

See discussions, stats, and author profiles for this publication at: <http://www.researchgate.net/publication/260407341>

Length-based indicators of fishery and ecosystem status: Glover's Reef Marine Reserve, Belize

ARTICLE *in* FISHERIES RESEARCH · OCTOBER 2013

Impact Factor: 1.84 · DOI: 10.1016/j.fishres.2013.03.011

CITATION

1

4 AUTHORS, INCLUDING:



[Elizabeth A Babcock](#)

University of Miami

64 PUBLICATIONS 1,765 CITATIONS

[SEE PROFILE](#)



[Mandy Karnauskas](#)

National Oceanic and Atmospheric Adminis...

20 PUBLICATIONS 88 CITATIONS

[SEE PROFILE](#)



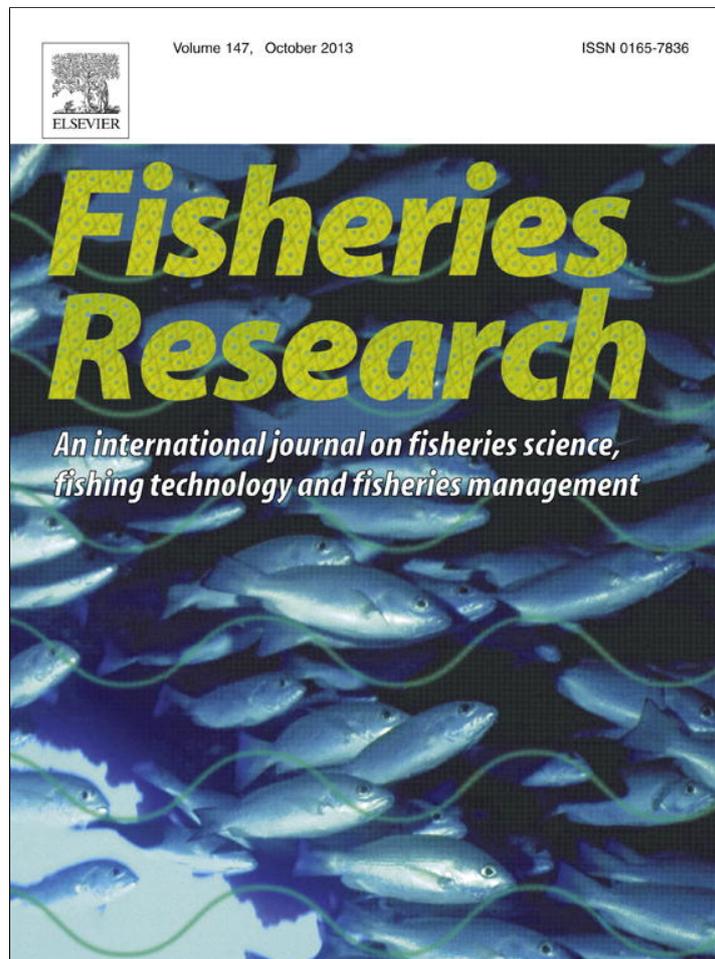
[Janet Gibson](#)

Wildlife Conservation Society

8 PUBLICATIONS 113 CITATIONS

[SEE PROFILE](#)

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>



Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Length-based indicators of fishery and ecosystem status: Glover's Reef Marine Reserve, Belize



Elizabeth A. Babcock^{a,*}, Robin Coleman^b, Mandy Karnauskas^{a,1}, Janet Gibson^b

^a University of Miami, Rosenstiel School of Marine and Atmospheric Sciences, 4600 Rickenbacker Cswy, Miami, FL 33149, USA

^b Wildlife Conservation Society, Belize, Global Conservation Program, P.O. Box 768, 1755 Coney Drive, 2nd Floor, Belize City, Belize

ARTICLE INFO

Article history:

Received 11 October 2012

Received in revised form 19 March 2013

Accepted 21 March 2013

Keywords:

Stock assessment

Indicators

Data-poor fisheries

Overfishing

Length-frequency

ABSTRACT

For the spear gun fishery at Glover's Reef, Belize, we used catch length frequencies to infer whether each of the eight most common species was likely to be overfished (spawning stock biomass < target) or experiencing overfishing (fishing mortality rate $F >$ natural mortality rate M). We used Monte Carlo simulations to determine whether the results were sensitive to uncertainty about natural mortality, asymptotic length, growth rate and length at maturity. We found that black grouper *Mycteroperca bonaci* is overfished, and Nassau grouper *Epinephelus striatus*, schoolmaster snapper *Lutjanus apodus* and mutton snapper *Lutjanus analis* are probably overfished, but hogfish *Lachnolaimus maximus*, stoplight parrotfish *Sparisoma viride*, French angelfish *Pomacanthus paru* and gray angelfish *Pomacanthus arcuatus* are probably not overfished. All species except French angelfish were experiencing overfishing across a range of life history parameters. Nassau grouper, black grouper and mutton snapper were often caught below the size at maturity L_m . The results were sensitive to different assumed values of the life history parameters. Life history parameters can vary regionally for many reef fishes, and there have been few life history studies in the western Caribbean; such studies would greatly improve estimates of stock status. We also calculated six multispecies indicators of fishery status. The mean length relative to L_m was greater than 1.0 and constant between 2005 and 2011. Mean trophic level, mean maximum size, and fraction piscivores increased between 2005 and 2011, partly due to the fact that parrotfish, previously an important component of the catch, have been prohibited beginning in 2009. Mean catch per unit effort declined. Given that black grouper, Nassau grouper, mutton snapper and schoolmaster snapper are found to be overfished and experiencing overfishing under most values of the life history parameters, we recommend size or catch limits for these species.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

The status of many fished stocks is unknown, particularly in the multispecies small-scale fisheries in the tropics (Worm et al., 2009). Tropical fisheries often lack historical catch and abundance trend data, which are necessary for traditional stock assessment methods. Simple indicators have been proposed to determine whether stocks are being harvested sustainably using length-frequency data (Ault et al., 1998, 2005, 2008; Cope and Punt, 2009; Ehrhardt and Ault, 1992; Froese, 2004), sometimes combined with catch per unit effort (CPUE) (Prince et al., 2011). These methods may be appropriate for

many tropical fisheries because they do not require historical catch and effort data or complex stock assessment models.

To assess the sustainability of a fishery, Froese (2004) suggested three length-based indicators: (1) P_{mat} , the fraction of the catch that is above the length at maturity (L_m), (2) P_{opt} , the fraction of the catch that is within $\pm 10\%$ of the optimal length of harvest (L_{opt}), and (3) P_{mega} , the fraction of fish that are more than 10% larger than L_{opt} ("mega-spawners"). To avoid recruitment overfishing, Froese (2004) suggested that the fraction of mature fish in the catch should be high, preferably 100%, so that each fish has a chance to spawn at least once before being harvested. To prevent growth overfishing, all or most of the fish caught should be within 10% of the optimal length of harvest (L_{opt}), which is the length at which the biomass of fish in a year-class is maximized. Where possible, maximum size limits to avoid capturing any of the mega-spawners would be appropriate because large fish are a critical source of fecundity (Berkeley et al., 2004). In the absence of a maximum size limit, the fraction of mega-spawners in the catch should be greater than 20% (Froese, 2004). Maintaining a substantial number of large fish in the population may be even more important for protogynous species in

* Corresponding author. Tel.: +1 305 421 4852; fax: +1 305 4214600.

E-mail addresses: ebabcock@rsmas.miami.edu (E.A. Babcock), rcoleman@wcs.org (R. Coleman), mandy.karnauskas@noaa.gov (M. Karnauskas), jgibson@wcs.org (J. Gibson).

¹ Present address: NOAA, National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149, USA.

which the change from female to male is socially mediated (Sadovy, 2001).

In the terminology of U.S. law, “overfished” is defined to mean that the spawning stock biomass is below a reference point, and “overfishing” is defined to mean that the fishing mortality rate is above a reference point (Magnuson-Stevens Fishery Conservation and Management Act, 2007). In a population that is overfished, there will be fewer large fish in the population to be caught by the fishery, which could reduce the values of P_{mat} , P_{opt} , and P_{mega} . However, the size selectivity of the fishery also influences the values of these indicators. Simulation studies by Cope and Punt (2009) have shown that a decision tree based on the Froese indicators can be used to infer overfished status with respect to spawning stock biomass benchmarks, unless the selectivity pattern makes the length-frequency data uninformative (e.g., a fishery that only targets large fish).

Length frequencies can also be used to calculate the fishing mortality rate (Ault et al., 2005; Ault et al., 2008) to determine whether the population is experiencing overfishing. The total mortality ($Z = F + M$) can be estimated from average length (\bar{L}) in the catch for fish within the size range commonly caught by the gear (Ehrhardt and Ault, 1992). The fishing mortality rate is estimated by subtracting the natural mortality rate from total mortality. The natural mortality rate is often used as a proxy for the fishing mortality rate that would maximize sustainable yield (F_{msy}) (e.g. Ault et al., 2008), and a population with F larger than M may be considered to be experiencing overfishing. A recent analysis has shown that F_{msy}/M may be lower than 1.0 for most teleosts (Zhou et al., 2012), so this assumption may underestimate the risk of overfishing. All of the sized-based indicators rely on the assumption that the age structure of the population is relatively stable over time; variability in fishing mortality, or in recruitment, may cause bias.

In the modern context of ecosystem-based fishery management, evaluating the broader impacts of fishing on marine ecosystems is becoming an important component of fisheries assessment (Fulton et al., 2005). Several indicators of the ecosystem-level impacts of fishing can be calculated from a sample of the length frequency and species composition of the catch (Fulton et al., 2005; Rochet and Trenkel, 2003; Ye et al., 2011). For example, the average value of P_{mat} across all the individual fish of all species in the catch is an indicator of the mean level of depletion of the harvested fish community (Rochet and Trenkel, 2003). This is particularly useful in multispecies fisheries where it is not possible to conduct single-species assessments of all species. Similarly, the average value of the maximum length L_{max} of fish species caught in the fishery has been proposed as an indicator of whether large species have been depleted (Rochet and Trenkel, 2003).

Unfished tropical marine systems often have a higher fraction of piscivorous fish relative to heavily fished systems, and it has been hypothesized that the fraction of piscivores can be used as an index of fishing intensity (Friedlander and DeMartini, 2002). With increasing fishing intensity, the proportion of piscivores in the catch would be expected to decline. The mean trophic level of the catch has also been proposed as an indicator of the effect of fishing on fish communities (Pauly et al., 1998; Pauly and Watson, 2005). With increased fishing intensity, the mean trophic level would be expected to decline. Recent research has shown that trends in the mean trophic level of fish in the catch may not be consistent with trends in the mean trophic level of fish in the ecosystem, especially if the fishery changes target species (Branch et al., 2010). Nevertheless, this indicator is a useful summary of the ecological roles of the fish being removed by the fishery.

The species diversity in the catch is also a potential indicator of the impact of the fishery on the ecosystem (Rochet and Trenkel, 2003). Biodiversity in the catch could decrease with increasing fishing pressure if some species become so depleted that they

are no longer caught. Finally, the average catch per unit of effort (CPUE) in numbers of fish caught per fisherman hour is often used as an ecosystem indicator (Fulton et al., 2005; Ye et al., 2011). With increasing fishing intensity, the total fishery CPUE would be expected to decline.

For these system-level indicators, appropriate reference levels that would indicate ecosystem overfishing have yet to be developed. However, the direction of change that the indicator should experience with increased fishing-induced change to the ecosystem is well understood (Shin et al., 2005). Thus, ecosystem-level indicators are commonly used to compare ecosystems across time and space rather than to evaluate the status of a particular system against fixed benchmarks (Shin et al., 2010). In this study, the ecosystem indicators were used to look for changes in the ecosystem or the fishery over time.

This paper presents an analysis of the status of several fish stocks in the spear gun fishery at Glover's Reef Marine Reserve, Belize, based on fish length and species composition data collected from fishermen by the Wildlife Conservation Society from 2004 through 2011.² We used Monte Carlo simulations to evaluate the sensitivity of the status indicators to the assumed values of the life history parameters. Finally, the potential impact of spear gun fishing on the broader ecosystem at Glover's Reef was evaluated with six multi-species indicators calculated from the length, species composition and CPUE of all fish caught in each year.

2. Methods

Glover's Reef (16°44'N, 87°48'W) is an atoll 25 km to the east of the Belize Barrier Reef, and is designated as a marine protected area (Fig. 1). Approximately one fifth of the atoll is designated as a no-take area; in the remainder of the atoll, called the general use zone, there are restrictions such as a ban on gillnets, traps and longlines in addition to the fishing regulations that apply throughout Belize (e.g. seasons and size limits for queen conch *Strombus gigas* and Caribbean spiny lobster *Panulirus argus*). In 2009, new fishery regulations imposed a ban on catching parrotfish throughout Belize, and a minimum and maximum size limit for Nassau grouper (Government of Belize, 2009). The law also included a ban on spear fishing for any species, the implementation of which has been indefinitely delayed. Beginning in 2011, the Belize Fisheries Department implemented a new Managed Access Program at Glover's Reef to restrict fishing to fishermen who have traditionally used Glover's Reef. As part of the managed access program, fishermen are required to keep logbooks documenting their catch.

The fishers at Glover's Reef come mainly from Sartaneja, in Northern Belize, and Hopkins on the mainland near Glover's Reef. The Sartaneja fishermen come to the atoll in sailboats, and then disperse in 7–14 dories per sailboat to fish individually for finfish using either spear gun or Hawaiian sling gear, or to free-dive for conch or lobster. More rarely they also fish with hook and line. The fishermen from Hopkins tend to use skiffs with outboard motors, and typically have a crew size of two or three and fish for finfish year round with hand lines, often on the outside of the atoll.³

Between 2004 and 2011, a Wildlife Conservation Society (WCS) employee, who is a former fisherman, visited the sailboats of the spear gun fishers while they were fishing at Glover's Reef, and

² Sampling program defined in Grant, S., 2004. Glover's Reef Marine Reserve Data Collection Plan (Part 2). Wildlife Conservation Society (Belize). www.caricom-fisheries.com/LinkClick.aspx?fileticket=fof%2FFW20K0s%3D&tabid=86 and Coleman, R., 2010. Glover's Reef Marine Reserve - Fisheries Catch Data Collection Program. Report for the period January 2005 to June 2010. Wildlife Conservation Society (Belize). www.gloversreef.org/grc/pdf/catch.data.05-10.pdf.

³ Ibid.

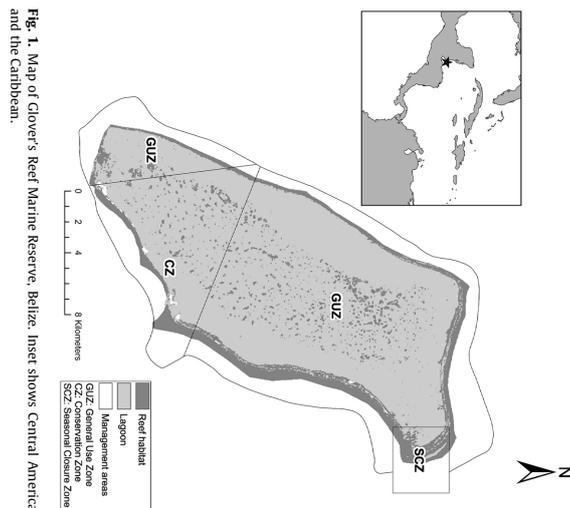


Fig. 1. Map of Glover's Reef Marine Reserve, Belize. Inset shows Central America and the Caribbean.

recorded the length, weight and species of every fish they had caught, as well as the number of hours each man had fished and the fishing gear used. The interviewer gathered data for approximately three arbitrarily chosen days every month, visiting as many as possible of the boats that were present on those days. Most months were sampled between January 2005 and June 2011.

We estimated species-specific length-based indicators of fishery sustainability using the entire dataset for the eight most common species (i.e. species with more than 50 individuals caught and identified to the species level). The species were recorded using local common names, so some fish were not identified to the species level (about 9% of the fish sampled, mainly porgies [Sparidae], parrotfishes [Scaridae] and angelfishes [Pomacanthidae]). All lengths were recorded as fork length.

The following life history parameters were needed for this analysis: the parameters of the von Bertalanffy growth equation (K and L_{∞}), length at maturity (L_m) and the maximum observed age (t_{max}), which was used to calculate natural mortality (M). We also used the maximum observed length (L_{max}) for some species to calculate L_{∞} . None of these population parameters have been estimated for reef fish populations in Belize. Therefore, we used values taken from the published values compiled in Fishbase (Froese and Pauly, 2013) or from other literature for populations of the same species elsewhere in Atlantic Ocean (Table 1). If more than one growth curve had been published, we used the median value of L_{∞} as the best estimate. Because K is strongly correlated with L_{∞} , the value of K from the same study as the L_{∞} was used as the best estimate. The upper range of L_{∞} was taken from the literature or calculated from L_{max} (Froese and Binohlan, 2000); the lower range was taken from the literature, unless this value was lower than the largest size caught at Glover's Reef, in which case the fishery value was used as a minimum for L_{∞} . For stoplight parrotfish (*Sparisoma viride*), most published values of L_{∞} were smaller than the mean size of stoplight parrotfish caught at Glover's Reef, so we used the median and range of the published values of L_{∞} larger than the mean size of stoplight parrotfish caught at Glover's Reef to define the range of L_{∞} and K . For gray angelfish (*Pomacanthus arcuatus*), the only published growth

Table 1
Life history parameters, with the ranges used for the simulations: K and L_{∞} are the parameters of the von Bertalanffy growth equation; L_m is length at maturity; L_{max} and t_{max} are the maximum published length and age, respectively; L_c and L_A are the minimum and maximum lengths that are frequently encountered in the spear gun fishery at Glover's Reef; and M is natural mortality rate.

Species	Family	Common name	L_c	L_A	L_{max}	t_{max}	K	L_{∞}	L_m	M
<i>Lachnolaimus maximus</i> ^a	Labridae	Hogfish	35	64	82	23	0.10 (0.08–0.26)	85 (64–92)	25 (17–45)	0.19 (0.13–0.35)
<i>Sparisoma viride</i> ^b	Scaridae	Stoptlight parrotfish	33	42	47.9	9	0.45 (0.45–0.71)	43 (42–50)	20 (18–26)	0.49 (0.33–0.86)
<i>Lutjanus analis</i> ^c	Lutjanidae	Mutton snapper	34	62	84.9	29	0.15 (0.1–0.25)	88 (78–118)	39 (28–52)	0.16 (0.1–0.43)
<i>Pomacanthus arcuatus</i> ^d	Pomacanthidae	Gray angelfish	32	46	55.98	24	0.12 (0.12–0.38)	58 (46–58)	22 (19–32)	0.19 (0.12–0.38)
<i>Lutjanus apodus</i> ^e	Lutjanidae	Schoolmaster	32	46	63.2	12	0.18 (0.18–0.35)	57 (46–66)	25 (14–32)	0.37 (0.25–0.47)
<i>Epinephelus striatus</i> ^f	Serranidae	Nassau grouper	41	71	120	29	0.10 (0.06–0.18)	93 (75–123)	52 (48–75)	0.16 (0.1–0.36)
<i>Mycteroperca bonaci</i> ^g	Serranidae	Black grouper	47	103	150	33	0.17 (0.12–0.17)	131 (120–153)	72 (67–72)	0.14 (0.09–0.46)
<i>Pomacanthus paru</i> ^h	Pomacanthidae	French angelfish	32	43	43	10	0.21 (0.21–0.28)	46 (43–46)	25 (25–26)	0.44 (0.3–0.52)

^a Hogfish L_{max} from McBride and Johnson (2007); t_{max} and L_m from Ault et al. (2008) with the upper limit of L_m calculated from L_{∞} and the lower limit from McBride et al. (2008); L_c and K from McBride and Richardson (2007).

^b Stoptlight parrotfish L_{max} from Randall (1978); L_{∞} , K and t_{max} from Choat et al. (2003) with the lower limit of L_{∞} equal to the maximum size commonly caught at Glover's reef, and the upper limit calculated from L_{max} ; L_m from Reeson (1983), Koltjes (1993) and García-Cagide et al. (1994).

^c Mutton snapper L_{max} from International Game Fish Association (2001); t_{max} from Burton (2002); K and L_{∞} from Manooch (1987) with upper and lower values from and Mason and Manooch (1985); L_m from Mason and Manooch (1985) with lower range from Ault et al. (2008).

^d Gray angelfish L_{max} from Aiken (1983) with lower range from Steward et al. (2009); t_{max} from Steward et al. (2009); L_{∞} calculated from L_{max} , and K from M (Jensen, 1996); L_m from Aiken (1983) with minimum and maximum calculated from L_{∞} .

^e Schoolmaster L_{max} from Cervigón (1993); t_{max} , K and L_{∞} from Ault et al. (2008) with upper range of L_{∞} calculated from L_{max} , and lower range of L_{∞} from Randall (1962); L_m from García-Cagide et al. (1994) with lower limit from Ault et al. (2008) and upper limit calculated from L_{∞} .

^f Nassau grouper L_{max} and t_{max} from Sadovy and Eklund (1999); K and L_{∞} from Valle et al. (1997) including lower limit of L_{∞} and both limits of K , upper limit of L_{∞} from Pauly (1978); L_m from García-Cagide et al. (1994) and Sadovy and Eklund (1999).

^g Black grouper L_{max} from International Game Fish Association (2001); t_{max} , K and L_{∞} from Crabtree and Bullock (1998) with lower limit of L_{∞} and upper limit of K from Manooch (1987) and upper limit of L_{∞} calculated from L_{max} ; L_m from Brule (2003), with lower limit calculated from L_{∞} .

^h French angelfish L_{max} from Glover's reef data; t_{max} from Florida Museum of Natural History (www.flmnh.ufl.edu/fish/gallery/descript/frenchangelfish/frenchangelfish.html); K and L_{∞} from Pauly (1978) with minimum and maximum L_{∞} calculated from L_{max} and minimum and maximum K calculated from M ; L_m from Feitosa et al. (2008) with minimum and maximum calculated from L_{∞} .

curve (Steward et al., 2009), found values of L_∞ smaller than the average size caught at Glover's reef. Thus, for gray angelfish we calculated the value of L_∞ from L_{\max} (Froese and Binohlan, 2000) and the value of K from M (Jensen, 1996).

For L_m , the median, minimum and maximum length at maturity for either unsexed or female fish was taken from the literature (Table 1). For L_{\max} and t_{\max} , the largest published value was used as the best estimate, because we assumed that each species was a single stock in the region. However, we did not use large values of L_{\max} and t_{\max} that did not seem to be well supported by data, for example those that came from guidebooks.

The optimal length L_{opt} was calculated from L_∞ , M and K using the equation of Beverton (1992):

$$L_{\text{opt}} = \frac{3L_\infty}{(3 + M/K)} \quad (1)$$

To determine a plausible range of values for natural mortality rate M , we calculated M using three commonly used methods: regression from longevity t_{\max} , an ad hoc method based on longevity, and regression from the growth parameter K . The regression from longevity is (Hewitt and Hoenig, 2005):

$$\ln(M) = 1.44 - 0.982 \ln(t_{\max}) \quad (2)$$

The ad hoc method is (Hewitt et al., 2007):

$$M = \frac{-\ln(a)}{t_{\max}} \quad (3)$$

where a is a small number corresponding to the fraction of recruits expected to survive to age t_{\max} . We used $a = 0.05$ to be consistent with Ault et al. (2008). The regression from K is (Jensen, 1996):

$$M = 0.21 + 1.45K \quad (4)$$

We used the median, minimum and maximum of these three values to define the range of values for M (Table 1).

The modes (or in the case of t_{\max} and L_{\max} , the maximum) values of the life history parameters were chosen as the best estimate of each parameter, in the absence of any data from Belize to improve the estimates. The values we chose as best estimates seemed to be consistent with each other (Froese and Binohlan, 2000; Jensen, 1996) and with the length frequency data we had collected. The values of L_∞ were within 20% of L_{\max} for each species. L_m was between 40 and 60% of L_∞ for every species except hogfish. For hogfish, the L_m was small relative to L_∞ in the published studies so we considered this value to be credible (Table 1). Finally, when M was estimated from either t_{\max} or K , the values were broadly consistent (Table 1).

The three Froese (2004) indicators were calculated as:

- (1) P_{mat} is the fraction of the catch greater than L_m .
- (2) P_{opt} is the fraction of the catch between $0.9L_{\text{opt}}$ and $1.1L_{\text{opt}}$.
- (3) P_{mega} is the fraction of the catch greater than $1.1L_{\text{opt}}$.

The 90% confidence intervals of each indicator were calculated by a simple bootstrap of the length frequency data, with 20,000 draws.

The decision tree of Cope and Punt (2009) was used to infer the selectivity pattern of the fishery for each species, and whether the biomass was likely to be above an overfished biomass reference point. The decision tree evaluates the values of the three Froese indicators, as well as their sum ($P_{\text{obj}} = P_{\text{mat}} + P_{\text{opt}} + P_{\text{mega}}$) and the ratio of L_m/L_{opt} to determine whether the selectivity pattern of the fishery is:

- (1) catch small, immature fish;
- (2) catch small and optimally-sized fish;
- (3) selectivity curve similar to the maturity ogive;
- (4) catch optimally-sized and bigger fish or;
- (5) catch optimally-sized fish.

Depending on the inferred selectivity, either P_{mat} or P_{opt} is compared to an empirically-derived reference point to infer whether the population is likely to be above or below the biomass reference point that corresponds to overfished status. The results of the Cope and Punt decision tree may be quite different from the results of the Froese indicators alone. For example, if the fishery selectivity pattern is to catch only small and immature fish, the Cope and Punt decision tree considers the population to be above the reference point (i.e. not overfished) if $P_{\text{mat}} > 0.25$, as compared to Froese's (2004) recommendation that all fish should be above this reference point to allow more fish to spawn. The Cope and Punt decision tree does not estimate the ratio of stock biomass to the reference point; rather, it infers whether the biomass is likely to be above or below the reference point. To determine the uncertainty in this estimate, we recalculated the reference point from the bootstrapped length frequency samples to calculate the probability that the population would be considered overfished.

For the overfishing indicator ($F > M$), the total mortality (Z) was estimated from average length (\bar{L}) using the method of Beverton and Holt (1957) as modified by Ehrhardt and Ault (1992). The original Beverton and Holt equation is:

$$Z = \frac{K(L_\infty - \bar{L})}{(\bar{L} - L_c)} \quad (5)$$

where K and L_∞ are the parameters of the von Bertalanffy growth function and L_c is the minimum fully-exploited size in the fishery. Ehrhardt and Ault (1992) showed that this method can be biased if the fishery does not exploit all older age classes of fish. They proposed the following formulation that includes a maximum size of capture (L_λ):

$$\left(\frac{L_\infty - L_\lambda}{\bar{L}_\infty - L_c} \right)^{Z/K} = \frac{Z(L_c - \bar{L}) + K(L_\infty - \bar{L})}{Z(L_\lambda - \bar{L}) + K(L_\infty - \bar{L})} \quad (6)$$

We estimated L_c for each species as the length at which a smoothed curve through the cumulative length-frequency histogram reached its maximum slope. This value was always close to the mode of the length-frequency histogram, so fish below that size were not fully recruited into the fishery. The maximum length in the fishery L_λ was the maximum observed length for most species. For some species, there were one or two fish in the data set that were more than 10 cm larger than the rest of the fish of that species; we excluded these outliers from the calculation of L_λ . The average length (\bar{L}) was calculated as the arithmetic mean of the lengths of all fish between lengths L_c and L_λ . Total mortality Z was calculated iteratively from Equation (6), using the function minimization algorithm *nlm* in R (R Development Core Team, 2012). Fishing mortality rate was calculated by subtracting M from Z . The 90% confidence interval for F/M was calculated by bootstrapping. If F was less than zero, it was assumed to be zero (this occurred only for one species, and in less than 8% of the samples for that species).

Monte Carlo simulations were used to evaluate the potential impact of uncertainty in the life history parameters L_m , L_∞ , K and M in the estimated values of the five indicators, using the minimum, maximum and mode values of the parameters from Table 1. We did the simulations two different ways: one with correlation among the four parameters, and one without. For the uncorrelated simulations, 20,000 random values of each of the uncertain parameters (L_m , L_∞ , K , and M), were drawn from a triangle distribution

Table 2
Correlation parameters used in simulations (Jensen, 1996; Pauly, 1980).

	L_{∞}	K	L_m	M
L_{∞}	1	-0.76	0.94	-0.61
K	-0.76	1	-0.65	0.81
L_m	0.94	-0.65	1	-0.61
M	-0.61	0.81	-0.61	1

(Carnell, 2011; Cortes, 2002; R Development Core Team, 2012), with mode, minimum and maximum values as shown in Table 1. For the correlated simulations, published values of the correlation between the parameters were used (Table 2, Froese and Binohlan, 2000; Pauly, 1980). The variance of each parameter was calculated so that the difference between the minimum and maximum value of the parameter was six standard deviations, and the variance-covariance matrix of the four parameters was calculated from the variances and correlations. We used the modal value of each parameter as the mean, and drew 20,000 sets of parameter values from the multivariate normal distribution. To avoid parameter sets that were not biologically possible, we threw out any parameter sets in which any of the parameter values drawn from the multivariate normal distribution were outside the range defined in Table 1.

For both correlated and uncorrelated simulations, L_{opt} was calculated from Equation 1 for each draw of the parameters. The values of the three Froese indicators were then calculated at these parameter values, and a bootstrapped sample of the length frequency data. The Cope and Punt decision tree was then applied to each draw, and Z , F and F/M were calculated. Monte Carlo intervals were calculated as the 5% and 95% quantiles of the estimated indicators across the 20,000 random draws. The probability of being overfished was calculated as the fraction of the 20,000 draws in which the Cope and Punt decision tree found that the population was below the overfished threshold. The probability of experiencing overfishing was calculated as the fraction of the 20,000 draws for which F was larger than M .

Using F/M to estimate whether a population is experiencing overfishing is only appropriate if M is a reasonable proxy for F_{msy} . A meta-analysis by Zhou et al. (2012) estimated a credible interval for F_{msy}/M from 0.77 to 0.97 for all teleosts combined. To determine whether the value of F_{msy}/M would change our perception of the overfishing status of these stocks, we recalculated the probability of overfishing using the lower limit of the credible interval from Zhou et al. (2012), $F_{msy}/M=0.77$. Finally, to evaluate whether the assumption that the fishery does not select larger fish influences the results, we recalculated the probability that F/M is greater than 1, using Equation (5), rather than Equation (6).

The potential impact of fishing on the finfish community at Glover's Reef was evaluated using six multispecies indicators calculated from the length and species composition of all fish caught in each year. They were:

- (1) mean length relative to L_m ,
- (2) mean maximum size L_{max} ,
- (3) fraction of piscivores,
- (4) mean trophic level,
- (5) Simpson species diversity, and
- (6) mean catch per unit of effort across all species.

Estimates of the parameters L_m and L_{max} were taken from Fishbase or from the literature (Table 1). To calculate the average length relative to length at maturity, the length of each fish was divided by the median length at maturity for its species. For species not listed in Table 1, the median values of L_m from Fishbase were used. For the few species for which no L_m data were available, values were estimated from L_{max} (Froese and Binohlan, 2000). For fish that had

Table 3
Sample sizes in the WCS survey of spear-gun fishermen.

Year	Days	Boats	Boat days	Fisherman days	Fish
2004	3	3	6	6	88
2005	14	8	16	29	386
2006	21	8	22	49	364
2007	16	9	19	38	193
2008	23	9	30	72	323
2009	17	8	19	59	481
2010	21	9	26	66	260
2011	8	8	12	27	177
Total	123	62	150	346	2272

only been identified to family, the median value for that family was used. The mean and standard error of L/L_m were then calculated for each year. The mean L_{max} and mean trophic level were calculated similarly using values of L_{max} and trophic level for each fish from Table 1 or from Fishbase. Fish were classified as herbivores, piscivores or other using diet information from McClanahan et al. (2011) and from Fishbase (Froese and Pauly, 2013), and the fraction of piscivores was calculated. Simpson's diversity index, defined as the probability that two fish chosen at random from the catch will be of different species, was calculated as (Hurlbert, 1971; Rochet and Trenkel, 2003):

$$D = 1 - \sum_j \left(\frac{n_j}{N} \right)^2 \tag{7}$$

where N is the total number of fish identified to species level in the catch, and n_j is the number of fish of species j .

The total CPUE was calculated by first calculating the mean catch in numbers of fish per fisherman hour for each sampled fishing boat, and then taking the average of the boat means across each year. This CPUE was not standardized, so it may not be proportional to abundance; nevertheless, it is expected to decline with increasing fishing intensity.

All of the analyses were conducted using R version 2.15.2 for Windows (R Development Core Team, 2012). ArcGIS was used to produce Fig. 1.

3. Results

3.1. Single species indicators

Length samples were collected on 123 days between August 2004 and June 2011, for a total of 346 fisherman-days sampled (Table 3). A total of 51 species were identified, and 2272 fish were identified to the species level, the most common of which were hogfish (*Lachnolaimus maximus*, 38%) and stoplight parrotfish (9%, Table 4). Eight species, comprising 70% of the catch, were caught in large enough numbers that we could estimate their status.

At the modal values of the parameters (light gray bars in Fig. 2, solid black line for bootstrapped confidence interval), most of the

Table 4
Number of length samples available by species.

Species	Common name	Number of fish
<i>Lachnolaimus maximus</i>	Hogfish	632
<i>Sparisoma viride</i>	Stoplight parrotfish	207
<i>Lutjanus analis</i>	Mutton snapper	191
<i>Pomacanthus arcuatus</i>	Gray angelfish	151
<i>Lutjanus apodus</i>	Schoolmaster	147
<i>Epinephelus striatus</i>	Nassau grouper	107
<i>Mycteroperca bonaci</i>	Black grouper	100
<i>Pomacanthus paru</i>	French angelfish	68
Other		669
Total		2272

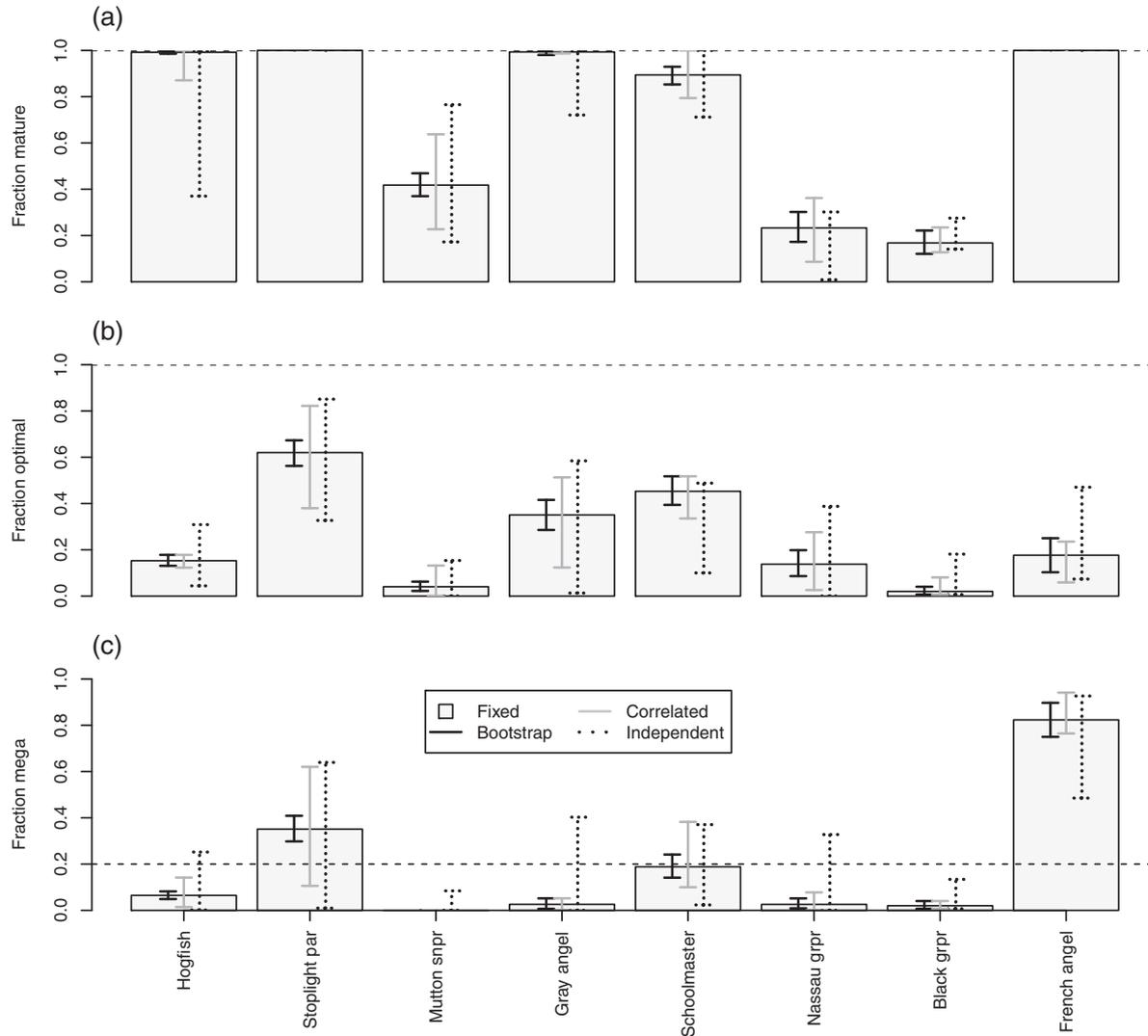


Fig. 2. Froese indicators for the most common species caught in the spear gun fishery at Glover’s Reef, Belize, including: (a) fraction mature P_{mat} ; (b) fraction within the optimal size range P_{opt} ; and (c) fraction of mega-spawners P_{mega} . Horizontal dashed lines are target levels of the indicators (below the line is not desirable). Gray bars indicate values calculated from the length frequency data with the life history parameters fixed at their most likely values. Error bars indicate 90% intervals calculated from bootstrap samples of the length–frequency data, with fixed life-history parameters (bootstrap) and with two alternative Monte Carlo simulations of parameter uncertainty (correlated and independent). Species are sorted by decreasing frequency in the catch.

fish of the eight common species caught at Glover’s Reef were larger than the assumed length at maturity (Fig. 2a). The species often caught below L_m were mutton snapper (*Lutjanus analis*), black grouper (*Mycteroperca bonaci*) and Nassau grouper (*Epinephelus striatus*). The fraction of the catch at optimal size (Fig. 2b) was less than 50% for most species. The fraction of mega-spawners in the catch (Fig. 2c) was below the 20% target for five of the eight species, with one (schoolmaster, *Lutjanus apodus*) including the 20% target in its confidence interval. Stoplight parrotfish and French angelfish (*Pomacanthus paru*) were commonly caught in the mega-spawner size range. There were four species for which more than 50% of the catch was smaller than the lower limit of the optimal size range, implying that they were experiencing growth overfishing: hogfish, mutton snapper, black grouper and Nassau grouper.

With fixed parameters, the confidence bounds around the estimated values of the Froese indicators were generally narrow, implying that the length–frequency sample sizes were large enough to provide adequate estimates of the indicators. Monte Carlo estimates of uncertainty in the indicators, given uncertainty in the life

history parameters (Fig. 2a–c), showed that the Froese indicators were fairly sensitive to the life history parameters, whether the parameters were correlated (Monte Carlo intervals solid gray) or not (Monte Carlo intervals dashed). For example, for hogfish with uncorrelated parameters, the P_{mat} indicator ranged from 38% to 100% depending on the values of the life history parameters. Nevertheless, the conclusions that many mutton snapper, black grouper and Nassau grouper are caught below the length at maturity, and that few fish of any species are caught at the optimal length holds across all the parameter values.

Using the Cope and Punt decision tree, at the modal values of the parameters (gray bars in Fig. 3a), the indicator relative to its target value was above 1.0 for hogfish, stoplight parrotfish, mutton snapper and gray angelfish, implying that they were not overfished. Schoolmaster, Nassau grouper and black grouper were overfished. The bootstrapped confidence intervals overlapped 1.0 for Nassau grouper and mutton snapper. The bootstrapped samples (Fig. 3d, black bars), found that there was some probability of being overfished for all species except French angelfish. Mutton snapper had a 28% probability of being overfished, while Nassau grouper had a

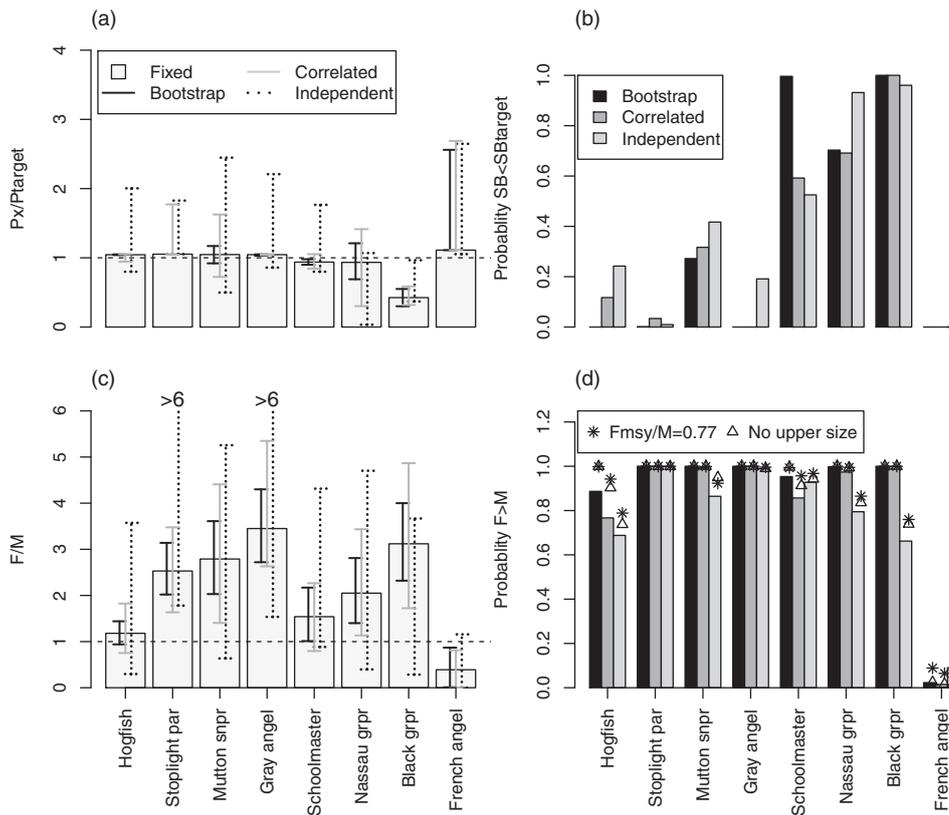


Fig. 3. Overfished and overfishing status, including: (a) the ratio of the appropriate Froese indicator to the target level in the Cope and Punt decision tree (values less than 1.0 imply an overfished population with $SB < SB_{target}$); (b) the fraction of Monte Carlo simulations in which $SB < SB_{target}$; (c) F relative to M ; and (d) the fraction of simulations with $F > M$.

70% probability of being overfished. For the Cope and Punt indicator, parameter uncertainty increased the probability that the stock was overfished for mutton snapper and Nassau grouper, and decreased it for schoolmaster and black grouper. The selectivity curves for the stocks were all classified as either type 2 (catch small and optimally-sized fish) or type 3 (selectivity curve similar to the maturity ogive), and the estimated selectivity pattern varied with the assumed life history parameters (Table 5).

The value of F relative to M at the modal parameter values implied that all species except French angelfish were experiencing overfishing (Fig. 3c). Even with fixed values of the parameters, the bootstrap confidence intervals for F/M were quite broad. For example, for black grouper, the 90% confidence interval of F/M was 2.2–4.2. This implies that larger sample sizes would be needed to achieve precise estimates of F/M from average length. Parameter uncertainty strongly influenced the results, particularly if the life history parameters were uncorrelated. With uncorrelated parameter uncertainty, the confidence interval of F/M included 1.0 for hogfish, mutton snapper, schoolmaster, Nassau grouper, and French angelfish. At the modal values of the parameters, or using correlated parameters, the probability that the population was experiencing overfishing was close to 1.0 for stoplight parrotfish, mutton snapper, gray angelfish, Nassau grouper and black grouper (Fig. 3d). With uncorrelated parameters, allowing for a broader range of possible life histories, the probability they were experiencing overfishing decreased slightly for mutton snapper and both groupers. All of these species, as well as hogfish and schoolmaster, were likely to be experiencing overfishing, with >60% probability that $F > M$ in all scenarios. Using a value of F_{msy}/M of 0.77 (the lower limit of the credible interval of Zhou et al. (2012), stars in Fig. 3d) increased the probability that the population was

experiencing overfishing, especially for hogfish. Assuming that there is no upper limit to the size of fish caught in the fishery (triangles in Fig. 3d) also increased the probability that the population was experiencing overfishing, especially for hogfish. Despite the wide Monte Carlo intervals, and the slightly different results with different modeling assumptions, the results are all consistent in finding that French angelfish are not experiencing overfishing, and all the other species are.

The average lengths of most of the eight species appeared to be stable over time (Fig. 4). Regression of individual fish length against

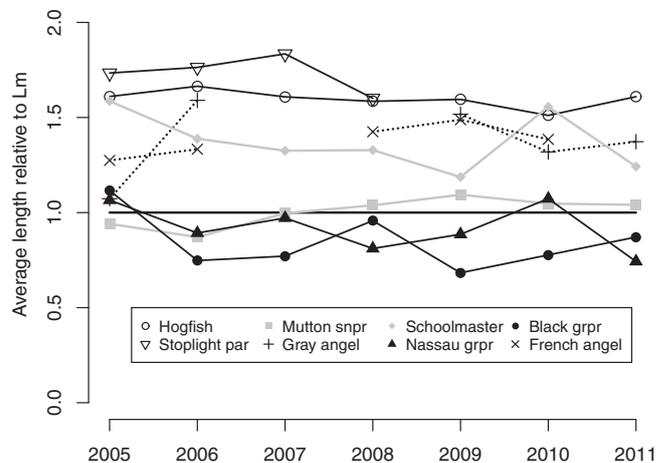


Fig. 4. Average lengths of the eight most common species relative to their length at maturity, by year.

Table 5

Values of estimated parameters and indicators at the modal value of the parameters, with 90% confidence intervals from the simulations with correlated parameters in parenthesis. P_x refers to whichever indicator is selected by the Cope and Punt decision tree. The selectivity is the selectivity estimated by the Cope and Punt decision tree, with the range of values in parenthesis. $SB < SB_{target}$ and $F > M$ refer to whether the population is overfished or experiencing overfishing; the probability of being overfished or experiencing overfishing is given in parentheses.

Species	L_{opt}	Selectivity	P_{mat}	P_{opt}	P_{mega}	$P_{xj}P_{target}$	$SB < SB_{target}$	F/M	$F > M$
Hogfish	51.2 (47.1–55.9)	3 (2–3)	0.99 (0.87–1.00)	0.15 (0.12–0.18)	0.06 (0.02–0.14)	1.04 (0.94–1.05)	N (0.11)	1.18 (0.76–1.83)	Y (0.77)
Stoplight parrotfish	31.6 (29.8–33.0)	3 (3–4)	1.00 (1.00–1.00)	0.62 (0.38–0.82)	0.35 (0.10–0.62)	1.05 (1.03–1.77)	N (0.04)	2.52 (1.64–3.48)	Y (1.00)
Mutton snapper	65.7 (56.5–73.7)	2 (1–3)	0.42 (0.23–0.63)	0.04 (0.00–0.14)	0.00 (0.00–0.00)	1.05 (0.72–1.63)	N (0.32)	2.78 (1.34–4.53)	Y (0.99)
Gray angelfish	37.9 (35.9–41.2)	3 (2–3)	0.99 (0.99–1.00)	0.35 (0.13–0.51)	0.03 (0.00–0.05)	1.05 (1.04–1.05)	N (0.00)	3.44 (2.63–5.33)	Y (1.00)
School-master	33.9 (31.0–36.0)	3 (2–3)	0.89 (0.80–1.00)	0.46 (0.33–0.52)	0.19 (0.10–0.38)	0.94 (0.84–1.05)	Y (0.59)	1.53 (0.77–2.32)	Y (0.85)
Nassau grouper	61.2 (54.8–69.6)	2 (1–3)	0.23 (0.07–0.36)	0.14 (0.03–0.27)	0.03 (0.00–0.07)	0.93 (0.30–1.42)	Y (0.67)	2.04 (1.13–3.47)	Y (0.97)
Black grouper	103.3 (93.9–109.2)	2 (1–2)	0.17 (0.12–0.24)	0.02 (0.00–0.09)	0.02 (0.00–0.05)	0.42 (0.30–0.62)	Y (1.00)	3.10 (1.64–5.09)	Y (1.00)
French angelfish	27.3 (26.1–27.9)	3 (3–4)	1.00 (1.00–1.00)	0.18 (0.06–0.24)	0.82 (0.76–0.94)	1.11 (1.11–2.69)	N (0.00)	0.38 (0.00–0.81)	N (0.02)

Table 6

Regressions of multispecies indicators against year.

Indicator	Slope	P	Regression model	Sample unit
L/L_m	–0.002	0.636	Linear regression	Fish
L_{max}	0.020	<0.001	Log linear regression	Fish
Fraction piscivores	0.081	0.003	Logistic regression	Fish
Mean trophic level	0.134	<0.001	Linear regression	Fish
Simpson's diversity	–0.013	0.253	Linear regression	Annual values
Total CPUE by boat	–0.134	<0.001	Log linear regression	Boat-days

year for each species (except stoplight parrotfish which was not caught in all years) found a significant increase in length for mutton snapper (slope = 1.35, $p < 0.01$), and significant decreases for school-master (slope = –0.82, $p = 0.03$) and black grouper (slope = –2.52, $p = 0.04$).

3.2. Ecosystem indicators

Four of the six ecosystem indicators showed a significant trend over time (Table 6). The mean length relative to length at maturity (Fig. 5a, Table 6) was stable over time. The mean L_{max} (Fig. 5b), fraction of piscivores (Fig. 5c) and mean trophic level of the catch (Fig. 5d) all showed small but significant positive trends over time (Table 6). Simpson diversity was lower in 2010 than in any other years (Fig. 5e) but showed no significant trend. CPUE declined significantly over time (Fig. 5f, Table 6).

The increased trophic level, fraction of piscivores, and mean L_{max} in the spear gun fishery may be caused by the fact that the spear gun fishery stopped targeting parrotfish from 2009 onward (Fig. 6), because of a regulation prohibiting parrotfish starting in 2009 (Government of Belize, 2009). There was a large catch of angelfish in 2009, but angelfish catches declined again in 2010. The current fishery catches mostly hogfish, groupers and snappers, which have higher trophic levels and larger maximum sizes than parrotfish and angelfish. The current mean trophic level of 3.9 is higher than the mean trophic levels in the catches of most fisheries (Branch et al., 2010) because there are so many snappers and groupers in the catch.

4. Discussion

4.1. Findings of the study

This study shows that, across the most plausible range of life history parameters, seven of the eight most commonly caught species in Glover's Reef spear gun fishery are currently overfished or experiencing overfishing. Only one species, the French angelfish, does not appear to be overfished or experiencing overfishing, and the sample size for this species was quite low. Estimated fishing mortality rates were several times the natural mortality rates for stoplight parrotfish, mutton snapper, gray angelfish, Nassau grouper and black grouper. According to the Cope and Punt decision tree, black grouper is overfished, and Nassau grouper, schoolmaster snapper and mutton snapper are probably overfished, but hogfish, stoplight parrotfish, gray angelfish and French angelfish are probably not overfished. Note that the Cope and Punt decision is an ad hoc method to infer overfished status based on length-frequencies, it is not a direct estimate of biomass relative to the biomass reference point. Nevertheless, the fact that the Cope and Punt indicators suggest overfished status for these species indicates that they may benefit from further assessment and improved management.

Mutton snapper, black grouper and Nassau grouper were caught in substantial numbers before they reached maturity, implying that there may be some risk of recruitment overfishing, if the fishing mortality rates continue to be large. The four species that were mainly caught before they reached the optimal size range (hogfish,

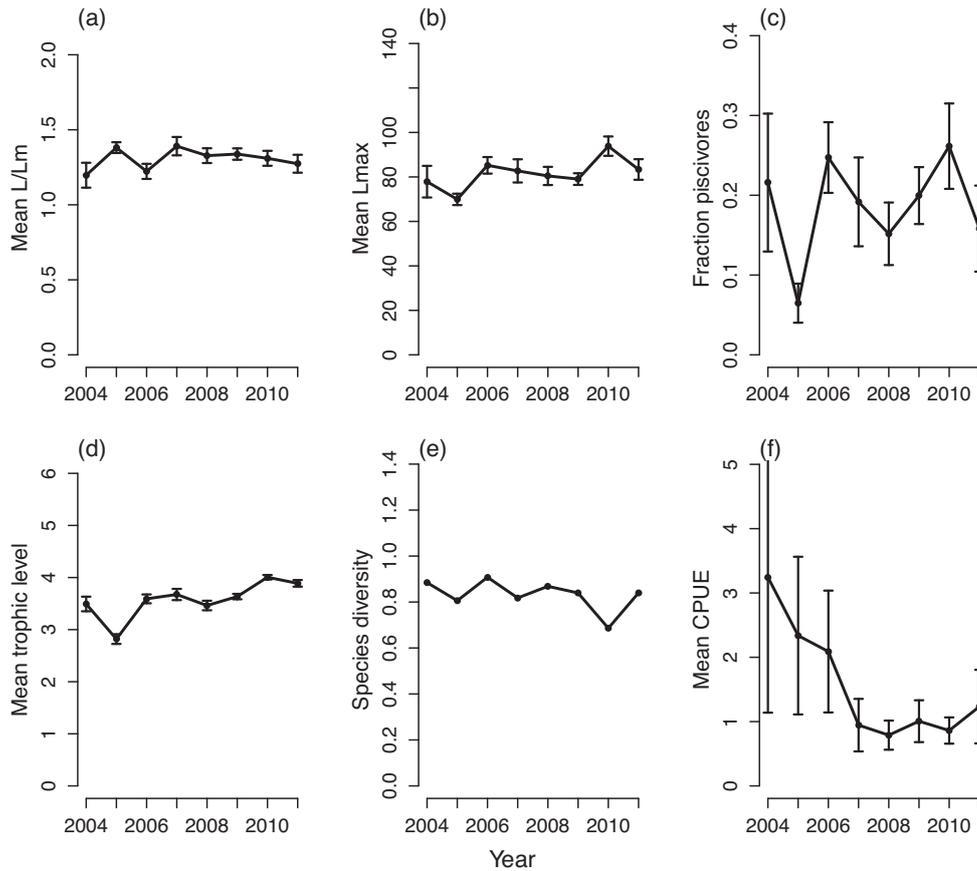


Fig. 5. Community indicators derived from catch monitoring data: (a) mean length relative to L_m ; (b) mean L_{max} ; (c) fraction of piscivores; (d) mean trophic level; (e) Simpson species diversity; and (f) total catch per unit of effort (fish per fishermen hour, with boat days as the sampling unit). Error bars indicate 95% confidence intervals.

mutton snapper, black grouper and Nassau grouper) may be experiencing growth overfishing. For hogfish, these results imply that the species is mainly caught at sizes larger than the size at maturity and smaller than the optimal size, which is possible because L_m (17–45 cm) is much smaller than the L_{opt} (47.1–55.9 cm) we calculated using L_∞ and other life history parameters. While L_m and L_{opt} are similar for most species (Froese and Binohlan, 2000), published estimates of L_m for hogfish are small relative to the published estimates of L_∞ (McBride and Johnson, 2007; McBride and Richardson,

2007; McBride et al., 2008), so it is plausible for this species to have an optimal size larger than its size at maturity.

4.2. Methodology and uncertainties

Given the lack of historical catch, abundance or effort trend data from the spear gun fishery at Glover's Reef, there were a limited number of methods that could be used to infer stock status. The length-based assessment methods turned out to be quite informative for these stocks. Our length-frequency sample of just 2272 fish was sufficient to provide estimates of the current status of the eight most common species in the fishery with reasonably narrow confidence intervals, given an assumed set of life history parameters.

Uncertainty in the life history parameters was the largest source of uncertainty in the estimates of status. Life history parameters vary considerably between studies for Caribbean reef fish (Ault et al., 2008; Froese and Pauly, 2013). The life history data used in this paper are from studies throughout the Caribbean and Florida and many come from a single local sample. None of the studies were conducted in Belize, and few were in the Western Caribbean. Thus, some of the numbers may not be applicable to populations in Belize, and some may be poorly estimated due to small sample sizes.

Our Monte Carlo simulations give some indication of how uncertainty in parameters propagates into wider intervals for the estimates of stock status, but there is no guarantee that our ranges for the life history parameters include the correct values for the populations at Glover's Reef. Nevertheless, despite the high level of parameter uncertainty, we were able to reach some conclusions about the status of the fish populations, for example that black

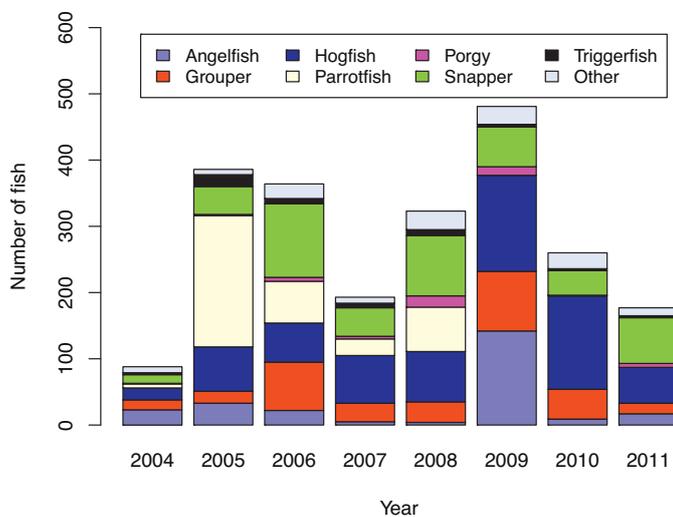


Fig. 6. Family composition of the catch by year.

grouper, Nassau grouper, and probably schoolmaster and mutton snapper are overfished and experiencing overfishing, while French angelfish are not.

Many methods for evaluating the status of low-data fisheries (Edwards et al., 2012) are dependent on the assumed values of life history parameters like length at maturity and maximum age (used to calculate natural mortality). Thus, methods such as Monte Carlo simulation should generally be used to evaluate the sensitivity of the status determinations to the uncertainty in life history parameters.

For species for which the fisheries are extremely size selective, the size-based indicators may not be useful for evaluating stock status. The Cope and Punt (2009) method cannot be used to estimate status for a fishery that catches only optimally-sized fish. Both stoplight parrotfish and French angelfish are caught at very large sizes at Glover's Reef, often in the mega-spawner size range. The smallest stoplight parrotfish reported in the spear gun catch was 28 cm, only 2 cm less than the upper limit of the optimal range. Stoplight parrotfish between 10 and 50 cm are seen in visual surveys at Glover's Reef (WCS unpublished data). Thus, the truncated size distribution in the parrotfish is likely the result of spear-fishermen targeting the largest fish they encounter, including large females and terminal phase males. According to the Cope and Punt decision tree, neither species is overfished; nevertheless, this result should be considered uncertain given the narrow range of sizes selected by the fishery. French angelfish also had the smallest sample size (68 fish) which gave wide confidence intervals to the status estimates.

All of the size-based indicators perform best if recruitment, fishing effort and the size selectivity of fisheries are fairly stable over time. Average lengths in the catch seemed to be relatively constant over time, which is consistent with these assumptions. However, the species composition of the catch was variable. Stoplight parrotfish and angelfish, for example, were significant components of the catch in some but not all years, due to a change in management (see below). Methods that account for changing fishing mortality rates might be particularly appropriate for these species.

4.3. Comparison to other studies

The finding that both Nassau and black grouper are overfished and experiencing overfishing is consistent with previous studies in the region. Black grouper are known to be depleted throughout their range (Sanches et al., 2010). Nassau grouper were overfished in the 1990s in Belize (Sala et al., 2001). Mutton snapper are also known to be experiencing overfishing elsewhere in Belize (Graham et al., 2008). As far as we know, this is the first study in Belize to find that schoolmaster snapper are probably overfished.

This is the first study to estimate status of fish populations at Glover's Reef, although there have been previous studies of changes in fish abundance. A fishery-independent survey at Glover's Reef compared fish densities in 1999, around the time the marine protected area was established, to fish densities in 2009, with data collected from random sites across the atoll both in the conservation zone and the general use zone. They found that mutton snapper, Nassau grouper and schoolmaster densities had not changed significantly, while black grouper, hogfish and gray angelfish densities had increased and stoplight parrotfish and French angelfish had declined (Karnauskas et al., 2011; Thoney, 2001). Stoplight parrotfish density decreased between 2002 and 2008 in another study (Mumby et al., 2012).

It may appear surprising that three species that appear to be experiencing high fishing mortality (black grouper, hogfish and gray angelfish) would be increasing in density. However, this discrepancy may be explained by the fact that the density data includes samples from the conservation zone. These species may be recovering from overfishing within the conservation zone while continuing

to be heavily fished in the general use zone. The fact that part of the population is protected from fishing in the conservation zone may allow the population to persist even with apparent high fishing mortality rates. More problematic is the decline in both stoplight parrotfish and French angelfish in the fishery-independent data. These species were not considered overfished in our analysis. However, considering that they are the two species with the narrowest range of sizes caught in the fishery, our results may be overly optimistic. It is also possible that the three species that our analysis found to be experiencing overfishing but not overfished (hogfish, stoplight parrotfish, and gray angelfish) are in fact experiencing high fishing mortality rates but have not yet declined below the overfished threshold.

4.4. Recommendations for future research

Further research to estimate the life history parameters for the fish populations in Belize would greatly improve our estimates of stock status. In particular, information on size at maturity of the important fishery species should be collected at Glover's Reef. Growth studies would be useful, particularly for the two species of angelfish, each of which had only one published growth study. The maximum sizes and growth rates of stoplight parrotfish are highly variable; therefore, a growth study of stoplight parrotfish in Belize would also be useful. There may also be geographic patterns in life history parameters for some species that could be used to provide better estimates of uncertainty in these parameters through meta-analysis.

Additional data that could be useful for Glover's Reef finfish fishery management are total catch and effort data. The catch data collection program that began in 2011 could generate such data, if species-specific data can be collected. The single-species and ecosystem-level indicators that we calculated would be useful for monitoring changes in the ecosystem over time. Therefore, length-frequency samples should continue to be collected, and the indicators should be recalculated regularly.

If resources become available, information on both the movement of adult fish at Glover's Reef, and the source of larval recruitment would also be useful, to determine whether the conservation zone is contributing to the sustainability of the fishery.

4.5. Effect of management and management recommendations

The fishing mortality rates for all species except French angelfish appear to be quite high. Therefore, reducing the fishing mortality rate for these species may be advisable. The species that are apparently overfished would be the highest priority for management action: black grouper, Nassau grouper, schoolmaster and mutton snapper. The species that do not yet appear to be overfished but are experiencing overfishing (hogfish, stoplight parrotfish and gray angelfish) may also benefit from lower fishing mortality rates. Imposing minimum size limits would be one way to reduce fishing mortality rates. Size limits could increase fishery yields by allowing more fish to grow to the optimal size before they are harvested, for the species that are currently caught at small sizes (Nassau grouper, black grouper, and mutton snapper). Except for Nassau Grouper, there are no size limits for finfish in Belize. Our data show that Nassau grouper have not yet recovered, despite protection at their spawning sites. The introduction (in 2009) of a minimum (51 cm) and maximum (76 cm) size limit for Nassau grouper may help the population recover (Government of Belize, 2009). The minimum size limit for Nassau grouper is around the size at maturity, and the maximum size is well into the mega-spawner size range. Thus, the minimum size limit allows fish to grow to reproductive size before they are harvested, and the maximum size limit protects older, highly fecund females

(mega-spawners) and males. Similar logic could be used to set limits for the other species that are overfished and caught at small sizes, black grouper, mutton snapper, and possibly schoolmaster snapper. Black grouper, Nassau grouper and mutton snapper are also caught by fishermen using hand lines at Glover's Reef (WCS unpublished data), which would need to be included in any management provision.

The other species-specific finfish regulation at Glover's Reef is the ban on catching parrotfish, implemented in 2009. Our data show that the fishery for parrotfish has indeed stopped. With no fishing mortality, the population should recover. However, now that parrotfish are not being caught, fishery-independent data, collected throughout the general use zone with an adequate sample size, would be the only way to monitor population recovery.

4.6. Ecosystem indicators

The increase in the ecosystem indicators mean L_{max} , mean trophic level and fraction piscivores are related to changes in the species composition of the catch from year to year, especially the catches of parrotfish. Most fish are taken when they are above the length at maturity, and the mean length is not changing with time, indicating a fishery that is neither collapsing nor rebuilding for most species (or a fishery that is highly size selective). The decline in CPUE over time is not easy to explain, because it occurred between 2004 and 2007 before the new regulations went into effect. The lower CPUE may be a result of declining abundance of some species, or changes in fishing practices.

Ecosystem-based fishery management requires the ability to monitor changes in ecosystems over time, especially those caused by fishing (Fulton et al., 2005; Rochet and Trenkel, 2003; Ye et al., 2011). Many proposed indicators require either ecosystem models or fishery-independent data sets, which are expensive and time consuming to collect. It would be convenient if the information gathered from a small, inexpensive, species and length-frequency sample from the fishery could give useful information about status and trends in the whole ecosystem. For the Glover's Reef data, the indicator of mean length relative to L_m was useful, because, in a fishery that catches more than 51 species, it would be difficult to get a large enough sample size to estimate status for every species. This indicator gives the useful information that most fish are growing to the age at maturity before being harvested. The trophic indicators and biodiversity indicators do not seem to give much information beyond what could be gleaned from examining the family composition of the catch. The fact that overall CPUE decreased over the time of the study was interesting, and warrants further study. Unfortunately, our sample sizes were not large enough to allow the calculation of single-species CPUE with any accuracy, and it is not clear whether the decrease in CPUE is caused by a decrease in abundance or some other factor.

5. Conclusion

The species composition, length and effort data collected at Glover's Reef since 2004 allowed the calculation of a range of single-species and ecosystem indicators appropriate for monitoring the status of the spear gun fishery. Given the result that Nassau grouper is overfished, the current size limits on Nassau grouper seem to be warranted. Additional protections for black grouper and perhaps schoolmaster and mutton snapper are advisable. We are able to make these recommendations despite the fact that we do not have reliable data from Belize on the age at maturity, maximum sizes and ages and growth curves for these finfish species,

because the overfishing indicators gave consistent results for a wide range of plausible values of the life history parameters for these species. Nevertheless, studies of the life history of these species should be conducted in Belize. It is also important to continue collecting length-frequency data from this fishery, to monitor status and trends over time.

Acknowledgments

This research has been conducted with the approval of the Belize Fisheries Department. Thanks to Danny Wesby and Randolph (Buck) Nuñez for the data collection and Natalyia Dennison and Virginia Burns for data entry. Thanks to Tim McClanahan for providing fish diet data. This work was supported by grants from Fundación AVINA, the USAID/EGAT Global Conservation Program II, the Oak Foundation, the Environmental Defense Fund and the USAID Regional Program for the Management of Aquatic Resources and Economic Alternatives. E. Babcock's work was partially supported by the University of Miami. Thanks to two anonymous reviewers who greatly improved the manuscript.

References

- Aiken, K.A., 1983. The biology, ecology and bionomics of the butterfly and angelfishes, Chaetodontidae. In: Munro, J.L.s (Ed.), Caribbean Coral Reef Fishery Resources. International Center for Living Aquatic Resources Management, Manila, pp. 155–165.
- Ault, J.S., Bohnsack, J.A., Meester, G.A., 1998. A retrospective (1979–1996) multi-species assessment of coral reef fish stocks in the Florida Keys. Fish B-NOAA 96, 395–414.
- Ault, J.S., Smith, S.G., Bohnsack, J.A., 2005. Evaluation of average length as an estimator of exploitation status for the Florida coral-reef fish community. ICES J. Mar. Sci. 62, 417–423.
- Ault, J.S., Smith, S.G., Luo, J.G., Monaco, M.E., Appeldoorn, R.S., 2008. Length-based assessment of sustainability benchmarks for coral reef fishes in Puerto Rico. Environ. Conserv. 35, 221–231.
- Berkeley, S.A., Chapman, C., Sogard, S.M., 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology 85, 1258–1264.
- Beverton, R.J.H., 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. J. Fish. Biol. 41, 137–160.
- Beverton, R.J.H., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations. Chapman and Hall, London.
- Branch, T.A., Watson, R., Fulton, E.A., Jennings, S., McGilliard, C.R., Publico, G.T., Ricard, D., Tracey, S.R., 2010. The trophic fingerprint of marine fisheries. Nature 468, 431–435.
- Brule, T., 2003. Reproduction in the protogynous black grouper (*Mycteroperca bonaci* (Poey)) from the southern Gulf of Mexico. Fish B-NOAA 101, 463–475.
- Burton, M.L., 2002. Age, growth and mortality of mutton snapper, *Lutjanus analis*, from the east coast of Florida, with a brief discussion of management implications. Fish. Res. 59, 31–41.
- Carnell, R., 2011. Triangle: Provides the Standard Distribution Functions for the Triangle Distribution. R package.
- Cervigón, F., 1993. Los Peces Marinos de Venezuela, Vol. 2. Fundación Científica Los Roques, Caracas, Venezuela.
- Choat, J.H., Robertson, D.R., Ackerman, J.L., Posada, J.M., 2003. An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride*. Mar. Ecol.-Prog. Ser. 246, 265–277.
- Cope, J.M., Punt, A.E., 2009. Length-based reference points for data-limited situations: applications and restrictions. Mar. Coastal Fish. 1, 1–18.
- Cortes, E., 2002. Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. Conserv. Biol. 16, 1048–1062.
- Crabtree, R.E., Bullock, L.H., 1998. Age, growth, and reproduction of black grouper, *Mycteroperca bonaci*, in Florida waters. Fish B-NOAA 96, 735–753.
- Edwards, C.T.T., Hillary, R.M., Levontin, P., Blanchard, J.L., Lorenzen, K., 2012. Fisheries assessment and management: A synthesis of common approaches with special reference to deepwater and data-poor stocks. Rev. Fish. Sci. 20, 136–153.
- Ehrhardt, N.M., Ault, J.S., 1992. Analysis of two length-based mortality models applied to bounded catch length frequencies. J. Am. Fish. Soc. 121, 115–122.
- Feitosa, C.V., Ferreira, B.P., De Araujo, M.E., 2008. A rapid new method for assessing sustainability of ornamental fish by-catch from coral reefs. Mar. Freshwater Res. 59, 1092–1100.
- Friedlander, A.M., DeMartini, E.E., 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Mar. Ecol.-Prog. Ser. 230, 253–264.
- Froese, R., 2004. Keep it simple: three indicators to deal with overfishing. Fish. Fish. 5, 86–91.

- Froese, R., Binohlan, C., 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *J. Fish. Biol.* 56, 758–773.
- Froese, R., Pauly, D., 2013. *FishBase*. World Wide Web Electronic Publication.
- Fulton, E.A., Smith, A.D.M., Punt, A.E., 2005. Which ecological indicators can robustly detect effects of fishing? *ICES J. Mar. Sci.* 62, 540–551.
- García-Cagide, A., Claro, R., Koshelev, B.V., 1994. Reproducción. In: Claro, R.s (Ed.), *Ecología de los peces marinos de Cuba*. Inst. Oceanol. Acad. Cienc. Cuba. and Cen. Invest. Quintana Roo, México, pp. 187–262.
- Government of Belize, 2009. Statutory Instrument No. 49 of 2009. Fisheries (Nassau grouper and Species Protection) Regulations. Government of Belize, p. 4.
- Graham, R.T., Carcamo, R., Rhodes, K.L., Roberts, C.M., Requena, N., 2008. Historical and contemporary evidence of a mutton snapper (*Lutjanus analis* Cuvier, 1828) spawning aggregation fishery in decline. *Coral Reefs* 27, 311–319.
- Hewitt, D.A., Hoening, J.M., 2005. Comparison of two approaches for estimating natural mortality based on longevity. *Fish B-Noaa* 103, 433–437.
- Hewitt, D.A., Lambert, D.M., Hoening, J.M., Lipcius, R.N., Bunnell, D.B., Miller, T.J., 2007. Direct and indirect estimates of natural mortality for Chesapeake Bay blue crab. *J. Am. Fish. Soc.* 136, 1030–1040.
- Hurlbert, S.H., 1971. Nonconcept of species diversity – critique and alternative parameters. *Ecology* 52, 577–586.
- International Game Fish Association, 2001. Database of IGFA angling records until 2001. International Gamefish Association. <http://wrec.igfa.org/>, Fort Lauderdale, USA.
- Jensen, A.L., 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Can. J. Fish. Aquat. Sci.* 53, 820–822.
- Karnauskas, M., Huntington, B.E., Babcock, E.A., Lirman, D., 2011. Pre-existing spatial patterns in fish abundances influence species-specific responses in a Caribbean marine reserve. *Mar. Ecol.-Prog. Ser.* 432, 235–246.
- Koltes, K.H., 1993. Aspects of the reproductive biology and social structure of the stoplight parrotfish (*Sparisoma viride*) at Grand Turk, Turks and Caicos Islands. *B. W. I. B. Mar. Sci.* 52, 792–805.
- Magnuson-Stevens Fishery Conservation and Management Act, 2007. Magnuson-Stevens Fishery Conservation and Management Act. (Public Law 94-265 As amended by the Magnuson-Stevens Fishery Conservation and Management Reauthorization Act (P.L. 109-479).
- Manooch, C.S.I., 1987. Age and growth of snappers and groupers. In: Polovina, J.J., Ralston, S.s (Eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press, Inc, Boulder, pp. 329–373.
- Mason, D.L., Manooch, C.S.I., 1985. Age and growth of mutton snapper along the east coast of Florida. *Fish. Res.* 3, 93–104.
- McBride, R.S., Johnson, M.R., 2007. Sexual development and reproductive seasonality of hogfish (Labridae: *Lachnolaimus maximus*), an hermaphroditic reef fish. *J. Fish. Biol.* 71, 1270–1292.
- McBride, R.S., Richardson, A.K., 2007. Evidence of size-selective fishing mortality from an age and growth study of hogfish (Labridae: *Lachnolaimus maximus*), a hermaphroditic reef fish. *B. Mar. Sci.* 80, 401–417.
- McBride, R.S., Thurman, P.E., Bullock, L.H., 2008. Regional variations of hogfish (*Lachnolaimus maximus*) life history: Consequences for spawning biomass and egg production models. *J. Northw. Atl. Fish. Sci.* 41, 1–12.
- McClanahan, T., Muthiga, N., Coleman, R., 2011. Testing for top-down control: can post-disturbance fisheries closures reverse algal dominance? *Aquat. Conserv. Mar. Freshwater Ecosyst.* 21, 658–675.
- Mumby, P.J., Steneck, R.S., Edwards, A.J., Ferrari, R., Coleman, R., Harborne, A.R., Gibson, J.P., 2012. Fishing down a Caribbean food web relaxes trophic cascades. *Mar. Ecol.-Prog. Ser.* 445, 13–24.
- Pauly, D., 1978. A Preliminary Compilation of Fish Length Growth Parameters Ber. Inst. Meeresk. Christian-Albrechts-Univ, Kiel, pp. 1–200.
- Pauly, D., 1980. On the interrelationships between natural mortality, growth-parameters, and mean environmental-temperature in 175 fish stocks. *J. Conseil.* 39, 175–192.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food webs. *Science* 279, 860–863.
- Pauly, D., Watson, R., 2005. Background and interpretation of the 'Marine Trophic Index' as a measure of biodiversity. *Philos. J. Roy. Soc. B* 360, 415–423.
- Prince, J.D., Dowling, N.A., Davies, C.R., Campbell, R.A., Kolody, D.S., 2011. A simple cost-effective and scale-less empirical approach to harvest strategies. *ICES J. Mar. Sci.* 68, 947–960.
- R Development Core Team, 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Randall, J.E., 1962. Tagging reef fishes in the Virgin Islands. *Proc. Gulf Caribbean Fish. Inst.* 14, 201–241.
- Randall, J.E., 1978. Scaridae. In: Fischer, W.s (Ed.), *FAO Species Identification Sheets for Fishery Purposes*. Western Central Atlantic (Fishing Area 31), FAO, Rome.
- Reeson, P.H., 1983. The biology, ecology and bionomics of the parrotfishes, Scaridae. In: Munro, J.L.s (Ed.), *Caribbean Coral Reef Fishery Resources*. International Center for Living Aquatic Resources Management, Manila, pp. 166–177.
- Rochet, M.J., Trenkel, V.M., 2003. Which community indicators can measure the impact of fishing? A review and proposals. *Can. J. Fish. Aquat. Sci.* 60, 86–99.
- Sadovy, Y., 2001. The threat of fishing to highly fecund fishes. *J. Fish. Biol.* 59, 90–108.
- Sadovy, Y., Eklund, A.M., 1999. Synopsis of the biological data on the Nassau Grouper, *Epinephelus striatus* (Block, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Technical Report NMFS.
- Sala, E., Ballesteros, E., Starr, R.M., 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: Fishery management and conservation needs. *Fisheries* 26, 23–30.
- Sanches, E.G., Pannuti, C.V., Sebastiani, E.F., Rodrigues, J.D., Garcia, C.E.D., Moreira, R.G., 2010. Threatened fishes of the world: *Mycteroperca bonaci* (Poey, 1860) (Serranidae: Epinephelinae). *Environ. Biol. Fish.* 88, 239–240.
- Shin, Y.J., Bundy, A., Shannon, L.J., Simier, M., Coll, M., Fulton, E.A., Link, J.S., Jouffre, D., Ojaveer, H., Mackinson, S., Heymans, J.J., Raid, T., 2010. Can simple be useful and reliable? Using ecological indicators to represent and compare the states of marine ecosystems. *ICES J. Mar. Sci.* 67, 717–731.
- Shin, Y.J., Rochet, M.J., Jennings, S., Field, J.G., Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62, 384–396.
- Steward, C.A., DeMaria, K.D., Shenker, J.M., 2009. Using otolith morphometrics to quickly and inexpensively predict age in the gray angelfish (*Pomacanthus arcuatus*). *Fish. Res.* 99, 123–129.
- Thoney, D., 2001. Glovers reef survey in Belize, a multi-Aquarium project. La surveillance du récif de Glovers à Bêlize, un projet multi-Aquariums. *Bull.Inst. Océanogr., Monaco* 20, 245–252.
- Valle, S.V., García-Arteaga, J.P., Claro, R., 1997. Growth parameters of marine fishes in Cuban waters. *Naga ICLARM Q* 20, 34–37.
- Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., Zeller, D., 2009. Rebuilding global fisheries. *Science* 325, 578–585.
- Ye, Y.M., Cochrane, K., Qiu, Y.S., 2011. Using ecological indicators in the context of an ecosystem approach to fisheries for data-limited fisheries. *Fish. Res.* 112, 108–116.
- Zhou, S.J., Yin, S.W., Thorson, J.T., Smith, A.D.M., Fuller, M., 2012. Linking fishing mortality reference points to life history traits: an empirical study. *Can. J. Fish. Aquat. Sci.* 69, 1292–1301.