. Biophysical dynamics of ocean fronts. The Sea 12: 187–218.

Oppel, F. and T. Meisel. 1871. Along the Florida Reef. Pages 265–309 *in* Tales of old Florida. Castle Press, Seacaucus.

Porter, J. W. and K. G. Porter (eds.). 2001. The Everglades, Florida Bay, and coral reefs of the Florida Keys. CRC Press, Boca Raton. 1000 p.

Prager, M.H. 1994. A suite of extensions to a non-equilibrium surplus-production model. Fish. Bull. 92: 374–389.

Quinn, T. J. and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, Oxford. 542 p.

Restrepo, V. R. and J. E. Powers. 1999. Precautionary control rules in U.S. fisheries management: specifications and performance. ICES J. Mar. Sci. 56: 846–852.

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

Rosenberg, A. A. 2003. Managing to the margins: the overexploitation of fisheries. Front. Ecol. Environ. 1: 102–106.

Rothschild, B. J. 1971. A systems view of fishery management with some notes on the tuna fisheries. FAO Fish. Tech. Pap No. 106. Rome, 45 p.

_____. 1973. Questions of strategy in fishery management and development. J. Fish. Res. Bd. Can. 30: 2017–2030.

_____, J. S. Ault, and S. G. Smith. 1996. A systems science approach to fisheries stock assessment and management. Pages 473–492 *in* V. F. Gallucci , S. Saila, D. Gustafson, and B. J. Rothschild, eds. Stock assessment: quantitative methods and applications for small scale fisheries. Lewis Publishers (Division of CRC Press), Chelsea.

Russell, E. S. 1931. Some theoretical considerations on the overfishing problem. J. Cons. Int. Explor. Mer. 6: 3–27.

Saaty, T. L. 1986. Axiomatic foundation of the analytical hierarchy process. Manage. Sci. 32: 16 p.

_____. 1990. The analytical hierarchy process: planning, priority setting, resource allocation. RWS Publications, Pittsburgh. 287 p.

_____ and L. G. Vargas. 1994. Decision making in economic, political, social, and technological environments. RWS Publications, Pittsburgh. 330 p.

Schmidt, T. W., J. S. Ault, and J. A. Bohnsack. 1999. Site characterization for the Dry Tortugas region: fisheries and essential habitats. Report to the Florida Keys National Marine Sanctuary and National Park Service. 113 p. plus app.

Stark, W. A. II. 1968. A list of fish of Alligator Reef, Florida with comments on the nature of the Florida reef fish fauna. Undersea Biol. 1: 4–40.

Sterman, J. D. 2000. Business dynamics: systems thinking and modeling for a complex world. Irwin McGraw-Hill, New York. 982 p.

Stommel, H. 1976. The Gulf Stream. University of California Press. Berkeley. 248 p.

Thompson, W. F. and F. H. Bell. 1934. Biological statistics of the Pacific halibut fishery. Rep. Int. Pac. Halibut Comm. 8: 49 p.

US Department of Commerce. 1996. Florida Keys National Marine Sanctuary Final Management Plan/Environmental Impact Statement (FMP/EIS), vol. 1: The management plan. NOAA, Washington DC. 319 p.

_____. 2002. Fisheries of the United States. 2001. National Marine Fisheries Service, Office of Sci. Tech., Silver Spring. 126 p.

Walters, C. J. 1986. Adaptive management of renewable resources. MacMillan, New York. 374 p.

Wagner, H. M. 1975. Principles of operations research: with applications to managerial decisions. Prentice-Hall, Inc., Englewood Cliffs. 1039 p.

Wang, J. D. 1978. Real time flow in unstratified shallow water. J. Watwy. Port Coastal Ocean. Div. ASCE 104 (WW1): 53–68.

_____, S. V. Cofer-Shabica, and J. Chin Fatt. 1988. Finite element characteristic advection model. J. Hyd. Eng. 114: 1098–1114.

_____, J. Luo, and J. S. Ault. 2003. Flows, salinity, and some implications for larval transport in south Biscayne Bay, Florida. Bull. Mar. Sci. 72: 695–723.

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