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Indicators for assessing the ecological dynamics and sustainability of southern Florida's coral reef and coastal fisheries

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ABSTRACT

Commercial and recreational fisheries target hundreds of fish and shellfish species across the seascape of southern Florida including inshore coastal bays, the flats of barrier islands, coral reefs and offshore pelagic waters. The ecological dynamics and economic sustainability of these valuable fishery resources are key conservation concerns. This study examined two ecological indicators of fishing impacts on exploited populations: (1) the more traditional metric catch per unit of fishing effort (CPUE); and (2) the non-traditional metric average length ($\bar{L}$) in the exploited life stage of a population. We show that both indicators were closely related to stock productivity via fisheries population dynamics theory, and that either indicator could be used to estimate fishing mortality rates (F). Data requirements are much less stringent for estimating F from the $\bar{L}$ indicator than CPUE, making it more practical for data-poor situations common to tropical marine fisheries. Using indicator-based estimates of $\hat{F}$ within a population dynamic modeling framework enabled an evaluation of fishing impacts on sustainability at both the species and community levels, an important step toward ecosystem-based fisheries assessment and management. A comparison of these approaches applied to the assessment of southern Florida coral reef fisheries suggested that fishing has fundamentally altered the ecological structure of the fish community by depleting the biomass of higher-trophic level carnivores to the extent that the stocks are unsustainable.

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1. Introduction

The coastal and coral reef ecosystem in southern Florida supports lucrative tourism and fishing industries that generate over US $6 billion in economic activity per year (Ault et al., 2005a). A variety of commercial and recreational fisheries operate across the seascape targeting many species of fish and shellfish representing a wide range of taxa and trophic groups (Fig. 1) with high economic value that includes, for example: shrimp, crabs, spotted seatrout, mullet, red drum, bonefish, snook and tarpon in coastal bays and nearshore flats of barrier islands; snappers, groupers, and lobsters in offshore hardbottom and coral reef habitats; and, pelagics such as mackerels, dolphinfish, tunas, and billfishes seaward of the barrier coral reefs. The ecological persistence and economic sustainability of these valuable marine species is a key conservation concern as demand for access and use of these fishery resources continues to increase with a growing human population in South Florida.

Overfishing, habitat degradation and prey reduction are the principal threats to sustainability of coral reef and coastal fisheries in Florida. In this context, fishery sustainability is defined as the ability of an exploited population to produce goods and services, including yields (i.e., landings) at suitable levels in the short term, while maintaining sufficient stock reproductive capacity to continue providing these goods and services at similar levels into the indefinite future (Ault et al., 2008). Food and sport fisheries intensively fish a complex of over 70 reef fish species including snappers, groupers, grunts, wrasses, jacks, and porgies (Ault et al., 1998; Coleman et al., 2000). Small ornamental reef fish and invertebrate species are captured for marine aquaria. Other fisheries are directed toward key prey species (shrimps, baitfish) of

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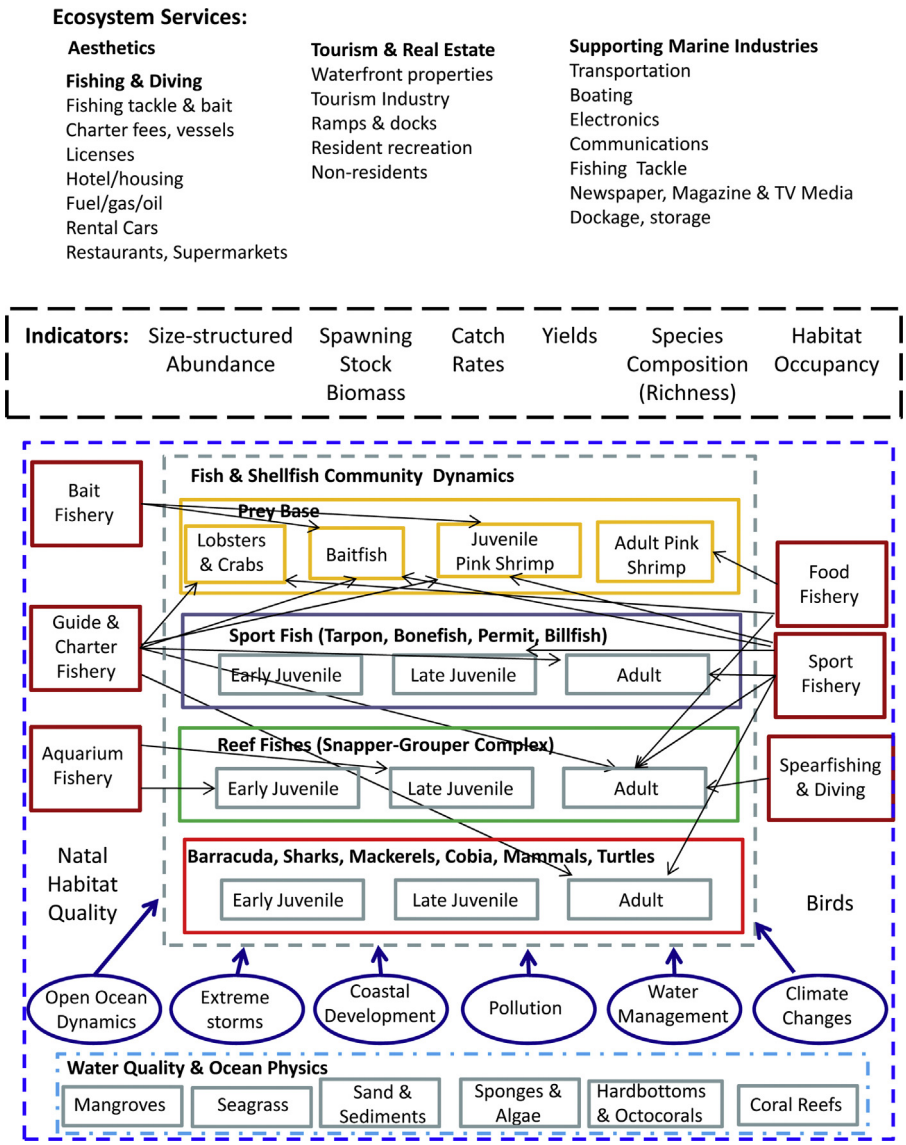

Fig. 1. Conceptual diagram of the ecological and fishery inter-relationships of the southern Florida marine ecosystem.

the snapper–grouper complex. Coral reef habitats are impacted by coral bleaching, disease, and vessel groundings, resulting in loss of both vertical structure and coral cover (Alvarez-Filip et al., 2009). Inshore nursery grounds of reef species are being altered by shoreline development, channel dredging, pollution, and changes in the volume, timing, and distribution of freshwater inflows (Lindeman et al., 2000; Wang et al., 2003; Ault et al., 1999, 2003, 2005a; Clua et al., 2005).

An interesting feature of the snapper–grouper complex is that any given fishing trip in the reef environment could potentially capture any one of the over 70 species. This is because the main reef fishing gears (e.g., hook-line, traps) are relatively non-selective and the species co-occur in similar habitats (Bohnsack and Ault, 1996; Ault et al., 2005b). The recreational and commercial fleets thus target the reef-fish complex as a whole rather than focus on any particular species. Efforts to manage coral reef fisheries from an ecological community perspective, however, have been hindered by the lack of data needed to evaluate sustainability status using conventional stock assessment methods. The required data for these conventional methods include demographic rates and historical time-series of age-size structured catches for each species, and the associated fishing effort by fleet and gear (Quinn and Deriso, 1999; Haddon, 2011). This paper describes the theoretical and empirical basis for an alternative approach to sustainability analysis at the species and community levels that bypasses the most problematic data requirements of conventional assessment methods, i.e., long time-series of catch and effort data. This alternative approach makes use of the indicator variable 'average length of the exploited life stage' ($\bar{L}$, L bar) that can be estimated from length composition data collected for most fisheries.

2. Methods

2.1. Indicators of sustainable fisheries: some theoretical inter-relationships

Here we explore the theoretical inter-relationship of two principal ecological indicators of fishing impacts on exploited populations: (1) catch (in weight or numbers) per unit of fishing effort (CPUE); and, (2) average size (in length or weight) in the exploited phase of the population, i.e., the mean of the distribution of size-structured relative abundance.

The CPUE indicator variable is an index of population productivity of the fishery resource, and mathematically relates to a dynamic

biomass (B) model that incorporates density-dependent birth and death rates. Adding a harvest term ($-FB$) creates a logistic surplus production model of the form

$$\frac{dB}{dt} = Bf(B) - FB = rB\left(1 - \frac{B}{B_0}\right) - FB, \quad (1)$$

where t is time, r is the intrinsic rate of increase in population biomass, B_0 is the unexploited population size (i.e., carrying capacity), and F is the instantaneous fishing mortality rate (Schaefer, 1957). At equilibrium, surplus production or yield in weight, Y_w, is given by

$$Y_w = F\bar{B} = qf\bar{B}, \quad (2)$$

the product of the instantaneous rate of fishing mortality F and $\bar{B}$, the average population biomass in a specified time interval (i.e., usually one year). From Eq. (2), fishing mortality F can be separated into two components, $F = qf$, where f is nominal fishing effort (e.g., the number of vessel-days or person-trips) and q is catchability, the fraction of the stock biomass removed per unit of f. It follows that catch per unit effort CPUE is defined as

$$\frac{Y_w}{f} = q\bar{B}, \quad (3)$$

and is thus a quantitative index (or indicator variable) proportional to average population size assuming that q is a constant.

Fundamental mathematical relationships exist among CPUE, surplus production (yield in weight from the fishery), stock biomass, and fishing effort as illustrated in Fig. 2. For the logistic surplus production model of Eq. (1), CPUE is linearly dependent on nominal fishing effort (Fig. 2A, solid line). Prior to being fished, stock CPUE is at its maximum value, fishing yields are zero (Fig. 2B), and stock biomass is at full carrying capacity B_0 (Fig. 2C). As fishing effort increases, stock biomass and its indicator CPUE both decline, whereas fishing yields steadily increase to a maximum value, MSY or maximum sustainable yield, which occurs in the logistic model at $0.5B_0$ or one-half of stock carrying capacity. As fishing effort increases past f_{msy}, surplus production, CPUE, and stock biomass all decline and approach zero.

Surplus production models assume that stock biomass components (i.e., ages or sizes) react similarly in terms of basic demographic processes (i.e., per capita births, growth, and deaths) irrespective of age. An alternative view derives from the basic idea that demographic processes of survivorship and growth are age-dependent (Beverton and Holt, 1957). The age-structured indicator variable $\bar{L}$, average length in the exploited phase of a stock, is defined as

$$\bar{L} = \frac{F\int_{a_c}^{a_\lambda} N(a)L(a)da}{F\int_{a_c}^{a_\lambda} N(a)da}, \quad (4)$$

where a_c is the age of first capture (i.e., the minimum age subject to exploitation), a_λ is the maximum age in the stock, $N(a)$ is numbers at age, and $L(a)$ is length at age (Ehrhardt and Ault, 1992). Two fundamental components of age-structured production models are the mathematical functions describing $N(a)$ and $L(a)$. A standard function for $N(a)$ is an exponential mortality model

$$N(a) = N(0)e^{-Za}, \quad (5)$$

where $N(0)$ is the "recruitment" (R) or addition of newborn to the population and Z is the total instantaneous mortality rate, i.e., the sum of fishing and natural mortality rates. The number of individuals in a birth cohort (i.e., age class) is presumed to decline exponentially from recruitment $R = N(0)$ at age 0 to the oldest age a_λ in the stock (Fig. 3A). For the model of Eq. (5), lifetime survivorship (i.e., the probability of surviving from recruitment to the maximum age) for an unexploited population is

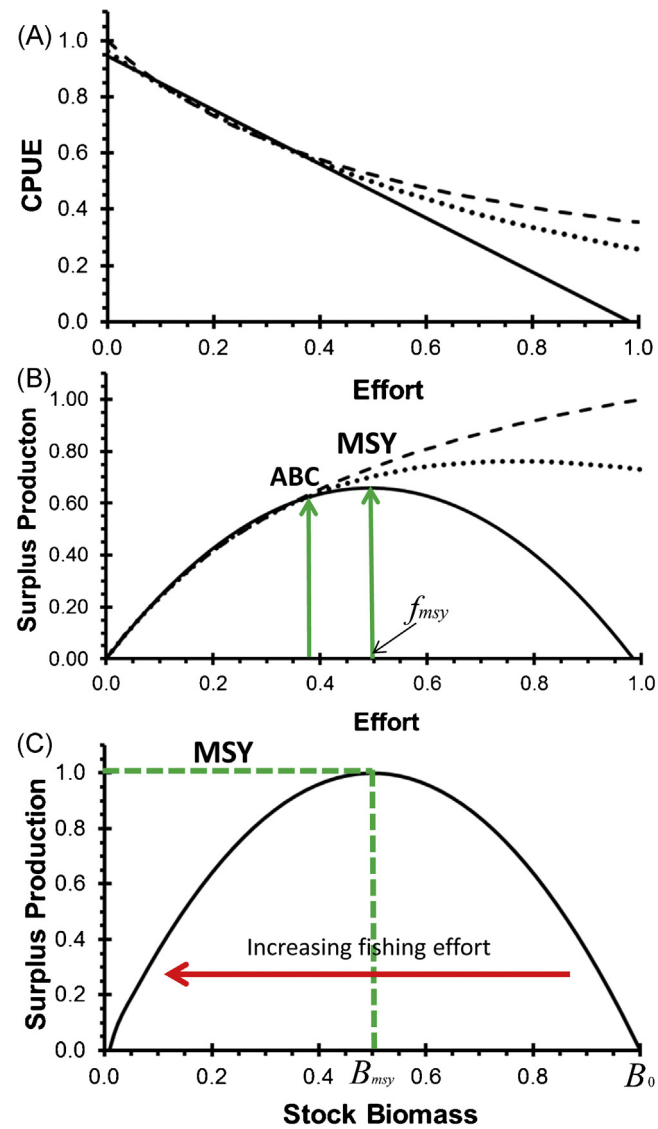

Fig. 2. Fundamental dynamics of logistic surplus production models: (A) linear relationship (solid line) of catch-per-unit-effort (indicator variable) to fishing effort; (B) model translation of stock surplus production (i.e., fishery yield) dependent on fishing effort (solid line); and (C) surplus production dependent on stock biomass. MSY = maximum sustainable yield; f_{msy} = fishing effort at MSY; ABC = allowable biological catch. Dashed lines in (A) and (B) show other possible exponential and hyperbolic model forms.

$S_\lambda = \frac{N(a_\lambda)}{R_0} = e^{-Ma_\lambda}$, where M is the instantaneous natural mortality rate (i.e., $Z = M$). The probability of surviving the exploited phase ($a_\lambda - a_c$) when fishing is occurring is

$S = e^{-(F+M)(a_\lambda - a_c)}$, where $Z = F + M$.

A standard function used to describe growth of an average individual in an age cohort over its lifespan is the von Bertalanffy model

$$L(a) = L_\infty(1 - e^{-K(a-a_0)}), \quad (6)$$

where L_∞, K, and a_0 are model parameters. Weight (individual biomass) at age is obtained from an allometric weight–length function

$$W(a) = \alpha(L(a))^\beta = \alpha(L_\infty(1 - e^{-K(a-a_0)}))^\beta \quad (7)$$

that uses $L(a)$ values from Eq. (6). For Eq. (7), the weight of an individual fish is expected to increase rapidly during its early years of life, then more slowly approach an asymptotic value during its later years (Fig. 3A).

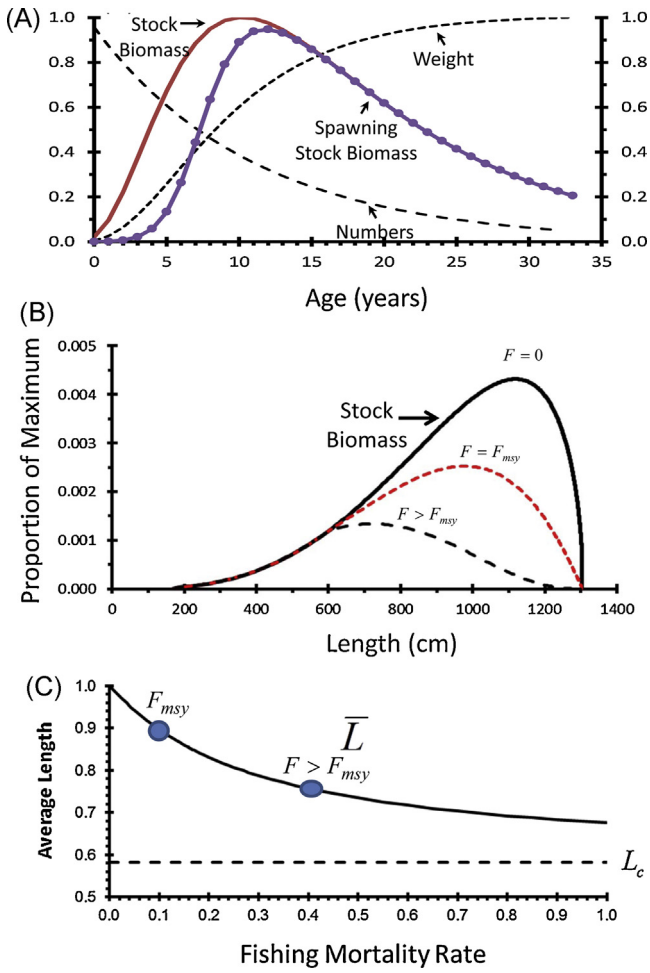

Fig. 3. Fundamentals of structured stock production dynamics: (A) survivorship at age (Eq. (5)), growth in weight at age (Eq. (7)), and the resulting stock biomass and spawning stock biomass at age; (B) stock biomass at length (cm) at three levels of fishing mortality (F); and, (C) response of the biological indicator average length (Eq. (4)) in the exploited phase of the stock for a range of fishing mortality rates F. Indicators are scaled as proportions of maximum values. L_c is the length at first capture.

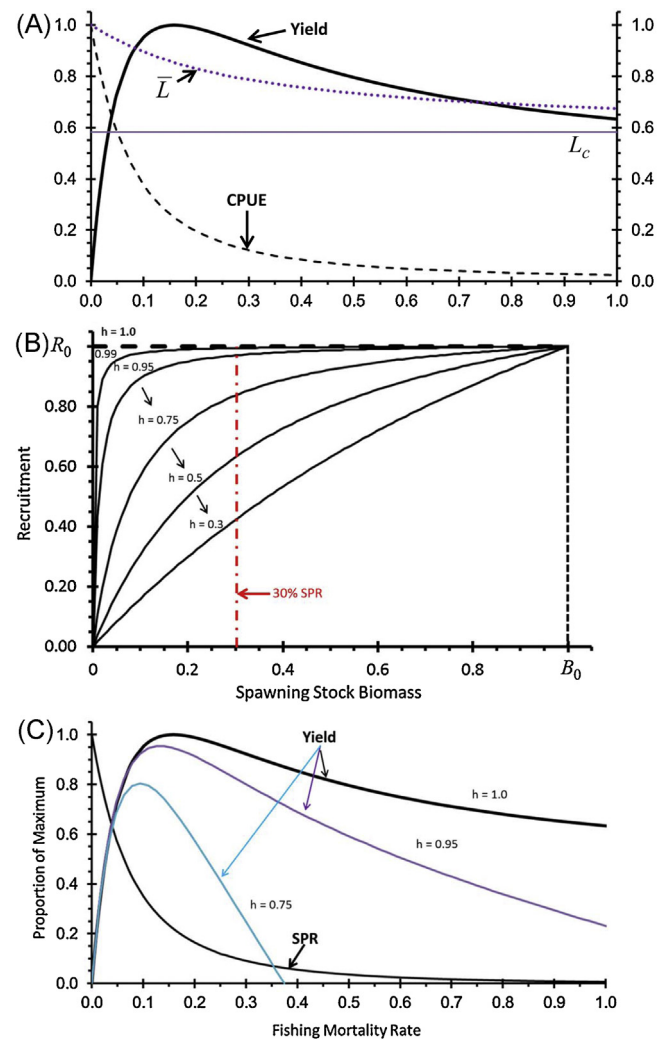

Fig. 4. Relationship of the age-structured production model to the logistic surplus production model. Panel (A) shows the relationship of the age-structured fishery yields (Y_w in weight, Eq. (8)) and CPUE (Eq. (3)) dependent on fishing mortality for the assumption of constant recruitment. Panel (B) shows recruitment (as a proportion of R_0, the unexploited recruitment in numbers) dependent on spawning stock biomass SSB (as a proportion of B_0, the unexploited SSB in weight, Eq. (9)) for several levels of steepness (h); higher h infers greater stock resilience. Panel (C) shows the relationship of SPR (Eq. (10)) and age-structured fishery yields for several levels of steepness (h) dependent on fishing mortality. Note that when steepness is lower than $h = 1.0$ the age-structured yield curves resemble the surplus production curve shown in Fig. 2B, with the effect on decreasing fishery yields at higher Fs with decreasing steepness h.

Given these functions for $N(a)$ and $W(a)$, biomass of a cohort ($B(a) = N(a)W(a)$) is maximized at some intermediate age (Fig. 3A). At young ages, cohort numbers are high but weights of individual fish are low, resulting in net lower biomass. At older ages the converse is true, i.e., weights of individual fish are high but cohort numbers are low. For an unexploited population in equilibrium, the functions shown in Fig. 3A represent numbers, weight, and biomass of age classes in the population in a given year t. Stock biomass is the sum of all cohorts alive during year t. Spawning stock biomass (SSB) is the proportion of stock biomass that is sexually mature. If the same population is considered from the perspective of length L, in contrast to age a, the biomass at length can be estimated as ensemble numbers at given length for cohorts, i.e., $N(L) = N(0)S(a)P(L|a)$, where $P(L|a)$ is the probability of being length L given the fish is age a, times the weight at length (c.f., Ault et al., 2008). When considered in terms of biomass at length (Fig. 3B), peak biomass occurs near the upper end of the length range for an unexploited population because many older age classes are compressed into a few large size classes. However, increasing the fishing mortality rate greatly truncates population biomass at age and size through a process known as juvenescence (i.e., "making the population younger"). This is reflected in the observed decrease in the indicator variable average length ($\bar{L}$) as fishing mortality increases (Fig. 3C).

From these relationships, yield in weight from the fishery in year t for an age-structured population is given by

$$Y_w(t) = \int_{a_c}^{a_\lambda} F(a)N(a)W(a)\,da = \int_{a_c}^{a_\lambda} F(a)B(a)\,da. \tag{8}$$

The inter-relationships of biological indicators for the age-structured production model for yield, CPUE and exploited population biomass (since $Y_w/f = q\bar{B}$) for a given age at first capture a_c, are demonstrated in Fig. 4. While CPUE decreases monotonically with increasing F, the yield maximizes at some intermediate value of F, just as with the logistic production model. There is a departure, however, between the yield curves for the surplus production and age-structured models at high rates of fishing. The age-structured model in Fig. 4A presumes that a constant level of newborn recruits will enter the population each year irrespective of spawning stock size, and further, predicts moderately high yields at high rates of F,

even though stock biomass is expected to be very low. This is in contrast to the surplus production model (Fig. 2B), which incorporates density-dependent per capita birth and death rates.

This lack of realism in the age-structured production model is addressed by accounting for the impact of fishing mortality on spawning stock biomass (SSB) and subsequent recruitment to the population. SSB is obtained by integrating over individuals in the population between the age/size of sexual maturity (a_m and L_m, respectively) and the maximum age/size (a_λ and L_λ, respectively),

$$\mathrm{SSB}(t) = \int_{a_m}^{a_\lambda} B(a)\,da \text{ or } \mathrm{SSB}(t) == \int_{L_m}^{L_\lambda} B(L|a)\,dL, \tag{9}$$

and represents the mature biomass that remains in the water after fishing. Maximum SSB is obtained under conditions of no fishing mortality when recruitment is at its maximum (i.e., R_0). Spawning potential ratio (SPR) is the ratio of exploited to unexploited SSB(t),

$$\mathrm{SPR} = \frac{\mathrm{SSB}_{\mathrm{exploited}}}{\mathrm{SSB}_{\mathrm{unexploited}}} \tag{10}$$

Recruitment dependent on SSB is shown in Fig. 4B for a range of "steepness" values h (Hilborn and Walters, 1992). Higher values of h imply greater recruitment at lower levels of spawning stock biomass after perturbations such as fishing (Mangel et al., 2010, 2013). A resilient stock can produce high levels of recruitment over a wide range of spawning biomass. As SSB declines toward zero with increasing exploitation, however, the expected recruitment also declines toward zero for all levels of steepness except $h = 1$, the scenario of constant (i.e., density-independent) recruitment. As illustrated in Fig. 4C, the age-structured yield model incorporating density-dependent recruitment (i.e., $h < 1$) more realistically predicts rapid declines in yields at high levels of F that have reduced the spawning stock biomass (or SPR) to low levels. Therefore, the link between the logistic and age-structured yield models, and thus the CPUE and $\bar{L}$ indicator variables, is more clearly seen when recruitment is dependent on SSB.

2.2. Estimation of fishing mortality rates from indicator variables

Estimates of fishing mortality rates over time for a given stock are required to conduct a formal sustainability analysis for a given stock. Fishing mortality rate F can be estimated from either one of two indicators, CPUE or $\bar{L}$. CPUE is estimated from catch and effort data collected from the fishery, ideally for each gear type and fleet (e.g., commercial, recreational). $\bar{L}$ is estimated from relative-abundance-at-length data for the exploited phase, ideally for each gear type and fleet. We compared the performance of the two indicators for three principal exploited species that dominate reef fish catches from southern Florida: black grouper (*Mycteroperca bonaci*), hogfish (*Lachnolaimus maximus*), and yellowtail snapper (*Ocyurus chrysurus*). The sources of catch-and-effort and length composition data from the various fleets (i.e., commercial, recreational, and charter) and gears (i.e., hook-line, spear, and trap) are given in Ault et al. (2005b) and were updated for this analysis. Fishing effort among fleets and gears was standardized using the fishing power method of Robson (1966) to produce a single combined index.

For the surplus production method (CPUE indicator), fishing mortality rates were estimated from catch-and-effort time-series using a non-equilibrium model employing maximum-likelihood procedures (Quinn and Deriso, 1999; Haddon, 2011).

For the length-based method ($\bar{L}$ indicator), fishing mortality rates were estimated following Ehrhardt and Ault (1992) and Ault et al. (1998) using estimates of $\bar{L}$ from catches and basic life history information on lifespan and size-at-age relationships (c.f., Supplemental information).

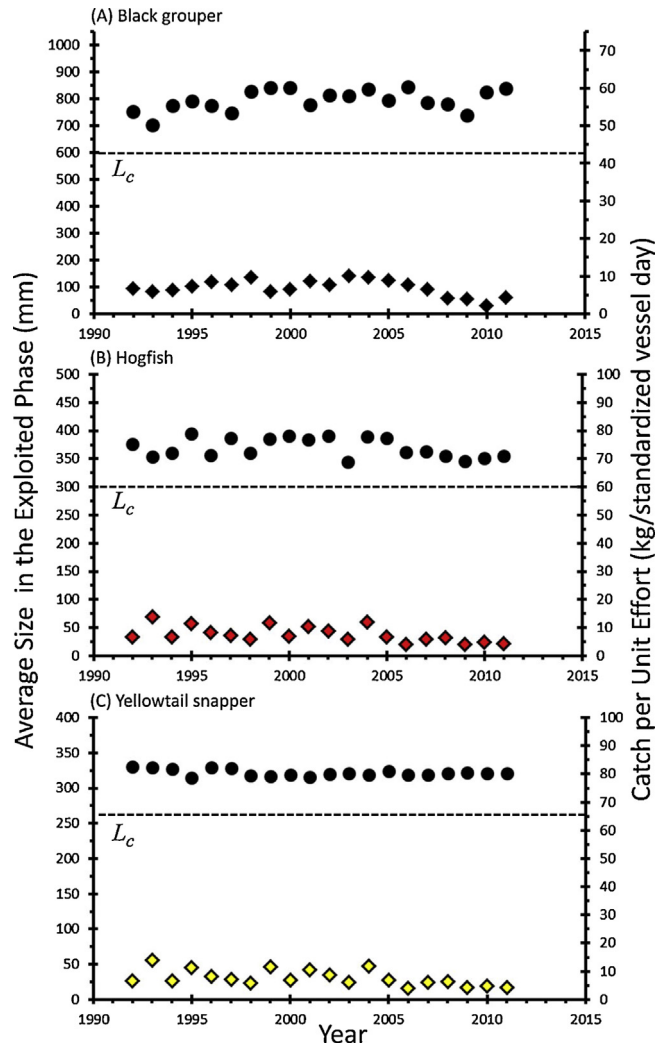

Fig. 5. Annual estimates of average length ($\bar{L}$) and CPUE during 1992–2011 for three principal reef fish species in southern Florida: (A) black grouper; (b) hogfish and (C) yellowtail snapper.

2.3. Model verifications and computation of sustainability benchmarks

We employed a stochastic numerical cohort-structured model (REEFS, Ault et al., 1998, 2008) to verify that fishing mortality rates estimated from CPUE and $\bar{L}$ matched the resulting observed population size structures. The REEFS model was also used to compute management benchmarks of stock status in a limit control rule context (Ault et al., 2008). These benchmarks were: F_{msy} (F generating maximum sustainable yield, MSY); B_{msy} (population biomass at MSY); and SPR (spawning potential ratio). We defined F_{msy} as $F = M$ (Francis, 1974).

3. Results

3.1. Comparison of indicator variables and fishing mortality rates

Comparisons of the empirical time-series of the two indicator variables, $\bar{L}$ and CPUE, for three exploited reef fishes in southern Florida (black grouper, hogfish, and yellowtail snapper) are shown in Fig. 5. Graphs are scaled to the expected maximum values of the indicator variables. The indicator variables for all three species were relatively stable over the past 20 year period (i.e., in equilibrium *per se*), but toward the low end of their respective ranges for all

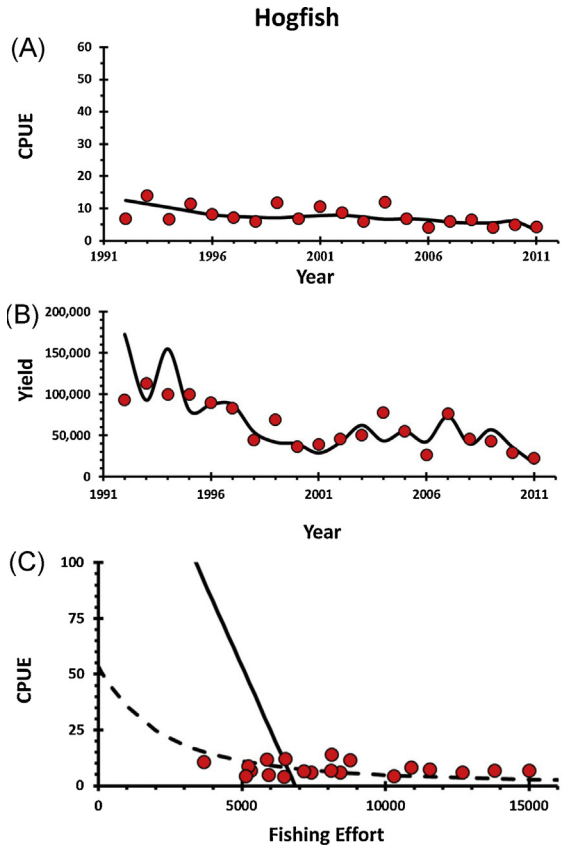

Fig. 6. Logistic surplus production model fits to 1992–2011 hogfish data: (A) CPUE; (B) surplus production and (C) CPUE dependent on fishing effort (solid line). The dashed line in (C) suggests that the production model is likely an exponential or hyperbolic function rather than the logistic function (see Fig. 2A).

cases.Surplus production (SP) model fits to observed hogfish annual CPUE (Fig. 6A) and yield (Fig. 6B) for 1992–2011 showed reasonable model performance. However, plotting CPUE against fishing effort (Fig. 6C), did not produce the expected trend for the logistic surplus production model (Fig. 6C, solid line). The underlying production model may approximate an exponential or hyperbolic function (Fig. 6C, dashed line; e.g., Fox, 1975); however, data were missing from the early years of the fishery, when fishing effort was low and stock biomass high, so CPUE did not even appear to be dependent on effort in the data plotted. Similar issues with SP methods were encountered with the other two species.

Despite the fitting issues of the SP method using CPUE data, similar estimates of fishing mortality rates were estimated with the structured length-based (LB) modeling method, at least for black grouper and yellowtail snapper (Fig. 7). The LB estimates exhibited lower variability. The departure between mean estimates from the two methods was more substantial for hogfish. Estimated fishing mortality rates for black grouper and hogfish were in excess of sustainable levels, irrespective of modeling method, whereas, yellowtail snapper was at or below the MSY limit.

We validated our *F*-estimates from the SP and LB methods by using them in the REEFS numerical model to compute the expected stock abundance at length. Comparisons of modeled and empirical size distributions matched well for the three species (Fig. 8). The estimated distribution of hogfish *F*s was somewhat lower from the SP model than from the LB model (Fig. 7), but the model-generated size structures from the LB estimates of *F* matched the empirical size structure more closely (c.f., Fig. 8A and B).

3.2. Limit control rules for assessing population sustainability

The "limit control rule" or "Kobe" diagram detailed in Ault et al. (2008) is a useful way to view the sustainability status of an exploited stock (Fig. 9A). The *y*-axis depicts the current level of *F* with respect to the fishing mortality rate that produces MSY (i.e., F_{msy}). The ratio value of $F/F_{msy} = 1$ represents the management limit; the ratio for a stock fished sustainably would be below this limit, i.e., $F < F_{msy}$. The *x*-axis depicts the current level of stock biomass with respect to the biomass value at MSY. Again, the ratio value of $B/B_{msy} = 1$ is the limit, but in this case the ratio of a sustainably fished stock would be above this limit, i.e., $B > B_{msy}$. Our cases—two overfished stocks, black grouper and hog snapper, and the case of a stock at MSY, yellowtail snapper—are shown on the Kobe plot (Fig. 9A, along with their expected trajectories of *F* and *B*, defined by the shape of the individual species' production curve.

As illustrated in Fig. 9B and C for black grouper, fishery management regulations generally address sustainability through implementation of changes in either fishing effort (reflected in *F*; *x*-axis), or size limits (i.e., restricting the age or size at first capture, a_c, L_c; *y*-axis), or both. The green line represents optimal yields (Fig. 9B) and SPR = 30% benchmark levels (Fig. 9C), respectively, for combinations of *F* and a_c. In addition to the obvious benefits in reductions of *F*, the situation depicted in Fig. 9B and C shows that it is also possible to achieve high yields and maintain stock reproductive capacity at acceptable levels even under very high rates of fishing, provided that a_c is set high enough to enable a sufficient proportion of the population to reproduce before being fished (e.g., Ault et al., 1998).

3.3. Applications to multiple species fished together

The analysis framework described above for a single species (or stock) can be used to evaluate situations where multiple species are fished together as a complex, a typical situation for coral reef fisheries. Results of community-level applications of fishing impacts on sustainability of reef-fishes are compared in a "community control rule" format for southern Florida (Fig. 10, Ault et al., 2005b). In this case, average length ($\bar{L}$) was the principal indicator variable used to estimate rates of fishing mortality for the reef fish community. Although these analyses were conducted one species at a time, plotting the results together on a control-rule graph provides a community perspective on sustainability status. It is evident that the majority of species analyzed have experienced unsustainably high rates of fishing mortality. The results also suggest that the severity of overfishing differed among species, even though nominal fishing effort in each area generally affects the reef-fish complex as a whole. This differential response to exploitation is linked to life history characteristics (Musick et al., 2000; Ault et al., 2005b, 2008), with slower-growing, longer-lived species such as groupers (Supplemental information) being more susceptible to fishing impacts compared to faster-growing, shorter-lived species such as grunts (i.e., F_{msy} for groupers is less than F_{msy} for grunts).

4. Discussion

The simple, thumbnail sketch of the southern Florida fisheries ecosystem in Fig. 1 underscores the need to move toward ecosystem-based fisheries management. This paper describes a framework for achieving this lofty goal. Using indicator variables estimated from empirical data within a population dynamic modeling framework, it is possible to evaluate fishing impacts on sustainability from a single species as well as community perspective. Either of two indicator variables, CPUE or $\bar{L}$, can be used to estimate *F*, which is then used to evaluate sustainability benchmarks (Figs. 9 and 10) conforming to the legal regulatory

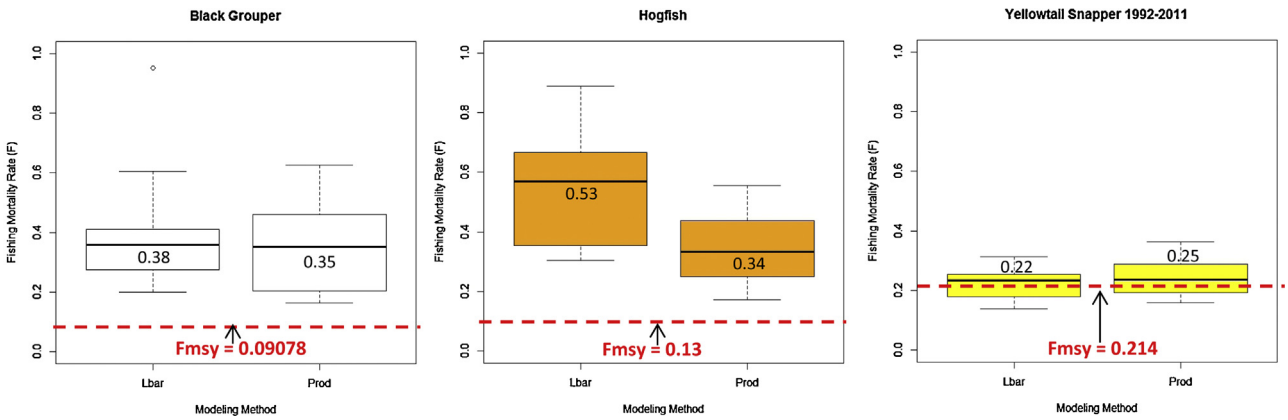

Fig. 7. Comparative estimates of the mean and distribution of annual fishing mortality rates for black grouper, hogfish and yellowtail snapper from 1992 to 2011 period using the length-based and surplus production models. Also shown are the *F*'s that produce MSY for each of the species.

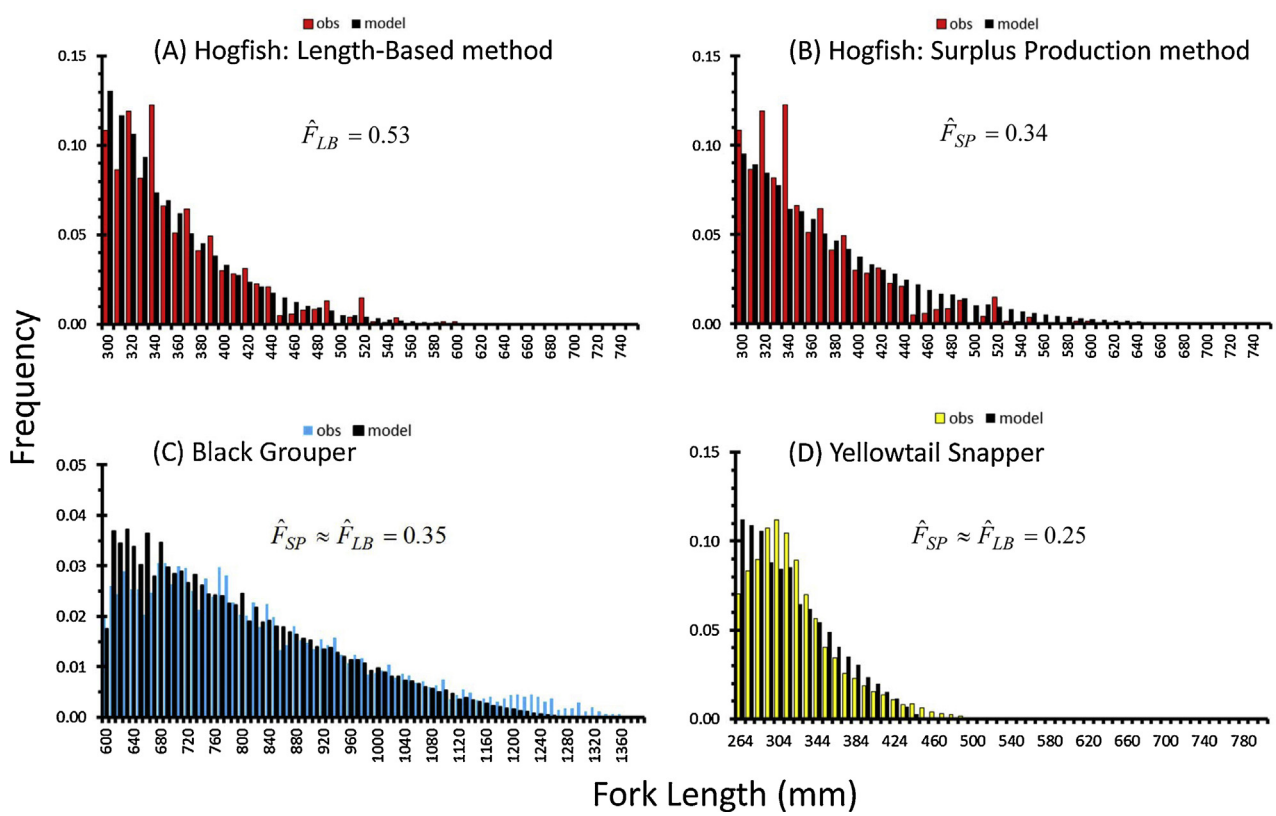

Fig. 8. Comparison of REEFS model-generated length frequencies (black bars) to observed length frequency distributions (colored bars) using estimated 20-year (1992–2011) mean fishing mortality rates from Fig. 7: (A) hogfish length-based ($\hat{F}_{LB} = 0.53$); (B) hogfish surplus production ($\hat{F}_{SP} = 0.34$); black grouper ($\hat{F}_{SP} \approx \hat{F}_{LB} = 0.35$); and, (D) yellowtail snapper ($\hat{F}_{SP} \approx \hat{F}_{LB} = 0.25$). Observed length frequencies were summed for 2002–2011.

framework for USA fisheries (Magnuson–Stevens Fisheries Conservation and Management Act; Restrepo and Powers, 1999; Ault et al., 2008).

Analysis methods for small-scale data limited fisheries have recently gained wide attention (Cope and Punt, 2009; Dick and MacCall, 2011; Jiao et al., 2011), although these have been the focus of stock assessment for some time (e.g., Beverton and Holt, 1957; Gallucci et al., 1996; Klaer et al., 2012). The length-based approach to estimate mortality rates presented here stems from a long tradition in fisheries science starting with Beverton and Holt (1957), and has been expanded in recent decades (Ehrhardt and Ault, 1992; Ault et al., 1998; Gedamke and Hoenig, 2006). It is interesting to note that a recent spate of length-based estimation methods for data-poor fisheries used Beverton–Holt life history ratios (e.g., M/K) to infer management benchmarks, without taking advantage of directly estimating stock mortality rates from length frequency data (i.e., Hordyk et al., 2014a,b; Prince et al., 2014).

As discussed in Ault et al. (2005b, 2008), the indicator $\bar{L}$ has some practical advantages over CPUE for coral reef fisheries, the most important of which is much less stringent data requirements. In many tropical fisheries, the requisite long time-series of species-specific catch and effort data by gear and fleet are simply not available, in contrast to species-specific length composition data collected by scientists at landing sites. Florida is no exception. For example, while catches and associated effort of prominent species in the reef-fish complex such as snappers and groupers are recorded

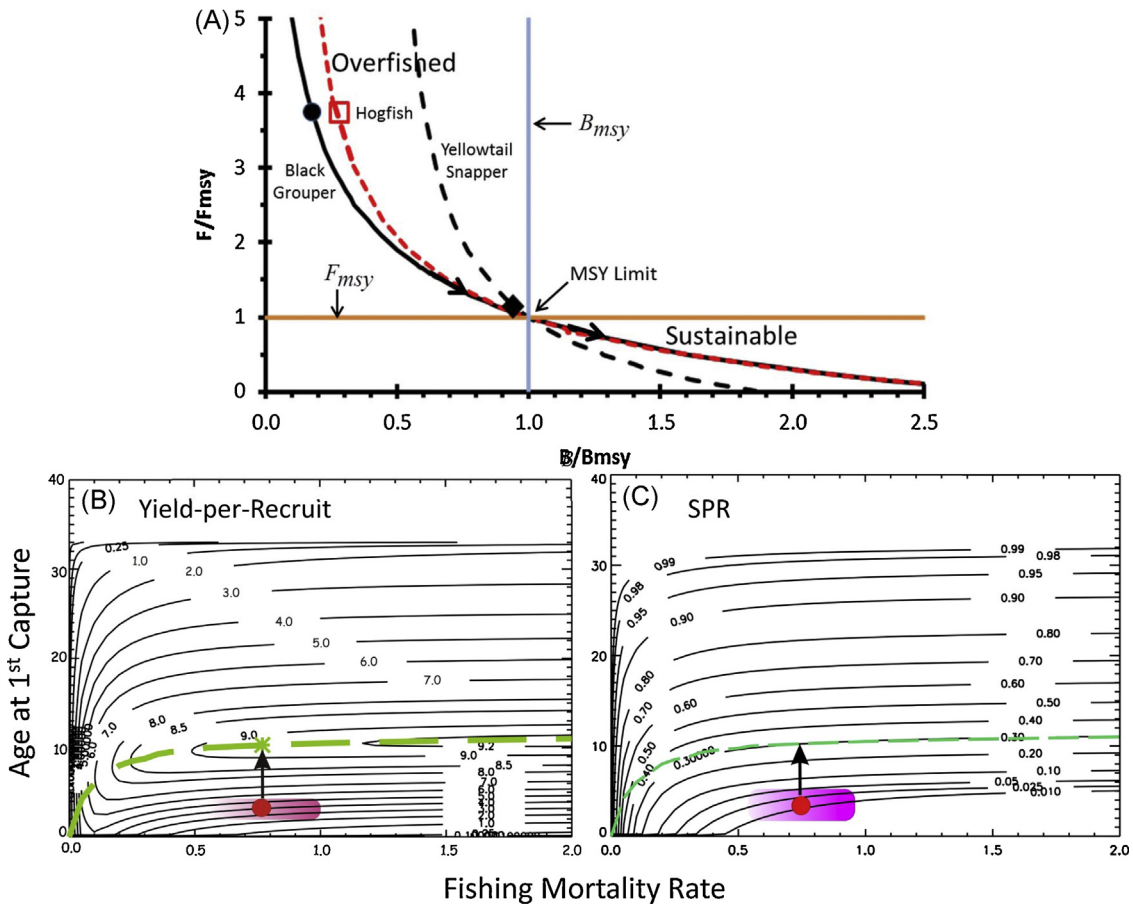

Fig. 9. (A) Limit control diagram for evaluating sustainable levels of fishing mortality rate *F* and stock biomass levels *B* with respect to the MSY management limit. (B and C) Illustration of resource management risks related to fishery yields (B) and spawning potential ratio (C) in the context of possible options to achieve sustainability. The shaded area of each panel shows current resource status (current estimated *F*), and the arrows denote required changes in age (or size) to reach optimum benefits (dashed green line).

for the commercial fleet at the species level, catches of most species of grunts and porgies are only recorded at the family level. Another issue we encountered was that even though a 20-year catch-effort series was available for our three example species (Fig. 5), data were not available from the earlier years of the fishery that would provide a more complete range of catch and effort values for a given stock, especially high catches at low effort. The effect of the restricted range of catch-effort values was apparent in the relationship between CPUE and effort (e.g., Fig. 6C), and created difficulties in application of the surplus production model for estimating fishing mortality rates.

The community perspective on sustainability shown in Fig. 10 suggests that fishing has substantially altered the trophic structure of reef-fish communities in southern Florida. Within the exploited snapper–grouper complex, the biomass of fishes that attain the largest sizes (groupers, large snappers) has been depleted more severely than the biomass of smaller-sized species (small snappers, grunts). The snapper–grouper complex contains most of the top-level carnivores in the wider reef-fish community, and it appears that most species in this trophic level have been fished at unsustainably high rates. The phenomenon of "fishing down the food chain" observed in many marine ecosystems around the world (Pauly et al., 1998) thus seems to be occurring in the coral reef ecosystems of Florida, and perhaps the wider Caribbean (e.g., Ault et al., 2008).

Other fishing impacts at the ecosystem scale are illustrated in Fig. 1. A number of fisheries in southern Florida target lower-trophic level species (shrimps, baitfish) that are key components of the prey base of higher-trophic-level species (coastal gamefishes,

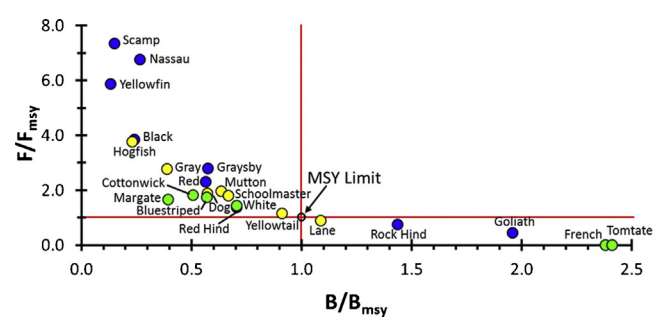

Fig. 10. Limit control plots showing estimated levels of spawning stock biomass (*x*-axis) and fishing mortality rate (*y*-axis) with respect to MSY levels for exploited reef-fish communities in southern Florida (redrawn from Ault et al., 2005b; blue circles, groupers; yellow circles, snappers and wrasses; green circles, grunts).

reef fishes) that are the targets of other fisheries (e.g., Ault, 2008). Thus both bottom-up and top-down fishing pressures are being exerted on the same food web. Fundamental alterations to trophodynamics from fishing, occurring along with other non-fishing impacts to sustainability from habitat and water quality alterations, make it questionable whether the ecosystem can continue to produce ecologically and economically viable goods and services into an uncertain future that likely involves climate change.

Evaluating fisheries sustainability in light of the full spectrum of threats—direct and indirect fishing, habitat alterations, climate change—will require extensions of population dynamics theory, models, and data, as well as more integrated coastal management

systems, along the lines described in Ault et al. (2005a). In the meantime, steps in the short term can be taken to address direct fishing impacts, perhaps the dominant stressor at present, on the southern Florida coastal and coral reef ecosystem. Scientifically, there is a need to expand the evaluation of fishing impacts to sustainability for as many exploited species in the ecosystem as possible, i.e., those that have sufficient life history (Supplemental information) and indicator (CPUE or $\bar{L}$) data. This analysis will provide a first-order view on which components of the ecosystem are being fished sustainably and which are not. This proposed synthesis of scientific results will set the stage for resource managers, scientists, and user groups to collectively develop corrective measures at the species, community, and ecosystem scales to reduce fishing impacts to sustainable levels that will hopefully begin to restore ecological balance to the trophic structure. These actions will in turn provide the foundation for achieving long-term economic sustainability of ecosystem goods and services.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2014.04.013.

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