A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys

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Abstract.–A baseline assessment of 35 economically and ecologically important Florida Keys reef fish stocks is provided by using a systems approach that integrates sampling, statistics, and mathematical modeling. Quantitative fishery-independent data from reef fish visual surveys conducted by SCUBA divers from 1979 to 1996 were used to develop estimates of population abundance, assemblage composition, and stock structures in relation to key physical and habitat factors. Exploitation effects were assessed with a new length-based algorithm that calculates total mortality rates from estimates of "average length of fish in the exploitable phase of the stock." These estimates were highly correlated for two statistically independent data sources on reef fish: fishery-independent diver observations and fishery-dependent head boat catches. We developed a reef fish equilibrium exploitation fishery simulation (REEFS) model and used estimates of fishing mortality to assess yield-per-recruit in relation to fishing intensity and gear selectivity and to assess spawning potential ratio (SPR) in relation to U.S. federal "overfishing" standards. Our analyses show that 13 of 16 groupers (Epinephelinae), 7 of 13 snappers (Lutjanidae), one wrasse (Labridae), and 2 of 5 grunts (Haemulidae) are below the 30% SPR overfishing minimum. Some stocks appear to have been chronically overfished since the late 1970s. The Florida Keys reef fishery exhibits classic "serial overfishing" in which the largest, most desirable, and vulnerable species are depleted by fishing. Rapid growth of the barracuda population (Sphyraenidae) during the same period suggests that fishing has contributed to substantial changes in community structure and dynamics.

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The Florida Keys support a rich tropical marine ecosystem, a productive multispecies coral reef fishery, and a billion dollar tourist economy. The Florida Keys are also considered an "ecosystem-at-risk" as one of the nation's most significant yet most stressed marine resources under management of the National Oceanic and Atmospheric Administration (NMFS, 1996). Concern about habitat degradation and escalating resource uses from a rapidly growing human population in southern Florida resulted in the establishment of the Florida Keys National Marine Sanctuary (FKNMS) in 1990. Because they are one of the most complex ecosystems on earth, coral reefs are a particular concern. The diverse fish community of these coral reefs is influenced by complicated biological and physical interactions (Sale, 1991; Lee et al., 1992; Polunin and Roberts, 1996). Reef fisheries can target a number of economically and ecologically important species (e.g. groupers, snappers, lobsters, conch, sponges, and corals). Over the past several decades, public use of and conflicts over fishery resources have increased sharply, while some fishery catches from historically productive snapper and grouper stocks have declined (Bohnsack et al., 1994). Concomitantly, the status and biological dynamics of these reef fishery resources are not well understood, and important stock assessment data are not available.

Another concern regarding reef fishery resources is the restoration of the Everglades north of the Florida Keys. Hydrological projects of historic proportions are expected to make a substantial change in the timing, volume, and location of freshwater outflows into the coastal marine environment (Harwell et al., 1996). These changes could affect the survivorship of juvenile reef fishes in critical shallow nursery areas of Florida Bay and Biscayne Bay and ultimately affect the productivity of the entire coral reef ecosystem.

The condition of most reef fish stocks is unknown because of the large number of species in the fishery, a lack of fishery-effort and landings data, and the quantity of population dynamics data needed to do traditional stock assessments. The goal of this paper is to develop a technically sound quantitative method for multispecies management assessments. For this purpose, we present an integrated baseline assessment to reference the status of the multispecies fishery so that the effects of management changes in the FKNMS may be accurately evaluated in the future (U.S. Dep. Commerce, 1996). Using fishery-independent data, we conducted an 18-year retrospective, analytical yield assessment of economically important Florida Keys reef fish stocks to elucidate the effects of fishing and to help define an effective fishery management strategy.

Hypothesis

A key to our ability to assess reef fish stocks was the use of "average size" (in length) of fish in the exploitable phase of the population ($\bar{L}$) as an indicator of stock status. Average size of fish was derived from visual survey data or headboat landings data. Headboats are party boats that carry more than 15 anglers per fishing trip (Dixon and Huntsman[1]). The use of $\bar{L}$ in stock assessment has deep roots in traditional fisheries management (Beverton and Holt, 1956, 1957; Ricker, 1975). The statistic provides a population level metric that integrates individual metabolic variables such as interdependent growth, mortality, and reproductive processes. The $\bar{L}$ statistic also is an important index of fishing effects because persistent heavy fishing reduces the average size of the population over time, making the stock younger through a process known as "juvenescence" which successively eliminates older, more fecund size classes (Ricker, 1963). This is extremely important in the context of stock and recruitment because the fecundity potential of individuals increases exponentially with size. In general, the average length of fish in the exploitable phase (i.e. between the size at first capture, L', and the maximum size, L_λ) is highly correlated with average population size and thus reflects the rate of fishing mortality operating in the fishery.

Theoretically, the average size of fish landed for any given species should be equal to the average size in the exploited phase of the remaining population just after fishing. In other words, we hypothesize that fishery-independent survey estimates of average length derived from visual data reported by divers should equal fishery-dependent estimates derived from catch data reported by headboat anglers. The greater the correlation between the two independent estimates of $\bar{L}$, the more robust "average length" should be as an indicator of stock status subject to exploitation.

[1] Dixon, R. L., and G. R. Huntsman. 1992. Estimating catches and fishing effort of the southeast United States headboat fleet, 1972–1982. Beaufort Laboratory, Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Beaufort, NC 28516. Draft report.

Methods and materials

Study area

The Florida Keys coral reef ecosystem is a unique tropical coastal marine environment stretching about 370 km from Key Biscayne southwest to the Dry Tortugas (Fig. 1). Situated parallel to the Florida current and Florida Bay, the coastal ecosystem encompasses many varied habitats comprising fresh- to saltwater marshes, estuaries, lagoons, mangrove stands, coral islands, sea grass beds, and coral reefs. Florida Bay and adjacent coastal estuaries serve as nursery areas for spiny lobster and many juvenile fishes that occupy reefs as adults. The clear water and high diversity of reef fish in the Florida Keys coral reef tract provide a unique environment to assess multispecies fisheries. Here we use a "systems approach" to facilitate effective decision making and to improve fishery management performance (Ault and Fox, 1989; Rothschild et al., 1996).

Reef fish surveys

Fishery-independent visual estimates of the abundance and size distributions of multispecies reef fish populations were taken along the Florida Keys reef track continuously from 1979 to 1996 (Table 1) by 12 highly trained and experienced divers using the stationary visual survey method of Bohnsack and Bannerot (1986). This nondestructive method provides reliable quantitative estimates of species abundance, frequency-of-occurrence, and size structure for the reef fish community. Divers recorded the abundance as well as the minimum, mean, and maximum lengths of each species seen during 5 minutes within randomly selected 7.5-m radius circular quadrats. Underwater visual estimates of reef fish size and abundance have frequently been made (Bellwood and Alcala, 1988; Harvey and Shortis, 1996); however, accurate and precise visual estimates of fish length require well-trained and experienced observers because objects in water appear magnified and closer than their actual range (Bell et al., 1985; Harvey and

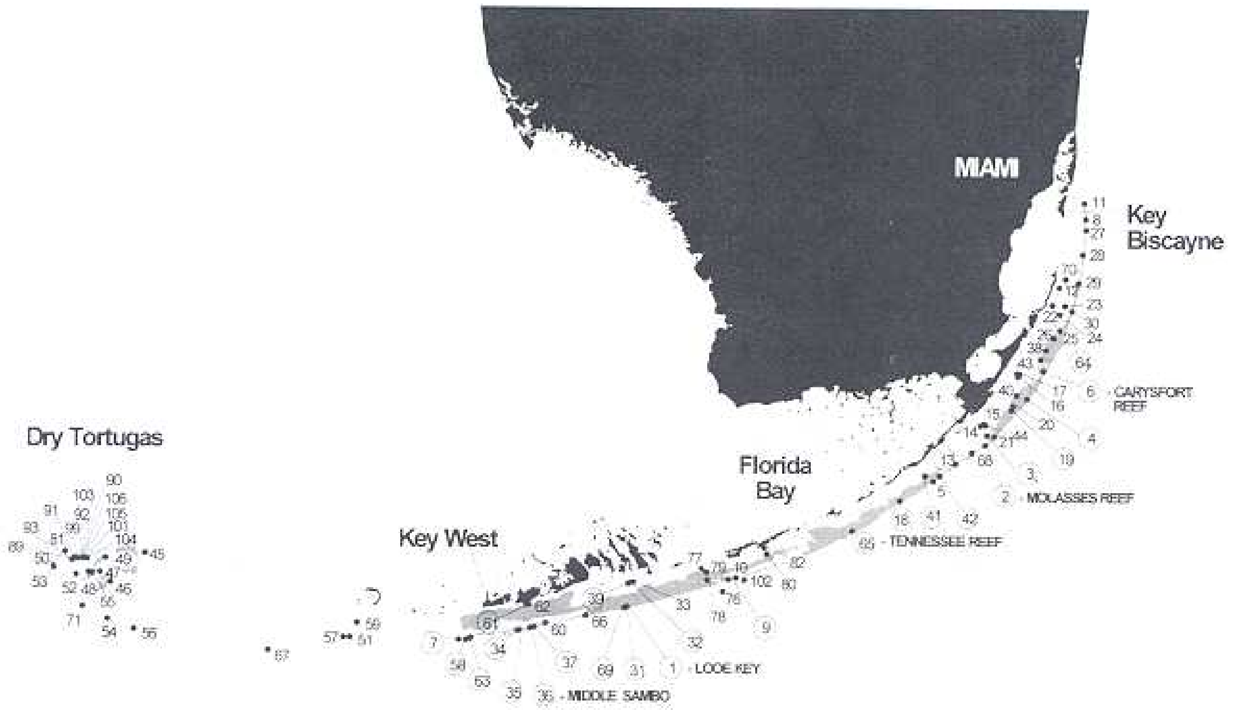

Figure 1

Map of the Florida Keys coastal marine ecosystem showing the coral reef tract (light gray) running offshore from Key Biscayne southwest to the Dry Tortugas, and the spatial relationships of Florida Bay, Key West, and the Miami urban center. Numbered darkened circles show the 89 reefs where 4,571 visual survey samples of the reef fish community were taken from 1979 to 1996. Open circles around numbers indicate sanctuary preservation areas (SPAs).

Table 1

Visual survey sampling effort (number of point samples) by habitat areas and depth intervals conducted from 1979 to 1996 in the Florida Keys reef tract. The offshore zone is exposed to the Florida Current.

Depth		Reef zone habitat type: Artificial reef	Coral reef		Hard bottom		Sand bottom	Totals	
Feet	Meters	Inshore	Inshore	Offshore	Inshore	Offshore	Inshore	Total	Percent
0–10	0–3.05	0	848	171	26	8	13	1,066	23.32
10–20	3.05–6.10	5	726	816	14	207	38	1,806	39.51
20–30	6.10–9.14	85	403	561	4	146	0	1,199	26.23
30–40	9.14–12.19	28	31	92	0	40	0	191	4.18
40–50	12.19–15.24	9	9	81	0	48	0	147	3.22
50–60	15.24–18.29	0	15	65	0	47	0	127	2.78
60–70	18.29–21.34	0	1	34	0	0	0	35	0.77
Total		127	2,033	1,820	44	496	51	4,571	
Percent		2.78	44.48	39.82	0.96	10.85	1.12		100.00

Shortis, 1996). To improve accuracy, divers continuously calibrated their length estimates with a 30-cm ruler attached perpendicular to the far end of a meterstick. Divers without calibration sticks have been shown to obtain a mean accuracy of 86% for length estimates (St. John et al., 1990).

Maximum use of the visual survey data required statistical intercalibration of the sampling efficiency of each diver. We used multiple regression analysis (Neter et al., 1996) to estimate relative sampling efficiency by adapting the "fishing power" model of Robson (1966)

$$C(d,t) = F(d,t)N(t)\xi(d,t) = q(d)f(d,t)N(t)\xi(d,t)$$
$$\rightarrow \frac{C(d,t)}{f(d,t)} = q(d)\overline{N}(d,t), \quad (1)$$

where $C(d,t)$ = the fish count of diver d at reef date t;
$N(t)$ = the average population size at reef date t;
$q(d)$ = the coefficient of sampling efficiency for diver d;
$f(d,t)$ = the nominal survey effort of diver d at reef date t, and
$\xi(d,t)$ = a log normally distributed error variable.

To account for any sampling bias that may have been introduced by differences among divers, a simple log-linear transformation of Equation 1 makes it possible to obtain minimum variance estimates of relative sampling efficiency, given fish counts by species, by diver, and by reef date. Data used for model development were derived from a series of controlled experiments conducted during a 9-day sampling expedition to the Dry Tortugas during June 1994. A matrix of estimated efficiency coefficients for divers by species was used to adjust an individual diver's results in relation to a standard-normal diver, here the most experienced diver in the group. After standardization, all the individual visual "catch-per-unit-of-effort" measurements were comparable over time and space (Ault et al.[2]). Spatial and temporal patterns in abundance and correlative linkages to habitat types were qualitatively analyzed with 3-D visualization software (IDL, 1995) by reef site throughout the Florida Keys for various survey years. Multivariate statistical analysis (Johnson and Wichern, 1992; Venables and Ripley, 1994) was used to assess variance-covariance and correlation structures between reef fish density and selected environmental and fish community auxiliary covariates.

We also used the 1981–95 NMFS headboat catch-and-effort data (Bohnsack et al., 1994; Dixon and Huntsman, 1992) to provide fishery-dependent population estimates comparable to those from the visual survey. Headboat data provide total numbers of individuals in the catch as well as total weight in the catch by species by year.

Stock assessment indicator variable

A stock assessment indicator variable is a quantitative measure that reflects the status of a population subjected to fishing or other environmental changes. Because reef fishes integrate aspects of the coastal ocean environment over their lifetime, a robust measure of population "health" or status can provide a sensitive indicator of direct and indirect stress on the stock, and perhaps on the regional marine ecosystem (Fausch et al., 1990). Population health for reef fish communities can best be described with the metabolic-based pool variable "average length in the exploitable phase of the stock." Therefore, to assess the health of each of the s stocks in the reef fish community over the past two decades, the statistic "average length in the exploitable phase of the stock," $\overline{L}(t)$, was found for each stock by integrating between the population age limits from t' (minimum age at first capture) to t_λ (oldest age in the stock), written as

$$\overline{L}(t) = \frac{F(t)\int_{t'}^{t_\lambda} N(a,t)L(a,t)da}{F(t)\int_{t'}^{t_\lambda} N(a,t)da}, \quad (2)$$

where $N(a,t)$ = abundance for age class a at time t;
$L(a,t)$ = length for class a at time t; and
$F(t)$ = the instantaneous fishing mortality rate at time t.

Estimates of the mean, variance, and 95% confidence interval of the mean were computed by the methods of Sokal and Rohlf (1969).

To estimate the annual total instantaneous mortality rate $Z(t)$ for each fish stock in each year t from population size structure and abundance statistics, we used a length-based method (Ault and Ehrhardt, 1991; Ehrhardt and Ault, 1992) particularly applicable to reef fish population dynamics

$$\left[\frac{L_\infty - L_\lambda}{L_\infty - L'}\right]^{\frac{Z(t)}{K}} = \frac{Z(t)\left(L' - \overline{L}(t)\right) + K\left(L_\infty - \overline{L}(t)\right)}{Z(t)\left(L_\lambda - \overline{L}(t)\right) + K\left(L_\infty - \overline{L}(t)\right)}, \quad (3)$$

where, L_λ = maximum size;
L' = the length at first capture;
$\overline{L}(t)$ = the average size in the exploitable phase in year t; and

[2] Ault, J. S., J. A. Bohnsack, and G. Meester. 1998. The relative fishing power of divers in tropical reef fish visual surveys. Unpubl. manuscript.

K and L_∞ = parameters of the von Bertalanffy equation.

Thus, the only unknown variable in Equation 3 is the total mortality rate in year t, $Z(t)$, which can be estimated fairly easily with an iterative algorithm called LBAR (Ault et al., 1996). Finally, by assuming that M, the annual instantaneous rate of natural mortality, is known and constant for the interval Δt, we can estimate the fishing mortality rate as $\hat{F}(t)=\hat{Z}(t)-M$.

Reef fish exploited-population simulation model

To achieve a better understanding of the dynamics of multispecies tropical coral reef fish stocks, their response to exploitation, and the accuracy and precision of statistical estimates from the sampling surveys, we developed an object-oriented computer simulation model for exploited reef fish populations in the Florida Keys fishery (REEFS [reef fish equilibrium exploitation fishery simulator (Ault[3])]). The fundamental population-dynamic processes of growth, mortality, and recruitment are relatively similar for fishes of the temperate, boreal, and tropical seas; however, some distinct differences in rates exist for tropical marine fishes as reflected by quasicontinuous growth, protracted spawning and recruitment, and competition-based population dynamics (Ault and Fox, 1990; Sparre and Venema, 1992; DeMartini, 1993). To represent the continuous time dynamics of a tropical coral-reef fish population in the numerical model, following Ault and Olson (1996), we formalized the conservation law for population abundance as

$$dN(a,t) = \frac{\partial N(a,t)}{\partial a}da + \frac{\partial N(a,t)}{\partial t}dt = -Z(a,t)N(a,t)dt. \tag{4}$$

This partial differential equation expresses population age structure in terms of the average number of fish by age over time. The term $\partial N/\partial a$ is the contribution to the change in $N(a,t)$ resulting from individuals getting older. Because the variable a is tied stepwise to chronological age, for each time step t, a gets one unit older, so that da/dt = 1. This condition holds for $t > 0$ and $a > 0$. Equation 4 requires two conditions on $N(a,t)$: one initial condition for $N(0,t)$; and a boundary condition in age 0 tied to reproduction for $N(0,t)$. Integration of Equation 4 with a growth function allows efficient estimation of population biomass and average size in the stock over time. In the numerical model REEFS, we modified Equation 4 to a stochastic age-independent length-based population dynamics model to simulate efficiently the average or ensemble number at a given length for the entire population age structure as

$$\overline{N}(L) = \int_{t_r}^{t_\lambda} R(\tau - a)S(a)\Theta(a)P(L|a)\,da\ , \tag{5}$$

where $R(\tau-a)$ = recruitment lagged back to cohort birth date;
$S(a)$ = survivorship to age a;
$\Theta(a)$ = sex ratio at age a; and
$P(L\,|\,a)$ = the conditional probability of a fish being length L given that it is age a.

The ensemble average length L at age a is represented by the von Bertalanffy growth function. The conditional probability distribution for length and age was assumed to be bivariate normal.

The reported maximum age of fish in the stock t_λ (equal to a generation), usually obtained from age and growth studies by using either scales or otoliths, allows application of a convenient and consistent method to normalize the annual instantaneous natural mortality rate M to life span. First, we assume that $S(t_\lambda)$, the fraction of the initial cohort numbers surviving from recruitment t_r to the maximum age, can be expressed as

$$\frac{N(t_\lambda)}{N(t_r)} = S(t_\lambda) = e^{-M(t_\lambda - t_r)}. \tag{6}$$

Then, assuming an unexploited equilibrium, by setting the probability of survivorship of recruits to the maximum age to be 5% (i.e. $S(t_\lambda)$=0.05), and letting t_r be equal to 0, we rearranged Equation 6 in order to provide an estimate of the natural mortality rate

$$\hat{M} = \frac{-\ln[S(t_\lambda)]}{t_\lambda}. \tag{7}$$

Mortality and growth estimation in tropical fishery populations are normally approached from a size-based perspective because of difficulties in ageing fish. Average size can be converted to mean age by making two assumptions: 1) that age a maps directly into, or is a function of, size $L(a)$; and 2) that mean length-at-age from the von Bertalanffy equation can be inverted as

$$a = \frac{-\ln\left[\dfrac{L_\infty - L(a)}{L_\infty}\right]}{K} + t_0. \tag{8}$$

[3] Ault, J. S. 1998. Tropical coral reef fishery resource decision dynamics. Unpubl. manuscript.

Numbers-at-length were converted to numbers-at-weight for each species by means of simple allometric relationships.

Assessment of exploitation effects

The REEFS model was configured to assess two fishery management decision-making endpoints, yield-per-recruit (YPR) and spawning potential ratio (SPR). Fishery management endpoints are relatively robust measures of potential yields and recruitment. As such, they help to focus on biological (size) and fishing (intensity) controls for managing current and future fishery production. Because biomass $B(a,t)$ is the product of numbers-at-age multiplied by weight-at-age, yield in weight Y_{u} from a given species s was calculated as

$$Y_{u}(F,L',t)=F(t)\int_{L'}^{L_{\lambda}}B(L|a,t)dL = F(t)\int_{L'}^{L_{\lambda}}N(L|a,t)W(L|a,t)dL. \tag{9}$$

Yield-per-recruit (YPR) is then calculated by scaling yield to average recruitment from the right-hand side of the above equation. Spawning stock biomass (SSB, in metric tons [t]) is a measure of the stock's reproductive potential or capacity to produce newborn, ultimately realized at the population level as successful cohorts or year classes. Spawning stock biomass is obtained by integrating over individuals between the minimum size of first maturity, L_{m}, and maximum reproductive size (here assumed to be the maximum size L_{λ}) in the stock

$$SSB(t)=\int_{L_m}^{L_{\lambda}}B(L|a,t)dL. \tag{10}$$

The size of first capture, L', is that regulated by regional fishery management. The modeled fishing mortality rate of headboats (and "viewing power" of divers) was assumed to remove (and sight) fish with a "knife-edged selectivity pattern" (see Gulland, 1983) over the range of exploitable sizes

$$F(t)=\begin{cases}0 & \text{if } L|a<L' \\ \hat{F}(t) & \text{if } L|a\geq L'\end{cases}. \tag{11}$$

Spawning potential ratio (SPR) is a contemporaneous management endpoint that measures the stock's potential capacity to produce optimum yields on a sustainable basis. SPR is a fraction expressed as the ratio of exploited spawning stock biomass in relation to the equilibrium unexploited SSB

$$SPR=\frac{SSB_{exploited}}{SSB_{unexploited}}. \tag{12}$$

Resultant estimated SPRs are then compared to the U.S. Federal standards which define 30% SPR as the "overfishing" threshold (Rosenberg et al., 1996). Linear regressions of estimated SPRs for snapper and grouper were made on 1996 average exvessel prices obtained from voluntary Monroe County dealer reports (NMFS[4]). Because sale of jewfish was prohibited, a theoretical 1996 jewfish price was estimated as 0.438 of the price of gag grouper on the basis of historical average annual price ratios (1987–90).

Management analyses

This assessment focuses on 35 reef fish species in 5 families: groupers, Epinephelinae; snappers, Lutjanidae; grunts, Haemulidae; the hogfish, *Lachnolaimus maximus*, Labridae; and the great barracuda, *Sphyraena barracuda*, Sphyraenidae. These are the primary targets of the recreational, commercial, and headboat fleets. Population dynamics parameters for each of these fish used in the analyses were gleaned from summaries in Claro (1994) and taxa-specific literature (Tables 2 and 3). The hogfish was grouped with snappers for analytical purposes.

The assessment used the following 7 steps (Fig. 2):

Step 1: Conduct visual survey for the reef fish community in year t and intercalibrate diver sampling efficiency by species, site, and year.

Step 2: Begin management analysis for species s using intercalibrated visual survey data to compute within-year estimates of $\bar{L}$ and associated 95% confidence intervals from the size and abundance data, by species, integrated over the range of exploitable sizes.

Step 3: Compute a statistically independent set of annual mean estimates of $\bar{L}$ using fishery-dependent headboat data and compare these with visual survey estimates.

[4] NMFS. 1996. Fishery Statistics Div., Southeast Fisheries Sci. Center, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami FL 33149-1003.

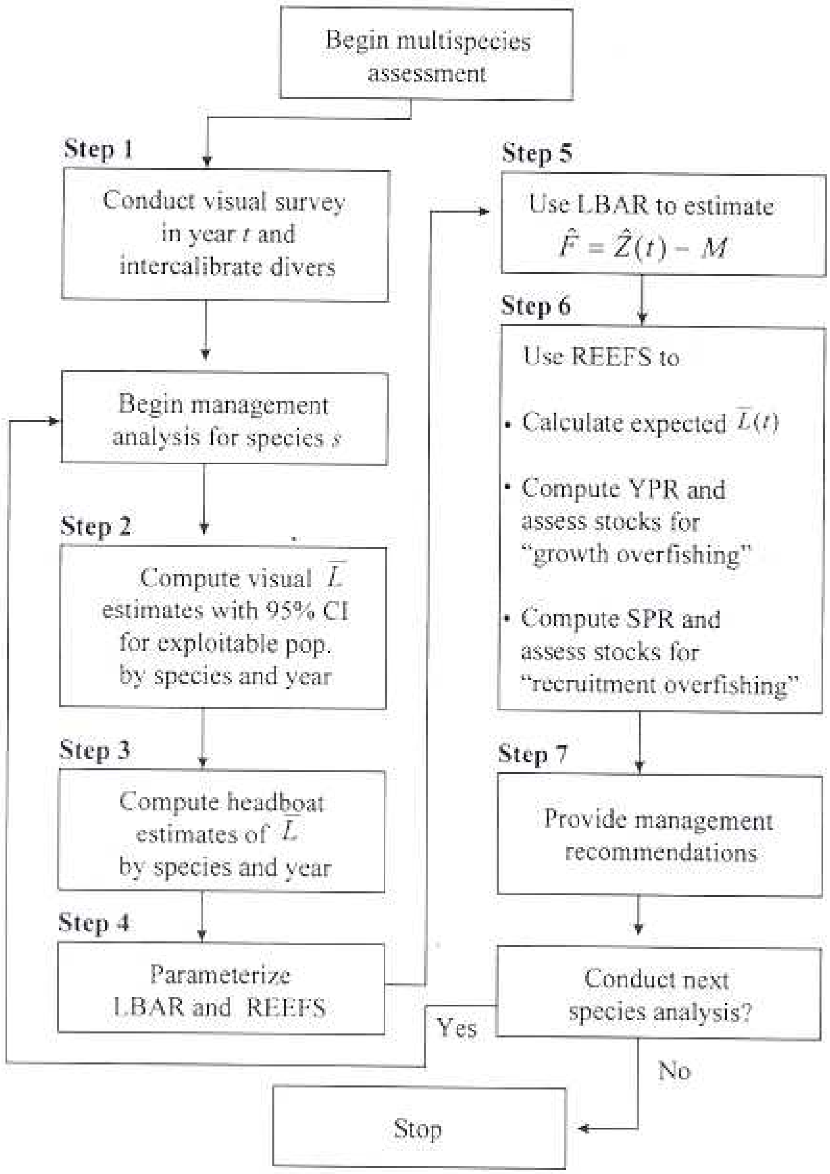

Figure 2

Flow chart showing the steps used in the multispecies reef fish assessment. See text for details.

Step 4: Use the population dynamics parameters of Table 3 to determine parameters of the LBAR (Ault et al., 1996) and the REEFS computer algorithms.

Step 5: Use $\bar{L}(t)$ estimate in LBAR to estimate by year fishing mortality rates for the two data sources; i.e. time series of visual and headboat data.

Step 6: Use the REEFS model to estimate: 1) expected $\bar{L}(t)$ given the reported population dynamics and $\hat{F}$ parameter values; 2) YPR and assess growth overfishing; and 3) spawning stock biomass (SSB) for the fishery in both exploited and unexploited states (i.e. $F = \hat{F}$, and F=0, respectively) and evaluate SPR to assess for recruitment overfishing.

Step 7: From these results, make specific fishery management recommendations on control strategies of F and L' consistent with eumetric fishing principles that minimize the potential for overfishing.

Results

Fishing effort and sampling intensity

Trends in nominal fishing effort, measured as the numbers of licensed recreational, commercial, and headboats vessels in Monroe County, show that recreational fishing effort has increased sharply since 1965 (Fig. 3). Since 1981, the largest increase has clearly come from the recreational sector and continues to increase whereas commercial and headboat sectors have been relatively stable.

In the 18-year (1979–96) visual survey, 4,571 point samples were collected over a variety of bottom types from 72 reefs located throughout the Florida Keys at depths to 21 m (Table 1; Fig. 1). The complete database contains information on 226 reef fish species in 55 families with 42 biological, habitat, and physical covariates.

Table 2

Parameters, definitions, and units for population dynamics variables common to the LBAR and REEFS numerical models used in simulation analysis of Florida Keys reef fish population dynamics. See Table 3 for parameter values.

Parameter	Definition	Units
s	Reef fish species (s=1, . . . ,n)	
a	Cohort age class (a=1, . . . , t_λ)	
t_r	Age of recruitment	months
L_r	Size at recruitment	mm
t_m	Minimum age of maturity	months
L_m	Minimum size of maturity	mm
t'	Minimum age of first capture	months
L'	Minimum size of first capture	mm
t_λ	Oldest (largest) age	years
L_λ	Largest (oldest) size	mm
W_∞	Ultimate weight	kg
L_∞	Ultimate length	mm
K	Brody growth coefficient	per year
t_0	Age at which size equals 0	years
α_{WL}	Scalar coefficient of weight-length function	dimensionless
β_{WL}	Power coefficient of weight-length function	dimensionless
$W(a,t)$	Weight at age a at time t	g
$L(a,t)$	Length at age a at time t	mm
$N(a,t)$	Numbers at age a at time t	number of fish
$M(a,t)$	Natural mortality rate at age a at time t	per year
$F(a,t)$	Fishing mortality rate at age a at time t	per year
$S(a)$	Survivorship to age a	dimensionless
$Z(t)$	Total mortality rate in year t	dimensionless
$\Theta(a)$	Sex ratio at age a	dimensionless
$B(a,t)$	Biomass at age a in year t	kg
$Y_w(t)$	Yield in weight in year t	metric tons
$SSB(t)$	Spawning stock biomass in year t	metric tons
$SPR(t)$	Spawning potential ratio in year t	percent

Average size and mortality

Average annual length was estimated for headboat catch statistics (1981–95) and for visual survey data (1979–96). Headboat data were used in the comparative analysis with the visual survey data because they provide consistent catch statistics and effort data. Typical comparisons of average length in the exploitable phase of the stock for the two data sets are shown for eight representative, economically important reef fishes: black grouper, red grouper, gray snapper, yellowtail snapper, white grunt, bluestriped grunt, hogfish, and great barracuda (Fig. 4). The 95% confidence intervals were computed for the visual estimates but could not be determined for the headboat data at this time owing to the survey estimation procedures used to calculate total numbers and total weight for the entire Florida Keys. In a few instances (e.g. 1985 and 1986), the computed confidence bounds were large owing to low sample sizes, but these mean estimates still correlated well with the rest of the data.

The estimated average lengths in the exploitable phase from the two independent data sources were highly correlated for groupers, snappers, and grunts (Fig. 4). The trend in average size also was relatively flat over the last 18 years and close to L' (Fig. 4).

Although the relation between $\bar{L}$ for visual and headboat data was similar for all groupers, snappers, and grunts, it differed somewhat for hogfish and barracuda (Fig. 4, G and H). Average length ($\bar{L}$) for hogfish was consistently smaller in visual samples than in headboat landings. In both data sets, however, $\bar{L}$ declined in the early 1980s but has steadily increased since the late-1980s (F=3.96, df=9, P<0.0001) (Fig. 4G). Average length for barracuda increased significantly (F=2.2, df=10, P<0.018) in visual surveys but declined in headboat landings beginning in the early 1980s (Fig. 4H). Increased mean barracuda size in visual samples indicates that there has been a corresponding increase in abundance because larger $\bar{L}$ requires increased survival. In visual samples, barracuda are now the top ranked species in biomass among all Florida Keys reef fishes.

Table 3

Florida Keys reef fish population dynamics parameters for 46 species used in mortality estimations and fishery simulations. Population dynamics parameter definitions and units are given in Table 2. The symbol ∗ indicates that the species is present in recreational catch but not headboat catches or the visual survey. The dash (—) indicates that insufficient population dynamic data were available to conduct a management analysis. Complete parameter sets were available for 35 species.

Species groups	Population parameters											
	M	t_λ	L_∞	W_∞	K	t_0	t_m	L'	t'	α_{wl}	β_{wl}	L_λ
Groupers (n=18)												
Black Grouper *Mycteroperca bonaci*	0.150	20	1200.0	31.6	0.160	–0.300	48	508.0	39	4.27E-06	3.2051	1153.1
Coney *Epinephelus fulvus*	0.180	17	698.9	1.5	0.145	–1.080	13	203.2	19	7.29E-05	2.5700	332.5
Gag Grouper *Mycteroperca microlepis*	0.200	13	1187.2	25.1	0.149	–0.802	60	508.0	36	1.21E-05	3.0305	1034.4
Graysby *Epinephelus cruentatus*	0.200	15	415.0	1.1	0.130	–0.940	36	203.2	52	1.22E-05	3.0439	362.5
Jewfish *Epinephelus itajara*	0.081	37	2394.0	244.9	0.054	–3.616	72	508.0	68	2.09E-05	2.9797	2328.0
Marbled Grouper ∗ *Epinephelus inermis*	—	—	—	—	—	—	—	—	—	—	—	—
Misty Grouper ∗ *Epinephelus mystacinus*	—	—	—	—	—	—	—	—	—	—	—	—
Nassau *Epinephelus striatus*	0.180	17	698.9	5.9	0.145	–1.080	83	508.0	95	3.83E-06	3.2292	648.2
Red Grouper *Epinephelus morio*	0.180	17	938.0	11.9	0.153	–0.099	48	508.0	61	1.13E-05	3.0350	869.0
Red Hind *Epinephelus guttatus*	0.180	17	392.7	1.1	0.207	–0.831	49	203.2	33	1.80E-04	2.6140	382.9
Rock Hind *Epinephelus adscensionis*	0.250	12	486.1	2.3	0.191	–2.160	48	203.2	9	6.00E-06	3.1930	453.3
Scamp *Mycteroperca phenax*	0.143	21	999.7	19.3	0.126	–1.357	48	508.0	52	2.02E-05	2.9932	932.2
Snowy Grouper *Epinephelus niveatus*	0.130	15	1091.3	19.5	0.113	–0.915	48	508.0	57	2.45E-05	2.9300	909.0
Speckled Hind *Epinephelus drummondhayi*	0.200	15	967.0	16.6	0.130	–1.010	48	508.0	58	1.11E-05	3.0730	861.0
Warsaw Grouper *Epinephelus nigritus*	0.080	41	2394.0	244.9	0.054	–3.616	48	508.0	68	2.09E-05	2.9797	2328.0
Yellowedge Grouper *Epinephelus flavolimbatus*	0.180	15	860.0	15.7	0.170	0.000	67	508.0	64	2.82E-05	2.9800	960.0
Yellowfin Grouper *Mycteroperca venenosa*	0.180	15	860.0	15.7	0.170	0.000	67	508.0	64	2.82E-05	2.9800	960.0
Yellowmouth Grouper *Mycteroperca interstitialis*	0.180	17	881.8	8.6	0.063	–9.030	36	508.0	56	2.58E-05	2.8937	710.7
Snappers (n=13) and hogfish (n=1)												
Black Snapper *Apsilus dentatus*	0.300	10	618.3	3.2	0.097	–1.728	29	203.2	30	4.52E-05	2.8146	418.4
Blackfin Snapper *Lutjanus buccanella*	0.230	9	729.7	2.4	0.084	–2.896	20	304.8	43	7.40E-06	2.9735	458.8
Cubera Snapper *Lutjanus cyanopterus*	0.150	20	1200.0	34.9	0.160	–0.300	28	304.8	19	1.32E-05	3.0601	910.0
Dog Snapper *Lutjanus jocu*	0.333	9	854.0	10.2	0.100	–2.000	28	304.8	30	4.28E-05	2.8574	790.0
Gray Snapper *Lutjanus griseus*	0.300	10	722.3	5.2	0.136	–0.863	24	254.0	29	3.05E-05	2.8809	556.2
Lane Snapper *Lutjanis synagris*	0.300	10	618.3	3.2	0.097	–1.728	29	203.2	30	4.52E-05	2.8146	418.4

continued

Table 3 (continued)

Species groups	Population parameters											
	M	t_λ	L_∞	W_∞	K	t_0	t_m	L'	t'	α_{wl}	β_{wl}	L_λ
Mahogony Snapper *Lutjanus mahogoni*	0.300	10	618.3	3.2	0.097	−1.728	29	304.8	64	8.18E-05	2.7190	418.4
Mutton Snapper *Lutjanus analis*	0.214	14	938.7	14.1	0.129	−0.738	24	304.8	29	1.57E-05	3.0112	797.8
Red Snapper *Lutjanus campechanus*	0.190	16	975.0	13.7	0.162	−0.010	28	508.0	55	2.04E-05	2.953	955.0
Schoolmaster *Lutjanus apodus*	0.250	12	570.0	3.3	0.180	0.000	20	254.0	40	2.04E-05	2.9779	503.8
Silk Snapper *Lutjanus vivanus*	0.230	9	781.1	9.3	0.092	−2.309	37	304.8	38	1.00E-05	3.1000	512.0
Vermillion Snapper *Rhomboplites aurorubens*	0.230	10	613.6	2.8	0.206	0.111	43	254.0	33	1.72E-05	2.9456	541.6
Yellowtail Snapper *Lutjanus chrysurus*	0.214	14	454.7	1.3	0.209	−0.712	24	304.8	56	7.75E-05	2.7180	433.4
Hogfish *Lachnolaimus maximus*	0.250	12	566.0	3.8	0.190	−0.776	18	203.2	20	2.55E-05	2.9700	439.0
Grunts (n=13) and barracuda (n=1)												
Black Margate *Anisotremus surinamensis*	—	—	—	—	—	—	33	203.2	—	2.39E-06	3.3916	—
Bluestriped Grunt *Haemulon sciurus*	0.500	6	289.6	0.47	0.484	−0.011	12	203.2	31	1.94E-05	2.9996	273.5
Caesar Grunt *Haemulon carbonarium*	—	—	—	—	—	—	27	203.2	—	1.29E-05	3.0559	—
Cottonwick *Haemulon melanurum*	—	—	—	—	—	—	27	203.2	—	2.52E-05	2.9527	—
French Grunt *Haemulon flavolineatum*	—	—	—	—	—	—	18	203.2	—	9.06E-06	3.1581	—
Margate *Haemulon album*	0.374	8	752.6	8.57	0.174	−0.450	34	203.2	17	1.52E-05	3.0423	578.4
Porkfish *Anisotremus virginicus*	—	—	—	—	—	—	25	203.2	—	1.01E-05	3.1674	—
Sailors Choice *Haemulon parrai*	0.428	7	400.2	1.24	0.220	−0.355	12	203.2	35	2.02E-05	2.9932	320.1
Smallmouth Grunt *Haemulon chrysargyreum*	—	—	—	—	—	—	24	203.2	—	2.77E-03	2.1567	—
Spanish Grunt *Haemulon macrostomum*	—	—	—	—	—	—	39	203.2	—	2.28E-05	3.0295	—
Striped Grunt *Haemulon striatum*	—	—	—	—	—	—	21	203.2	—	1.39E-05	3.0988	—
Tomtate *Haemulon aurolineatum*	0.333	9	441.6	1.89	0.091	−2.095	24	203.2	57	6.19E-06	3.2077	279.9
White Grunt *Haemulon plumieri*	0.375	8	511.9	3.06	0.186	−0.776	18	203.2	24	8.35E-06	3.1612	410.3
Great Barracuda *Sphyraena barracuda*	0.200	15	1238.3	14.03	0.172	−0.461	36	619.2	44	4.11E-06	3.0825	1151.5

Management analyses

We also conducted a multispecies stock assessment and management analysis with the estimates of fishing mortality to examine if current exploitation levels are commensurate with sustainable fisheries. Although 46 exploited reef fish species had been seen or captured in the visual and headboat surveys, only 35 species had population dynamics parameter sets sufficient to conduct a management analysis (Table 3). We noted striking similarities in key relations within taxa as shown by the somewhat discrete clusters of taxa when maximum size dependent on maximum age for a variety of species was plotted (Fig. 5). Mean F estimates for visual survey and headboat data were used to encompass conservatively the range of feasible fishing mortality rates experienced in the fishery over the last two decades. A comparison of methods and data sources also allowed us to consider risks associated with the overall uncertainty bounds for each stock assessment. Results of an example assessment analysis is shown for gray snapper in which

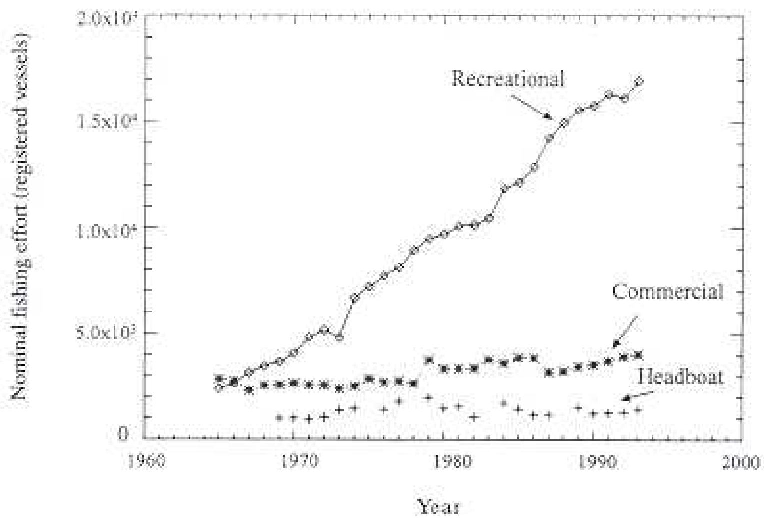

Figure 3

Time series of three types of nominal fishing effort directed at Florida Keys reef fish from 1965 to 1993 based on numbers of recreational ( ) and commercial (✱) vessels registered in Monroe County, Florida. Headboats (+) are considered to be a subset of the commercial fishing fleet.

management endpoints like yield-per-recruit (YPR) and spawning potential ratio (SPR) are provided (Fig. 6). These results are typical of the management information provided for each species.

Our analyses indicated that the average size in the exploitable phase for many economically important reef fish populations was marginally above the minimum size of capture regulated by fishery management agencies (i.e. South Atlantic Fishery Management Council and the Florida Marine Fisheries Commission). To assess the impact of these mortality rates on the stock production, we performed an analytical yield analysis to estimate the YPR for each stock, and evaluated the current YPR status in relation to "eumetric" (cf. Beverton and Holt, 1957) or well-balanced fishing in terms of the minimum size of fish captured and level of fishing effort (Fig. 6A). An issue of paramount concern in assessing analytical yield models are the settings of the two dynamic control variables, F and L' (Fig. 6A). From the perspective of optimal decision making, any transition of the fishery over the yield surface should minimize negative risks, while maximizing the economic, ecological, social, and aesthetic aspects. The YPR analysis for gray snapper suggests that the current size (or age) of first capture, L' at 254 mm (=10 in), likely results in "growth overfishing." To maximize the YPR for the range of F operating in the fishery for the last two decades, L' should be increased to greater than 350 mm (Fig. 6B).

Figure 6C shows progressive reductions of gray snapper stock biomass when F is increased to the estimate's lower bound shown in Figure 6B. The likelihood range of $\hat{F}$ (i.e. $\hat{F}$=[0.5,1.1]) is likely also contributing to a very low SPR for gray snapper. In fact, it is below the Federal minimum of 30% SPR (Fig. 6D). The minimum estimated F still reduces SPR to about 29% of the unexploited state, whereas the upper bound estimate results in 15% SPR. The majority of the range of estimated F suggest that the gray snapper stock is also "recruitment overfished" as reflected by reduced spawning potential.

The summary of the SPRs for Florida Keys reef fish (Fig. 7) shows that a total of 13 of 16 groupers, 7 of 13 snappers, and 2 of 5 grunts, for which there are data, are below the SPR that constitutes overfishing by Federal definitions. Overall, 63% of the 35 stocks that could be analyzed were overfished. Linear regressions of SPR on exvessel price showed a significantly negative ($F_{1,14}$=7.55, P=0.0157) slope for grouper and a marginally significant ($F_{1,11}$=4.77, P= 0.0514) negative slope for snapper (Fig. 8).

Discussion

Fishery dynamics

Our results indicate that Florida Keys reef fish populations have been heavily fished for at least the last

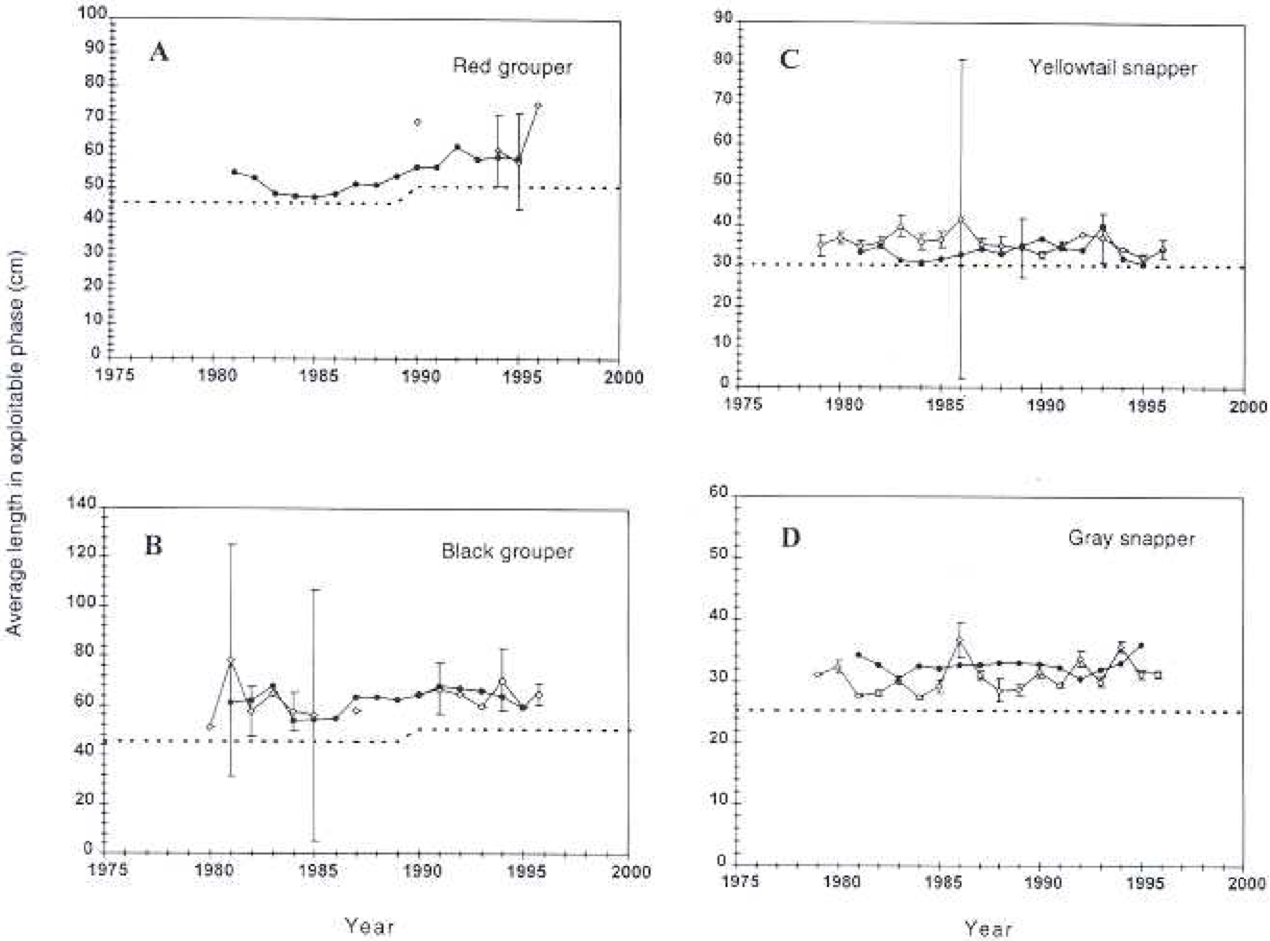

Figure 4

Average length (cm) in the exploitable phase of the stock estimated from headboat (●) and visual survey ( ) data for several reef fish stocks during the period 1979 to 1996: (**A**) red grouper, (**B**) black grouper, (**C**) yellowtail snapper, (**D**) gray snapper, (**E**) white grunt, (**F**) bluestriped grunt, (**G**) hogfish, and (**H**) great barracuda. Bars around visual survey estimates are 95% confidence intervals of the mean. Horizontal dotted lines show the minimum size at first capture L' regulated by regional fishery management.

two decades. Total fishing effort has increased substantially because of greater average fishing power per vessel and a much larger recreational fishery. Mace (1997) estimated that the average "fishing power" per vessel (i.e. the average proportion of the stock removed per unit of fishing effort) has increased 4-fold over the previous 25 years mainly because of improved technology involving better vessel designs, hydroacoustics, hydraulics, and navigation (GPS, Loran C, charts). The arithmetic increase of recreational fishing vessels is an important factor also, although its absolute effect on reef fish stocks is unknown because the recreational fleet is distributed diffusely and heterogeneously and has not been well sampled to date.

Stock assessment indicator variable

The estimated average lengths (size) of reef fish in the exploitable phase, determined from statistically independent visual and headboat data, were highly comparable for groupers, snappers, and grunts, supporting their use in the multispecies assessment. Average sizes of hogfish and barracuda, however, differed between the two data sets. The larger average hogfish size in headboat samples appears to be the result of life history patterns and different responses to fishing gears with depth. Hogfish tend to move from shallow to deeper water with age (Davis, 1976) and are more vulnerable to spearfishing than hook-and-line gear. Divers, however, are effectively

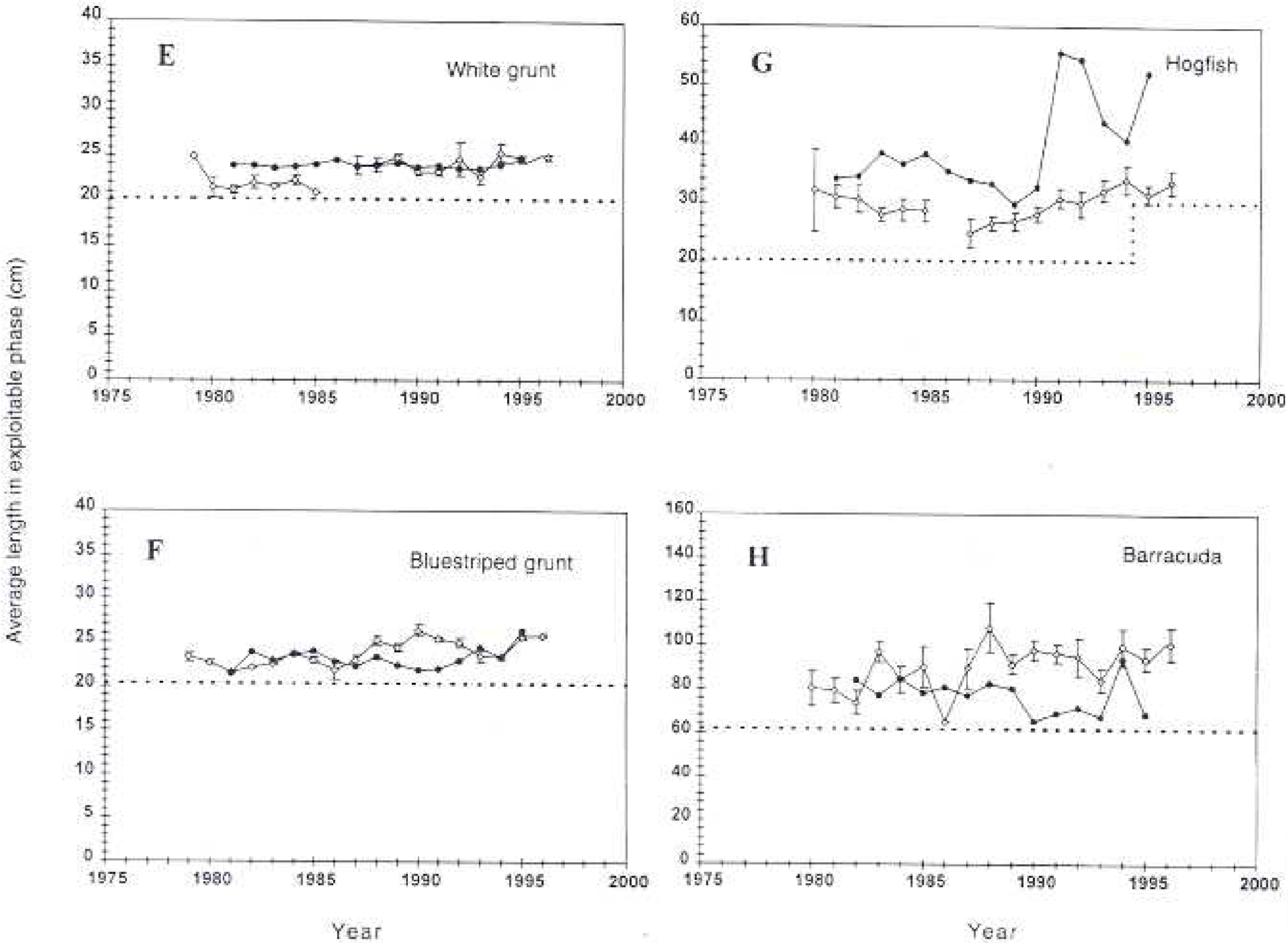

Figure 4 (continued)

restricted to shallower depths for safety reasons. Thus, large hogfish that inhabit depths below safe diving limits are available to only the headboat fleet. In shallow water, divers are more likely to see small hogfish because they are more abundant and because large hogfish are more likely to be selectively depleted by spearfishing. The increased average size in both data sets since the mid-1980s (Fig. 4G) is most likely the result of increased spearfishing regulation, imposed recreational bag limits, and initiation of minimum size limits.

The average size of barracuda diverged in visual samples and headboat landings since the early 1980s (Fig. 4H). This pattern is likely the result of the promotion and expansion of catch-and-release fishing for barracuda during that time period. Decreased fishing mortality resulting from more released barracuda would increase the average size of fish in the exploitable phase and be detected in visual samples. Headboat landings, however, could trend toward smaller fish because more large barracuda increase the frequency of angler "breakoffs" (i.e. fish biting through lines or leaders) and the proportion of releases because only small barracuda are normally retained for human consumption. Large barracuda are avoided because they carry greater risk of ciguatera poisoning, which can result in convulsions and death for humans (de Sylva, 1994).

The trend in average size for grouper, snapper, and grunt stocks was relatively flat over the past 18 years and close to the minimum exploitable length (Fig. 4). The flatness is explained by considering expected $\bar{L}$ from a modeled range of F in an analytical model, given knowledge about current values of $\hat{F}$. The slope of $\bar{L}$ on F was very shallow in the range of the analytical model (Fig. 9), corroborating the empirical estimates in Figure 4. Some stocks appear to have been chronically overfished since the late 1970s. We

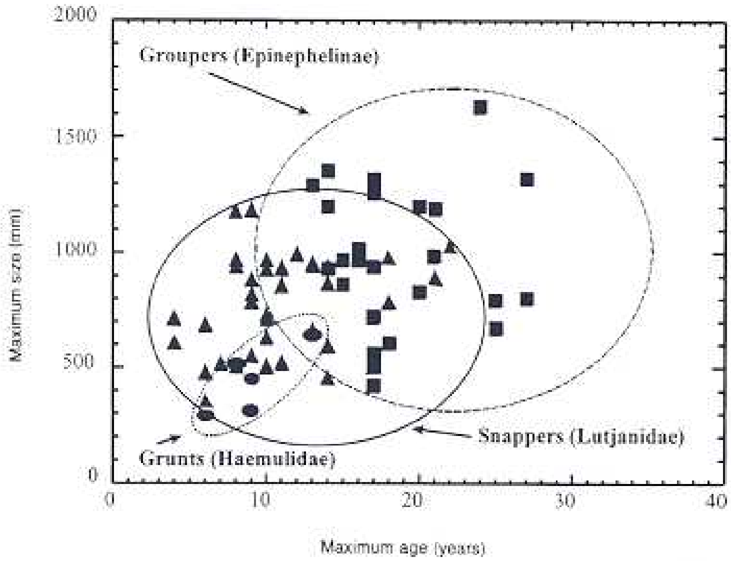

Figure 5

Relationship between the population dynamic parameters maximum size L_λ and maximum age t_λ for three economically important Florida Keys reef fish taxa: groupers, Epinephelinae (■); snappers, Lutjanidae (▲); and grunts, Haemulidae (●).

also noted similarities in key relations within various taxa that separated out into somewhat discrete clusters when maximum size versus maximum age by species is plotted (Fig. 5). This pattern of species clusters suggests that species within the various taxa groupings will likely respond to exploitation in a similar manner. The sensitivity to exploitation is highest for groupers, followed by snappers, and then grunts.

Overfishing and community shifts

Despite conservative assumptions, the estimated fishery exploitation rates suggest that many Florida Keys reef fish stocks are overfished according to definitions for U.S. fisheries (Rosenberg et al., 1996) (Figs. 7 and 9). Many desirable grouper and snapper stocks have low spawning potential ratios (SPRs). Inverse relationships between increased fishing effort (particularly by the recreational sector) (Fig. 3) and the long-term decreased average size and stock biomass (e.g. Fig. 6C) of the most desirable species (e.g. groupers and snappers) are particular concerns.

The Florida Keys reef fishery shows the classic pattern of serial overfishing, in which the more vulnerable species are progressively depleted (Munro and Williams, 1985; Russ and Alcala, 1989). The longest-lived, latest-maturing, and lowest mortality (M) stocks [i.e. groupers] are those first to experience significant declines in population biomass, followed in sequence by intermediate-lived stocks [snappers], and finally by short-lived stocks [grunts] [Fig. 7]). Within families, the inverse relations between the spawning potential ratio and exvessel market price (Fig. 8) are consistent with serial overfishing. As expected, the most valuable snapper and grouper also tend to have the lowest spawning potentials. During the time frame of this study, numerous measures were taken to reduce fishing mortality in state and federal waters. Fish traps were progressively eliminated between 1980 and 1992, and numerous bag limits and minimum size limits were imposed. Fisheries were closed for queen conch (*Strombus gigas*), jewfish (*Epinephelus itajara*), and Nassau grouper (*E. striatus*). These actions are evidence of trends reported in this study.

Our data suggest that there may have been substantial changes in the composition of the biomass and abundance of the reef fish community over the past several decades. Although many groupers and snappers have declined, apparently in response to growing fishing effort, some grunts have increased in relative abundance. Claro (1991) noted a similar process in the Golfo de Batabano, Cuba, and hypothesized that chronic overharvesting of snappers resulted in shifts in community composition in favor

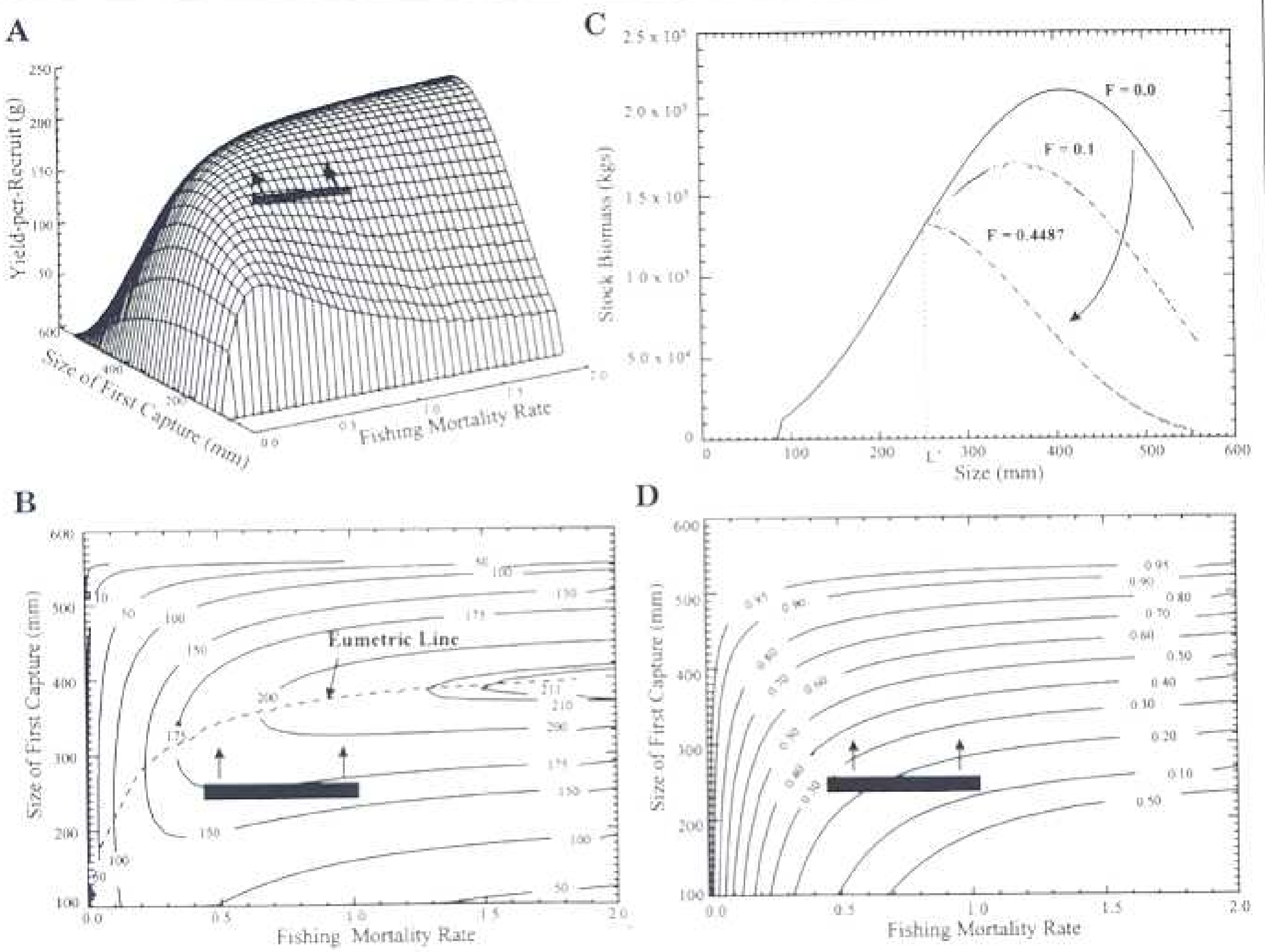

Figure 6

Example calculation of an analytical yield model management analysis for gray snapper: (**A**) 3-dimensional yield-per-recruit YPR surface (g) as a function of the fishing mortality rate F (per yr) and size at first capture L' (mm); (**B**) YPR isopleths in lifetime yield-per-recruit; (**C**) stock biomass dependent on size for several exploitation levels; and (**D**) spawning potential ratio (SPR) as a function of F and L'. REEFS model input parameter values are from Table 3. Shaded rectangles in panels A, B, and D show estimated range of F and L'. Darkened rectangle in panel D indicates the range of F estimates that exceed the Federal 30% SPR overfishing definition following Rosenberg et al. (1996).

of grunts. Another indication of significant change was the explosive growth of barracuda (Fig. 4H) which may be explained by several factors. First, there is little directed commercial or recreational fishing for barracuda as food because of health concerns. Second, growth of catch-and-release fishing by sport anglers and reduced emphasis on spearfishing may have substantially lowered barracuda mortality. Third, other top predators, such as groupers, snappers, and sharks, have been intensively fished, therefore probably lowering competition for food, while, at the same time, barracuda still retain a large and possibly increasing prey base of grunts and other small fishes. Increased abundance and biomass of a top predator like barracuda could be a management concern if barracuda substantially impact reef fish community dynamics. For example, excessive predation on popular sport fishes like snappers could counteract potential reductions in fishing mortality sought by traditional management.

An adjustment of minimum sizes of first capture (L') and fishing mortality rates (F) may mitigate the apparent growth and recruitment overfishing conditions in the fishery. This adjustment should be done in a multispecies context to optimize the biotic and fishery potential of the reef fish assemblage. However, traditional management actions alone are unlikely to be sufficient because they can be circum-

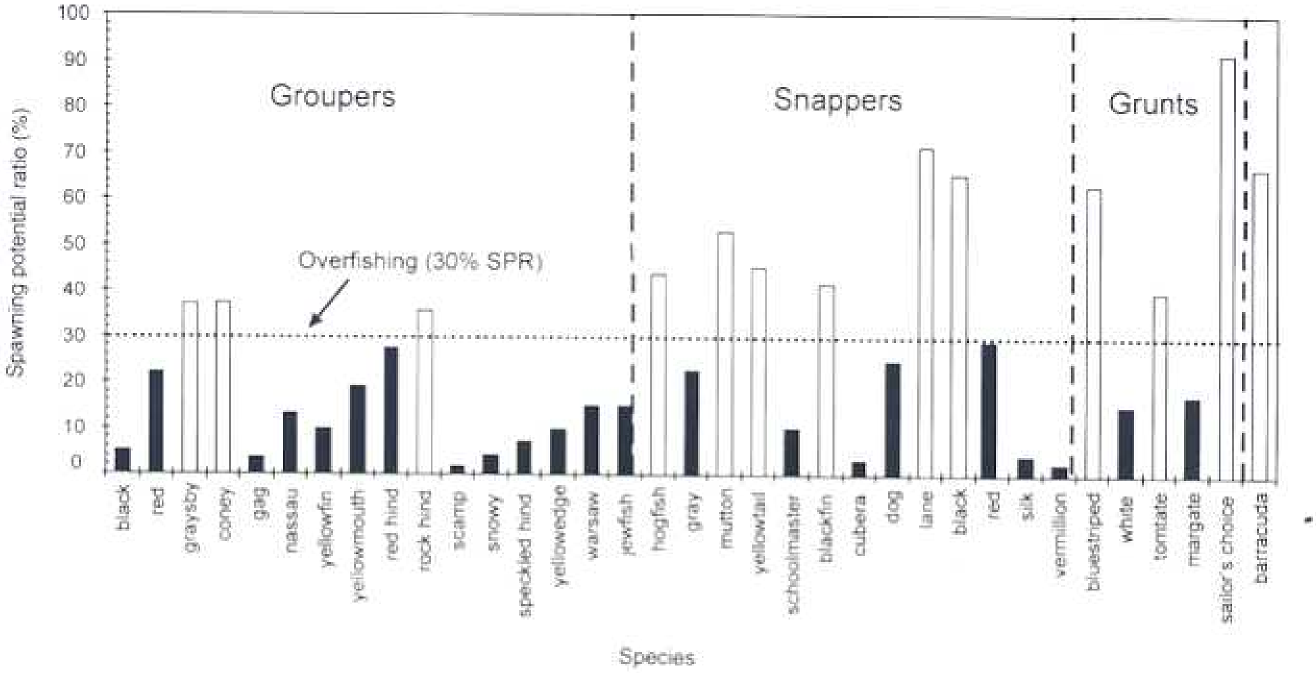

Figure 7

Estimates of percent spawning potential ratio (SPR%) for 35 species of Florida Keys reef fish comprise groupers, snappers, grunts, hogfish, and great barracuda. Darkened bars indicate stock "overfishing," and open bars indicate the stock is above the 30% SPR U.S. Federal standard.

vented and habitually fail to control fishing effort effectively, particularly in an open access fishery (Waters, 1991; Bohnsack and Ault, 1996). For example, bycatch mortality and high fishing effort from the expanding fleets can make size limits ineffective. In theory, every fish can be caught once it reaches minimum legal size with the result that insufficient mature adults survive to reproduce. The tradition of open-access management systems coupled with risk-prone management decisions remains a principal obstacle to achieving renewable resource sustainability (Rosenberg et al., 1993).

Reversing adverse trends in the Keys reef fishery are likely to require other innovative approaches for controlling exploitation rates. Rothschild et al. (1996) recommended that fishery management maintain a systems view of the resources, emphasizing strategy over tactics. With this in mind, we recommend coupling traditional management measures with a spatial network of areal closures called "no take" marine reserves. Marine reserves provide an ecosystem management strategy for achieving long-term goals of protecting biodiversity while maintaining sustainable fisheries. The establishment of a network of small (16 to 3,000 ha) no-take reserves in the FKNMS on 1 July 1997 (U.S. Dep. Commerce, 1996) is a first step. A key to the success of this effort is a conscientious, continuous assessment program for integrating fishery-independent and fishery-dependent data to evaluate the effectiveness of these reserves (Bohnsack and Ault, 1996). With adaptive management (Walters, 1986), improvements can be implemented over time.

Multispecies assessment

Our overall goal was to improve the scientific basis for managing tropical multispecies fisheries by providing an efficient, quantitative framework to assess multispecies fisheries. New assessment methods are particularly needed for complex fisheries that have been poorly documented, are not well understood, and face increased exploitation. Traditional single-species stock assessment methods are at times inappropriate or inadequate to deal with the dynamics and structure of multispecies assemblages with large numbers of exploited species (Caddy, 1981; Ault and Fox, 1990; Appledorn, 1996). Owing to a lack of data and basic biological information, only a few reef species in the entire southeastern U.S. have had comprehensive stock assessments.

We emphasized a multispecies ecosystem approach because traditional fishery models have been ineffectual in creating sustainable fisheries (Ludwig et al., 1993; Sharp, 1995; Caddy, 1996; Russ, 1996).

Single-species fishery management models built to maximize fishery yield and economic rent ignore critical biological and physical interactions and cumulative stresses on habitats. Reef fish stocks are likely to be regulated by trophic interactions at the individual, population, and community levels. Also, application of "traditional" fishery management models developed for temperate species to tropical coral reef assemblages is tenuous. In response to these problems, the National Research Council Committee on Fisheries (1994) recommended developing multispecies ecosystem management programs for building sustainable fisheries. Successful implementation of such programs will require innovative research, new management strategies, less destructive and wasteful fishing methods, protection of critical and sensitive habitats, and more effective education.

Our retrospective analysis emphasized fishery-independent data. Although fishery-independent assessments can provide reliable measures of fish abundance, population dynamics, and community composition (Gunderson, 1993), their application in multispecies fishery assessments have been limited. We predict an increasing need to rely on such data for assessment purposes because fishery-dependent data will become less available and less useful as new regulations are imposed that will establish larger size limits, closed seasons, closed fishing areas, and species prohibited from being fished. Also, the shifting emphasis from commercial to recreational fishing makes collecting fishery-dependent data much more difficult and expensive.

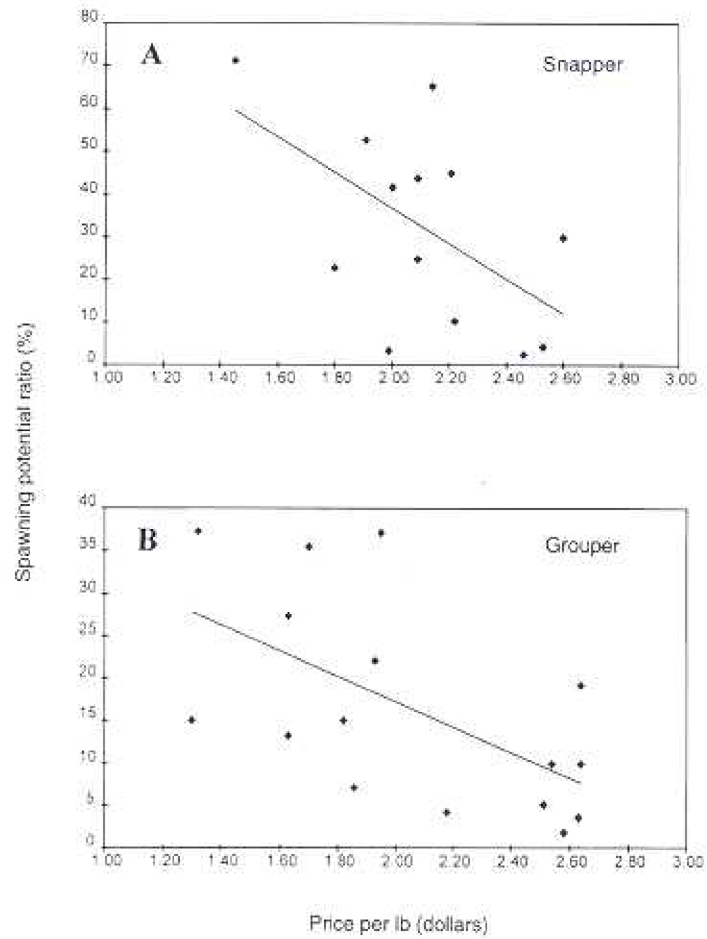

Figure 8

Linear regressions of estimated species spawning potential ratio (y) on average 1996 Monroe County exvessel price (x) for: (**A**) snapper: $y = 119.59 - 41.38x$; and, (**B**) grouper: $y = 47.35 - 15.03x$.

Results from this 18-year retrospective assessment are encouraging in providing estimates of stock status. However, several assumptions that simplify the population dynamics of the various species make it prudent to consider population estimates first-order approximations. The error intrinsic in population-rate estimates derived from surveys depends on the accuracy and precision of the basic survey. Errors ultimately propagate upwards during a series of calculations used to determine the average size, total mortality rates, fishing mortality rates, yield-per-recruit, and finally the spawning potential ratio, which is the current focus of management decisions. Also, although the Florida Keys fishery represents a major fishing area, it does not necessarily represent the entire stock range for an individual species. It is possible that mature stock components exist outside the fishing area.

Six actions could improve future assessments. First, develop suitably structured spatial models for linkages between habitat use and fish ontogeny to "fill-in" the map of population estimates for areas not sampled. Second, calibrate the relative statistical power of diver surveys and headboat fishing gear. Ideally, diver observations should relate to what fishermen catch. Because the fishing mortality rate of headboats (and viewing power of divers) are considered strictly proportional to average population abundance, we must understand the fraction of the stock assessed per unit of effort and the interrelationship of the efficiency of the two "gear" types. Third, increase temporal and spatial sampling coverage to increase survey precision and resolution. Fourth, tune fishery-independent surveys with other indices of stock abundance. In this retrospective analyses, no attempt had been made to have the two survey

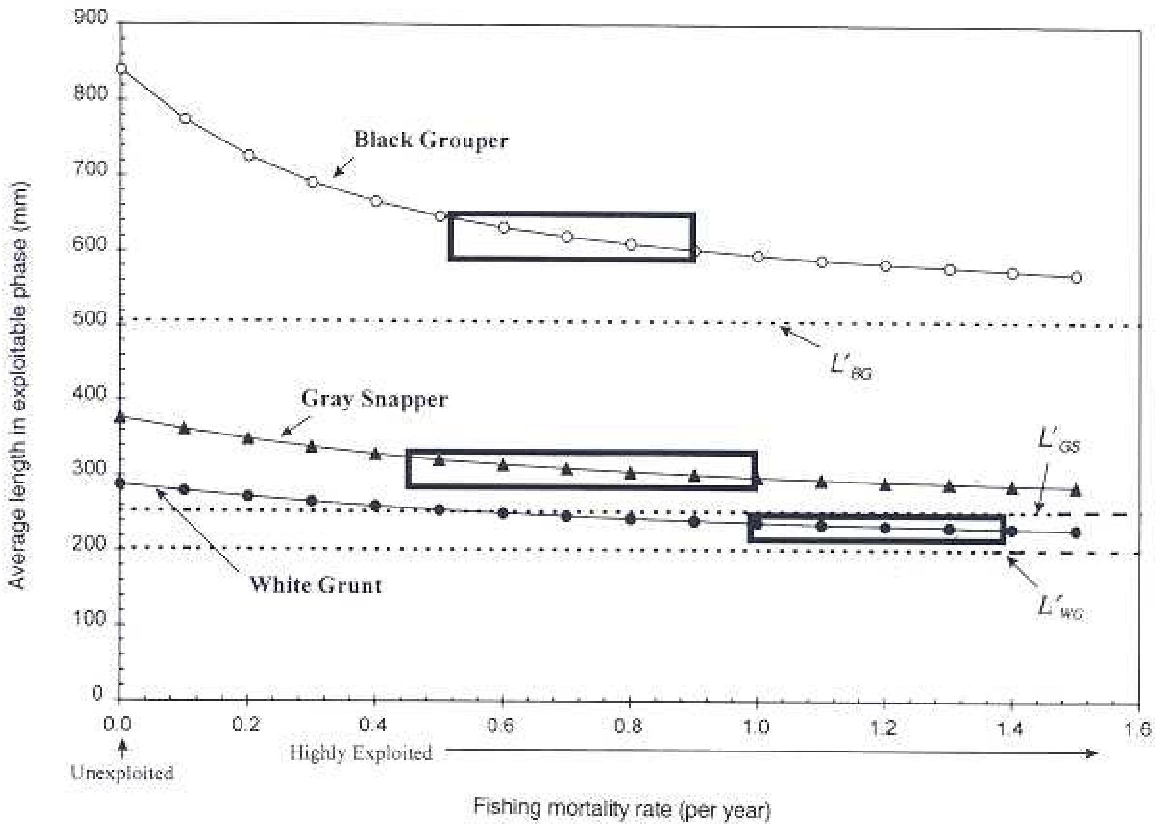

Figure 9

Simulation of equilibrium relationship of average length in the exploitable phase $\bar{L}$ dependent on fishing mortality rate F using the REEFS model for several reef fish taxa: (**A**) black grouper (○); (**B**) gray snapper (▲); and (**C**) white grunt (●). Boxes around species curves show the range of F estimates from the retrospective analyses.

types coincide with respect to sampling effort or locations within the Florida Keys. Fifth, employ new sampling technologies, such as hydroacoustics, green band lasers, and stereo video cameras to improve the accuracy and cost effectiveness of biomass and abundance estimates. Sixth, improve basic biological information on growth, reproduction, mortality, feeding, and recruitment, which are fundamental elements of stock assessment. The models and conclusions presented here are strongly influenced by the accuracy of the parameter estimates and the source for these estimates is not always reliable.

Conclusions

We used a new approach involving fishery-independent data to conduct a quantitative retrospective multispecies assessment of changes in the Florida Keys multispecies reef fish community. Our results show that fishing effort and mortality levels are very intense, that many stocks are "overfished," and that exploitation has likely altered the structure and dynamics of the reef fish community. Inevitable increases in fishing effort, particularly by recreational anglers, combined with habitat degradation by rapid growth of human populations in the region, if unabated, will increase the potential for overfishing and ecosystem changes. Without effective intervention by regional fishery management to bring fishing effort under control, reef fish stocks will likely continue to decline. A spatial network of "no take" marine reserves, combined with traditional management measures, have the potential to reverse these trends for many species and to allow the long-term goals of building sustainable fisheries and protecting biodiversity to be achieved.

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