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Evaluation of average length as an estimator of exploitation status for the Florida coral-reef fish community

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Simulation and empirical analyses were conducted to evaluate the utility and robustness of average length (Lbar) of animals in the exploited population as an estimator of fishing mortality (F), and therefore as an indicator of exploitation status for Florida coral-reef fish. Simulation results showed that the Lbar estimator of fishing mortality was relatively insensitive to trends in recruitment, and demonstrated favourable properties for detecting statistical differences between sustainable and non-sustainable rates of exploitation. Rates of F estimated from fishery-dependent size composition data were comparable to F estimates from catch-and-effort time-series. Average length was also estimated from fishery-independent diver surveys for 22 species in the exploited snapper−grouper complex. A majority of snapper−grouper species are currently fished unsustainably in the Florida Keys, though overfishing appears most severe for long-lived, slow-growing fish.

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Introduction

The Florida Keys coral-reef ecosystem (24.7°N 81.0°W) is inhabited by more than 400 fish species and supports multibillion-dollar fishing and tourism industries (Johns *et al.*, 2001). Over recent decades, reef-fish populations have declined, owing to a variety of human-related stressors, most notably fishing and habitat alterations (Ault *et al.*, in press). The fish are intensively exploited (Ault *et al.*, 1998, 2003), but fishing mortality affects the species differentially (Coleman *et al.*, 2000; Musick *et al.*, 2000).

Our research focus has been to quantify the reef-fish community response to exploitation in the Florida Keys (Ault *et al.*, 1998). The principal data source is fishery-independent, synoptic diver-based visual surveys of species composition, abundance, and size structure, including target and non-target species (Bohnsack *et al.*, 1999; Ault *et al.*, 2002). The principal stock assessment indicator variable to quantify population status is average length (Lbar) of the exploited part of the population, which is a metabolic-based indicator that is highly correlated with population size (Beverton and Holt, 1957; Ricker, 1963; Pauly and Morgan,

1987; Ault and Ehrhardt, 1991; Ehrhardt and Ault, 1992; Kerr and Dickie, 2001). For exploited species, Lbar reflects the rate of fishing mortality. Because body size is broadly correlated with trophic level, large individuals and species are often top predators. Biomass declines of such animals are usually the most marked community response to exploitation (Ault *et al.*, 1998; Gislason and Rice, 1998; Pauly *et al.*, 1998; Kerr and Dickie, 2001). Previous studies showed that the Lbar estimator of mortality rate is unbiased under conditions of constant annual recruitment to the exploited stock (Ehrhardt and Ault, 1992; Quinn and Deriso, 1999). However, resulting mortality estimates may exhibit positive bias under conditions of an increasing trend in recruitment. In the Florida Keys, recruitment of the most severely depleted stocks may be increasing at present, in response to a series of recent management actions for the snapper−grouper complex, including gear restrictions, minimum size and bag limits, and spatial closures (Ault *et al.*, in press).

To evaluate the utility and robustness of average size as an estimator of exploitation status for Florida reef fish, our objectives here are to: (i) examine uncertainty in Lbar

estimates of mortality rates and potential bias caused by trends in recruitment; (ii) compare estimates of mortality rates based on a variety of methods and different data sources; (iii) apply the Lbar estimator of mortality simultaneously to a suite of reef-fish species under the same nominal fishing effort, to evaluate its potential as a first-order indicator of community response to exploitation.

Methods

Table 1 shows the sources of length composition and catch-and-effort data used. Life history parameters for Florida reef fish (Table 2) were taken from Ault *et al.* (1998, 2002, 2003) and Claro *et al.* (2001). Natural mortality rate (M) was estimated from lifespan, applying the procedure of Alagaraga (1984).

Total instantaneous mortality rate (Z) was estimated using the method of Ehrhardt and Ault (1992), which is based on length at first capture (L_c), maximum length in the stock (L_λ), and average length in the exploited stock (Lbar), in conjunction with the Bertalanffy growth parameters K and L_∞. Estimates of Z were computed using an iterative numerical algorithm (LBAR; Ault *et al.*, 1996; FAO, 2003), and annual estimates of F were obtained by subtracting M from Z. All input values are given in Table 2.

Theoretically, Lbar in year t is expressed as

$$\overline{L}(t) = \frac{F(t)\int_{a_c}^{a_\lambda} N(a,t)L(a,t)da}{F(t)\int_{a_c}^{a_\lambda} N(a,t)da} \tag{1}$$

where a_c is the minimum age at first capture, a_λ the oldest age in the stock, N(a,t) the abundance for age class a, L(a,t) the length-at-age, and F(t) is the instantaneous fishing mortality rate at time t. In practice, Lbar is usually estimated in the length range $L_c - L_\lambda$. Estimates of average

length and the corresponding variances were obtained from fishery-dependent and -independent length composition data, applying standard statistical procedures (Sokal and Rohlf, 1981). Non-normality of length observations was corrected by log-transformation. Fishery-dependent estimates were obtained by weighting recreational and commercial fleet estimates by their respective proportions of the catch, and fishery-independent estimates by weighting estimates of population abundance from data collected inside and outside marine protected areas by their respective proportions.

In addition, two methods were used to estimate F from Florida-wide catch-and-effort time-series: the ASPIC non-equilibrium surplus production model (Prager, 1994), and a continuous formulation (i.e. no age or size structure) of a general stock-synthesis model (Methot, 1990; Quinn and Deriso, 1999), employing maximum-likelihood procedures (Haddon, 2001). These time-series methods generally produce more reliable estimates for the most recent years. Effort among fleets and gears was standardized using the fishing power method of Robson (1966).

Finally, a numerical cohort-structured model (Ault and Olson, 1996; Ault *et al.*, 1998) was used to compute management benchmarks of stock status and to conduct simulation analyses of uncertainty and bias properties of F estimates based on average size. The benchmarks used to evaluate sustainable exploitation in terms of a limit control rule were: F_{msy} (F generating maximum sustainable yield, MSY); B_{msy} (population biomass at MSY); and SPR (spawning potential ratio; Mace, 1997; Restrepo and Powers, 1999). We define F_{msy} as F = M.

The bias in F resulting from potentially increasing trends in recruitment to the exploited stock was evaluated for hogfish (*Lachnolaimus maximus*) with the cohort-structured model. Hogfish was used here because reliable long-term fishery-dependent and -independent data were available for methodological comparisons, and because its life history demographics are characteristic of the snapper−grouper complex. Simulations were run over a range of exploitation rates (F = 0.0−0.8) and increasing recruitment trends (0−10% y^{-1}). Recruitment of fish entering the population at age t_r was assumed to have an exponential trend (with recruitment rate parameter r; $N_{t_r,t} = N_0 e^{rt}$), and was presumed to occur over the entire lifespan (Quinn and Deriso, 1999). These analyses represent a ''worst-case'' scenario for potential bias in F estimates.

Results

The analytical relationship between Lbar and F, some aspects of uncertainty in average length mortality estimates, and the expected stochastic population length compositions at three levels of fishing mortality (F = 0; F = F_{msy}; F = F_{2001}) are depicted in Figure 1. The most recent Florida-wide estimate of F is about four times higher than F_{msy}. Means and 95% confidence intervals (CI) of Lbar for

Table 1. Sources of length composition (lc) and catch-and-effort (c−e) data used to evaluate average length as an estimator of exploitation status for Florida reef fish (MRFSS, Marine Recreational Fisheries Statistics Survey; TIP, Trip Interview Program; TTD, Trip Ticket Data Base; RVC, Reef-fish Visual Census).

Type of data	Database	Period	Comments
Florida-wide			
lc/c−e	MRFSS*	1993−2002	Sport fishing fleet
lc	TIP*	2001−2002	Commercial fleet
c−e	TTD**	1993−2001	Commercial fleet
Florida Keys			
lc	RVC***	2000−2002	Fishery-independent

Sources: * National Oceanic and Atmospheric Administration, ** Florida Fish and Wildlife Conservation Commission, *** Bohnsack and Bannerot (1986), Bohnsack *et al.* (1999); Ault *et al.* (2002).

Table 2. Life history input parameters and estimated population parameters for Florida reef fish (a_0 and W_∞, parameters of the von Bertalanffy equation; L_m, length at maturity; B_{msy}, expressed as proportion of unfished stock biomass; for other symbols see text).

Species	Input parameters								Estimated parameters					
	a_λ (y)	K (y^{-1})	L_∞ (mm)	a_0 (y)	W_∞ (kg)	L_m (mm)	L_c (mm)	L_λ (mm)	M (y^{-1})	Lbar (mm)	F (y^{-1})	SPR (%)	B_{msy}	B/B_{msy}
Groupers (Serranidae)														
Rock hind (*Epinephelus adscensionus*)	12	0.19	486	−2.16	2.27	336	200	454	0.25	288	0.19	31	0.22	1.44
Graysby (*E. cruentatus*)	15	0.13	415	−0.94	1.14	198	200	363	0.20	233	0.56	36	0.63	0.57
Red hind (*E. guttatus*)	17	0.21	393	−0.83	1.09	251	180	383	0.18	251	0.24	24	0.34	0.70
Goliath grouper (*E. itajara*)	37	0.05	2 394	−3.62	244.9	978	600	2 178	0.08	1 161	0.04	53	0.27	1.96
Red grouper (*E. morio*)	17	0.15	938	−0.10	11.9	437	500	869	0.18	592	0.41	27	0.47	0.57
Nassau grouper (*E. striatus*)	17	0.15	940	−1.08	12.0	480	600	870	0.18	635	1.19	13	0.47	0.26
Black grouper (*Mycteroperca bonaci*)	20	0.16	1 200	−0.30	31.6	597	600	1 153	0.15	709	0.60	10	0.41	0.26
Scamp (*M. phenax*)	21	0.13	1 000	−1.36	19.3	491	500	932	0.14	550	1.05	6	0.42	0.15
Yellowfin grouper (*M. venenosa*)	15	0.17	860	0.00	15.7	527	500	792	0.20	542	1.18	6	0.45	0.13
Snappers (Lutjanidae)														
Mutton snapper (*Lutjanus analis*)	14	0.13	939	−0.74	14.1	279	400	798	0.21	493	0.41	29	0.45	0.63
Schoolmaster (*L. apodus*)	12	0.18	570	0.00	3.28	148	250	504	0.25	315	0.45	31	0.46	0.67
Gray snapper (*L. griseus*)	12	0.14	722	−0.86	5.25	233	250	557	0.25	309	0.70	15	0.39	0.39
Dog snapper (*L. jocu*)	12	0.10	854	−2.00	10.2	300	300	790	0.25	368	0.47	22	0.39	0.57
Lane snapper (*L. synagris*)	10	0.10	618	−1.73	3.24	205	200	418	0.30	258	0.27	42	0.39	1.09
Yellowtail snapper (*Ocyurus chrysurus*)	14	0.21	455	−0.71	4.24	197	250	433	0.21	297	0.53	27	0.49	0.56
Wrasses (Labridae)														
Hogfish (*Lachnolaimus maximus*)	23	0.08	913	−1.78	14.1	166	300	786	0.13	340	1.00	6	0.36	0.18
Grunts (Haemulidae)														
Margate (*Haemulon album*)	10	0.17	753	−0.45	8.57	426	200	578	0.30	297	0.50	8	0.21	0.39
Tomtate (*H. aurolineatum*)	11	0.09	310	−1.28	1.89	130	150	280	0.28	203	0.00	100	0.42	2.41
French grunt (*H. flavolineatum*)	12	0.18	295	0.00	0.57	176	160	235	0.25	205	0.00	100	0.42	2.38
Cottonwick (*H. melanurum*)	9	0.32	350	−0.50	0.82	203	160	333	0.33	208	0.61	17	0.34	0.51
Bluestriped grunt (*H. sciurus*)	8	0.30	413	0.00	1.36	205	180	404	0.37	233	0.65	21	0.37	0.57
White grunt (*H. plumieri*)	8	0.19	512	−0.78	3.06	177	170	411	0.37	227	0.54	25	0.35	0.70

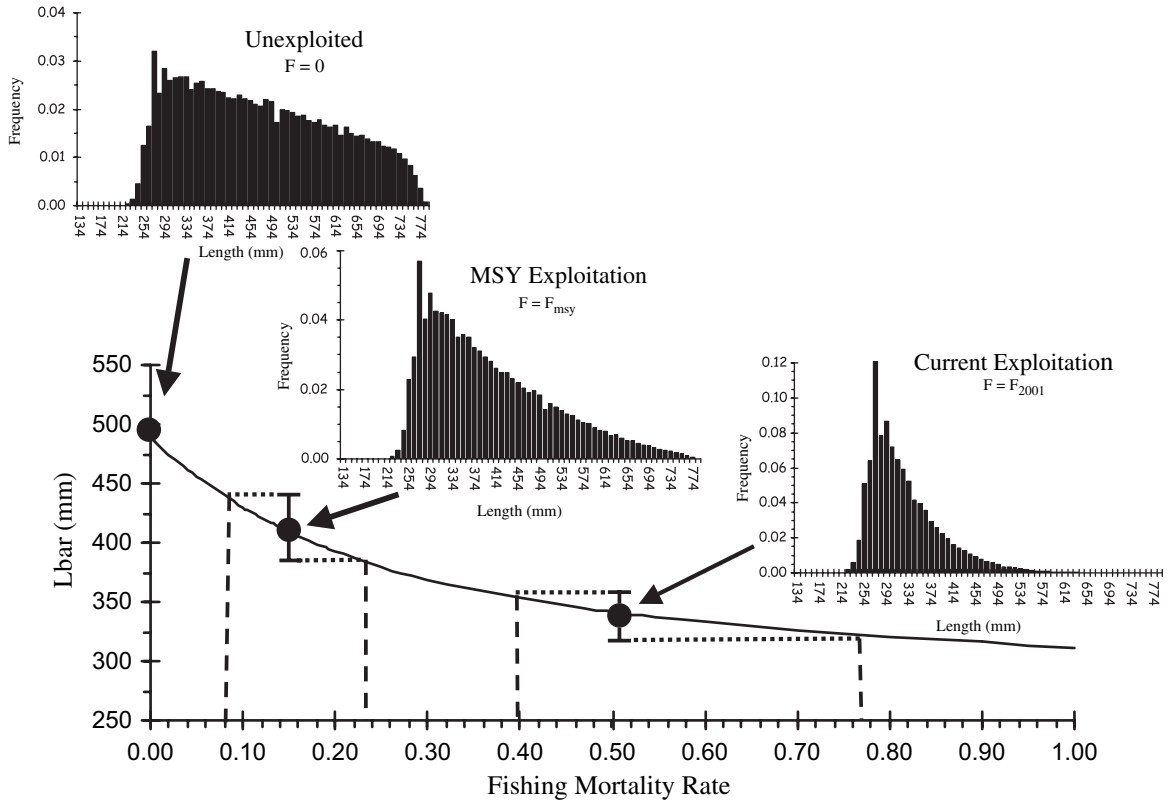*Average length as estimator of exploitation status for Florida reef fish*

Figure 1. Relationship of Lbar in the exploited phase and fishing mortality F for hogfish, and the variation in F estimates (dotted horizontal bars) resulting from variation in Lbar (dashed vertical bars). Insets show representative population length frequency compositions at F_0, F_{msy}, and F_{2001}.

the cases F_{msy} and F_{2001} were used to estimate the respective means and 95% CIs of F. Although the CI of Lbar is larger at F_{msy} than at F_{2001}, the corresponding CI of F is higher at F_{2001} owing to the non-linear relationship between Lbar and F. The non-linear relationship also results in asymmetric CIs of F that are more pronounced at higher exploitation rates.

A contour diagram of the proportional bias in Z estimates at different rates of recruitment r and F (Figure 2) shows that bias increases with decreasing F and increasing r. Based on the F-range observed in Florida-wide estimates during the past 10 years and an upper bound of r = 0.04 (corresponding to a 251% increase over a full lifespan; at most a 200% increase has been observed for snapper–grouper species over 20 years of the fishery-independent surveys), the feasible realm of bias for hogfish ranges from 3% to 7%. At values of F near F_{msy} = 0.13, the bias is <15%, and probably much lower, because recruitment would be expected to increase less for a stock fished sustainably.

A comparison of estimates for hogfish based on different methods and data sources (Figure 3) indicates that annual F for the non-equilibrium production and stock-synthesis models were nearly identical over the period 1993–2001,

whereas Florida-wide Lbar estimates of F from fishery-dependent data for the years 2001 and 2002 generally corresponded with the estimates from catch-and-effort time-series. Florida Keys estimates from fishery-independent
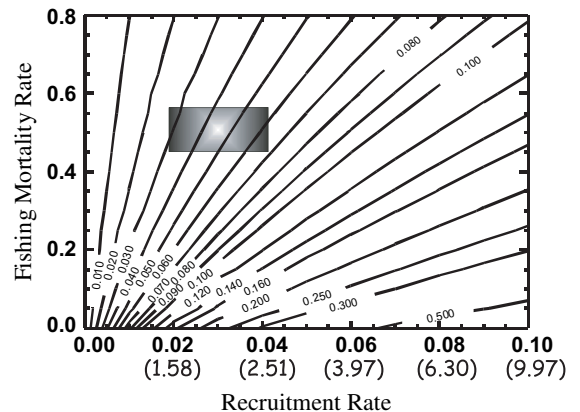

Figure 2. Contours of proportional bias in Lbar mortality estimates for hogfish at various annual rates of recruitment (r) and F (values in parenthesis: lifetime factor increase in recruitment corresponding to r).
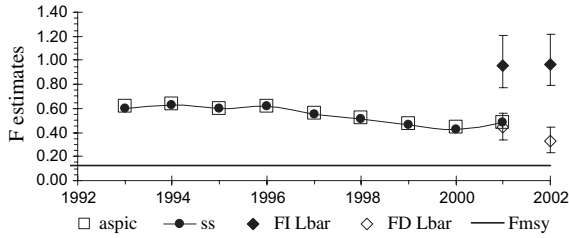
Figure 3. Comparison of estimates of fishing mortality for hogfish based on different assessment methods and data sources: non-equilibrium production model (aspic), stock-synthesis model (ss), and fishery-dependent average length (FD Lbar) methods used Florida-wide data; fishery-independent average length (FI Lbar) method used only Florida Keys RVC data (horizontal line: management benchmark F_{msy}).

data were higher than the Florida-wide estimates for 2001 and 2002. One likely reason for this is that the Florida Keys comprises most of the coral-reef habitats in Florida, so generating most of the commercial and recreational landings of this species (Ault *et al.*, 2003).

Lbar mortality estimates, based on fishery-independent size composition data collected between 2000 and 2002, and management benchmarks for 22 species of reef fish, are provided in Table 2. Values of the F/F_{msy} ratio plotted against the B/B_{msy} ratio (Figure 4) suggest that most species of the snapper—grouper complex experience overfishing (F-ratio > 1, B-ratio < 1; Restrepo and Powers, 1999) and have been subject to unsustainable rates of exploitation in recent years. Notable exceptions are two small grunt species not targeted by the fishery (French grunt, *Haemulon flavolineatum*, and tomtate, *H. aurolineatum*), and the goliath grouper (*Epinephelus itajara*), which has been under a fishing moratorium since 1990. Overfishing appears most severe for long-lived, slow-growing fish (cf. Table 2, Figure 4).

Discussion

The Lbar method for estimating total mortality exhibits relatively robust properties for assessing exploitation impacts on the Florida coral-reef community. Apart from being unique by having zero-bias properties at equilibrium (Ehrhardt and Ault, 1992; Quinn and Deriso, 1999), the method appears to be relatively insensitive to trends in likely recruitment for Florida Keys reef-fish species (Ault *et al.*, 1998, 2001, 2002). Temporal variation in recruitment, in contrast to a deterministic trend, would result in an even smaller bias than the simulated extreme trends. The estimator also showed desirable properties for detecting statistical differences at the lower range of exploitation rates that should allow discrimination between sustainable and non-sustainable rates. Finally, estimates of F from fishery-dependent size composition data were comparable to those from catch-and-effort time-series.

The use of Lbar as an estimator of fishing mortality, and therefore indirectly as an indicator of exploitation, has several practical advantages: (i) relatively simple data requirements (i.e. accurate and precise information on the age-and-size relationship, length frequency compositions for the exploited stock, and estimates of M); (ii) the method applies to both fishery-independent and -dependent data, and therefore may help to resolve incongruencies that exist among individual data sets; (iii) relatively simple computational requirements for the Lbar algorithm, because length-to-age transformation is not required, unlike most contemporaneous age-based mortality estimators (Quinn and Deriso, 1999); (iv) the method might be used to generate a "community control rule" indicator of exploitation status, when used in the context of synoptic fishery-independent survey data.

The principal fleet targeting the reef-fish complex of approximately 50 species is recreational, and the principal gear is hook and line, which is relatively non-selective
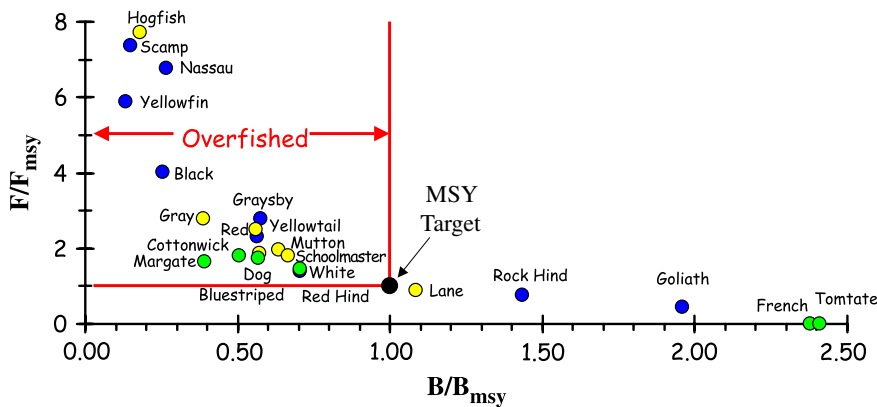

Figure 4. Plot of F/F_{msy} ratio against B/B_{msy} ratio for 22 fish species in the Florida Keys coral-reef ecosystem for the years 2000—2002 (blue, groupers; yellow, snappers and wrasses; green, grunts).

(Ault *et al.*, 2003). Because many of the species co-occur in similar habitats, capture probability for most species on any given trip at any location is greater than zero. Therefore, nominal fishing effort in the Florida Keys affects the snapper−grouper complex as a whole, but acts differentially on individual species, depending on their life history characteristics. The impact of exploitation was more severe for the slow-growing, long-lived groupers and hogfish than for other species (Figure 4). In addition, exploitation rates appear to differ throughout Florida, but are most intense in the Florida Keys. Because of these factors, management to build sustainable fisheries may need to consider the entire reef-fish complex and perhaps invoke a spatial context to interventions.

Acknowledgements

References

Alagaraga, K. 1984. Simple methods for estimation of parameters for assessing exploited fish stocks. Indian Journal of Fisheries, 31: 177−208.

Ault, J. S., Bohnsack, J. A., and Meester, G. A. 1998. A retrospective (1979−1996) multispecies assessment of coral reef fish stocks in the Florida Keys. Fishery Bulletin, US, 96: 395−414.

Ault, J. S., Bohnsack, J. A., and Smith, S. G. Towards sustainable multispecies fisheries in the Florida USA coral reef ecosystem. Bulletin of Marine Science, 76(2) (in press).

Ault, J. S., and Ehrhardt, N. M. 1991. Correction to the Beverton and Holt Z-estimator for truncated catch length-frequency distributions. ICLARM Fishbyte, 9(1): 37−39.

Ault, J. S., McGarvey, R. N., Rothschild, B. J., and Chavarria, J. 1996. Stock assessment computer algorithms. *In* Stock Assessment: Quantitative Methods and Applications for Small Scale Fisheries, pp. 501−515. Ed. by V. F. Gallucci, S. Saila, D. Gustafson, and B. J. Rothschild. Lewis Publishers (Division of CRC Press), Chelsea, MI.

Ault, J. S., and Olson, D. B. 1996. A multicohort stock production model. Transactions of the American Fisheries Society, 125: 343−363.

Ault, J. S., Smith, S. G., Diaz, G. A., and Franklin, E. 2003. Florida hogfish fishery stock assessment. Report to the Florida Fish and Wildlife Conservation Commission. 67 pp. + Figures and Tables.

Ault, J. S., Smith, S. G., Luo, J., Meester, G. A., Bohnsack, J. A., and Miller, S. L. 2002. Baseline multispecies coral reef fish stock assessments for the Dry Tortugas. NOAA Technical Memorandum NMFS-SEFSC-487. 117 pp.

Ault, J. S., Smith, S. G., Meester, G. A., Luo, J., and Bohnsack, J. A. 2001. Site characterization for Biscayne National Park: assessment of fisheries and habitats. NOAA Technical Memorandum NMFS-SEFSC-468. 185 pp.

Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food, Fishery Investigations Series II, vol. 19. Lowestoft, England. 533 pp.

Bohnsack, J. A., and Bannerot, S. P. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report, NMFS 41. 15 pp.

Bohnsack, J. A., McClellan, D. B., Harper, D. E., Davenport, G. S., Konoval, G. J., Eklund, A. M., Contillo, J. P., Bolden, S. K., Fischel, P. C., Sandorff, G. S., Javech, J. C., White, M. W., Pickett, M. H., Hulsbeck, M. W., Tobias, J. L., Ault, J. S., Meester, G. A., Smith, S. G., and Luo, J. 1999. Baseline data for evaluating reef fish populations in the Florida Keys, 1979−1998. NOAA Technical Memorandum NMFS-SEFSC-427. 61 pp.

Claro, R., Lindeman, K. C., and Parenti, L. R. 2001. Ecology of the Marine Fishes of Cuba. Smithsonian Institution Press, Washington, D.C. 253 pp.

Coleman, F. C., Koenig, C. C., Huntsman, G. R., Musick, J. A., Eklund, A. M., McGovern, J. C., Chapman, R. W., Sedberry, G. R., and Grimes, C. B. 2000. Long-lived reef fishes: the grouper−snapper complex. Fisheries, 25(3): 14−21.

Ehrhardt, N. M., and Ault, J. S. 1992. Analysis of two length-based mortality models applied to bounded catch length frequencies. Transactions of the American Fisheries Society, 121: 115−122.

FAO. 2003. FiSAT II: FAO−ICLARM stock assessment tools. User's guide. Ed. by F. C. Gayanilo, P. Sparre, and D. Pauly. FAO, Rome.

Gislason, H., and Rice, J. 1998. Modelling the response of size and diversity spectra of fish assemblages to changes in exploitation. ICES Journal of Marine Science, 55: 362−370.

Haddon, M. 2001. Modeling and Quantitative Methods in Fisheries. Chapman and Hall/CRC Press, Boca Raton, FL.

Johns, G. M., Leeworthy, V. R., Bell, F. W., and Bonn, M. A. 2001. Socioeconomic study of reefs in southeast Florida: final report. Hazen and Sawyer Environmental Engineers & Scientists. 349 pp.

Kerr, S. R., and Dickie, L. M. 2001. The Biomass Spectrum: a Predator−Prey Theory of Aquatic Production. Columbia University Press, New York.

Mace, P. 1997. Developing and sustaining world fishery resources: state of science and management. *In* Proceedings of the Second World Fishery Congress, pp. 1−20. Ed. by D. A. Hancock, D. C. Smith, A. Grant, and J. P. Beumer. Brisbane, Australia.

Methot, R. D. 1990. Synthesis model: an adaptive framework for analysis of diverse stock assessment data. International North Pacific Fisheries Commission Bulletin, 50: 259−277.

Musick, J. A., Harbin, M. M., Berkeley, S. A., Burgess, G. H., Eklund, A. M., Findley, L., Gilmore, R. G., Golden, J. T., Ha, D. S., Huntsman, G. R., McGovern, J. C., Parker, S. J., Poss, S. G., Sala, E., Schmidt, T. W., Sedberry, G. R., Weeks, H., and Wright, S. G. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). Fisheries, 25(11): 6−30.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. Science, 279: 860−863.

Pauly, D., and Morgan, G. R. 1987. Length-based methods in fisheries research. ICLARM Conference Proceedings, 13. 468 pp.

Prager, M. H. 1994. A suite of extensions to a non-equilibrium surplus-production model. Fishery Bulletin, US, 92: 374−389.

Quinn, T. J., and Deriso, R. B. 1999. Quantitative Fish Dynamics. Oxford University Press. 542 pp.

Restrepo, V. R., and Powers, J. E. 1999. Precautionary control rules in U.S. fisheries management: specifications and performance. ICES Journal of Marine Science, 56: 846−852.

Ricker, W. E. 1963. Big effects from small causes: two examples from fish population dynamics. Journal of the Fisheries Research Board of Canada, 20: 257−264.

Robson, D. S. 1966. Estimation of the relative fishing power of individual ships. ICNAF Research Bulletin, 3: 5−15.

Sokal, R. R., and Rohlf, F. J. 1981. Biometry, 2nd edn. Freeman & Co., San Francisco. 859 pp.