



Fish community and single-species indicators provide evidence of unsustainable practices in a multi-gear reef fishery

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ABSTRACT

Using information on the species composition and length-frequencies of fish caught in the spear and hook and line fisheries of Glover's Reef Marine Reserve, Belize, we evaluated changes between 2004–2010 and 2011–2017 in single-species and ecosystem sustainability indicators. The two gears differed in species caught, and both changed species composition between time periods, with the line fishers targeting smaller species, and the spear fishers responding to a parrotfish ban by catching more snappers and small groupers, as well as grey angels. Both gears caught smaller fish in 2011–2017 compared to 2004–2010, indicating overfishing. Species often caught immature were black grouper, Nassau grouper and mutton snapper with spears, and black snapper with lines. Most fish of other species were mature, but many were smaller than the optimal size for harvest. Fishing mortality rates were higher than natural mortality rates for most species in both gears in both time periods, whether calculated from average length or by length-based spawning potential ratio (LBSPR), implying that most populations were experiencing overfishing. Many species also had a low spawning potential ratio, implying a high probability that they were overfished. In general, many species were subject to unsustainable levels of fishing, and, according to the Froese indicators, some would benefit from size limits to protect immature individuals. These results are supported despite uncertainty in life history parameters for fishes in Belize, and differences between data poor assessment methods.

1. Introduction

Small-scale fisheries, including fisheries around tropical coral reefs, are an important source of livelihood and food security for often-impoorished coastal communities worldwide (Andrew et al., 2007; Newton et al., 2007). Thus, improving the sustainability of these fisheries is a necessary step toward poverty alleviation (Bene et al., 2010). In the Western Caribbean, over one million local people are directly dependent on the integrity and health of the Mesoamerican Reef system for their livelihood, and the national economies of four countries (Belize, Guatemala, Honduras, and Mexico) substantially benefit from the reef's fisheries resources and appeal as an international tourist destination (Zeller et al., 2011). Therefore, the sustainable management of small-scale fisheries associated with the Mesoamerican Reef system, much of which falls within the territorial waters of Belize, is imperative in light of food security and income generation as well as maintaining biodiversity and other essential ecosystem services. However, small-scale fisheries are difficult to assess and manage because they lack the quantity and/or quality of data needed for conventional stock

assessment and have limited enforcement capacity across dynamic multi-species and multi-gear systems (Costello et al., 2012).

A first step in assessing the status of a small-scale fishery is to evaluate the species and length composition of the catch. Samples of species composition and length-frequencies may be easier to obtain than time series of total catch or abundance. Thus, length-based methods are commonly used for assessing the sustainability of data-limited fisheries, and to evaluate changes in status over time (Dowling et al., 2016). Such information can be used to evaluate whether large-scale community shifts have occurred, such as changes in the trophic level of fish that are caught, or a shift toward smaller species or smaller individuals, which can indicate unsustainable exploitation rates (Hobday et al., 2011; Rochet and Trenkel, 2003). Differences between gears may be important for designing management strategies that take into account the species and size selectivity of each component of the fishery.

For individual species that are commonly caught, the length composition of the catch can be informative about whether the fishery is focused on small or immature individuals (Froese, 2004), and whether

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Table 1

Details on the symbols used in the analysis. Indicators are given separately in Table 2.

Symbol	Units	Definition	Source, method and use
Calculated from species composition data			
N		Number of fish identified to species in the catch	Used to calculate Simpson diversity
n_j		Number of fish of species j in the catch.	Used to calculate Simpson diversity
Calculated from length composition data			
L_c	cm	Length fully recruited into fishery	Calculated from mode of length frequency distribution (Babcock et al., 2013)
L_λ	cm	Maximum fully recruited length in fishery	Observed maximum length in the catch, excluding any outliers more than a few cm larger than the rest of the distribution. (See Supplement for details)
SL_{50}	cm	Length at 50% selection in logistic selectivity curve	Estimated by LBSPR function in R (Hordyk et al., 2015b)
SL_{95}	cm	Length at 95% selection in logistic selectivity curve	Estimated by LBSPR function in R (Hordyk et al., 2015b)
Taken from the literature or given an assumed value			
$CV(L)$		CV in length at age	Assumed equal to 0.1
K		von Bertalanffy growth coefficient	From literature (Table 3 and Supplement), has Monte Carlo distribution
L_m	cm	Median length at first reproduction	From literature (Table 3 and Supplement), has Monte Carlo distribution
L_{max}	cm	Maximum observed length	From literature (Table 3 and Supplement), assumed constant
L_∞	cm	Asymptotic length in the von Bertalanffy growth curve	From literature (Table 3 and Supplement), has Monte Carlo distribution
t_{max}	yr	Maximum observed age	From literature (Table 3 and Supplement), assumed constant
Calculated from literature values for each Monte Carlo draw			
L_{opt}	cm	Optimal length, at which the total biomass of a cohort is maximized	$L_{opt} = \frac{3L_\infty}{(3 + M/K)}$ (Beverton, 1992) or $\log_{10}(L_{opt}) = 1.053 \cdot \log_{10}(L_m) - 0.0565$ (Froese and Binohlan, 2000)
M	yr ⁻¹	Natural mortality rate	$M = 4.899t_{max}^{-0.916}$ or $M = 4.188K^{0.73}(10L_\infty)^{-0.33}$ where L_∞ is in cm (Then et al., 2015) or $M = \frac{-\ln(0.05)}{t_{max}}$ (Ault et al., 2008)
Calculated from data and parameters for each Monte Carlo and bootstrap draw			
\bar{L}	cm	Mean length of fish between L_c and L_λ	Needed to calculate Z (Ehrhardt and Ault, 1992)
Z	yr ⁻¹	Total mortality, calculated from \bar{L}	$\left(\frac{L_\infty - L_\lambda}{L_\infty - L_c}\right)^{\frac{Z}{K}} = \frac{Z(L_c - \bar{L}) + K(L_\infty - \bar{L})}{Z(L_\lambda - \bar{L}) + K(L_\infty - \bar{L})}$ (Ehrhardt and Ault, 1992) calculated iteratively using nlminb function in R.
F	yr ⁻¹	Fishing mortality rate	$F = Z - M$

the population is overfished, defined as being below a biomass threshold (Cope and Punt, 2009). Given information about growth and natural mortality rates, length-frequencies can be also used to estimate fishing mortality rates (Beverton and Holt, 1957; Ehrhardt and Ault, 1992; Hordyk et al., 2015b), where a fishing mortality rate (F) larger than the natural mortality rate (M , i.e. $F/M > 1$) is an indicator that the population is experiencing overfishing (See Table 1 for definitions of all parameters, and Table 2 for the indicators). Length-based spawning potential ratio (LBSPR) (Hordyk et al., 2015b, 2016) is a methodology that can be used to estimate both fishing mortality rates and spawning potential ratio (SPR). SPR, defined as the current spawning stock biomass (SSB) relative to the unfished SSB, is a metric of whether the population is overfished, with values less than 0.3–0.5 (depending on the life history of the fish population) indicative of overfished status (Goodyear, 1993).

Using data collected by the Wildlife Conservation Society (WCS) between 2004 and 2011 at Glover's Reef, Belize, Babcock et al. (2013) applied several length-based methods to determine whether the spear component of the fishery was sustainable (Ault et al., 1998, 2005, 2008; Cope and Punt, 2009; Ehrhardt and Ault, 1992; Froese, 2004), and also used a range of multispecies indicators to evaluate the ecosystem impacts of the fishery (Rochet and Trenkel, 2003). Because life history data were not available from Belize, they used a Monte Carlo method to include uncertainty about the values of life history parameters in the estimates of status, along with bootstrapping to estimate the sampling error. The objective of this paper is to expand the analysis of Babcock et al. (2013) by: (1) using multivariate statistics to compare the species composition caught in the spear versus hook and line gears over time; (2) including six more years of data through May 2017 to calculate sustainability indicators; (3) calculating the indicators for the hook and line gear as well as the spear gear; (4) updating the life history data used to calculate the indicators; and (5) adding the LBSPR method (Hordyk et al., 2015b) to estimate both SPR and F/M .

2. Methods

2.1. Study site and data collection

Glover's reef (16°44' N, 87°48' W) is an atoll 25 km to the east of the Belize barrier reef, which is designated as a multi-zone marine reserve (i.e. marine protected area) (Tewfik et al., 2017). Approximately one fifth of the atoll is a replenishment zone (i.e. no-take area), while the remainder of the atoll is zoned as general use where commercial fishing is only allowed by licensed users and under a set of regulations enforced by the Belize Fisheries Department. The regulations within Glover's atoll include a ban on gillnets, traps, artificial habitats (i.e. shades to attract lobsters) and longlines in addition to other fishing regulations that apply throughout Belize (Government of Belize, 2003; Tewfik et al., 2017). Since 2009 regulations specific to finfish in Belize include a ban on catching herbivorous fish (specifically parrotfish and surgeonfish) and a minimum and maximum size limit (50–74 cm total length) for the Nassau grouper (Government of Belize, 2009). Beginning in 2011, the Belize Fisheries Department implemented a pilot study for the spatial management of fishing grounds, called the "Managed Access Program", at Glover's Reef, which restricted fishing rights to individuals who have traditionally used Glover's Reef through a new electronic licensing system. The fishers at Glover's Reef originate mainly from Sarteneja, in Northern Belize, and Hopkins on the mainland opposite Glover's Reef (Grant, 2004; Tewfik et al., 2017). The Sarteneja fishers come to the atoll aboard 10–15 m sailboats, and then disperse in 4–7 dories per sailboat to fish individually for finfish using either spear gun or Hawaiian sling gear (hereafter both referred to as spear fishing), or to free-dive for conch or lobster mostly within the atoll's lagoon and associated patch reefs but occasionally on the fore-reef (Tewfik et al., 2017). More rarely they also fish with hook and line. The fishermen from Hopkins tend to use 7–10 m skiffs with outboard motors, and typically have a crew size of two or three and fish for

Table 2
Indicators of fishery status.

Symbol	Definition	Source and interpretation
(\bar{L}/L_m)	Mean length relative to the length at maturity L_m across all fish in the catch	$(\bar{L}/L_m) < 1$ indicates overfishing, decrease indicates increasing fishing pressure (Rochet and Trenkel, 2003; Hobday et al., 2011)
\bar{L}_{max}	Mean maximum size L_{max}	L_{max} taken from literature, mean calculated across all fish in the catch. Decrease indicates increasing fishing pressure
P_{pisc}	Fraction of piscivores, defined as fish with a diet > 75% fish	Diet fractions from Fishbase (Froese and Pauly, 2017) and from Randall (1968) (Supplement Table A1). Indicates changes in abundance or targeting
P_{spong}	Fraction of spongivores, defined as fish with a diet > 75% sponges	Indicates changes in abundance or targeting
P_{invert}	Fraction of invertivores, defined as fish with a diet > 75% invertebrates	Indicates changes in abundance or targeting
\bar{TL}	Mean trophic level	Indicates changes in abundance or targeting
D	Simpson species diversity $D = 1 - \sum_j \left(\frac{n_j}{N} \right)^2$	May decline with overfishing (Hurlbert, 1971; Rochet and Trenkel, 2003)
\bar{CPUE}	Mean catch per unit of effort across all species (fish/fisher hour)	Indicator of fishery profitability. Calculations done as in Babcock et al. (2013)
P_{mat}	Proportion of fish in catch that are mature ($L \geq L_m$)	$P_{mat} < 1$ indicates immature fish being caught (Froese, 2004)
P_{opt}	Proportion of fish caught that are within 10% of L_{opt}	$P_{opt} < 1$ indicates potential growth overfishing (Froese, 2004)
P_{mega}	Proportion of fish caught that are mega-spawners ($L \geq 1.1L_{opt}$)	$P_{opt} < 0.2$ indicates possible depletion of mega-spawners (Froese, 2004)
DT	Overfished metric based on the Froese metrics and a decision tree	Infers selectivity of the fishery (e.g. target immature fish only, selectivity similar to the maturity ogive, etc.) from P_{mat} , P_{opt} , and P_{mega} , and L_m/L_{opt} , and then whether the population is overfished (= below a biomass threshold) or not. (Cope and Punt, 2009)
$(F/M)_{ML}$	F/M from mean length	$F/M > 1$ is overfishing (Ehrhardt and Ault, 1992)
SPR	Length based spawning potential ratio	Calculated using R library LBSPR (Hordyk et al., 2015b) $LBSPR < 0.4$ indicates overfished status
$(F/M)_{LBSPR}$	F/M from the LBSPR method	$F/M > 1$ is overfishing (Hordyk et al., 2015b)

finfish year-round mainly with hook and line, often on the outside of the atoll but still within the general use zone of the marine reserve (Tewfik et al., 2017).

Between 2004 and 2017, WCS researchers approached boats fishing at Glover's Reef, and recorded the length, mass and species of every fish they had caught, as well as the number of hours each person had fished and the fishing gear used. Fishers were not obligated to participate in the data collections. A one-gallon gas coupon was used as an incentive to individual fishers who did participate. Because the sample sizes were small, we combined years into two time periods (2004–2010 and 2011–2017) for all analyses, rather than evaluating changes by year.

2.2. Species composition and fish community indicators

We used multivariate statistics to evaluate differences in species composition between time periods (2004–2010 or 2011–2017), gear types (spear or hook and line), and boat types (skiff or sail boat). First, we produced a community table indicating the number of individuals of each fish species caught in each season (Months 1–3, 4–6, 7–9, 11–12) of each year, with boat types and gear types counted separately. Fish that were not identified to species were excluded, as were species with fewer than 30 observations, and species that were observed in fewer than 3 samples. To normalize for the differences in sample sizes, the species composition in each sample (year, season, gear type, boat type) was divided by the total number of fish caught to give the proportional species composition. To test for the effects of gear type, time period and boat type on the species composition of these most common species, we used PERMANOVA (permutational analysis of variance) (Anderson, 2001; Anderson and Walsh, 2013). PERMANOVA was applied to both the proportion data, using the Bray-Curtis distance metric, and presence/absence, using the Jaccard distance metric. NMDS (non-metric multidimensional scaling) (Minchin, 1987) was used to visualize the differences in species composition between gears, time periods and boat types using the same data. All multivariate analyses were done in R version 3.4.2, using the Vegan community ecology package (Oksanen et al., 2017).

To estimate the impact of fishing on the fish community in general at Glover's Reef, we calculated the following indicators for each gear

type in each time period (Babcock et al., 2013) (See Table 2 for definitions, references, and interpretations):

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

All the multispecies indicators except CPUE were calculated across all individual fish that had been identified to species (Table 2, Supplement Table A1). However, if length data were missing, or no data were available on diet for the species the sample size was sometimes reduced. For the most commonly-caught species, the median values of L_m and L_{max} were used from all the values found in Fishbase and an independent literature search (Table 3). For less common species, we used the median values from Fishbase, found using the Rfishbase library (Boettiger et al., 2012). For the few species for which no L_m data were available, values were estimated from L_{max} (Froese and Binohlan, 2000). The total CPUE was calculated as the mean catch in numbers of fish per fisher-hour for each sampled fishing boat in each day, keeping the two gear types separate (Babcock et al., 2013). For each indicator, a linear model was used to determine whether the mean values differed between gears (spear versus line), and whether they had changed between time periods (2004–2010 versus 2011–2017). A logit-link generalized linear model was used for all the proportions. All other models were simple 2-way ANOVA, with both CPUE and L_{max} log-transformed to achieve normality.

2.3. Single-species fishery indicators

For species with a large enough samples size, we estimated the following single-species indicators of fishery sustainability (Table 2): proportion mature (P_{mat}) (Froese, 2004),

Table 3

Life history parameters (see details in Table 1), with the ranges used for the Monte Carlo simulations. All lengths are fork lengths in cm. See Table 3 for common names.

Family	Species	L_{max}	t_{max}	K	L_{∞}	L_m	M	L_{opt}
Haemulidae	<i>Haemulon sciurus</i> ^a	41	12	0.3(0.22,0.3)	37(34,41)	20(17,21)	0.5(0.25,0.52)	23(21,25)
Labridae	<i>Lachnolaimus maximus</i> ^b	82	23	0.1(0.08,0.26)	85(64,92)	25(17,45)	0.17(0.13,0.28)	39(23,54)
Lutjanidae	<i>Apsilus dentatus</i> ^c	60	29	0.48(0.3,0.65)	58(56,62)	40(32,44)	0.22(0.1,0.63)	46(41,52)
	<i>Lutjanus analis</i> ^d	84	29	0.15(0.1,0.25)	88(77,118)	39(28,52)	0.22(0.1,0.24)	51(40,62)
	<i>Lutjanus apodus</i> ^e	63	42	0.18(0.12,0.35)	57(46,66)	25(14,32)	0.16(0.07,0.31)	35(24,45)
	<i>Lutjanus buccanella</i> ^f	73	NA	0.12(0.08,0.7)	60(53,73)	28(23,36)	0.23(0.22,0.38)	34(28,42)
	<i>Lutjanus purpureus</i> ^g	104	18	0.1(0.09,0.13)	90(79,107)	41(37,44)	0.17(0.08,0.35)	49(42,61)
	<i>Lutjanus synagris</i> ^h	50	19	0.22(0.08,0.4)	47(44,58)	22(18,31)	0.33(0.16,0.38)	27(22,32)
	<i>Lutjanus vivanus</i> ⁱ	74	NA	0.1(0.05,0.32)	73(60,76)	39(22,57)	0.19(0.19,0.36)	43(33,49)
Pomacanthidae	<i>Pomacanthus arcuatus</i> ^j	60	24	0.38(0.17,0.6)	62(46,62)	25(23,34)	0.27(0.12,0.52)	37(25,49)
	<i>Pomacanthus paru</i> ^k	43	10	0.17(0.12,0.21)	47(43,47)	25(23,27)	0.31(0.3,0.59)	27(25,29)
Scaridae	<i>Sparisoma viride</i> ^l	45	9	0.45(0.45,0.71)	43(42,46)	20(18,26)	0.65(0.33,0.66)	25(20,29)
Scombridae	<i>Scomberomorus cavalla</i> ^m	173	23	0.15(0.07,0.51)	140(138,176)	63(40,77)	0.2(0.13,0.28)	83(69,101)
Serranidae	<i>Epinephelus guttatus</i> ⁿ	76	22	0.24(0.12,0.24)	52(47,57)	25(25,29)	0.29(0.14,0.39)	33(27,39)
	<i>Epinephelus striatus</i> ^o	120	29	0.1(0.06,0.18)	93(72,123)	52(48,75)	0.17(0.1,0.22)	59(53,67)
	<i>Mycteroperca bonaci</i> ^p	150	33	0.17(0.12,0.17)	131(120,153)	72(67,72)	0.2(0.09,0.23)	86(79,94)
Sphyrnidae	<i>Sphyrna barracuda</i> ^q	180	18.4	0.11(0.09,0.26)	140(132,183)	66(64,85)	0.16(0.16,0.34)	83(72,96)

^a Bluestriped grunt L_{max} (Claro, 1994), K and L_{∞} (Appeldoorn, 1992), lower limit of L_{∞} (Valle et al., 1997), upper limit of L_{∞} and L_m (Ault et al., 2008), L_m and lower limit of L_m (García-Cagide et al., 1994).

^b Hogfish L_{max} , L_{∞} , K , range of K and upper limit of L_{∞} (McBride and Johnson, 2007), t_{max} and L_m (Ault et al., 2008), lower limit of L_{∞} from largest size encountered at Glover's Reef, upper limit of L_m calculated from L_{∞} , lower limit of L_m (McBride et al., 2008).

^c Black snapper L_{max} (Allen, 1985), t_{max} (Ault et al., 1998), L_{∞} , upper limit of K , and upper limit of L_m (García-Cagide et al., 1994), L_m (Thompson and Munro, 1983), median value of K from the mean of the upper and lower values, upper limit of L_{∞} calculated from L_{max} , lower limit of L_m calculated from L_{∞} .

^d Mutton snapper L_{max} (International Game Fish Association, 2001), t_{max} (Burton, 2002), K and L_{∞} (Manooch, 1987), range of K and L_{∞} , and L_m (Mason and Manooch, 1985), lower limit of L_m (Ault et al., 2008).

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

^f Blackfin snapper L_{max} (Appeldoorn et al., 1987), the only available t_{max} was only 9 years (Ault et al., 2008) so we did not use this estimate; K and L_{∞} from (Valle et al., 1997), with the minimum value of L_{∞} set equal to the largest observed value at Glover's Reef, maximum L_{∞} and minimum K (Ault et al., 2008), K maximum (Thompson and Munro, 1983); L_m (Ault et al., 2008; Boardman and Weiler, 1980; García-Cagide et al., 1994).

^g Southern red snapper L_{max} (Trindade-Santos and Freire, 2015); t_{max} (Allen, 1985); K and L_{∞} (Pauly, 1980), range of K and L_{∞} (Baker et al., 2001; Claro and García-Arteaga, 1994; Manickchand-Heileman and Phillip, 1996; Menezes and Gesteira, 1974); L_m and range of L_m (García-Cagide et al., 1994; Trindade-Santos and Freire, 2015).

^h Lane snapper L_{max} (International Game Fish Association, 2001), t_{max} (Luckhurst et al., 2000); K and L_{∞} (Freitas et al., 2014), minimum L_{∞} from largest typical size at Glover's Reef, maximum L_{∞} (Manooch, 1987); K range (Aiken, 2001; Luckhurst et al., 2000), L_m (Aiken, 2001), range of L_m (García-Cagide et al., 1994; Manickchand-Dass, 1987).

ⁱ Silk snapper L_{max} (International Game Fish Association, 2001); K and L_{∞} (Claro and García-Arteaga, 1994), range of L_{∞} (Lessa et al., 2004; Valle et al., 1997), range of K (Lessa et al., 2004; Tabash and Sierra, 1996); L_m calculated from L_{∞} because this gave a value near the center of the reported range, minimum L_m (Lessa et al., 2004), maximum L_m (García-Cagide et al., 1994).

^j Grey angel L_{max} (Aiken, 1983), minimum L_{max} , t_{max} (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_{∞} .

^k French angel L_{max} from Glover's reef data, t_{max} from Florida Museum of Natural History (2011), 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_{∞} .

^l Stoplight 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), Koltz (1993) and García-Cagide et al., (1994).

^m King mackerel L_{max} (Collette and Nauen, 1983), t_{max} (Shepard et al., 2010); K and L_{∞} (Sturm and Salter, 1990), range of K (Shepard et al., 2010; Sutter et al., 1991), lower limit of L_{∞} from the largest common size at Glover's Reef, upper limit of L_{∞} calculated from L_{max} , L_m and its upper limit (Trindade-Santos and Freire, 2015) and lower limit (Rickman et al., 2000).

ⁿ Red hind L_{max} and t_{max} (Sadovy et al., 1992), K , L_{∞} and upper limit of K (Thompson and Munro, 1983), lower limit of K and upper limit of L_{∞} (Munro and Williams, 1985), lower limit of L_{∞} (Chan and Sadovy, 2002), L_m (García-Cagide et al., 1994), upper limit of L_m calculated from L_{∞} .

^o 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).

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

^q Barracuda L_{max} (Torres, 1991), t_{max} , lower limit of L_{∞} , upper limit of K and L_m (Kadison et al., 2010), L_{∞} , K and lower limit of K (Pauly, 1978), lower limit of L_{∞} calculated from L_{max} , L_m (García-Cagide et al., 1994), and lower limit of L_m (Whitfield, 1998).

- (1) proportion optimal sized (P_{opt}) (Froese, 2004),
- (2) proportion mega-spawners (P_{mega}) (Froese, 2004),
- (3) F/M from mean length, $(F/M)_{ML}$ (Ehrhardt and Ault, 1992),
- (4) overfished status from the decision tree approach (DT) (Cope and Punt, 2009),
- (5) spawning potential ratio (SPR) from the LBSPR method (Hordyk et al., 2015b), and
- (6) F/M from the LBSPR method $(F/M)_{LBSPR}$ (Hordyk et al., 2015b).

All indicators were calculated for each species, gear (spear vs. hook and line), time period (2004–2010 and 2011–2017) combination for which at least 60 fish were measured. Combining the data across years implies the assumption that recruitment, fishing mortality and size selectivity are relatively consistent across the time period, since the combined length frequency is assumed to represent the entire time period. For stoplight parrotfish, no fish were caught after 2008 due to the herbivore ban, so the indicators calculated for the early time period only apply for 2004–2008.

The following life history and selectivity parameters were needed to calculate these indicators: K , L_∞ , L_m , t_{max} , M , L_{opt} , L_c , L_λ , SL_{50} , SL_{95} , and $CV(L)$ (See Table 1 for definitions). The ranges of uncertainty in K , L_∞ , L_m and M were also needed for the Monte Carlo analysis. None of the life history parameters have been estimated for reef fish populations in Belize. Therefore, we used the published values K , L_∞ , L_m and t_{max} compiled in Fishbase (Froese and Pauly, 2017) and other literature for populations of the same species elsewhere in the central Western Atlantic region and Caribbean basin (Table 3, see Supplementary information and Babcock et al. (2013) for details). To determine a most likely value and a plausible range of values for natural mortality rate M , we calculated M using three alternative methods and used the median, minimum and maximum of these three values (Table 3). For most species, two of the three methods were taken from Then et al. (2015), who compiled a dataset of more than 200 populations with empirical estimates of M , and estimated the best predictors of M from either t_{max} or the von Bertalanffy growth parameters (Table 1). The third method was based on the assumption that 5% of the population would survive to the recorded t_{max} (Ault et al., 2008) (Table 1). For the two species lacking a value of t_{max} (Table 3), the three methods used to calculate the most likely and range of values for M were Then et al. (2015)'s equation based on K and two alternative equations to calculate M from K from Jensen (1996). The optimal length L_{opt} was calculated either from L_∞ , M and K (Beverton, 1992) or from L_m (Froese and Binohlan, 2000) (Tables 1 and 3).

The mean length $(F/M)_{ML}$ and LBSPR (SPR and $(F/M)_{LBSPR}$) methods make different assumptions about selectivity. In the mean length method of Ehrhardt and Ault (1992) maximum size L_λ is used to account for fish that may not be susceptible to the fishery as they grow larger. This may be applicable for some species at Glover's Reef, because they exhibit ontogenetic migration from the mostly shallow-water fishing grounds within the lagoon, where spear fishing occurs, into deeper water (Collins and McBride, 2011; Andradi-Brown et al., 2016). The minimum and maximum size caught, L_c and L_λ , were calculated separately for each gear, but both time periods were combined because there have been no observed changes in the gear or fishing methodology that would cause a change in selectivity (Babcock et al., 2013). The LBSPR method simulates the population dynamics, including variability in length at age, to estimate the F/M and SPR that would produce the observed length frequency in the fishery. We assumed that the selectivity curve was logistic, and allowed LBSPR to estimate SL_{50} and SL_{95} . The selectivity curves were estimated for each gear and time period separately for convenience, although they were similar between time periods. The $CV(L)$ was assumed to be 0.1. The LBSPR method generally assumes a logistic maturity curve. However, we assumed a knife-edge maturity at L_m to be consistent with the assumptions used in the Froese indicators.

To calculate confidence intervals of the seven indicators and the probabilities of either overfishing or overfished status, we used Monte Carlo simulation to include parameter uncertainty, as well as bootstrapping of the length frequency data (Babcock et al., 2013). The life history parameters L_m , L_∞ , K and M were drawn from a truncated multivariate normal distribution. 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 these variances and a correlation matrix taken from the literature (Supplement Table A2, (Babcock et al., 2013)). L_{opt} was calculated from both equations (Table 1) for each draw of the parameters, and then a single value was drawn from a uniform distribution between the two values. This method was used to admit the uncertainty in L_{opt} in cases where the growth and size at maturity information did not give consistent estimates of L_{opt} . The values of the indicators (P_{mab} , P_{ovb} , P_{mega} , DT and $(F/M)_{ML}$) were then calculated for each of the 10,000 parameter value draws, each combined with one bootstrapped sample of the length frequency data. For the LBSPR methods, a preliminary analysis found

that many bootstrap samples were unable to estimate values of SPR and $(F/M)_{LBSPR}$, perhaps because the model was not able to estimate selectivity due to relatively small sample sizes. Thus, we used the total length-frequency rather than bootstrap samples for the LBSPR method, although we used the Monte Carlo samples to include parameter uncertainty.

For all indicators, 90% confidence intervals were calculated as the 5% and 95% quantiles of the estimated indicators across the 10,000 draws. If $(F/M)_{ML}$ or $(F/M)_{LBSPR}$ was estimated to be greater than 4, the value was truncated to 4. The probability of experiencing overfishing according to the average length or the LBSPR method was calculated as the fraction of the draws for which $(F/M)_{ML}$ or $(F/M)_{LBSPR}$ was greater than a reference point. A reference point of $F/M = 1$ was used, as $F = M$ is a commonly used proxy for the fishing mortality rate that would sustain maximum sustainable yield (F_{MSY}) (Zhou et al., 2012). The probability of overfished status according to the DT was calculated as the fraction of the draws in which the DT found that the population was below the overfished threshold. The probability of overfished status according to LBSPR was calculated as the fraction of draws where SPR was less than a reference point. An SPR of 40% was used as the reference point because it is an intermediate value. The appropriate reference points to define both overfished status and overfishing vary with the life history of the fish, with lower F/M targets and higher SPR targets for more long-lived, slow growing species (O'Farrell and Botsford, 2005; Zhou et al., 2012). To evaluate whether uncertainty in the reference points influences the results we ran sensitivity analyses in which the value of the F/M and SPR reference points were drawn from distributions. A meta-analysis by Zhou et al. (2012) estimated a posterior distribution of F_{MSY}/M that was lognormal with a mean of 0.866 and a CV of 0.21. We therefore drew values of the F_{MSY}/M target from this lognormal distribution for each of the 10,000 Monte Carlo iterations. For the SPR reference point, we assumed that the value of SPR_{MSY} decreased linearly from 50% to 30% when the species' median M increased from the lowest level in our dataset (0.1) to the highest level (0.33). For each Monte Carlo simulation, we drew random values from a normal distribution with the mean defined by the linear relationship with M , and a CV of 0.1. All the overfished and overfishing probabilities were calculated as above.

Finally, to evaluate whether the size composition of each species in each gear had changed between time periods for the commonly caught species, we used ANOVA to test for differences in mean individual fish length for those species caught in both time periods. For species caught in both gears, we used 2-way ANOVA to test for differences between gears and time periods. We also plotted the seasonal distribution of catches by species in each gear to evaluate whether each species was likely to be caught during its spawning season, as identified from the literature. All analyses were conducted in R version 3.4.2 (R Development Core Team, 2017).

3. Results

3.1. Species composition and fish community indicators

The catch dataset included measurements of 6604 individual fish, of which 6214 were identified to species. There were 62 species in 20 families. However, only 26 species were sufficiently common in the catch to be included in the multispecies analysis. When the analysis was limited to these species, there were 89 samples composed of unique combinations of year, season, gear type and boat type. PERMANOVA applied to either the proportions or the presence/absence data from these samples gave similar results (Table 4). Both models found that only gear explained a large fraction of the variance in species composition (24% in the proportions, 14% in presence/absence). For the proportions, gear, time period and boat type were significant ($P < 0.05$), and none of the interactions were significant, while for presence/absence only gear, time period and the gear x time period

Table 4
PERMANOVA where the response variable is the species composition in samples consisting of all fish sampled in the same year, season, boat type and gear type. Pr (> F) is the P value associated with each variable and R² is the proportion of variance explained.

(a) Bray Curtis proportions						
	Df	Sums of Sqs	Mean Sqs	F	R ²	Pr(> F)
gear	1	7.14	7.14	28.55	0.24	< 0.001
time period	1	0.75	0.75	3.00	0.02	0.005
boat type	1	0.50	0.50	1.98	0.02	0.044
gear × time period	1	0.48	0.48	1.92	0.02	0.052
gear × boat type	1	0.44	0.44	1.75	0.01	0.078
time period × boat type	1	0.30	0.30	1.20	0.01	0.270
Residuals	82	20.50	0.25		0.68	
Total	88	30.10			1.00	

(b) Jaccard presence/absence						
	Df	Sums of Sqs	Mean Sqs	F	R ²	Pr(> F)
gear	1	3.91	3.91	14.78	0.14	< 0.001
time period	1	1.28	1.28	4.83	0.04	< 0.001
boat type	1	0.32	0.32	1.20	0.01	0.262
gear × time period	1	0.74	0.74	2.78	0.03	0.002
gear × boat type	1	0.33	0.33	1.24	0.01	0.232
time period × boat type	1	0.28	0.28	1.05	0.01	0.394
Residuals	82	21.67	0.26		0.76	
Total	88	28.51			1.00	

interaction were significant. For presence/absence, time period, and the time period × gear interaction together explained an additional 7% of the variation, while boat type and its interactions explain less than 3%. Thus, gear and to a lesser extent time period influenced species composition, but boat type was less important.

The NMDS based on presence/absence data fit the data adequately with 2 dimensions, with stress of 0.18, and showed that there was little overlap between the species composition of the spear and hook and line catches (Fig. 1). Also, the hook and line species composition changed more than the spear species composition between time periods. The proportions of the commonly caught species in each gear in each time period (Fig. 2) indicate that the species composition of the hook and line catch shifted over time, from a fishery dominated by a few species of snappers, along with barracuda, to one that catches a variety of snappers along with grunts, porgies and red hind. The spear fishers stopped catching parrotfish due to the ban, but otherwise caught a similar mix of species in both periods. Many species were caught in only one gear, including parrotfishes and angelfishes by spear, and silk snapper, red snapper and king mackerel by hook and line. Species caught with both gears included mutton snapper and black grouper.

There were significant differences in the values of the indicators between the two gears for all the indicators except Simpson species diversity (Table 5, Fig. 3). Fraction spongivores (i.e. angelfish) was only calculated for the spear catch, because the hook and line gear caught no spongivores. In the first time period, the spear catch had a higher L/L_m and fraction invertivores, and lower L_{max} , fraction piscivores, and trophic level than hook and line. All indicators except Simpson diversity varied between time periods for at least one of the gears. For hook and line, there were decreases over time in L/L_m , L_{max} , and fraction piscivores, and increases in fraction of invertivores, trophic level and CPUE (Table 5, Fig. 3). The hook and line species composition was dominated by large snappers in both time periods; however, porgies, grunts, and small groupers such as red hind became more common in the catch over time (Fig. 2, Supplement Table A4). For the spear catches, there was a decrease between time periods in L/L_m , and increases in trophic level and the fraction of spongivores (Table 3). These results are consistent with the disappearance of parrotfishes from the spear catch, along with an increase in catch of angelfishes (Fig. 2). Interestingly, the variance of the trophic levels decreased between time periods for both gears (F test, $p < 0.001$). For the spear gear, the higher trophic level and lower

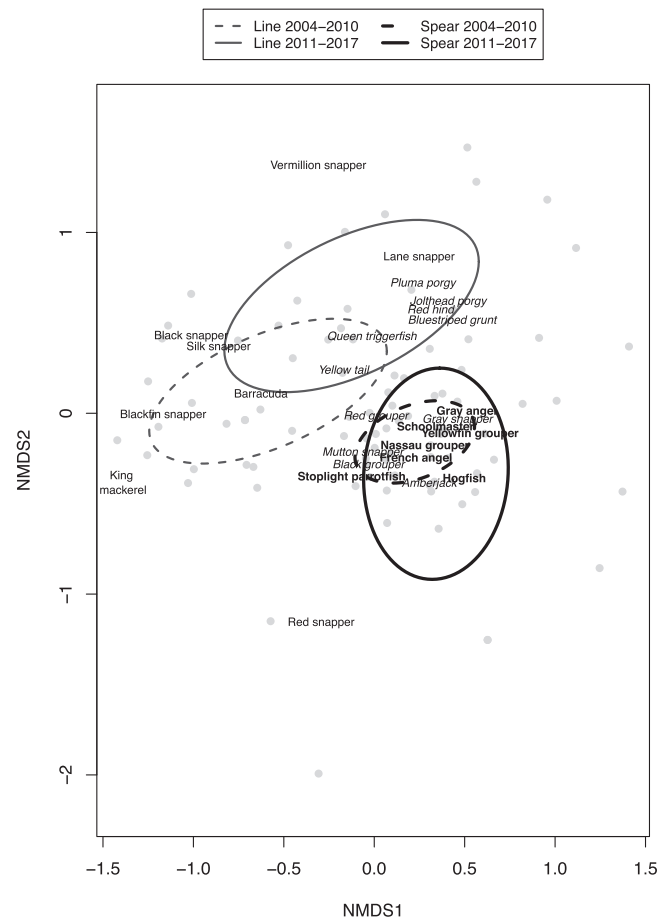


Fig. 1. NMDS results for species composition of the most common 26 species in the catch, showing sites (points) defined as a combination of year, season, boat type and gear type, and the ellipses defined by the means and standard deviations of NMDS1 and NMDS2 for each combination of gear type and time period (see legend). The mean for each species is labeled, with plain text indicating species caught primarily (> 10%) on spears, bold indicating species caught primarily on hook and line, and italics indicating species caught on both gears. Stress = 0.18.

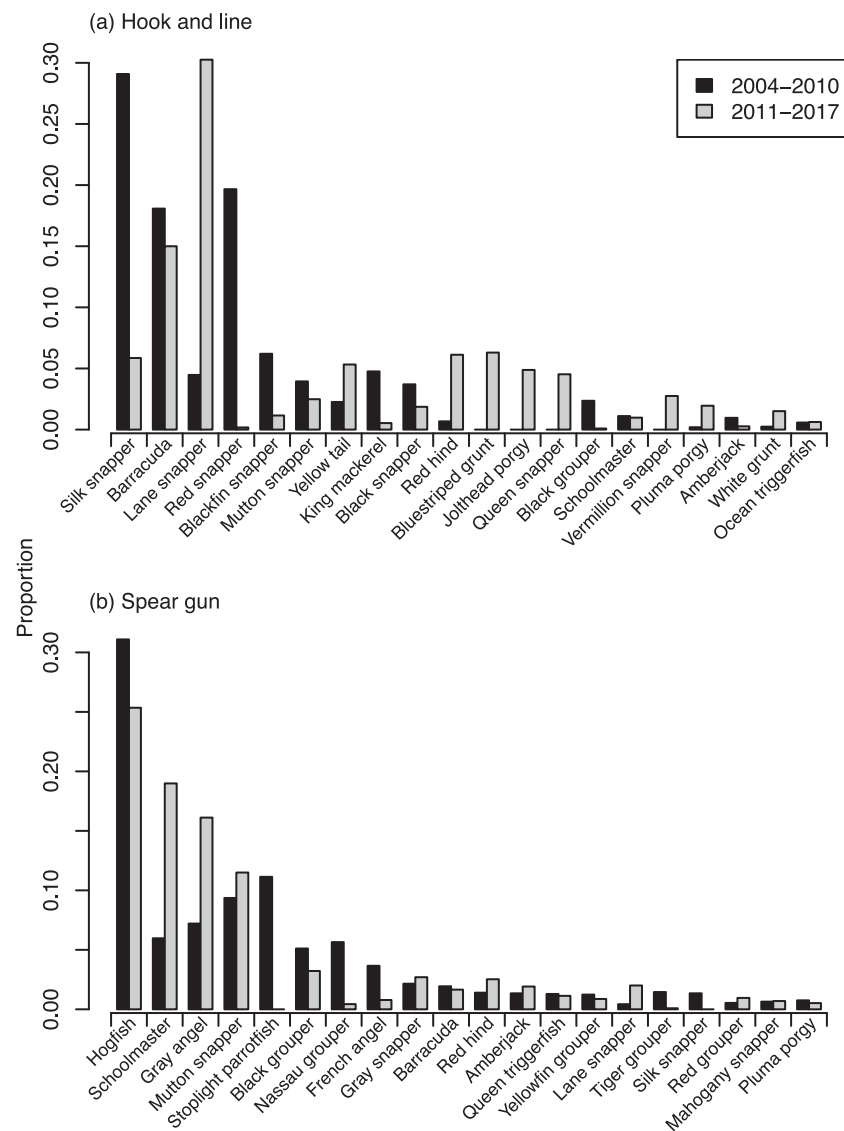


Fig. 2. Proportion of landings for the top 20 species in each of hook and line and spear fisheries on Glover's atoll during the two time periods. Rankings based on the total numbers of fish landed between 2004 and 2017. The top 20 species represent 96% of the hook and line catch and 93% of the spear catch that was identified to species (total $n = 6214$) (See Supplement Table A4 for details).

variance in trophic level in the later period was caused by the loss of herbivores (trophic level = 2) in the catch. For hook and line, the change seems to be related to the different mix of snapper species in the catch (Fig. 2, Supplement Table A4).

3.2. Single-species fisheries indicators

The total sample size of fish with a valid length measurement was 6544, split evenly between gear types (spear: $n = 3248$, hook and line: $n = 3296$). The sample size was larger in 2004–2010 ($n = 4208$) than in 2011–2017 ($n = 2338$). The sample size was large enough to estimate the indicators for 25 combinations of time period, gear and

Table 5

Linear models to test for change in ecosystem indicators between gears (spear vs. hook and line) and time periods (2004–2010 vs. 2011–2017). P values refer to the difference between gears in the first time period (P gear), the difference between time periods for hook and line (P time), and the interaction, which tests for a difference between gears in the time trend (P interaction).

Indicator	Model	Sample unit	n	P gear	P time	P interaction
L/L_m	linear	Fish	6157	< 0.001	< 0.001	0.707
L_{max} (cm)	log-linear	Fish	6214	< 0.001	< 0.001	< 0.001
Piscovore fraction	logistic	Fish	6181	< 0.001	< 0.001	0.001
Spongivore fraction	logistic	Fish	2981	NA	< 0.001	NA
Invertivore fraction	logistic	Fish	6181	< 0.001	< 0.001	< 0.001
Trophic level	linear	Fish	6214	< 0.001	< 0.001	< 0.001
Simpson diversity	linear	Years	26	0.137	0.475	0.884
CPUE (fish/hour)	log-linear	Boat-days	308	0.009	0.054	< 0.001

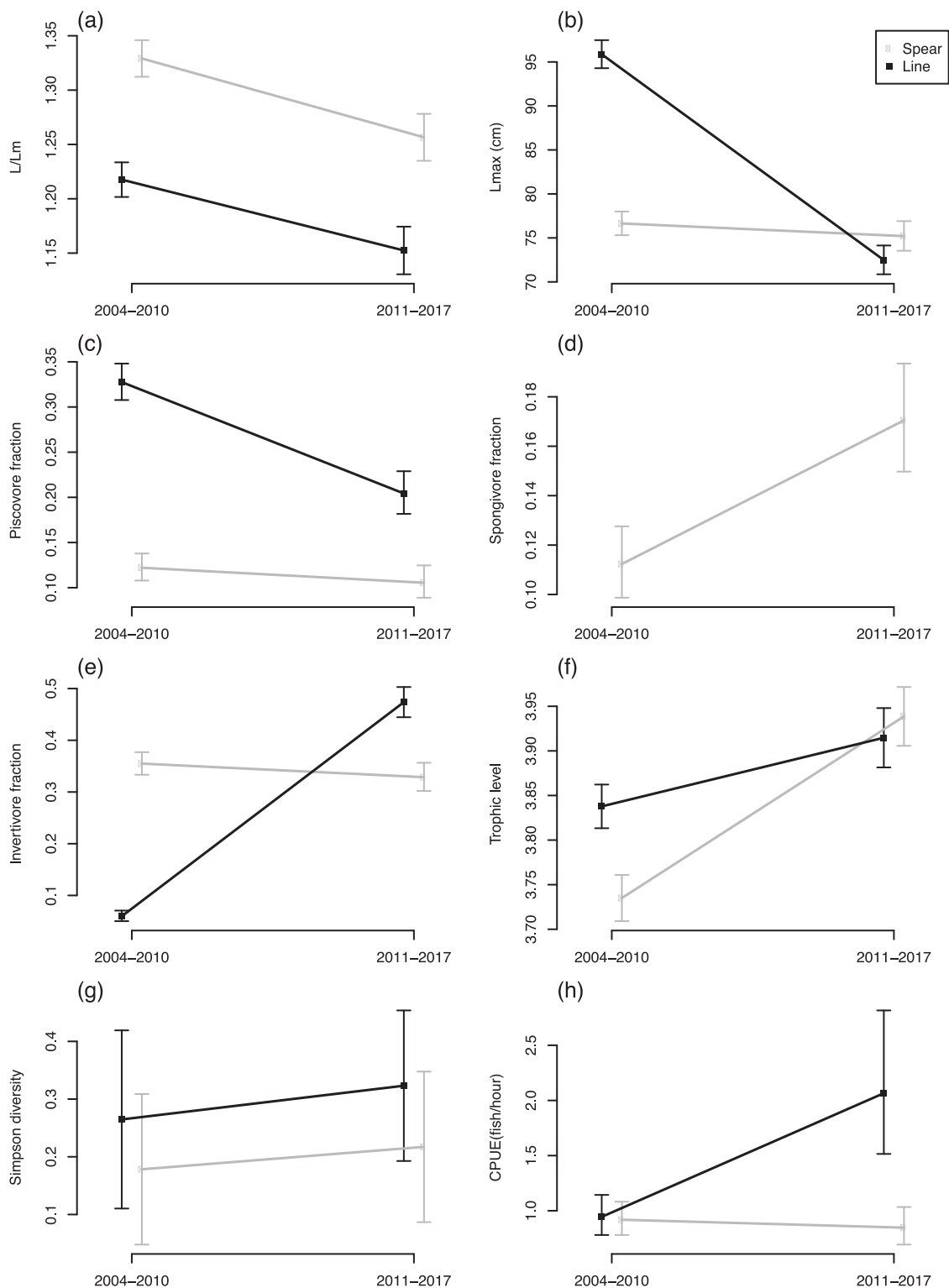


Fig. 3. Means with 95% confidence intervals of the ecosystem indicators for each gear, from the models described in Table 5.

species (Number of species = 17) (Table 3, Table 6). For the hook and line gear, the commonly caught species differed between the two time periods, with only silk snapper, lane snapper and barracuda among the most common species in both periods (Fig. 2). Black snapper, blackfin snapper, mutton snapper, and king mackerel were common in the early period, while red hind and bluestriped grunt were common in the later period (Fig. 2). Of the eight species that were caught in 2004–2010 by spear and analyzed in Babcock et al. (2013), only four were caught in

large numbers after 2011. Stoplight parrotfish are no longer caught due to the herbivorous fish ban. Black grouper, Nassau grouper and French angel were caught but not in large enough numbers to calculate the length-based indicators. The species analyzed in both periods were hogfish, mutton snapper, schoolmaster and grey angel (Table 6).

The Froese indicators (Fig. 4) showed that most species were caught when they were larger than the size at maturity with both gears in both time periods. However, with spears, mutton snapper, black grouper and

Table 6

Sample sizes (n) and sample size between the minimum (L_c) and maximum (L_λ) fully selected size (n in range) for each gear type, time period, and species. Only species with sample sizes of 60 or more were included in the analysis.

Gear	Time period	Species	Common name	n	n in range	L_c	L_λ
Line	2004–2010	<i>Apsilus dentatus</i>	Black snapper	76	47	35	45
		<i>Lutjanus analis</i>	Mutton snapper	82	59	48	62
		<i>Lutjanus buccanella</i>	Blackfin snapper	129	84	39	53
		<i>Lutjanus purpureus</i>	Red snapper	409	383	35	70
		<i>Lutjanus synagris</i>	Lane snapper	93	89	22	44
		<i>Lutjanus vivanus</i>	Silk snapper	605	486	35	53
		<i>Scomberomorus cavalla</i>	King mackerel	99	66	79	138
		<i>Sphyræna barracuda</i>	Barracuda	376	199	88	132
Line	2011–2017	<i>Epinephelus guttatus</i>	Red hind	69	24	35	42
		<i>Haemulon sciurus</i>	Bluestriped grunt	71	44	23	32
		<i>Lutjanus synagris</i>	Lane snapper	341	210	22	44
		<i>Lutjanus vivanus</i>	Silk snapper	66	29	35	53
		<i>Sphyræna barracuda</i>	Barracuda	169	43	88	132
Spear	2004–2010	<i>Epinephelus striatus</i>	Nassau grouper	104	61	43	72
		<i>Lachnolaimus maximus</i>	Hogfish	578	331	36	64
		<i>Lutjanus analis</i>	Mutton snapper	174	109	34	62
		<i>Lutjanus apodus</i>	Schoolmaster	111	78	30	46
		<i>Mycteroperca bonaci</i>	Black grouper	95	61	48	103
		<i>Pomacanthus arcuatus</i>	Grey angel	134	97	30	46
		<i>Pomacanthus paru</i>	French angel	68	31	34	43
		<i>Sparisoma viride</i>	Stoplight parrotfish	207	129	33	42
Spear	2011–2017	<i>Lachnolaimus maximus</i>	Hogfish	291	179	36	64
		<i>Lutjanus analis</i>	Mutton snapper	132	81	34	62
		<i>Lutjanus apodus</i>	Schoolmaster	218	110	30	46
		<i>Pomacanthus arcuatus</i>	Grey angel	185	80	30	46

Nassau grouper were often caught before they matured. With hook and line gear, black snapper were mainly caught before maturity, while red snapper were about 50% mature. Barracuda, lane snapper, and silk snapper were less frequently mature in the later time period than in the early time period. The optimal size L_{opt} was highly uncertain for most species, so that the confidence intervals for P_{opt} and P_{mega} were quite broad. Most fish were not in the optimal size interval in either gear in either period, and most species were caught in small numbers in the mega-spawner size range. However, large fractions of the catch of French angel and stoplight parrotfish with spears, and blackfin snapper and king mackerel with hook and line were mega-spawners.

The estimated fishing mortality rates relative to natural mortality were quite consistent between the LBSPR and the mean length methods, with a correlation between $(F/M)_{ML}$ and $(F/M)_{LBSPR}$ of 0.96 (Fig. 5a, b). The fishing mortality rates were generally high, with $(F/M)_{ML}$ and $(F/M)_{LBSPR} > 1$ for most species. For both methods, the confidence intervals were wide reflecting the uncertainty around the estimate of M , except in the cases where F/M was truncated to the maximum allowed value of 4, for example for grey angels. The confidence intervals of both $(F/M)_{ML}$ and $(F/M)_{LBSPR}$ for French angel by spear in 2004–2010 included 1, while the confidence intervals of both $(F/M)_{ML}$ and $(F/M)_{LBSPR}$ for king mackerel by hook and line in 2004–2010 were below 1. For hogfish in 2011–2017, the confidence interval of $(F/M)_{ML}$ overlapped 1, and both $(F/M)_{ML}$ and $(F/M)_{LBSPR}$ were lower in 2011–2017 than in 2004–2010. The average length and the LBSPR method were consistent in finding that all species except king mackerel and French angel have a high probability of experiencing overfishing (Table 7). The probabilities were similar whether $F/M = 1$ was used as the overfishing reference point (Table 7) or the overfishing reference points was drawn from a distribution (Supplement Table A6). For hogfish caught by spears, both methods implied that the probability of overfishing decreased between time periods. King mackerel in 2004–2010 hook and line and French angel in 2004–2010 spears had a low probability of overfishing from both methods.

The SPR calculated with LBSPR was variable between species but had fairly narrow confidence intervals (Fig. 5c). On spear gear in 2004–2010 French angelfish were not overfished according to this

metric (i.e. median SPR > 0.4) but all species were below the overfished threshold in 2011–2017. With hook and line gear, blackfin snapper and king mackerel were not overfished in 2004–2010, but all species were overfished in 2011–2017. In general, species with a very high F/M tended to have a lower SPR and vice versa, as expected since overfishing eventually leads to overfished status (e.g. compare king mackerel to mutton snapper).

Although the probabilities of overfished status from DT and LBSPR are not directly comparable they produced consistent results for several species (Table 7). Both methods found a probability of overfished status greater than 0.5 for black snapper in 2004–2010, and silk snapper in 2011–2017 and barracuda in both time periods with hook and line, and Nassau grouper and black grouper in 2004–2010, schoolmaster in both time periods, and mutton snapper in 2011–2017 by spear. However, for some species, the two methods gave contradictory results. For red snapper the probability of overfished status was 0.18 for DT and 0.96 for SPR. Grey angel also had low overfished probability with DT and high with SPR, while king mackerel had the opposite pattern. This inconsistency was probably caused by the fact that the two methods make different assumptions about the size selectivity of the fishery. See Supplement Table A5 for the selectivities inferred by the DT, and Supplement Figs. A1 and A2 for the selectivities estimated by LBSPR. Allowing the SPR reference point to vary by species and including stochasticity did not change the estimated probabilities of overfished status by SPR, except for the short-lived stoplight parrotfish, which had a lower probability of being overfished with a lower reference point (Supplement Table A6).

For the species caught in both time periods in hook and line, lane snapper did not change in size (ANOVA, $p = 0.699$), but there were significant declines in mean size for silk snapper ($p < 0.001$, mean difference = -4.24 cm) and barracuda ($p < 0.001$, mean difference = -10.85 cm). For spears, hogfish ($p = 0.204$) and mutton snapper ($p = 0.107$) did not change in size between time periods, but schoolmaster ($p < 0.001$, mean difference = -2.98 cm) and grey angel ($p < 0.001$, mean difference = -3.76 cm) decreased significantly in size. Mutton snapper, which was the only species caught in large numbers in both gears, was significantly larger when caught by

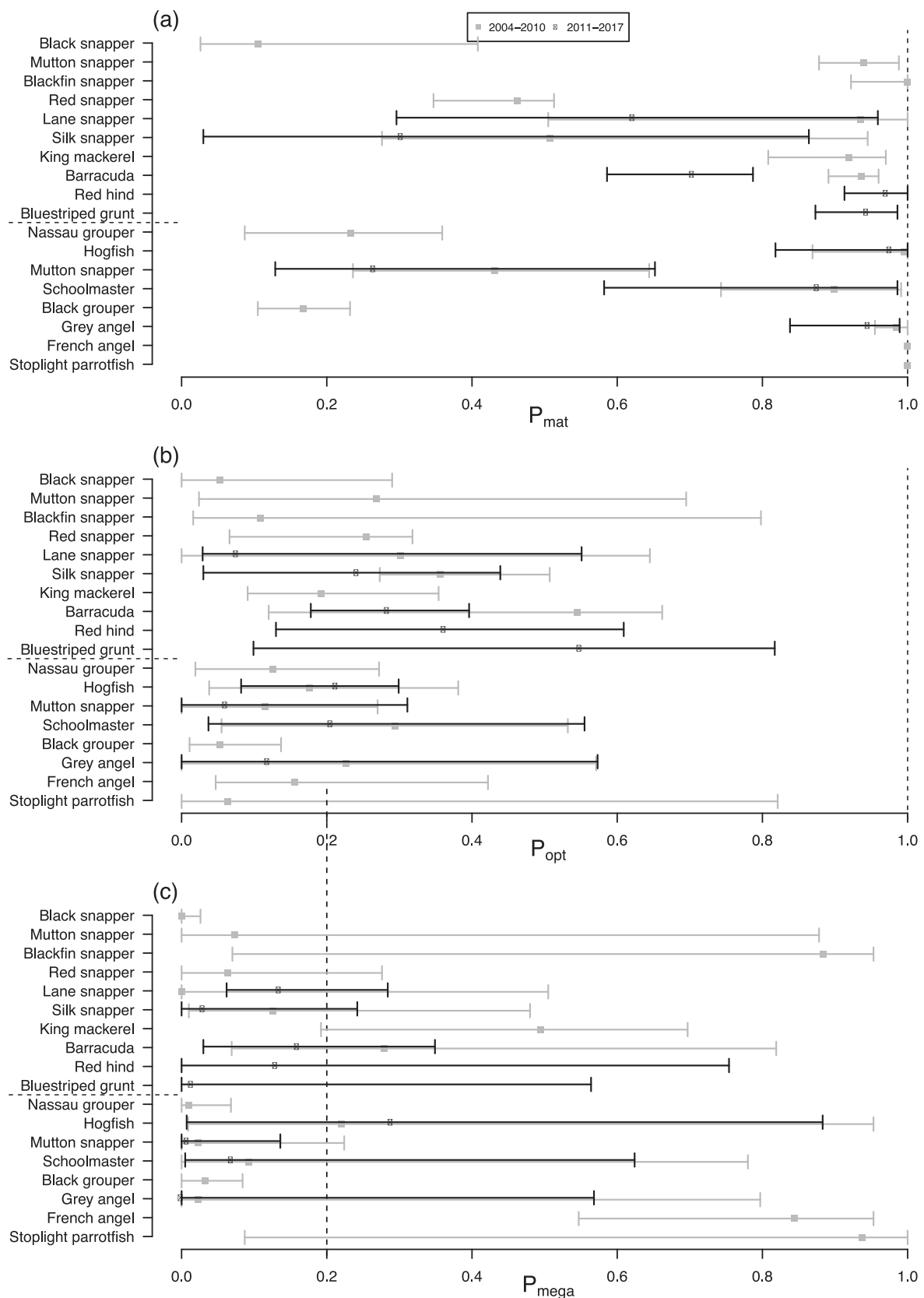


Fig. 4. Froese (2004) indicators: (a) P_{mat} = proportion mature, (b) P_{opt} = proportion in the optimal size range, (c) P_{mega} = proportion mega-spawners with 90% bootstrap and Monte Carlo confidence intervals. Species above the horizontal dashed line were caught on spears, and below were caught on hook and line. The vertical dashed line is a target level, both P_{mat} and P_{opt} should be around 1, while P_{mega} should be to the right of 0.2.

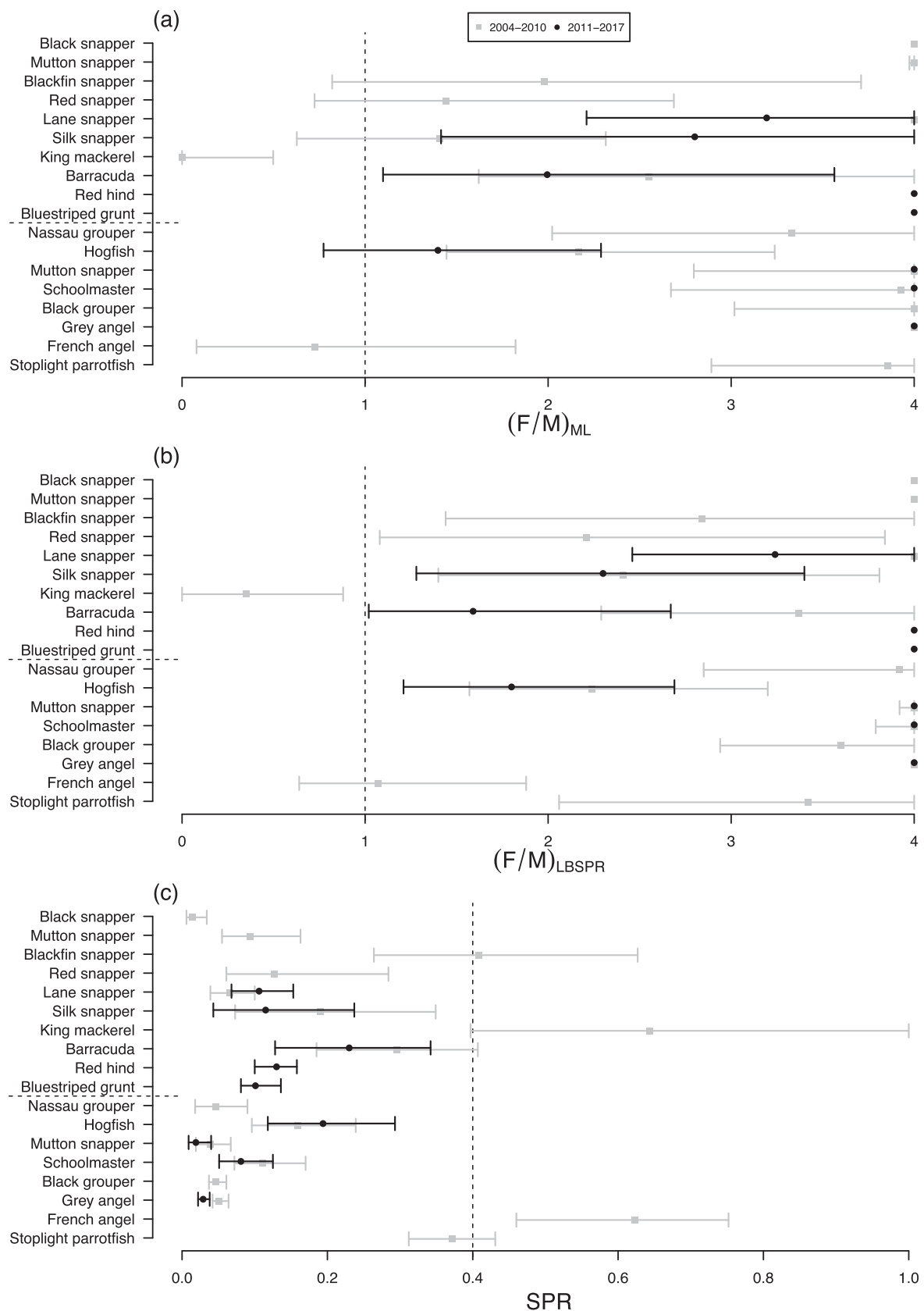


Fig. 5. (a) F/M calculated from average length (Ehrhardt and Ault, 1992), (b) F/M calculated using LBSPR (Hordyk et al., 2015b), and (c) spawning potential ratio (SPR) computed with LBSPR, all with 90% Monte Carlo confidence intervals. Species above the horizontal dashed line were caught on spears, and below were caught on hook and line. The vertical dashed line is a target level, such that $F/M < 1$ is not overfishing) and SPR should be to the right of the line ($SPR > 0.4$ is not overfished).

Table 7

Probabilities associated with overfishing and overfished reference points. The probability of overfishing ($F > M$) was calculated either from mean length (F/M)_{ML} (Ehrhardt and Ault, 1992) or from the LBSRP method (F/M)_{LBSRP} (Hordyk et al., 2015b). The probability of being overfished was calculated either by using a decision tree to infer $B < B_{\text{target}}$ (DT) (Cope and Punt, 2009) or from LBSRP ($\text{SPR} < 0.4$). Darker shading implies higher probabilities.

Time		P(Overfishing)		P(Overfished)	
Gear	period	Common name	(F/M) _{ML}	(F/M) _{LBSRP}	DT SPR<0.4
Line	2004	Black snapper	1.00	1.00	0.92 1.00
		Mutton snapper	1.00	1.00	0.35 1.00
		Blackfin snapper	0.91	0.99	0.47 0.47
		Red snapper	0.81	0.97	0.18 1.00
		Lane snapper	1.00	1.00	0.28 1.00
		Silk snapper	0.80	0.99	0.48 0.98
		King mackerel	0.29	0.03	0.73 0.05
		Barracuda	1.00	1.00	0.56 0.94
Line	2011	Red hind	1.00	1.00	0.22 1.00
		Bluestriped grunt	1.00	1.00	0.33 1.00
		Lane snapper	1.00	1.00	0.42 1.00
		Silk snapper	0.99	0.99	0.59 1.00
		Barracuda	0.97	0.96	0.79 0.99
Spear	2004	Nassau grouper	1.00	1.00	0.74 1.00
		Hogfish	1.00	1.00	0.13 1.00
		Mutton snapper	1.00	1.00	0.38 1.00
		Schoolmaster	1.00	1.00	0.59 1.00
		Black grouper	1.00	1.00	0.99 1.00
		Grey angel	1.00	1.00	0.04 1.00
		French angel	0.32	0.59	0.88 0.02
		Stoplight parrotfish	1.00	1.00	0.78 0.70
Spear	2011	Hogfish	0.85	0.99	0.29 1.00
		Mutton snapper	1.00	1.00	0.63 1.00
		Schoolmaster	1.00	1.00	0.47 1.00
		Grey angel	1.00	1.00	0.21 1.00

hook and line (2-way ANOVA $p < 0.001$).

4. Discussion

4.1. Findings of the analysis

The species composition of the catch differed between gears and between time periods for both gears. For hook and line, in particular, some species were caught in large numbers in one time period only. This variability in species caught implies that hook and line fishers may be opportunistically targeting species that are transitory or form spawning aggregations. The commonly caught species in the Glover's Reef fishery that are known to form spawning aggregations include all

the groupers (Nassau grouper, black grouper, and red hind), as well as mutton snapper, schoolmaster, and lane snapper (Sadovy de Mitcheson et al., 2008). It is not known whether the deepwater snappers (red, black, blackfin and silk snappers) form aggregations. Spear fishers generally do not target aggregations because the aggregations are located on the outer forereef in areas associated with deep promontories, with high relief and strong wave action (Graham et al., 2008; Kobara and Heyman, 2010), which are not amenable to free diving from small canoes. Changes in regulations as well as changes in markets and fishing practices may also have caused the change in species composition of the catch over time.

The ecosystem indicators were quite different between gears and between time periods. The hook and line catch saw a decrease in size of fish caught between time periods, along with an increase in both CPUE and trophic level, corresponding to a change in the species composition of the catch focusing on smaller species, including snappers, groupers, and grunts, which are either piscivores, invertivores or both. The increase in trophic level combined with a decrease in the fraction of piscivores can be explained by the increasing number of invertivores (e.g. lane snapper, bluestriped grunt, jolthead porgy) or mixed invertivore-piscivore (e.g. yellowtail snapper, red hind) species in the catch. For the spear catch, the decrease in size of fish combined with an increase in trophic level is consistent with a shift away from parrotfishes toward smaller snappers (lane, schoolmaster) and groupers (red hind) while catching larger numbers of grey angelfish.

The only species caught in large numbers in both gears was mutton snapper. This species had a high probability of experiencing overfishing and a relatively high probability of being overfished in all gears and time periods, and this result was well-supported because all methods gave consistent results. It is also consistent with a finding from fishery-independent data that mutton snapper density is declining at Glover's Reef (Tewfik et al., 2017). The somewhat larger fish caught on hook and line gear may be explained by the fact that hook and line fishers tend to fish in deeper water, often outside the reef crest of the atoll, while the spear fishers are largely limiting activities to the shallow lagoon in part due to the prohibition on using SCUBA (Tewfik et al., 2017). Mutton snappers are found in depths up to 200 m (Teixeira et al., 2010), while spear fishers are unlikely to fish below 30 m and generally much shallower, implying that the deeper component of the population is only susceptible to hook and line fishing. Larger fish in deeper water may be a result of either ontogenetic migration (Graham et al., 2008) or lower fishing mortality rates in the deeper water. It is also likely that at least some of the hook and line catch is taken from spawning aggregations. Mutton snappers aggregate to spawn at promontories on the forereef at several locations in Belize, including known sites at Glover's atoll, between March and June, and the aggregations that are not protected have been depleted (Graham et al., 2008; Kobara and Heyman, 2010). Some, but not all, of the mutton snapper catch by hook and line was taken during the spawning season (Supplement Fig. A3).

For hook and line, the species that were commonly caught in both time periods were barracuda, silk snapper, and lane snapper. For barracuda all the analyses were consistent in finding that barracuda are experiencing high fishing mortality rates, which are causing the population to decline. The highly significant decrease in size of barracuda in the catch indicates that this species is in need of management attention (Kadison et al., 2010).

Silk snapper also experienced a significant decrease in size, and showed a decrease in the median values of all three Froese indicators in the hook and line catch. However, the confidence intervals of P_{mat} were very broad due to the uncertainty in size at maturity. The probability of experiencing overfishing was high and the probability of being overfished increased between time periods. Silk snapper are a deepwater species, found at depths up to 378 m (Sylvester and Dammann, 1973). They have been recorded spawning year-round, and they are thought to form spawning aggregations; however, this has not been proven, and the locations of possible spawning aggregations are not known

(Boardman and Weiler, 1980). The majority of the hook and line catches at Glover's Reef took place in October, and it is not known whether this involved targeting an aggregation. The biology of the deepwater snappers such as silk snapper is not as well-known as that of the more shallow reef associated species, so there is a need for further biological research for these species to support management of the fishery.

Lane snapper in the hook and line fishery had a high probability of overfishing. Although F/M appeared to decrease between time periods, the fraction mature also decreased. This species is caught within the lagoon and in deeper water on the forereef. They spawn in the late spring and summer in the Caribbean (García-Cagide et al., 1994), and are known to form spawning aggregations (Sadovy de Mitcheson et al., 2008). However, most of the catches of lane snapper were not during the spawning season (Supplement Fig. A3). The indicators for lane snapper imply that fishing mortality rates remain too high.

For hook and line, the commonly caught species in 2004–2010 that were not common in 2011–2016 were black snapper, blackfin snapper, red snapper and king mackerel. For some of these species, the low catch in 2011–2017 may be due to either changes in targeting or sampling error related to the fact that the samples come from a small number of boat-days sampled. Red snapper, for example, were caught in very large numbers in late 2008 by two boats; in one case a single boat caught 67 red snappers in one day. It may be that sampling in 2011–2017 never happened to intercept a vessel targeting red snappers.

Blackfin snapper caught on hook and line in 2004–2010 had a low probability of being overfished and a high probability of experiencing overfishing. This species is found in depths up to 150 m, and spawns from spring through autumn, but spawning aggregations have not been documented (Allen, 1985; García-Cagide et al., 1994). The majority of the fish were caught in November, so the fishery probably was not targeting spawners although the fish caught were mainly mature. Black snapper, on the other hand, were primarily caught when immature, and had a high probability of both experiencing overfishing and being overfished. Black snapper spawns year-round with peaks in spring and fall, and is usually found in depths up to 180 m (Allen, 1985; García-Cagide et al., 1994). The catches at Glover's Reef peaked in November, so fishers were probably not targeting spawning fish. King mackerel were mainly caught while mature, with a high fraction of the catch in the optimal or mega-spawner size range, and this species had a low probability of experiencing overfishing. For all four of the species caught in large numbers in the early time period only, the lack of data on recent catches is problematic, since the size composition may have changed in the last seven years. For black snapper, particularly, there is a risk that the fishery continues to target undersized fish.

Finally, the species that were caught only in the recent time period for hook and line were red hind and bluestriped grunt. These are both small species, that may have become more important to the fishery as larger species became harder to find, as shown by the large decline in mean L_{max} in the hook and line catch. Both species had a high probability of experiencing overfishing from both methods and their probability of being overfished was low with DT and high with LBSPR. Both were mainly mature when caught, and both had a large fraction of the catch in either the optimal or mega-spawner size range (Fig. 4). These species seem to be less depleted than other species caught by hook and line based on the Froese indicators. However, they are experiencing overfishing, which will cause them to become more depleted if fishing mortality rates are not reduced. They may be more important target species than they have been in the past, which could cause fishing pressure to continue to increase.

For the spear gear, the species caught in large numbers in both time periods were hogfish, schoolmaster and grey angels, along with mutton snapper (discussed above). For hogfish, there was no significant change in size between time periods, but the probability of both experiencing overfishing and being overfished decreased between time periods. Hogfish have increased in size and density in the replenishment zone (Tewfik et al., 2017), which may be supporting the overall population

at Glover's Reef. Schoolmaster had a significant decrease in average size. The probability of experiencing overfishing remained high, while the probability of being overfished remained high for the LBSPR method and somewhat lower for the DT. For grey angels, the average size decreased significantly. The DT and LBSPR methods disagree on whether the population is overfished, with the DT finding that the fishery was selective for small individuals, and not overfished. The fishing effort with spears has decreased at Glover's Reef (Belize Fisheries, unpublished logbook data). Thus, we would expect that these species should be increasing in size and less likely to be assessed as overfished or experiencing overfishing. In this context, the continuing decrease in size of grey angels and schoolmasters is problematic.

The species caught in large numbers by spear only in the first time period were black grouper, Nassau grouper, stoplight parrotfish, and French angel. The two large groupers had a high probability of experiencing overfishing and being overfished and they were also mainly immature when caught. Both these species form spawning aggregations, and have a history of being overfished in Belize, including at spawning aggregations (Burns-Perez and Tewfik, 2015; Sala et al., 2001). With the smaller sample size in 2011–2017, along with the size limits that have been imposed for Nassau grouper, it is not surprising that few individuals were caught ($n = 5$ Nassau groupers caught and $n = 37$ black groupers with spears from 2011 to 2017). Both these species are overfished and at risk for continued overfishing. French angels, on the other hand, tended to be large when caught, with many in the optimal size range. Thus, they had a relatively low probability of experiencing overfishing, although they were considered overfished by the DT because P_{opt} was quite low. Stoplight parrotfishes are no longer caught due to the herbivore ban. This ban has been shown to increase the abundance of large parrotfishes, which includes stoplight parrotfish, at Glover's Reef (Tewfik et al., 2017); however, there is a risk that the loss of this target species may have increased fishing pressure on other species including the overfished groupers and angelfish.

Finally, it should be noted that many of the species caught at Glover's Reef are important species in the fisheries throughout Belize. This includes silk, lane, mutton, black and schoolmaster snapper, as well as red hind and barracuda. All of these species were among the top 14 species by abundance ($n = 2377$) in a survey of fish markets throughout Belize in 2017 (Tewfik and Burns-Perez, 2017). The Glover's Reef fishery also catches species that were once important, but have been depleted, including Nassau grouper (Sala et al., 2001). Thus, it is possible that similar changes are occurring in the fisheries in the rest of the country, and this should be investigated.

4.2. Methods and uncertainties

The largest source of uncertainty remains the values used for the life history parameters for all these methods. One reason for the slight differences between our results and the results of Babcock et al. (2013) is the use of new values of M for this analysis that are somewhat higher than the previous values (Then et al., 2015). This analysis also allowed for a greater range in uncertainty in L_{opt} than Babcock et al. (2013), because we wanted to admit the uncertainty caused by using growth and maturity studies from different studies in different regions, which implied different values of L_{opt} .

The values of L_m and L_∞ are key uncertainties, so it is a priority to estimate these values for populations in Belize. It is possible, for example, that the findings that most king mackerel are mature and most blackfin snapper are immature are based on incorrect lengths at maturity, if the populations in Belize are different from those where the published life history parameters were estimated. We used the median and range of values from Fishbase and the literature to estimate each parameter and its uncertainty. For highly studied species like mutton snapper, which has 9 published growth studies, the published estimates probably bound the range of plausible values for a mutton snapper population. However, for less studied species such as grey angel, which

has only one growth study, our estimated range of parameter values may not include the true value. Also, the confidence intervals are quite wide for some species. For example, for lane snapper caught with hook and line, the fraction mature varies from less than 0.4 to nearly 1.0, because of large range of values used for L_m for this species. Having life history parameters estimated for the populations in Belize would allow us to use a smaller range of plausible values. Local estimates would also ensure that the values of L_m , L_∞ , K and M are consistent with each other, which is not necessarily the case when using values taken from studies of different populations which may have different growth or maturity schedules. Although there have been many studies on the expected relationships between life history parameters (Beverton, 1992; Froese and Binohlan, 2000; Hordyk et al., 2015a; Prince et al., 2015; Thorson et al., 2017), which can indicate whether assumed values are consistent, it is difficult to know which values to believe if, for example, all the published L_m values are lower than would be expected given all the published L_∞ values, because the growth studies are all in one region and the maturity studies are in another. Thus, life history studies within Belize are critical.

In the absence of regional life history studies, more could also be done to evaluate the implications of different assumptions about the life history parameters. We chose to use the median and range of the published values of each parameter for each species to bound uncertainty. Meta-analyses involving data from a larger group of species could also provide improved estimates for some of the less studied species, such as the angelfishes (Thorson et al., 2017). Also, the LBSPR method was designed to work using life history ratios M/K and L_m/L_∞ , which are less variable between species, and show consistent patterns among taxonomic groups (Hordyk et al., 2015a, 2015b; Jardim et al., 2015; Prince et al., 2015). We did not use the ratios because we wanted to use published values for the species of interest, and to use consistent inputs for all the methods, but the ratios are worth exploring.

This analysis identified some interesting similarities and differences between the commonly-used length-based methods for assessing overfishing and overfished status. Estimates of whether the population was experiencing overfishing ($F/M > 1$) from the mean length in a fully selected range ($(F/M)_{ML}$), versus fitting the whole length frequency with an estimated logistic selectivity ($(F/M)_{LBSPR}$) were very consistent. This is somewhat surprising because one of the reasons for using the Ehrhardt and Ault (1992) method is to account for the possibility that larger fish may be present but not caught in the fishery (dome-shaped selectivity). It would be interesting to allow the LBSPR method to estimate a dome shaped selectivity curve to see if the estimated value of $(F/M)_{LBSPR}$ would differ. However, this would probably require larger sample sizes, since dome-shaped selectivity patterns are difficult to estimate from length-frequency data (Hordyk et al., 2016). The consistency between results implies that our finding that most species are experiencing overfishing is robust to the method used or the selectivity assumption.

Estimates of whether the population was overfished were somewhat less consistent between the LBSPR and DT methods for some species, due in part to their different assumptions about selectivity. The LBSPR method is more sophisticated about modeling the growth of spawner biomass in a cohort with variable size at age, combined with the effects of fishing and natural mortality, but it makes the assumption (in this implementation) that selectivity is logistic. Thus, it interprets low catches of larger fish as evidence of overfished status, as in the case of grey angel. The DT, on the other, is willing to infer that the failure to catch larger fish is caused by selectivity, rather than overfished status, if the fraction mature is high. Of course, the question of whether selectivity is dome-shaped is important for all forms of stock assessment, not just data-poor methods such as these (Punt et al., 2014). Dome-shaped selectivity implies a pool of larger, older fish that are not vulnerable to the fishery, so dome-shaped selectivity would make higher fishing mortality rates sustainable. However, wrongly assuming dome-shaped selectivity when larger fish actually are vulnerable to the fishery can

lead to over-optimistic estimates of status and the risk of continued overfishing. Dome shaped selectivity could occur in either the spear or the line fishery, if larger, older fish are not present in the areas that are fished. Thus, it is important to verify dome-shaped selectivity, for example by using fishery independent data or by evaluating changes over time in the length-composition of the catch. To be precautionary, it is probably better to use the LBSPR results rather than DT results if the selectivity pattern is “small fish only.”

We estimated all indicators of status by combining data into two time periods, rather than applying the methods to a time series of length-frequency data. This runs the risk of bias if there have been changes in fishing mortality rate over time, or if recruitment is variable. In fact, fishing mortality rates have probably changed over time. Both $(F/M)_{LBSPR}$ and $(F/M)_{ML}$ can be estimated with time series of length-frequency data, to estimate annual changes in F/M (Hordyk et al., 2015b, 2016; Then et al., 2017). However, the sample sizes we have are not large enough to do this. Thus, we have to assume that our estimates approximate the average for each time period, but F in any year may be different. In addition, the length-based methods all assume that any change in the length frequency is caused by fishing; an increase in small fish caused by strong recruitment would be misinterpreted as a higher probability of overfishing or overfished status. Gathering larger length datasets in each year would also make it easier to identify strong recruitment years to avoid this bias. Large samples would also make it possible to use length-based control rules to manage the fishery, for example by limiting catches when the mean length of a species falls below some agreed upon reference point, perhaps in addition to other sources of information (Jardim et al., 2015; McDonald et al., 2017).

4.3. Conclusion

Some of the species caught in the Glover's Reef fishery are caught when they are quite small, implying that their fisheries have a history of overfishing and are not likely to be sustainable without reducing fishing pressure. These include black grouper, Nassau grouper, mutton snapper and black snapper. For most of the species that dominate both the spear and hook and line catches at Glover's Reef, the fish are caught when they are mature, but small relative to the size that would optimize yield. In addition, the average size of fish caught with both gears has decreased over time, as has the size of several of the important species in the fishery, including silk snapper, barracuda, schoolmaster and grey angel. Thus, reducing the catch on small, immature fish is likely to increase yields and improve the sustainability of the fishery for both gears. Species that are targeted while they form spawning aggregations, such as black grouper, Nassau grouper, mutton snapper for at least some of the catch, and perhaps some of the deepwater snappers, are particularly at risk of overfishing due to the potential for fishers to rapidly remove a large fraction of the spawning population (Sadovy and Domeier, 2005). Thus, further research on the timing and location of additional spawning aggregation sites is necessary in order to protect these aggregations from excessive fishing (Burns-Perez and Tewfik, 2015). In addition, and despite a number of uncertainties and data limitations, fishing mortality rates should be reduced for most species examined here to maintain long-term stability of livelihoods, food security and broader ecosystem services. On a more positive note, mutton snapper had a somewhat lower risk of overfishing in 2011–2017 than in 2004–2010, and stoplight parrotfish are no longer caught in the fishery. Thus, current regulations, including the no-take zone since 1993, (Tewfik et al., 2017), gear restrictions, license limitation, and in the case of parrotfish, the herbivore ban, appear to be having a positive effect on these two species. However, many other species were subject to unsustainable levels of fishing, and, according to the Froese indicators, some would benefit from size limits to protect immature individuals.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2018.07.003>.

References

- Aiken, K.A., 1983. The biology, ecology and bionomics of the butterfly and angelfishes, Chaetodontidae. In: Munro, J.L. (Ed.), Caribbean Coral Reef Fishery Resources. International Center for Living Aquatic Resources Management, Manila, pp. 155–165.
- Aiken, K.A., 2001. Aspects of reproduction, age and growth of the lane snapper, *Lutjanus synagris* (Linnaeus, 1758) in Jamaican coastal waters. *Proc. Gulf Caribbean Fish. Inst.* 52, 116–134.
- Allen, G.R., 1985. FAO species catalogue. Snappers of the World. An Annotated and Illustrated Catalogue of Lutjanid Species Known to Date, vol. 6 FAO, Rome.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46.
- Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecol. Monogr.* 83, 557–574.
- Andradi-Brown, D.A., Gress, E., Wright, G., Exton, D.A., Rogers, A.D., 2016. Reef fish community biomass and trophic structure changes across shallow to upper-mesophotic reefs in the Mesoamerican Barrier Reef, Caribbean. *PLoS One* 11 (6), e0156641.
- Andrew, N.L., Bene, C., Hall, S.J., Allison, E.H., Heck, S., Ratner, B.D., 2007. Diagnosis and management of small-scale fisheries in developing countries. *Fish. Fish.* 8, 227–240.
- Appeldoorn, R.S., 1992. Interspecific relationships between growth parameters, with application to haemulid fishes. In: 7th International Coral Reef Symposium. Guam. pp. 899–904.
- Appeldoorn, R.S., Dennis, G.D., Lopez, O.M., 1987. Review of shared demersal resources of Puerto Rico and the Lesser Antilles region. FAO Fish. Rep. 383, 36–104.
- Ault, J.S., Bohnsack, J.A., Meester, G.A., 1998. A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys. *Fish. Bull.* 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.
- Babcock, E.A., Coleman, R., Karnauskas, M., Gibson, J., 2013. Length-based indicators of fishery and ecosystem status: Glover's Reef Marine Reserve, Belize. *Fish. Res.* 147, 434–445.
- Baker, M.S.J., Charles, A.W., Gent, D.L.V., 2001. Age validation of red snapper, *Lutjanus campechanus*, and red drum, *Sciaenops ocellatus*, from the northern Gulf of Mexico using 210Pb disequilibrium in otoliths. *Proc. Gulf Caribbean Fish. Inst.* 52, 63–73.
- Bene, C., Hersoug, B., Allison, E.H., 2010. Not by rent alone: analysing the pro-poor functions of small-scale fisheries in developing countries. *Dev. Policy Rev.* 28, 325–358.
- 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.
- Boardman, C., Weiler, D., 1980. Aspects of the life history of three deep water snappers around Puerto Rico. *Proc. Gulf Caribbean Fish. Inst.* 32, 158–172.
- Boettiger, C., Lang, D.T., Wainwright, P.C., 2012. rfishbase: exploring, manipulating and visualizing FishBase data from R. *J. Fish. Biol.* 81, 2030–2039.
- Brule, T., 2003. Reproduction in the protogynous black grouper (*Mycteroperca bonaci* (Poey)) from the southern Gulf of Mexico. *Fish. Bull.* 101, 463–475.
- Burns-Perez, V., Tewfik, A., 2015. Brief history of management and conservation of Nassau grouper and their spawning aggregations in Belize: a collaborative approach. *Proc. Gulf Caribbean Fish. Inst.* 68, 188–222.
- 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.
- Cervigón, F., 1993. Los peces marinos de Venezuela, vol. 2 Fundación Científica Los Roques, Caracas, Venezuela.
- Chan, T.T.C., Sadovy, Y., 2002. Reproductive biology, age and growth in the chocolate hind, *Cephalopholis boenak* (Bloch, 1790), in Hong Kong. *Mar. Freshwater Res.* 53, 791–803.
- 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.
- Claro, R., 1994. Características generales de la ictiofauna. In: Claro, R. (Ed.), Ecología de los peces marinos de Cuba. Instituto de Oceanología Academia de Ciencias de Cuba and Centro de Investigaciones de Quintana Roo (CIQRO), México, pp. 55–70.
- Claro, R., García-Arteaga, J.P., 1994. Crecimiento. In: Claro, R. (Ed.), Ecología de los peces marinos de Cuba. Instituto de Oceanología Academia de Ciencias de Cuba and Centro de Investigaciones de Quintana Roo (CIQRO), México, pp. 321–402.
- Collette, B.B., Nauen, C.E., 1983. FAO species catalogue. Scombrids of the World. An Annotated and Illustrated Catalogue of Tunas, Mackerels, Bonitos and Related Species Known to Date, vol. 2 FAO, Rome.
- Collins, A.B., McBride, R.S., 2011. Demographics by depth: spatially explicit life-history dynamics of a protogynous reef fish. *Fish. Bull.* 109, 232–242.
- Cope, J.M., Punt, A.E., 2009. Length-based reference points for data-limited situations: applications and restrictions. *Mar. Coastal Fish.* 1, 1–18.
- Costello, C., Ovando, D., Hilborn, R., Gaines, S.D., Deschenes, O., Lester, S.E., 2012. Status and solutions for the world's unassessed fisheries. *Science* 338, 517–520.
- Crabtree, R.E., Bullock, L.H., 1998. Age, growth, and reproduction of black grouper, *Mycteroperca bonaci*, in Florida waters. *Fish. Bull.* 96, 735–753.
- Dowling, N.A., Wilson, J.R., Rudd, M.B., Babcock, E.A., Caillaux, M., Cope, J., Dougherty, D., Fujita, R., Gedamke, T., Gleason, M., Gutierrez, N., Hordyk, A., Maina, G.W., Mous, P.J., Ovando, D., Parma, A.M., Prince, J., Revenga, C., Rude, J., Szuwalski, C., Valencia, S., Victor, S., 2016. FishPath: a decision support system for assessing and managing data- and capacity-limited fisheries. In: Quinn H.T.J., Armstrong, J.L., Baker, M.R., Heifetz, J., Witherell, D.M.E. (Eds.), Assessing and Managing Data-Limited Fish Stocks. Alaska Sea Grant, University of Alaska, Fairbanks.
- Ehrhardt, N.M., Ault, J.S., 1992. Analysis of two length-based mortality models applied to bounded catch length frequencies. *Trans. 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.
- Florida Museum of Natural History, 2011. French Angelfish. (Accessed 18 June 2018). www.floridamuseum.ufl.edu/fish/discover/species-profiles/pomacanthus-paru/.
- Freitas, M.O., Rocha, G.R.A., Chaves, P.D.D., De Moura, R.L., 2014. Reproductive biology of the lane snapper, *Lutjanus synagris*, and recommendations for its management on the Abrolhos Shelf, Brazil. *J. Mar. Biol. Assoc. U. K.* 94, 1711–1720.
- 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., 2017. FishBase. (Accessed 18 June 2018). www.fishbase.org.
- García-Cagide, A., Claro, R., Koshelev, B.V., 1994. Reproducción. In: Claro, R. (Ed.), Ecología de los peces marinos de Cuba. Inst. Oceanol. Acad. Cienc. Cuba. and Cen. Invest., Quintana Roo, México, pp. 187–262.
- Goodyear, C.P., 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *Can. Spec. Publ. Fish. Aquat. Sci.* 120, 67–81.
- Government of Belize, 2003. The subsidiary laws of Belize revised edition 2003. Fisheries (Glover's Reef Marine Reserve) Regulations. Chapter 210.
- Government of Belize, 2009. Statutory instrument No. 49 of 2009. Fisheries (Nassau Grouper and Species Protection) Regulations.
- 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.
- Grant, S., 2004. Glover's Reef Marine Reserve Data Collection Plan (Part 2). Wildlife Conservation Society (Belize), Belize City, Belize.
- Hobday, A.J., Smith, A.D.M., Stobutzki, I.C., Bulman, C., Daley, R., Dambacher, J.M., Deng, R.A., Dowdney, J., Fuller, M., Furlani, D., Griffiths, S.P., Johnson, D., Kenyon, R., Knuckey, I.A., Ling, S.D., Pitcher, R., Sainsbury, K.J., Sporic, M., Smith, T., Turnbull, C., Walker, T.I., Wayte, S.E., Webb, H., Williams, A., Wise, B.S., Zhou, S., 2011. Ecological risk assessment for the effects of fishing. *Fish. Res.* 108, 372–384.
- Hordyk, A., Ono, K., Sainsbury, K., Loneragan, N., Prince, J., 2015a. Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. *ICES J. Mar. Sci.* 72, 204–216.
- Hordyk, A., Ono, K., Valencia, S., Loneragan, N., Prince, J., 2015b. A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES J. Mar. Sci.* 72, 217–231.
- Hordyk, A.R., Ono, K., Prince, J.D., Walters, C.J., 2016. A simple length-structured model based on life history ratios and incorporating size-dependent selectivity: application to spawning potential ratios for data-poor stocks. *Can. J. Fish. Aquat. Sci.* 73, 1787–1799.
- 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, Fort Lauderdale, USA (Accessed 18 June 2018). <http://wrec.igfa.org/>.
- Jardim, E., Azevedo, M., Brites, N.M., 2015. Harvest control rules for data limited stocks using length-based reference points and survey biomass indices. *Fish. Res.* 171, 12–19.
- 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.
- Kadison, E., D'Alessandro, E.K., Davis, G.O., Hood, P.B., 2010. Age, growth, and reproductive patterns of the great barracuda, *Sphyrna barracuda*, from the Florida Keys. *Bull. Mar. Sci.* 86, 773–784.
- Kobara, S., Heyman, W.D., 2010. Sea bottom geomorphology of multi-species spawning aggregation sites in Belize. *Mar. Ecol. Prog. Ser.* 405, 243–254.
- 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.

- Bull. Mar. Sci. 52, 792–805.
- Lessa, R.P., Nóbrega, M.F., Bezerra, J.L.J., 2004. Dinâmica de populações e avaliação de estoques dos recursos pesqueiros da região nordeste, vol. II DIMAR, Departamento de Pesca-Universidade Federal Rural de Pernambuco, Recife-Brazil.
- Luckhurst, B.E., Dean, J.M., Reichert, M., 2000. Age, growth and reproduction of the lane snapper *Lutjanus synagris* (Pisces: Lutjanidae) at Bermuda. Mar. Ecol. Prog. Ser. 203, 255–261.
- Manickchand-Dass, S., 1987. Reproduction, age and growth of the lane snapper, *Lutjanus synagris* (Linnaeus), in Trinidad, West-Indies. Bull. Mar. Sci. 40, 22–28.
- Manickchand-Heileman, S.C., Phillip, D.A.T., 1996. Reproduction, age and growth of the Caribbean red snapper *Lutjanus purpureus* in waters off Trinidad and Tobago. In: Arreguín-Sánchez, F., Munro, J.L., Balgos, M.C., Pauly, D. (Eds.), Biology, Fisheries and Culture of Tropical Groupers and Snappers, ICLARM Conf. Proc. 48.
- Manooch, C.S.I., 1987. Age and growth of snappers and groupers. In: Polovina, J.J., Ralston, 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., 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.
- McDonald, G., Harford, B., Arrivillaga, A., Babcock, E.A., Carcamo, R., Foley, J., Fujita, R., Gedamke, T., Gibson, J., Karr, K., Robinson, J., Wilson, J., 2017. An indicator-based adaptive management framework and its development for data-limited fisheries in Belize. Mar. Policy 76, 28–37.
- Menezes, M.F.d., Gesteira, T.C.V., 1974. Idade e crescimento do pargo, *Lutjanus purpureus* Poey, no norte e nordeste do Brasil. Arquivos de Ciências do Mar 14, 81–85.
- Minchin, P.R., 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69, 89–107.
- Munro, J.L., Williams, D.M., 1985. Assessment and management of coral reef fisheries: biological, environmental and socio-economic aspects. In: Proceedings of the Fifth International Coral Reef Congress. Tahiti, 27 May–1 June 1985. Antenne Museum-EPHE, Moorea, French Polynesia. pp. 543–578.
- Newton, K., Cote, I.M., Pilling, G.M., Jennings, S., Dulvy, N.K., 2007. Current and future sustainability of island coral reef fisheries. Curr. Biol. 17, 655–658.
- O'Farrell, M.R., Botsford, L.W., 2005. Estimation of change in lifetime egg production from length frequency data. Can. J. Fish. Aquat. Sci. 62, 1626–1639.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. Vegan: Community Ecology Package. Library for R.
- Pauly, D., 1978. A Preliminary Compilation of Fish Length Growth Parameters. Ber. Inst. Meereskd. 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.
- Prince, J., Hordyk, A., Valencia, S.R., Loneragan, N., Sainsbury, K., 2015. Revisiting the concept of Beverton - Holt life-history invariants with the aim of informing data-poor fisheries assessment. ICES J. Mar. Sci. 72, 194–203.
- Punt, A.E., Hurtado-Ferro, F., Whitten, A.R., 2014. Model selection for selectivity in fisheries stock assessments. Fish. Res. 158, 124–134.
- R Development Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.
- Randall, J.E., 1962. Tagging reef fishes in the Virgin Islands. Proc. Gulf Caribbean Fish. Inst. 14, 201–241.
- Randall, J.E., 1968. Caribbean Reef Fishes. T.F.H. Publications, Inc. Ltd., Hong Kong.
- Randall, J.E., 1978. Scaridae. In: Fischer, W. (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.
- Rickman, S.J., Dulvy, N.K., Jennings, S., Reynolds, J.D., 2000. Recruitment variation related to fecundity in marine fishes. Can. J. Fish. Aquat. Sci. 57, 116–124.
- 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., Domeier, M., 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24, 254–262.
- 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 Fisheries Technical Report NMFS 146.
- Sadovy, Y., Figuerola, M., Roman, A., 1992. Age and growth of red hind *Epinephelus guttatus* in Puerto Rico and St. Thomas. Fish. Bull. 90, 516–528.
- Sadovy de Mitcheson, Y., Cornish, A., Domeier, M., Colin, P.L., Russell, M., Lindeman, K.C., 2008. A global baseline for spawning aggregations of reef fishes. Conserv. Biol. 22, 1233–1244.
- 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.
- Shepard, K.E., Patterson, W.F., DeVries, D.A., Ortiz, M., 2010. Contemporary versus historical estimates of king mackerel (*Scomberomorus cavalla*) age and growth in the US Atlantic ocean and Gulf of Mexico. Bull. Mar. Sci. 86, 515–532.
- 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.
- Sturm, M.G.D., Salter, P., 1990. Age, growth, and reproduction of the king mackerel *Scomberomorus cavalla* (Cuvier) in Trinidad waters. Fish. Bull. 88, 361–370.
- Sutter, F.C., Williams, R.O., Godcharles, M.F., 1991. Growth and mortality of king mackerel *Scomberomorus cavalla* tagged in the Southeastern United-States. Fish. Bull. 89, 733–737.
- Sylvester, J.R., Dammann, A.E., 1973. Contribution to biology of silk snapper *Lutjanus vivanus* from Virgin-Islands. Trans. Am. Fish. Soc. 102, 843–845.
- Tabash, F.A.B., Sierra, L.M.S., 1996. Assessment of *Lutjanus vivanus* and *Lutjanus bucanella* in the North Caribbean coast of Costa Rica. Naga ICLARM Q. 19, 48–51.
- Teixeira, S.F., Duarte, Y.F., Ferreira, B.P., 2010. Reproduction of the fish *Lutjanus analis* (mutton snapper; Perciformes: Lutjanidae) from Northeastern Brazil. Rev. Biol. Trop. 58, 791–800.
- Tewfik, A., Burns-Perez, V., 2017. Community Catch Data – Pilot Study: February – May 2017. Wildlife Conservation Society, Belize.
- Tewfik, A., Babcock, E.A., Gibson, J., Burns-Perez, V.R., Strindberg, S., 2017. Benefits of a replenishment zone revealed through trends in focal species at Glover's Atoll, Belize. Mar. Ecol. Prog. Ser. 580, 37–56.
- Then, A.Y., Hoenig, J.M., Hall, N.G., Hewitt, D.A., 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES J. Mar. Sci. 72, 82–92.
- Then, A.Y., Hoenig, J.M., Huynh, Q.C., 2017. Estimating fishing and natural mortality rates, and catchability coefficient, from a series of observations on mean length and fishing effort. ICES J. Mar. Sci. 75, 610–620.
- Thompson, R., Munro, J.L., 1983. The biology, ecology and bionomics of Caribbean reef fishes: Lutjanidae (snappers). In: Munro, J.L. (Ed.), Caribbean Coral Reef Fishery Resources. ICLARM, pp. 94–109.
- Thorson, J.T., Munch, S.B., Cope, J.M., Gao, J., 2017. Predicting life history parameters for all fishes worldwide. Ecol. Appl. 27, 2262–2276.
- Torres, F.S.B.J., 1991. Tabular data on marine fishes from Southern Africa, part II: growth parameters. Fishbyte 9, 37–38.
- Trindade-Santos, I., Freire, K.M.F., 2015. Analysis of reproductive patterns of fishes from three large marine ecosystems. Front. Mar. Sci. 2, 1–10.
- Valle, S.V., García-Arteaga, J.P., Claro, R., 1997. Growth parameters of marine fishes in Cuban waters. Naga ICLARM Q. 20, 34–37.
- Whitfield, A.K., 1998. Biology and Ecology of Fishes in Southern African Estuaries. J.L.B. Smith Institute of Ichthyology, South Africa.
- Zeller, D., Graham, R., Harper, S., 2011. Reconstruction of total marine fisheries catches for Belize, 1950–2008. In: Palomares, M.L.D., Pauly, D. (Eds.), Too Precious to Drill: The Marine Biodiversity of Belize. Fisheries Centre, University of British Columbia, pp. 142–151.
- 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.