

ARTICLE

# Length-Based Assessment of an Artisanal Albulid Fishery in the South Pacific: a Data-Limited Approach for Management and Conservation

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## Abstract

Data-limited fisheries assessment methods have great potential to help inform small island communities on the status of their fisheries resources. In this paper, we provide a length-based assessment of an artisanal fishery that primarily targets spawning aggregations of Shortjaw Bonefish *Albula glossodonta* at Anaa Atoll in the Tuamotu Archipelago of French Polynesia. We assessed the length-frequency distribution of the spawning stock across a 3-year period (2016–2018). During this time, male and female Shortjaw Bonefish were fully recruited to the fishery at age 4 and age 5, respectively. Fishing mortality was over two times the range of natural mortality for this species (i.e., 0.21–0.32), and based on these estimates of natural mortality, the annual spawning potential ratio of the population was between 7% and 20% across the sampling years. The majority of the catch was sexually mature, with 78,

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95, and 95% of the annual female catch in 2016, 2017, and 2018, respectively, being equal to or greater than the length of first maturity (i.e., 48 cm FL). However, every fisheries indicator and biological reference point suggested that the fishery was overexploited and in need of management intervention. To this aim, the community of Anaa (1) established an Educational Managed Marine Area, which overlaps with the Shortjaw Bonefish migratory corridor adjacent to Tukahora village and (2) instated a temporal rahui (a traditional conservation method) inside the Educational Managed Marine Area during the peak months of the spawning season.

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Fisheries resources are threatened by a wide range of anthropogenic activities, including overexploitation, habitat modification, and climate change (Jackson et al. 2001; Pauly et al. 2002; Allison et al. 2009). Many of the most severe fisheries declines are in data-deficient artisanal fisheries (Pauly 1997; Allison and Ellis 2001; Neil et al. 2007; Worm et al. 2009; Johnson et al. 2013), where communities lack the capacity to conduct research and monitor the status of their yields and where robust governance structures or formal monitoring programs are absent (Hughes et al. 2010; Fenner 2012). This paradigm is universal in the artisanal fisheries of the tropical Pacific Ocean, where low fish biomass and altered reef ecosystems are associated with human inhabitation (Friedlander and DeMartini 2002; DeMartini et al. 2008; Sandin et al. 2008), and there is an urgent need to manage these fisheries on local and regional scales (Bell et al. 2009; Houk et al. 2012, 2017, 2018; Cuetos-Bueno et al. 2018).

Most fisheries stock assessments are expensive and require a combination of life history parameters and time series catch-and-effort data to evaluate the status of a harvested species (Walters and Pearse 1996; Prince et al. 2015). However, these prerequisites are rare in remote island communities, which happen to be the jurisdictions where science-based management is urgently needed (Johannes 1998; Prince et al. 2011, 2015). Fortunately, novel low-cost data-limited methods are emerging that permit the assessment of data-deficient fisheries without the once essential context provided by historic abundance and long-term trends in fisheries landings (Froese 2004; Cope and Punt 2009; Prince et al. 2011; Hordyk et al. 2015b). These methods utilize a combination of life history parameters and the length-frequency distribution of a harvested fish population to reveal its status in a given fishery and have made substantial contributions to the management of numerous data-poor fisheries (Ault et al. 2008; Nadon et al. 2015; Prince et al. 2015; Usseglio et al. 2016). Additionally, to compensate for the lack of biological and catch data, other approaches suggest assessing fisheries systems from three different viewpoints: the ecology of targeted populations, their exploitation, and the broader socioeconomic fishery context. This information can illuminate the need for intervention in unmanaged fisheries and assist in the development of fisheries conservation

actions that are necessary to sustain coral reef fisheries (Clua et al. 2005).

Spawning-aggregation fisheries that target coral reef species are of particular conservation concern, as the predictable spatial and temporal concentrations of reproductively mature fish from a broad geographic area renders their populations highly vulnerable to over exploitation (Sadovy 2005; De Mitcheson et al. 2008; De Mitcheson and Erisman 2012; Gruss et al. 2014; Erisman et al. 2017). These biomass concentrations provide benefits to fishers, including minimized search time, reduced overhead, and large predictable catches that yield short-term economic benefits (De Mitcheson and Erisman 2012; Secor 2015). However, market saturation can result in price gluts where fishers receive less value per fish, waste due to excess fish that cannot be sold, and heterogenous food supply (De Mitcheson and Erisman 2012). Furthermore, if improperly managed, overfishing of these aggregations can result in population-wide effects on harvested species (Claydon 2004; Sasikumar et al. 2015; Secor 2015). Even in spawning-aggregation fisheries where managers have the resources to effectively monitor the harvest, fishery-dependent data collected from spawning aggregations known to be hyper stable and can mask declines in stock abundance (i.e., catch per unit effort remains stable, while the abundance of the stock continues to decline), and in consequence exploitation can cryptically erode the resilience of a population (De Mitcheson and Erisman 2012).

Shortjaw Bonefish *Albula glossodont* (hereafter referred to as “bonefish”) have historically played a vital role in the subsistence and commercial fisheries in Anaa Atoll, a remote island in the Tuamotu Archipelago of French Polynesia. Locally known as *kiokio*, bonefish are captured in the lagoon with a variety of methods, including hand lines and gill nets; however, this species is principally harvested with artisanal fish traps during their spawning migrations between the lagoon and the open ocean (Allen 2014; Torrente 2015; Filous et al. 2019b). The artisanal trap fishery has existed for centuries but the addition of chicken wire to the end of the rock traps and the expansion of the total number of fish traps since the late 1980s has increased the efficiency of the fishery and yields have declined from their historical abundance (A. Filous, personal communications with residents of Anaa Atoll). This

scenario and the consequential overexploitation of bonefish populations is commonplace in analogous fisheries across the Pacific Islands, and the bonefish of Tarawa, Kiriritimati, Aitutaki, and Hawai'i have all been overexploited with the modernization of traditional fishing techniques (Beets 2000; Johannes and Yeeting 2000; Friedlander et al. 2007; Adams et al. 2013; Allen 2014). Congruently, fisheries harvests at Anaa Atoll were nonregulated throughout the 20th century, and to compound the absence of fisheries management, the phenomenon of shifting baselines in fisheries resource abundance confounds the ability of the community to evaluate the current state of the fishery (Pauly 1995). Until recently, there was insufficient biological data to evaluate the impact of fishing on the stock; however, research into the life history of the species has filled these knowledge gaps and paved the way for its assessment with the data-limited methods (Filous et al. 2019a).

Data-limited length-based fisheries methods have great potential to help inform this small island community on the status of this fishery and provide management recommendations to improve its sustainability (Froese 2004; Thorson and Prager 2011; Hordyk et al. 2015b). To this aim, this paper provides an assessment of the bonefish fishery by describing the sex composition of the harvested bonefish stock and assessing its length-frequency distribution across a 3-year period with three data-limited fisheries methods. These include the following: (1) an estimation of fishing mortality and recruitment of male and female bonefish in the trap fishery with an age-based catch curve, (2) the estimation of the spawning potential ratio (SPR) of the atoll's bonefish population and how far the fishery deviates from the biological reference point ( $F_{40\%}$ ), and (3) the application of the Froese (2004) fisheries indicators to assess the sustainability and status of this fishery. Based on these results and a synthesis of previous research, we propose community-based management recommendations that will allow the continued harvest of the resource while protecting the essential components of the population's spawning stock.

## STUDY SITE

Anaa is a small coralline atoll (38 km<sup>2</sup>) 350 km east of Tahiti, in the Tuamotu Archipelago of French Polynesia (Figure 1). The atoll is bordered by a coral reef that encircles a shallow lagoon with 11 small islands known as "motu" and fringing sand flats. Anaa is closed and lacks a deep oceanic pass between its interior lagoon and outer reef. There are a few small and shallow passes that allow movement between the lagoon and oceanic habitats, which are situated in the northeastern area of the atoll (Figure 1). An artisanal trap fishery targets the spawning migrations of bonefish, which are funneled through these migratory

passages, and there are 36 artisanal fish trap structures located throughout Anaa Atoll (Figure 1). Each lunar month during the spawning season, migrating schools of bonefish are captured in the trap complex while moving between the lagoon and the open ocean during the waning gibbus moon. Privately owned traps are operated by individuals that hold a concession from the Direction Des Ressources Marines to operate and sell captured marine life and are outfitted with chicken wire mesh (5 × 3.5 cm), thereby selecting any fish with girths greater than 3.5 cm that encounter the trap. In contrast, public traps are constructed entirely of stone and harvested on a first-come, first-served basis by any member of the community (Figure 2). Upon capture, bonefish schools typically remain blockaded in the cod end of the trap for periods of 1 to 4 d. The fish are then brailed or netted out of the trap as needed to meet local market demand. Bonefish are sold fresh on the atoll for 1,000 French Pacific francs (CFP) per packet (about five bonefish; 1,000 CFP = US\$9.33 as of October 2019), and when bonefish are abundant, they are salted, dried, and sold for 1,000 CFP per fish if exported to Tahiti (Figure 2). This fishery provides sustenance and economic opportunities for the atoll's approximately 500 residents, but previous research suggests that the bonefish stock is overexploited and in need of a quantitative fisheries assessment (Filous et al. 2019b).

## METHODS

Fisheries landings surveys were conducted alongside local fishers to record the length and sex of bonefish harvested in the artisanal trap fishery. Catches were sampled from all public and private traps that operated in the migratory corridors of the atoll, and sampling coincided with monthly spawning runs during the waning moon phases from 2016 to 2018. A scientist (the first author) accompanied local fishermen during harvesting events and each captured fish was counted, measured to the nearest centimeter (FL) on a purpose-built measuring cradle, and sexed externally by pressing the abdomen anterior to the cloaca. Males were identified by the presence of milt and females by the presence of oocytes. These observations provided length-frequency distributions of the male and female components of the bonefish spawning population during the annual fishing seasons from 2016 to 2018. In this forthcoming analysis, all values are means and SDs of the mean, unless otherwise stated, and statistics were done in R (version 3.4.3).

*Sex ratios and size differences between male and female bonefish.*—To determine if the overall sex ratio of the bonefish population differed significantly from 1:1, the sex ratio (F:M) was taken across all sampled fish and tested with a chi-square test using the `chisq.test` function.

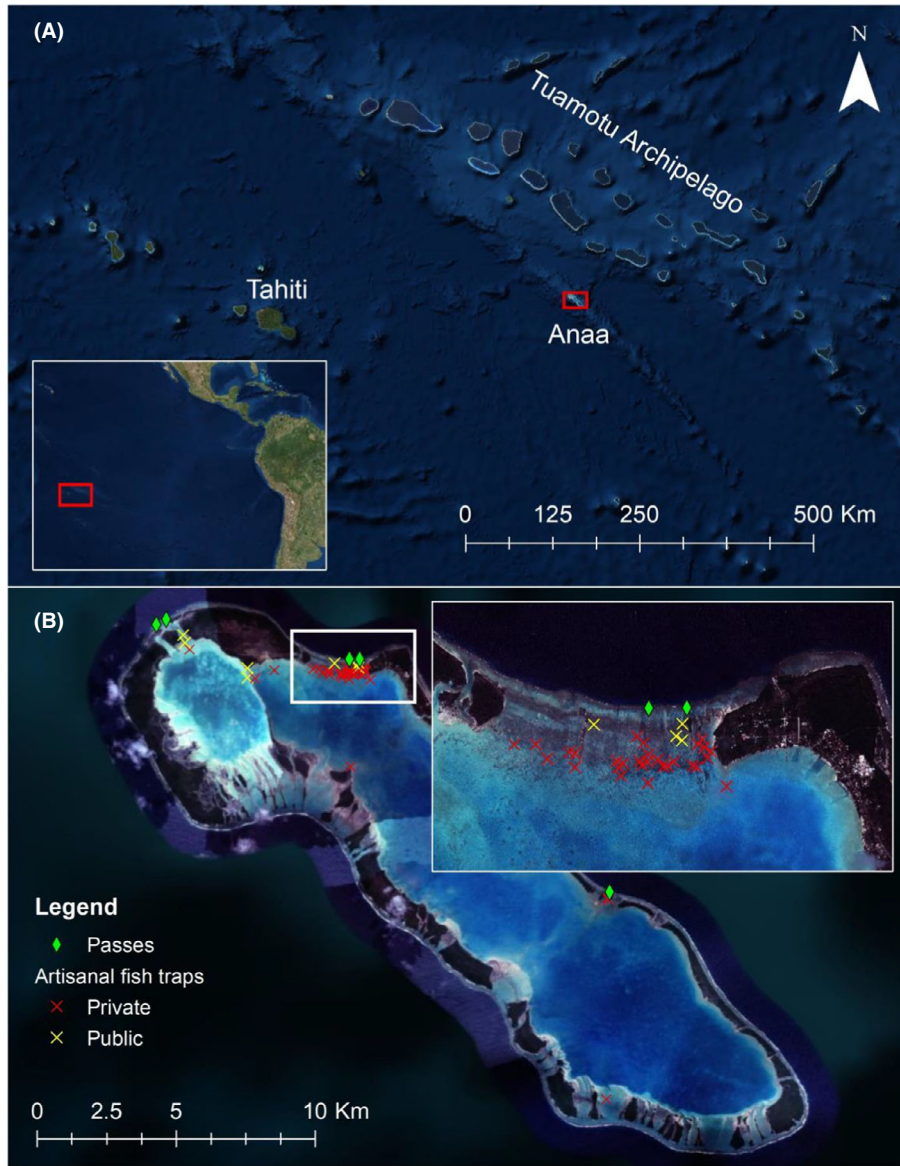


FIGURE 1. The location of (A) Anaa, the eastern most atoll in the Tuamotu Archipelago of French Polynesia, and (B) a map of Anaa, showing the locations of artisanal fish traps (red Xs indicate the locations of private fish traps, yellow Xs indicate the locations of public fish traps, green diamonds indicate the locations of migratory passageways used by Shortjaw Bonefish).

Differences in the average size of male and female bonefish were evaluated with a Student's *t*-test. The ages of each fish were determined with length–age conversions using the sex-specific growth parameters, mean asymptotic length ( $L_{\infty\text{Female}} = 78$  cm FL,  $L_{\infty\text{Male}} = 58$  cm FL), growth rate ( $K_{\text{Female}} = 0.21$ ,  $K_{\text{Male}} = 0.38$ ), and the theoretical age at which length is zero ( $t_0 = -0.40$ ) described in Filous et al. (2019a), and the differences in average age of male and female bonefish were tested with a Student's *t*-test as described above. Changes in the sex ratio of spawning schools were evaluated throughout the spawning season by determining the number of females

and males in each catch and testing for differences in the sex ratio of catches between months of the spawning season with a binomial generalized linear model using the glm function. Post hoc multiple comparisons were then performed with the Tukey's honestly significant difference test with the glht function in the multcomp package.

*Age-based catch curve.*—The total annual fishing mortality experienced by female and male components of the bonefish population was estimated with an age-based catch curve (Chapman and Robson 1960). Following the methods of Smith et al. (2012), a catch curve was

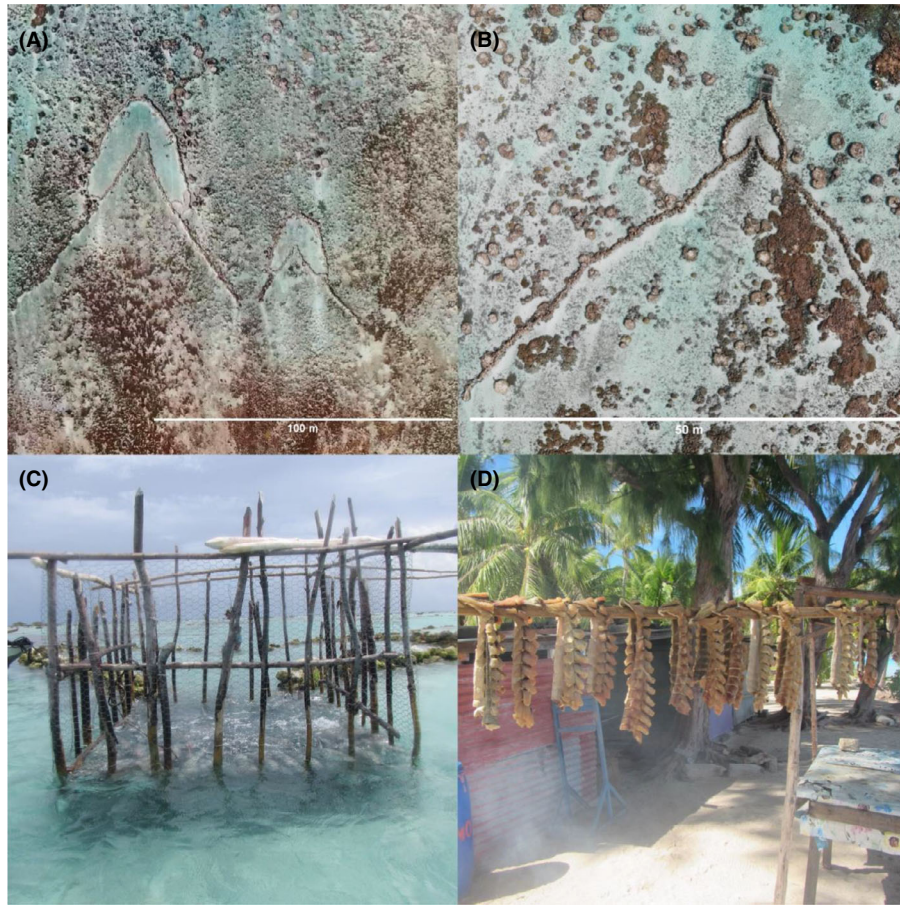


FIGURE 2. Artisanal fish trap design at Anaa Atoll, with (A) public traps made exclusively from coral rock and (B) private traps comprised of coral rock and chicken wire mesh. Panel (C) shows a close up view of the chicken wire mesh holding a catch of Shortjaw Bonefish in the cod end of a private trap, and (D) shows dried Shortjaw Bonefish, which is the principal product of the trap fishery.

constructed by taking the annual fork length measurements of male and female bonefish captured in the artisanal trap fishery and converting length to age, with the sex-specific von Bertalanffy growth parameters as described above. Total mortality ( $Z$ ) was then estimated with a modified Chapman–Robson method that corrected for overdispersion with the FSA package (Ogle et al. 2019). The apex in the catch curve for each sex reveals the age at which male and female bonefish are fully recruited to the fishery, and this method estimates the total (natural and fishing) instantaneous mortality ( $Z$ ) and annual survival ( $S$ ) experienced by these two segments of the population (Smith et al. 2012). From these estimates of total instantaneous mortality, we calculated a range of respective fishing mortalities for male and female bonefish by subtracting the natural mortality ( $M$ ) of 0.21 derived from the Hoenig (1983) fish equation and an  $M$  of 0.32 derived from the Then et al. (2015) Hoenig<sub>nl</sub>s equation (Filous et al. 2019a). The range of fishing mortality to obtain a maximum sustainable yield ( $F_{msy}$ )

was then estimated using these two values with the following equation:

$$F_{msy} = 0.87M, \quad (1)$$

where  $F_{msy}$  is the fishing mortality and  $M$  is the instantaneous rate of natural mortality (Zhou et al. 2012).

Finally, generation time ( $GT$ ) was estimated with the following equation:

$$GT = AM + \frac{T_{max} - AM}{2}, \quad (2)$$

where  $AM$  is the age at first maturity (4 years) in females and  $T_{max}$  (20 years) is the maximum recorded age (Depczynski and Bellwood 2006; Filous et al. 2019a).

*Spawning potential ratio.*—The SPR of a fish stock is defined as the proportion of unfished reproductive potential remaining in a population at any given level of fishing pressure (Goodyear 1993; Hordyk et al. 2015b) and is a ratio of the number of eggs an average recruit could produce over its lifetime in a fished stock versus the number

of eggs an average recruit could produce over its lifetime in an unfished stock (Brooks et al. 2010). The SPR of the bonefish population and fishery selectivity at Anaa Atoll was estimated with the age-structured methods outlined in Hordyk et al. (2015a) with the LBSPRfit function and model type “absel” in the R package LBSPR using the life history characteristics and the two separate estimates of  $M$  described above (Hordyk 2019). The plots of selectivity and the annual length-frequency distributions of the harvested fish compared with a simulated population with an SPR of  $F_{40\%}$  were extracted with the plotMat and plotTarg functions in the R package LBSPR.

**Froese sustainability indicators.**—Froese (2004) proposed three guiding principles to avoid overexploitation: (1) let them spawn, (2) let them grow, and (3) let the megaspawners live. According to these principles (i.e., immature fish are not harvested, fish are harvested at their optimal length, and megaspawners are protected), a fishery should be sustainable if it is managed to insure that the size of fish harvested adhere to these guidelines (Froese 2004). To assess the status of the bonefish fishery at Anaa Atoll, we evaluated the annual length-frequency distributions of harvested female bonefish in the context of these three principles. Following the methods of Froese (2004), we used the female life history characteristic growth rate ( $K=0.21$ ), mean asymptotic length ( $L_{\infty}=78$  cm FL), and the two natural mortality rates described above to determine optimum harvest lengths ( $L_{opt}$ ) for female bonefish:

$$L_{opt} = L_{\infty} \times [3/(3 + M/K)], \quad (3)$$

where  $L_{opt}$  is the optimal harvest length (Beverton 1992; Froese 2004).

From these optimal harvest lengths, optimum harvest length intervals were estimated as  $\pm 10\%$  of the  $L_{opt}$ , the length of a megaspawner was estimated as lengths greater than 1.10 of the  $L_{opt}$ , and the length at 50% maturity ( $L_{mat}$ ) was estimated to be 48 cm FL in Filous et al. (2019a). According to the methods of Cope and Punt (2009), if the combined percentages of mature, optimal, and megaspawners in the catch ( $P_{obj}$ ) is between 100% and 200%, the selectivity of the fishery fits the maturity ogive. Given this selectivity pattern, if  $L_{mat}$  is less than or equal to 0.75 of the  $L_{opt}$  and the proportion of mature individuals in the catch is greater than 95% or if  $L_{mat}$  is equal to 0.9 of the  $L_{opt}$  and the proportion of mature individuals in the catch is greater than 90%, the spawning biomass is likely greater than or equal to both 40% and 25% of the unfished spawning biomass (Cope and Punt 2009).

## RESULTS

From 2016 to 2018, we sampled 3,420 bonefish from the artisanal trap fishery. The sex ratio of these fish was

1,666 females to 1,754 males and was not significantly different from 1:1 ( $\chi^2=2.2643$ ,  $df=1$ ,  $P<0.13$ ). The average length of male and female bonefish was significantly different ( $t=49.23$ ,  $df=2,705$ ,  $P<0.005$ ), with females being larger ( $55 \pm 5$  cm FL) than males ( $49 \pm 3$  cm FL). When these lengths were converted to age, the mean age of males ( $4.65 \pm 0.93$  years) and females ( $5.55 \pm 1.14$  years) was also significantly different ( $t=25.151$ ,  $df=3,215$ ,  $P<0.005$ ). There was a significant difference in the sex ratio of spawning aggregations across the reproductive season, wherein females dominated the catch during March, April, and May but declined throughout the remainder of the season, yielding to a male-dominated catch ( $P<0.005$ ; Figure 3). In the following length-based analysis we separated the female and male components of the population to derive sex-specific population estimates for each year (Table 1).

### Age-Based Catch Curve

The catch curve analysis indicates that male and female bonefish are fully recruited to the trap fishery at age 4 and age 5, respectively (Figure 4). Based on a visual analysis of the peaks and right tails of the age-frequency distributions, we included ages 4–8 from 2016 to 2017 and ages 5–8 in 2018 when modeling male catch curves. For female catch curves, we included ages 5–10 from 2016 to 2018.

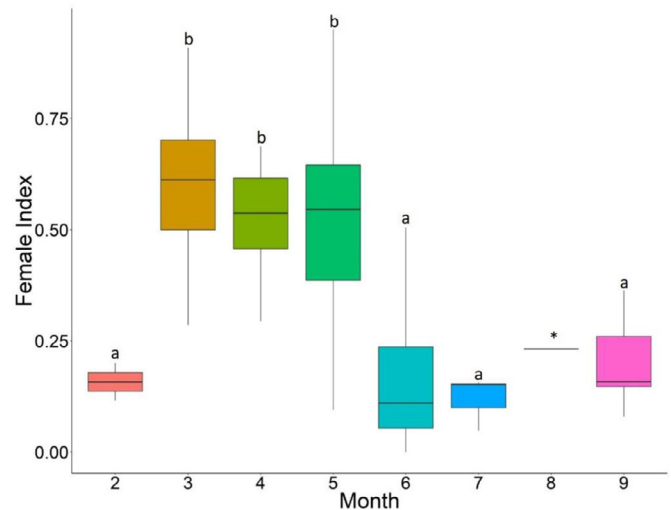


FIGURE 3. The female to male sex ratio of Shortjaw Bonefish in the catches harvested throughout the months of the spawning season for 2016–2018 in aggregate. For the box plot, the horizontal line in each box indicates the median, the box dimensions represent the 25th to 75th percentile ranges, and the whiskers show the 10th to 90th percentile ranges. Different letters above the boxes indicate significant differences between months based on Tukey–Kramer honestly significant difference multiple comparisons with a  $P<0.005$ . Note that the month of August (marked with an asterisk) was removed from statistical comparisons due to low sample size.

TABLE 1. Estimates of survival ( $S$ ), total mortality ( $Z$ ), and fishing mortality ( $F$ ) derived from age-based catch curves for male and female Shortjaw Bonefish from 2016 to 2018. Note that two different natural mortality rates ( $M$ ) were used to provide a range of  $F$  estimates: one based on the Hoenig (1983) fish equation ( $M=0.21$ ) and one on the Hoenig<sub>nls</sub> equation ( $M=0.32$ ), each denoted by the subscript (available estimates of 95% confidence intervals are provided in parentheses).

Year	Sex	$N$	$S$	$Z$	$F_{M=0.21}$	$F_{M=0.32}$
2016	Female	144	50 (43.16–56.84)	0.69 (0.57–0.80)	0.48	0.37
	Male	126	43 (36.12–49.88)	0.84 (0.57–1.1)	0.63	0.52
2017	Female	631	44.78 (41.72–47.84)	0.8 (0.59–1.01)	0.59	0.48
	Male	893	38.01 (35.37–40.64)	0.97 (0.76–1.18)	0.76	0.65
2018	Female	891	43.86 (41.23–46.49)	0.82 (0.69–0.95)	0.61	0.50
	Male	735	25.28 (21.86–28.70)	1.37 (1.28–1.46)	1.16	1.05

The modified Chapman–Robson method yielded annual survival rates ranging between 43.86% and 50.00% ( $46 \pm 3\%$ ) for females and between 25.28% and 43.86% ( $35 \pm 9\%$ ) for males. After subtracting the two  $M$  values from the total mortality estimates, the rate of fishing mortality ranged from 0.48 to 0.61 ( $0.56 \pm 0.07$ ) in females and 0.63 to 1.16 ( $0.85 \pm 0.28$ ) in males when using the Hoenig (1983)  $M$  and 0.37 to 0.50 ( $0.45 \pm 0.05$ ) in females and 0.52 to 1.05 ( $0.74 \pm 0.22$ ) in males with the Hoenig<sub>nls</sub>  $M$ . Finally, we estimated the  $F_{msy}$  to be between 0.18 and 0.28, and with the species living to maximum life span of 20 years in the absence of fishing, the generational turnover time is estimated to be 12 years.

### Spawning Potential Ratio

The SPR of the bonefish population between 2016 and 2018 was estimated to be between 7% and 11% ( $9 \pm 2\%$ ) with the Hoenig (1983)  $M$  and between 13% and 20% ( $17 \pm 3\%$ ) with the Hoenig<sub>nls</sub>  $M$  (Table 2). The truncated length composition of the bonefish population along with its associated theoretical egg production is evident in reference to the simulated length-frequently distribution of a theoretical population with Hoenig (1983)  $M$  and a 40% SPR, a well-established biological reference point for the maintenance of sustainable fisheries (Figure 5). A selectivity curve indicates that bonefish are fully selected to the fishery shortly after reaching sexual maturity (Table 2; Figure 6).

### Froese Sustainability Indicators

Given a female von Bertalanffy growth parameter ( $K$ ) of 0.21, we estimated the ratio of  $M/K$  to be 1.00 for a population with a Hoenig (1983)  $M$  and 1.52 for a population with a Hoenig<sub>nls</sub>  $M$ , which yielded optimum lengths of harvest for female bonefish of 58 and 52 cm FL, respectively. From these  $L_{opt}$  estimates we derived an optimal harvest size range between 52 and 64 cm FL, and we estimated the size at which a female bonefish becomes a megaspawner to be greater than 64 cm FL based on a Hoenig (1983)  $M$ . In a population with a Hoenig<sub>nls</sub>  $M$ ,

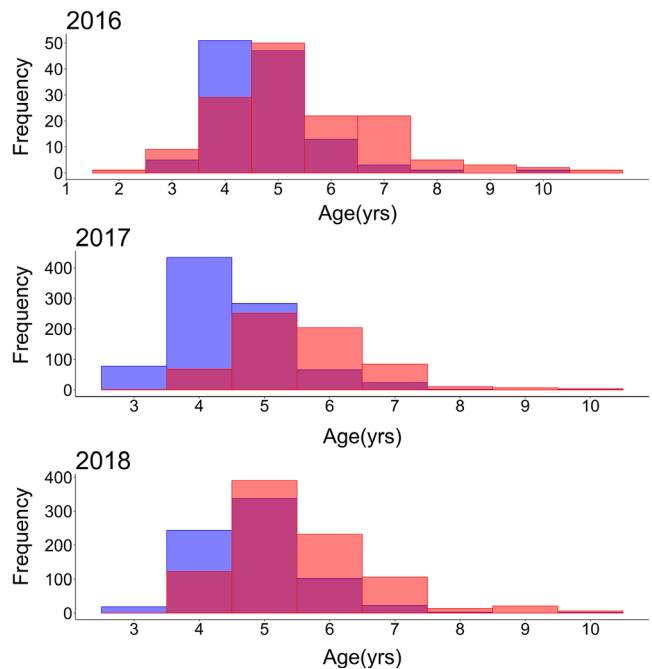


FIGURE 4. Age-frequency distribution of the annual Shortjaw Bonefish catches harvested in the artisanal trap fishery at Anaa Atoll from 2016 to 2018 (blue bars represent harvested males, pink bars represent harvested females, and the overlapping size distributions of the two sexes is indicated by the darker shading).

the optimum harvest size range was estimated to be between 47 and 57 cm FL, and the length of a megaspawner was estimated to be greater than 57 cm FL. An analysis of the annual length-frequency distributions of harvested fish with Froese's indicators demonstrated that the majority of harvested fish were sexually mature with 78, 95, and 95% ( $89 \pm 10\%$ ) of the annual female catch being equal to or greater than 48 cm FL (i.e., the  $L_{mat}$  for female bonefish) across the three sampling years, respectively. Given the estimates of  $L_{opt}$  derived from the Hoenig (1983)  $M$ , over half of the harvested fish were within the optimal size range of 52 to 64 cm FL, with an average of  $65 \pm 9\%$  of the catch being within this range during the

TABLE 2. The fisheries selectivity, length-based spawning potential ratio (SPR), and Froese fisheries indicators for female Shortjaw Bonefish harvested at Anaa Atoll from 2016 to 2018. Note that two different natural mortality rates ( $M$ ) were used to provide a range of SPR and Froese estimates: one based on the Hoening (1983) fish equation ( $M=0.21$ ) and one on the Hoening<sub>nls</sub> equation ( $M=0.32$ ). Abbreviations are as follows: SL50 = the length at which 50% of individuals are selected to the fishery, SL95 = the length at which 95% of individuals are selected to the fishery, %<sub>mat</sub> = percent of mature individuals in the catch, %<sub>mega</sub> = percent of mega-spawners in the catch, %<sub>opt</sub> = percent of individuals in the catch that are within the optimal size range.

Year	Total females	SL50	SL95	% <sub>mat</sub> $L_{>48}$ cm	$M_{\text{Hoening}(1983)} = 0.21$			$M_{\text{Hoening}_{\text{nls}}} = 0.32$		
					SPR	% <sub>opt</sub> $L_{52-64}$ cm	% <sub>mega</sub> $L_{>64}$ cm	SPR	% <sub>opt</sub> $L_{47-57}$ cm	% <sub>mega</sub> $L_{>57}$ cm
2016	144	52	62	78	11	56	5	20	52	32
2017	631	54	59	95	7	74	2	13	56	42
2018	891	50	54	95	9	64	3	17	64	35

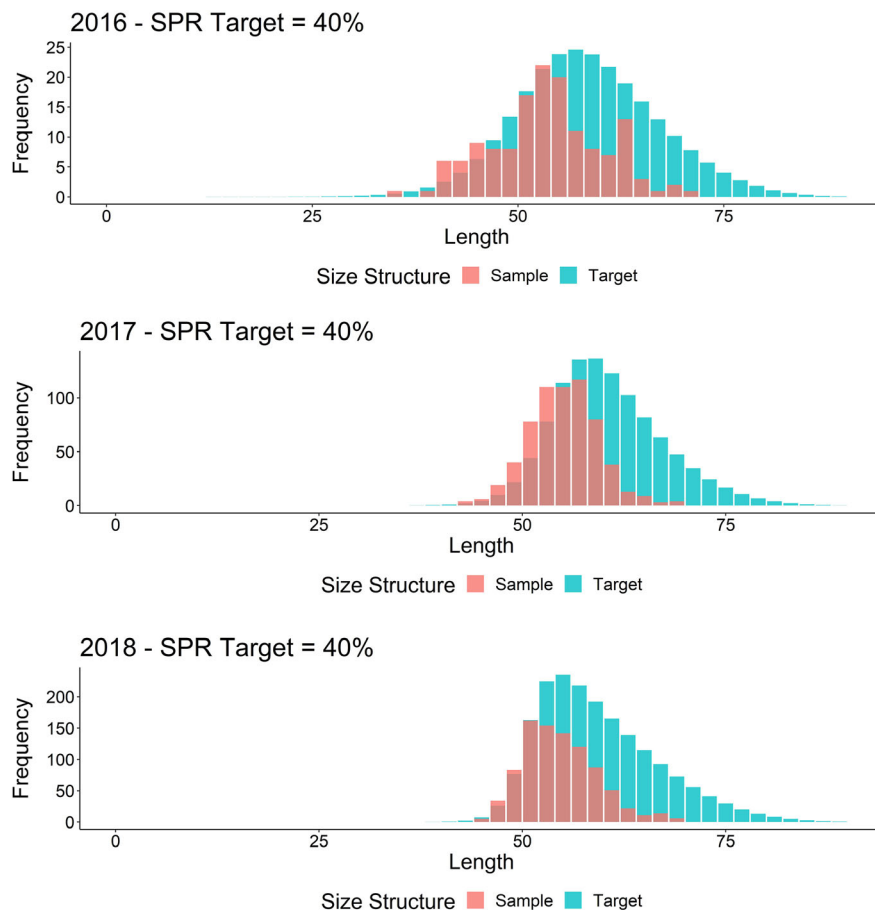


FIGURE 5. The size distribution of female Shortjaw Bonefish harvested in the artisanal trap fishery at Anaa Atoll from 2016 to 2018 during the spawning season, overlaid on a theoretical size structure if the population were to have an SPR of 40% and a natural mortality rate ( $M=0.21$ , derived from the Hoening 1983 fish equation). Green bars indicate the observed size frequency of harvested fish, and pink bars indicate the theoretical size distribution under a 40% SPR scenario.

study period. However, the annual percentage of megaspawners in the catch was low and averaged  $3 \pm 1\%$  (Table 2). In contrast, when using the of  $L_{\text{opt}}$  derived from the Hoening<sub>nls</sub>  $M$ , on average  $54 \pm 2\%$  of the catch was within the optimal size range and  $36 \pm 4\%$  of the catch was

considered a megaspawner. Following the principles for length-based reference points outlined by Cope and Punt (2009), for both the  $L_{\text{opt}}$  estimates derived from the Hoening (1983)  $M$  and Hoening<sub>nls</sub>  $M$  (i.e., 58 and 52 cm FL, respectively), the  $P_{\text{obj}}$  ranged from 139% to 171% and



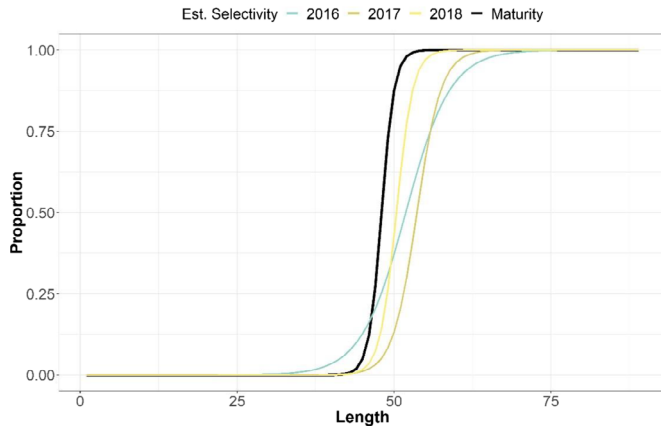


FIGURE 6. The artisanal fish trap selectivity curve from 2016 to 2018, plotted in reference to the length at maturity (the blue line indicates fisheries selectivity in 2016, the orange line indicates fisheries selectivity in 2017, the yellow line indicates fisheries selectivity in 2018, and the black line indicates the maturation schedule of female Shortjaw Bonefish).

130% to 193%, respectively, suggesting that the selectivity of this fishery follows the maturity ogive of this species. For this selectivity pattern, according to the decision tree presented in Cope and Punt (2009), an analysis of the relationship between the  $L_{mat}$  and the two estimates of  $L_{opt}$  indicates that the  $L_{mat}$  (i.e., 48 cm FL) is not less than or equal to 0.75 of the  $L_{opt}$  (i.e., 44 and 39 cm FL, respectively). Furthermore, in both cases, the  $L_{mat}$  is not equal to 0.9 of the  $L_{opt}$  (i.e., 52 and 47 cm FL, respectively). Therefore, although the percentage of mature individuals in the catch is relatively high, the spawning biomass is likely less than 40% or 25% of the unfished spawning stock.

## DISCUSSION

The management of small-scale, data-limited fisheries can benefit from cost-effective methodologies such as the length-based methods applied in this study. However, there are a variety of assumptions that could affect the outcomes of these length-based fisheries models. First, all of the methods we utilized rely on an estimate of natural mortality, which is a poorly understood life history characteristic and difficult to estimate (Vetter 1987; Pascual and Iribarne 1993; Hewitt and Hoenig 2005; Kenchington 2014; Then et al. 2015). Errors in the estimation of this parameter would affect our catch curve estimates of fishing mortality, optimal harvest length, and SPR. In recognition of this uncertainty, we modeled these estimates across a range of plausible values for  $M$ . Furthermore, these methods assume the population is at equilibrium, meaning both recruitment and fishing mortality are constant. This assumption is rarely met in wild populations, and environmental stochasticity could affect the recruitment strength of the year-classes that we modeled in our study and bias our results (Hordyk et al. 2015b). Nevertheless, given the limited resources in many communities

like Anaa Atoll, these methods provide an important tool for the management of their fisheries, and although there is uncertainty in the exact values of our results, collectively they suggest this population is overexploited.

Our estimates of total mortality ( $Z$ ) are high for this genus, for which estimates of  $Z$  in locations with no active commercial fisheries are between 0.21 to 0.27 (roughly equivalent to natural mortality) and 0.643 in fished populations (Crabtree et al. 1994; Ault et al. 2007; Friedlander et al. 2007; Kamikawa et al. 2015). Traditionally, in order to maintain maximum sustainable yields, managers strived to limit fishing mortality so that it does not exceed natural mortality (Francis 1974); however, this paradigm has been revised (i.e.,  $F_{msy} = 0.87M$ ) to provide a more conservative biological reference point (Francis 1974; Zhou et al. 2012). Our study revealed that in some years fishing mortality is two to three times the instantaneous range of natural mortality and exceeds the range of  $F_{msy}$  for this species (Gulland and Boerema 1973; Murawski et al. 2001; Kenchington 2014). These figures are concerning given the historical collapse of analogous fisheries. For instance, fishing mortality in the bonefish fishery of Hawaii was estimated at 0.59 and commercial landings have declined to less than 1% of their historic yields (Friedlander et al. 2007, 2015; Kamikawa et al. 2015).

Our estimate of fishing mortality for males is consistently higher than for females, which supports our “differential spawning behavior” theory in which male bonefish engage in spawning events more frequently than females and as a result are more vulnerable to harvest in the trap complex. Previous research indicates that female bonefish exhibit group synchronous oocyte development, with three developmental stages present in the gonads of spawning-capable fish (i.e., primary growth, cortical alveolar, and vitellogenic 3). Therefore, we suggest that females need time to develop their oocytes between batches, while in contrast, males appear to be capable of spawning during every monthly lunar phase (Filous et al. 2019a). These life history characteristics are corroborated by unpublished acoustic tracking data that showed that males visited the spawning grounds more frequently than females (A. Filous, unpublished data). The apparent differences in spawning frequency between the two sexes may be responsible for the higher rate of fishing mortality in the male component of the spawning stock and the shift toward male-dominated catches that we observed during the latter part of the spawning season.

The selectivity curve of this fishery is asymptotic, with any individual greater than their age of maturity vulnerable to harvest. However, the average age of both male and female bonefish captured in this fishery is equal to their age of first recruitment, illustrating the truncated life span of an average recruit and the limited egg production it could provide over its lifetime (Goodyear 1993). Given

the current level of fishing mortality, the more conservative SPR analysis with a Hoenig (1983)  $M$  suggests that the SPR of the atoll's spawning stock is critically low and, if taken at its 3-year average, the population has lost over 91% of its theoretical egg production. A SPR between 20% to 40% is considered to be the minimum egg production required to maintain fish stocks, while SPRs less than 20% are symptomatic of overexploitation (Clark 2002; Ault et al. 2008; Nadon et al. 2015; Kindsvater et al. 2016). This is because the rate of increase in compensatory survival required per unit decrease in SPR is significantly higher when a population's SPR is less than or equal to 20% (Goodyear 1993). With this in mind, the SPR estimates derived from the Hoenig<sub>nls</sub>  $M$  suggest that the population's SPR was at this 20% threshold in 2016 and descended below it throughout the remainder of the study. Furthermore, previous work has suggested that in scenarios where the spawner–recruit relationship is unknown, the recommended maximum fishing mortality should be at least  $F_{40\%}$  (i.e., a level that would maintain 40% of the population SPR) because  $F_{msy}$  cannot be reliably estimated (Mace 1994; Clark 2002). Given our results, the longevity of bonefish, the unidentified spawner–recruit relationship, and the fact that the artisanal trap fishery intensively harvests their spawning aggregations in a way that has led to the collapse of analogous fisheries (Beets 2000; Johannes and Yeeting 2000), a  $F_{40\%}$  should be the target for the management of this fishery (Goodyear 1993; Mace 1994). Yet, both estimates suggest that the population is presently well below this reference point, and although the fishery continues to provide yield, the population could be highly sensitive to environmental stochasticity and other factors that may affect recruitment (Stacey and Taper 1992; Hutchings and Reynolds 2004; Reynolds et al. 2005).

Our results demonstrate that the artisanal trap fishery partially adheres to Froese's first principle of sustainable fisheries of “let them spawn” as few females are harvested at sizes less than the length of first maturity (L50). However, there is an important distinction between harvest at L50 and the opportunity to spawn. The length at which 95% of female bonefish reach sexual maturity (L95) is 51 cm FL, and female bonefish are fully recruited to the fishery at 5 years of age (i.e., 51–55 cm FL). This evidence suggests that although the L50 for the species is 48 cm FL (age 4), some individuals may not make their first spawning run until their 5th year of life. Consequently, because the trap fishery primarily captures bonefish en route to their spawning locations, much of the population's spawning stock is harvested before their first spawning event, therefore violating the “let them spawn at least once” principle (Myers et al. 1997; Myers and Mertz 1998). Similarly, our results indicate growth overfishing may be occurring, in that a significant proportion of the harvested

bonefish were outside of the optimum size ranges that were predicted by both the estimates made with Hoenig (1983) and Hoenig<sub>nls</sub> rates of  $M$  (Diekert 2012). To improve food security and ensure that the maximum yield (i.e., edible biomass) can be obtained from an individual fish, a well-managed fishery will allow new recruits to grow to an optimum length before they are harvested, thus increasing the yield obtained from the resource (Holt 1958; Froese and Binohlan 2000; Froese 2004). Finally, our results based on the Hoenig (1983)  $M$  provide evidence of longevity overfishing, wherein the proportion of megaspawners ( $L_{\text{mega}} = 64$  cm FL) in the population is critically low (Beamish et al. 2006). These older, larger, and more fecund fish are disproportionately important to the population (Berkeley et al. 2004b; Hixon et al. 2014), and an increasing body of evidences suggests that in addition to increased fecundity with female body size, maternal age is positively related to larval survival and recruitment (Longhurst 2002; Berkeley et al. 2004a; Birke-land and Dayton 2005; O'Farrell and Botsford 2006). Therefore, the loss of these more experienced spawners may lead to higher larval mortality rates and recruitment failure as the aptitude of the collective spawning stock is reduced (Walsh et al. 2006; Venturelli et al. 2012). Moreover, the population's spawning biomass may be depleted to a point where depensation could limit the overall reproductive success of fish that escape the trap fishery (Rowe and Hutchings 2003; Gascoigne and Lipcius 2004; Secor 2015). A well-managed fishery will minimize the harvest of these age-classes with a goal of 0%. In the assessment of an unmanaged fishery like that of Anaa Atoll, the presence of 30% to 40% of megaspawners in a stock would be considered a healthy age structure and less than 20% of megaspawners in the catch composition would suggest that a state of overexploitation exists (Froese 2004). However, the estimated size of a megaspawner was different between the two Hoenig (1983) and Hoenig<sub>nls</sub> rates of  $M$  and the later ( $L_{\text{mega}} = 57$  cm FL) suggests that the proportion of megaspawners is relatively high. This discrepancy is a result of the two rates of natural mortality used in this study, and given the uncertainty in the estimation of this parameter, we were unable to definitively assess the status of megaspawners in this stock. The limitations of the interpretation of Froese indicators have been explored in Cope and Punt (2009), and following their recommendations, both outputs suggest that the spawning biomass is likely less than 40% or 25% of its unfished potential and recruitment overfishing could be effecting this population (Cope and Punt 2009).

Historically, there was a limited number of traps in this fishery, and it was likely sustainable due to the inefficiency of rudimentary fishing technology and the limited capacity to preserve large amounts of fish (Torrente 2015). However, after a series of cyclones devastated the atoll in the

early 1980s (Dupon 1984), small-scale economic development and food acquisition during the reconstruction of the atoll was supported by a rapid proliferation in the number of traps (Filous, personal communications with residents of Anaa Atoll), and this is a classic case of overcapitalization of a fishery (Greboval and Munro 1999; Clark and Munro 2002). In the adjacent Rangiroa Atoll, the maximum economic yield was estimated to be 10 traps and well below the predicted maximum sustainable yield of 53 traps (Chauvet and Galzin 1996). Furthermore, the pulse nature of spawning and correlated surges in catch leads to oversupply (De Mitcheson and Erisman 2012), and during peak spawning activity fishers are frequently forced to sell bonefish in seven fish per packet as opposed to the standard five, and in some cases fish are released in poor condition after being held for weeks due to lack of market demand (A. Filous, personal observation). This suggests that in addition to overfishing the current trapping effort does not increase economic benefits to fishers but rather reduces individual catches, leads to oversupply, and marginalizes profits, with worrying long-term consequences to the fishery.

Although our data provides only a recent window into the time series changes in this fishery, our results suggest that the stock is being fished at a level that is economically inefficient and at risk of impairing recruitment. While the fishery continues to provide yield, the collapse of fisheries under heavy exploitation is often preceded by a period of stability in catch rates, and these plateau-style collapses, which are often a result of depensation (i.e., Allee effects from reduced spawner abundance), provide false impressions of fisheries equilibrium (Mullon et al. 2005). Catch rates are known to be hyperstable in spawning aggregations, and declines are first realized in adjacent sectors of the fishery (De Mitcheson and Erisman 2012). There is some evidence to suggest that this phenomenon is occurring on Anaa, as local ecological knowledge indicates that bonefish have become increasingly harder to catch in the traditional fishing holes in the lagoon, where they were customarily targeted with hook and line. Furthermore, elder residents indicate that prior to the late 1980s bonefish spawning aggregations were so plentiful that during their migrations the original stone traps would become completely saturated and thousands of the fish could be captured throughout the entire breadth of the passageways where the artisanal fish traps now operate (Filous, personal communications with residents of Anaa Atoll). The apparent consistency of our results and the observations of the community's elder generations citing marked declines highlight the utility of the SPR in modeling the current status of a fishery in data-limited scenarios (Prince et al. 2011; Hordyk et al. 2015a, 2015b, 2015c; Ault et al. 2018).

The albulid fisheries of Oceania are integral to the region's culture, food security, and economic development but have been impacted by anthropogenic harvest and habitat modification throughout their range (Beets 2000; Johannes and Yeeting 2000; Friedlander et al. 2007; Adams et al. 2013; Allen 2014; Wallace 2015). The bonefish fishery at Anaa Atoll exhibits symptoms of overexploitation of its spawning aggregations and epitomizes the challenges faced by this species and society (Sadovy 2005; Sadovy and Domeier 2005; Domeier 2012). Given the severity of overexploitation, there is an urgent need to manage this fishery as recovery from collapse often takes decades and requires more extreme regulations (Myers et al. 1995; Hutchings 2006). However, any action must appreciate the humanitarian importance of the trap fishery and its contribution to commercial markets, food security, and the cultural heritage of the residents of Anaa Atoll. We emphasize the need to manage the fishery to preserve both the ecosystem and the cultural services that bonefish provide to this socioecological system. Here we discuss potential management solutions that will improve the sustainability of the trap fishery while maintaining a judicious level of subsistence harvest.

Although this albulid is fished with a variety of gear types throughout the atoll, management should focus on the harvest of spawning aggregations (Danylchuk et al. 2011; Adams et al. 2013, 2018). To this aim, the establishment of a slot limit that protects both newly mature spawning females and megaspawners is a commonly utilized catch control in fisheries management (Froese 2004; Gwinn et al. 2015). However, though theoretically effective, given the nature of the fishery where catches are brailed or netted from the traps in large quantities, we believe this solution will be hard to implement and there are many unanswered questions regarding the postrelease fate of these fish after interactions with humans (Coggins et al. 2007; Lennox et al. 2017). Furthermore, owing to the nature of this spawning-aggregation fishery in which bonefish are not vulnerable to capture until sexual maturity, the lower bound of the size limit is naturally enforced by the reproductive biology of the species. Given the uncertainty surrounding the estimation of natural mortality and the discrepancy in our results on the exact size of a megaspawner, we were unable to specify the effective size to protect that would conserve this component of the spawning stock. Finally, even if length-based harvest restrictions are implemented, if fishing mortality remains high and unmanaged in younger age-classes, not enough recruits will survive to reach the size of a megaspawner for this management strategy to be effective. Thus, the establishment of length-based harvest restrictions should not be a management priority. Alternatively, as noted above, the fishery is overcapitalized and the migratory passes from the lagoon to the ocean are saturated with traps. Although

the number of traps actively fishing is only a fraction of the number historically available, fishing effort (i.e., the number of traps) must be adjusted to match population size and the overall health of the resource. Therefore, we propose fishers, local government, and the regional fisheries authority work together to cap the number of active traps permitted in the atoll's migratory corridors so that fishing capacity can be matched to the size of the resource. However, this is a long-term solution that will require considerable effort and collaboration with stakeholders, both at the local and national level. The critical state of the population indicates more immediate action is required to prevent the collapse of this fishery.

Consequently, spatiotemporal closures in the atoll's migratory corridors during peak reproductive activity provide an easily enforceable, low-economic-impact, and biologically effective management solution (Heppell et al. 2012; Gruss et al. 2014; Erisman et al. 2017). The most significant finding of this research in regard to this management option is the apparent difference in the sex ratios of bonefish aggregations throughout the course of the spawning season. This suggests that the majority of the population's females synchronize their egg development and spawn together during the beginning of the season. Previous work has proposed the resurgence of traditional management in the form of a rahui (the traditional conservation method of Eastern Polynesia) during the waning gibbous moon phase (Filous et al. 2019a, 2019b). The results of the present study demonstrate that the most efficient period to institute a rahui, while at the same time maintain a level of traditional harvest, may be to protect the first three moon phases of the spawning season in March, April, and May by the removal of chicken wire from the cod end of the traps and subsequently open the fishery for the remainder of the year. In doing so, a significant proportion of females would be allowed to spawn (i.e., maximizing egg production), ensuring a series of reproductive events and reducing overall fishing mortality to both the female and male components of the population. Along with these management actions, continued yearly monitoring of the size structure of fish harvested during the open season would allow the efficacy of these seasonal closures to be evaluated.

Given the urgent need for management and the failure of many top-down management regimes in Oceania (Johannes 1978, 1998; Friedlander 2018), we recommend a community-based management approach to implementing these conservation actions based on local participation in the monitoring of the resource (McClanahan et al. 1997; Wilson et al. 2006; Danielsen et al. 2007; Jokieli et al. 2011; Ayers and Kittinger 2014; Schemmel et al. 2016; Vaughan et al. 2017). Rahui is the traditional conservation method of Eastern Polynesia in which a community can choose to restrict the use of an area or resource that is in decline

and provides a socially robust method of management. Rahui can include spatial closures, seasonal closures, size limits, or any other form of regulatory measure that is enacted to preserve a scarce resource (Bambridge 2016). To this aim, our results were presented to the community of Anaa Atoll by the local school and the government established an Educational Managed Marine Area (EMMA), which overlaps with the bonefish migratory corridor adjacent to Tukahora village (<https://www.radio1.pf/anaa-a-son-aire-marine-educative/>). As part of this EMMA, the atoll's school children were taught the biology of bonefish and the importance of megaspawners and their representatives worked with the atoll's fishers and stakeholder groups to petition the community for the institution of a temporal rahui inside the EMMA during the three critical months described above. Given that their habitat is pristine and the high fecundity of bonefish, we project the bonefish population will recover under this management regime. Our estimate of generational turnover time suggests that it will take 12 years to yield a meaningful recovery of the resource, but given the age of maturity and recruitment to the fishery, we expect measurable changes in population abundance within 4–5 years. In light of these positive management outcomes, our results provide an important reference point from which this population can be monitored in future years.

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## REFERENCES

- Adams, A. J., A. Z. Horodysky, R. S. McBride, K. Guindon, J. Shenker, T. C. Macdonald, H. D. Harwell, R. Ward, and K. Carpenter. 2013. Global conservation status and research needs for tarpons (Megalopidae), ladyfishes (Elopidae) and bonefishes (Albulidae). *Fish and Fisheries* 15:280–311.
- Adams, A. J., J. M. Shenker, Z. Jud, J. Lewis, E. Carey, and A. J. Danylchuk. 2018. Identifying pre-spawning aggregation sites for the recreationally important bonefish (*Albula vulpes*) to inform conservation. *Environmental Biology of Fishes* 102:159–173.
- Allen, M. S. 2014. The historical role of bonefishes (*Albula* spp.) in Polynesian fisheries. Pages 51–72 in W. K. McElroy and E. Komori, editors. Hawaiian archaeology special publication no. 4, papers in honor of Dr. Yoshihiko Sinoto. Society for Hawaiian Archaeology, Honolulu.
- Allison, E. H., and F. Ellis. 2001. The livelihoods approach and management of small-scale fisheries. *Marine Policy* 25:377–388.
- Allison, E. H., A. L. Perry, M. C. Badjeck, W. Neil Adger, K. Brown, D. Conway, A. S. Halls, G. M. Pilling, J. D. Reynolds, N. L. Andrew, and N. K. Dulvy. 2009. Vulnerability of national economies to the impacts of climate change on fisheries. *Fish and Fisheries* 10:173–196.
- Ault, J., R. Humston, M. Larkin, E. Perusquia, N. Farmer, J. Luo, N. Zurcher, J. Posada, S. Smith, L. Barbieri, and M. Posada. 2007. Biology and management of the world tarpon and bonefish fisheries. Pages 217–258 in J. Ault, editor. Population dynamics and resource ecology of atlantic tarpon and bonefish. CRC Press, Boca Raton, Florida.
- Ault, J. S., S. G. Smith, J. A. Bohnsack, J. Luo, M. H. Stevens, G. T. DiNardo, M. W. Johnson, and D. R. Bryan. 2018. Length-based risk analysis for assessing sustainability of data-limited tropical reef fisheries. *ICES Journal of Marine Science* 76:165–180.
- Ault, J. S., S. G. Smith, J. Luo, M. E. Monaco, and R. S. Appeldoorn. 2008. Length-based assessment of sustainability benchmarks for coral reef fishes in Puerto Rico. *Environmental Conservation* 35:221–231.
- Ayers, A. L., and J. N. Kittinger. 2014. Emergence of co-management governance for Hawai'i coral reef fisheries. *Global Environmental Change* 28:251–262.
- Bambridge, T., editor.. 2016. The rahui: legal pluralism in Polynesian traditional management of resources and territories. ANU Press, Canberra, Australia.
- Beamish, R. J., G. A. McFarlane, and A. Benson. 2006. Longevity over-fishing. *Progress in Oceanography* 68:289–302.
- Beets, J. 2000. Declines in finfish resources in Tarawa lagoon, Kiribati, emphasize the need for increased conservation effort. *Atoll Research Bulletin* 490.
- Bell, J. D., M. Kronen, A. Vunisea, W. Nash, G. Keeble, A. Demmke, S. Pontifex, and S. Andrefouet. 2009. Planning the use of fish for food security in the Pacific. *Marine Policy* 33:64–76.
- Berkeley, S. A., C. Chapman, and S. M. Sogard. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* 85:1258–1264.
- Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29(8):23–32.
- Beverton, R. J. H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *Journal of Fish Biology* 41:137–160.
- Birkeland, C., and P. K. Dayton. 2005. The importance of fishery management of leaving the big ones. *Trends in Ecology and Evolution* 20:356–358.
- Brooks, E. N., J. E. Powers, and E. Cortés. 2010. Analytical reference points for age-structured models: application to data-poor fisheries. *ICES Journal of Marine Science* 67:165–175.
- Chapman, D. G., and D. S. Robson. 1960. The analysis of a catch curve. *Biometrics* 16:354–368.
- Chauvet, C., and R. Galzin. 1996. The lagoon fisheries of French Polynesia. *Naga the ICLARM Quarterly* 19:37–40.
- Clark, C. W., and G. R. Munro. 2002. The problem of overcapacity. *Bulletin of Marine Science* 70:473–483.
- Clark, W. G. 2002.  $F_{35\%}$  revisited ten years later. *North American Journal of Fisheries Management* 22:251–257.
- Claydon, J. 2004. Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. *Oceanography and Marine Biology: An Annual Review* 42:265–302.
- Clua, E., B. Beliaeff, C. Chauvet, G. David, J. Ferraris, M. Kronen, M. Kulbicki, P. Labrosse, Y. Letourneur, D. Pelletier, O. Thébaud, and M. Léopold. 2005. Towards multidisciplinary indicator dashboards for coral reef fisheries management. *Aquatic Living Resources* 18:199–213.
- Coggins, L. G., M. J. Catalano, M. S. Allen, W. E. Pine, and C. J. Walters. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries* 8:196–210.
- Cope, J. M., and A. E. Punt. 2009. Length-based reference points for data-limited situations: applications and restrictions. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 1:169–186.
- Crabtree, R. E., C. W. Harnden, and C. Stevens. 1994. Age, growth, and mortality of bonefish, *Albula vulpes*, from the waters of the Florida Keys. U.S. National Marine Fisheries Service Fishery Bulletin 94:442–451.
- Cuetos-Bueno, J., D. Hernandez-Ortiz, C. Graham, and P. Houk. 2018. Human and environmental gradients predict catch, effort, and species composition in a large Micronesian coral-reef fishery. *PLoS ONE* [online serial] 13(5):e0198068.
- Danielsen, F., M. M. Mendoza, A. Tagtag, P. A. Alviola, D. S. Balete, A. E. Jensen, M. Enghoff, and M. K. Poulsen. 2007. Increasing conservation management action by involving local people in natural resource monitoring. *Ambio* 36:566–570.
- Danylchuk, A. J., S. J. Cooke, T. L. Goldberg, C. D. Suski, K. J. Murchie, S. E. Danylchuk, A. D. Shultz, C. R. Haak, E. J. Brooks, A. Oronti, J. B. Koppelman, and D. P. Philipp. 2011. Aggregations and offshore movements as indicators of spawning activity of bonefish (*Albula vulpes*) in The Bahamas. *Marine Biology* 158:1981–1999.
- DeMartini, E. E., A. M. Friedlander, S. A. Sandin, and E. Sala. 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology Progress Series* 365:199–215.
- Depczynski, M., and D. R. Bellwood. 2006. Extremes, plasticity, and invariance in vertebrate life history traits: insights from coral reef fishes. *Ecology* 87:3119–3127.

- De Mitcheson, Y. S., A. Cornish, M. Domeier, P. L. Colin, M. Russell, and K. C. Lindeman. 2008. A global baseline for spawning aggregations of reef fishes. *Conservation Biology* 22:1233–1244.
- De Mitcheson, Y. S., and B. Erisman. 2012. Fishery and biological implications of fishing spawning aggregations, and the social and economic importance of aggregating fishes. *Fish and Fisheries Series* 35: 225–284.
- Diekert, F. K. 2012. Growth overfishing: the race to fish extends to the dimension of size. *Environmental and Resource Economics* 52: 549–572.
- Domeier, M. L. 2012. Revisiting spawning aggregations: definitions and challenges. *Fish and Fisheries Series* 35:1–20.
- Dupon, J. F. 1984. Where the exception confirms the rule: the cyclones of 1982–1983 in French Polynesia. *Disasters* 8:34–47.
- Erisman, B., W. Heyman, S. Kobara, T. Ezer, S. Pittman, O. Aburto-Oropeza, and R. S. Nemeth. 2017. Fish spawning aggregations: where well-placed management actions can yield big benefits for fisheries and conservation. *Fish and Fisheries* 18:128–144.
- Fenner, D. 2012. Challenges for managing fisheries on diverse coral reefs. *Diversity* 4:105–160.
- Filous, A., R. R. Lennox, Robert J. Coleman, A. Friedlander, E. E. G. Clua, and A. J. Danylchuk. 2019a. Life-history characteristics of an exploited bonefish *Albula glossodonta* population in a remote South Pacific atoll. *Journal of Fish Biology* 95:562–574.
- Filous, A., R. J. Lennox, E. E. G. Clua, and A. J. Danylchuk. 2019b. Fisheries selectivity and annual exploitation of the principal species harvested in a data-limited artisanal fishery at a remote atoll in French Polynesia. *Ocean and Coastal Management* 178: 104818.
- Francis, R. C. 1974. Relationship of fishing mortality to natural mortality at the level of maximum sustainable yield under the logistic stock production model. *Journal of the Fisheries Board of Canada* 31:1539–1542.
- Friedlander, A. M. 2018. Marine conservation in Oceania: past, present, and future. *Marine Pollution Bulletin* 135:139–149.
- Friedlander, A. M., J. E. Caselle, J. Beets, C. G. Lowe, B. W. Bowen, T. K. Ogawa, and B. S. Anderson. 2007. Biology and ecology of the recreational bonefish fishery at Palmyra Atoll National Wildlife Refuge with comparisons to other Pacific islands. Pages 27–56 in J. S. Ault, editor. *Biology and management of the world tarpon and bonefish fisheries*. CRC Press, Boca Raton, Florida.
- Friedlander, A. M., and E. E. DeMartini. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Marine Ecology Progress Series* 230:253–264.
- Friedlander, A. M., J. Nowlis, and H. Koike. 2015. Improving fisheries assessments using historical data: stock status and catch limits. Pages 91–118 in J. N. Kittinger, L. McClenachan, K. B. Gedan, and L. K. Blight, editors. *Marine historical ecology in conservation: applying the past to manage for the future*. University of California Press, Berkeley.
- Froese, R. 2004. Keep it simple: three indicators to deal with overfishing. *Fish and Fisheries* 5:86–91.
- Froese, R., and C. Binohlan. 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. *Journal of Fish Biology* 56:758–773.
- Gascoigne, J., and R. N. Lipcius. 2004. Allee effects in marine systems. *Marine Ecology Progress Series* 269:49–59.
- Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *Canadian Special Publication of Fisheries and Aquatic Sciences* 120:67–81.
- Greboval, D., and G. Munro. 1999. Overcapitalization and excess capacity in world fisheries: underlying economics and methods of control. Food and Agriculture Organization of the United Nations Fisheries Technical Paper 386.
- Gruss, A., J. Robinson, S. S. Heppell, S. A. Heppell, and B. X. Semmens. 2014. Conservation and fisheries effects of spawning aggregation marine protected areas: what we know, where we should go and what we need to get there. *ICES Journal of Marine Science* 71:1515–1534.
- Gulland, J., and L. K. Boerema. 1973. Scientific advice on catch levels. U.S. National Marine Fisheries Service Fishery Bulletin 71:325–335.
- Gwinn, D. C., M. S. Allen, F. D. Johnston, P. Brown, C. R. Todd, and R. Arlinghaus. 2015. Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. *Fish and Fisheries* 16:259–281.
- Heppell, S. A., B. X. Semmens, S. K. Archer, C. V. Pattengill-Semmens, P. G. Bush, C. M. McCoy, S. S. Heppell, and B. C. Johnson. 2012. Documenting recovery of a spawning aggregation through size frequency analysis from underwater laser calipers measurements. *Biological Conservation* 155:119–127.
- Hewitt, D. A., and J. M. Hoenig. 2005. Comparison of two approaches for estimating natural mortality based on longevity. U.S. National Marine Fisheries Service Fishery Bulletin 103:433–437.
- Hixon, M. A., D. W. Johnson, and S. M. Sogard. 2014. BOFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science* 71:2171–2185.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. U.S. National Marine Fisheries Service Fishery Bulletin 82:898–903.
- Holt, S. J. 1958. The evaluation of fisheries resources by the dynamic analysis of stocks, and notes on the time factors involved. International Commission for the Northwest Atlantic Fisheries Special Publication 1:77–95.
- Hordyk, A., K. Ono, K. Sainsbury, N. Loneragan, and J. Prince. 2015a. Some explorations of the life history ratios to describe length composition, spawning-per-recruit and the spawning potential ratio. *ICES Journal of Marine Science* 72:204–216.
- Hordyk, A., K. Ono, S. Valencia, N. Loneragan, and J. Prince. 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 Journal of Marine Science* 72:217–231.
- Hordyk, A. R. 2019. Package LBSPR. Available: <https://cran.r-project.org/web/packages/LBSPR/index.html>. (November 2019).
- Hordyk, A. R., N. R. Loneragan, and J. D. Prince. 2015c. An evaluation of an iterative harvest strategy for data-poor fisheries using the length-based spawning potential ratio assessment methodology. *Fisheries Research* 171:20–32.
- Houk, P., J. Cuetos-Bueno, B. Tibbatts, and J. Gutierrez. 2018. Variable density dependence and the restructuring of coral-reef fisheries across 25 years of exploitation. *Scientific Reports* 8:5725.
- Houk, P., K. Rhodes, J. Cuetos-Bueno, S. Lindfield, V. Fread, and J. L. McIlwain. 2012. Commercial coral-reef fisheries across Micronesia: a need for improving management. *Coral Reefs* 31:13–26.
- Houk, P., R. Tilfas, M. Luckymis, O. Nedlic, B. Ned, J. Cuetos-Bueno, and M. McLean. 2017. An applied framework to assess exploitation and guide management of coral-reef fisheries. *Ecosphere* 8:e01727.
- Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution* 25:633–642.
- Hutchings, J. A. 2006. Collapse and recovery of marine fishes. *Letters to Nature* 406:882–885.
- Hutchings, J. A., and J. D. Reynolds. 2004. Marine fish population collapses: consequences for recovery and extinction risk. *BioScience* 54:297.
- Jackson, J. B., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A.

- Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637.
- Johannes, R. E. 1978. Traditional marine conservation methods in Oceania and their demise. *Annual Review of Ecology and Systematics* 9:349–364.
- Johannes, R. E. 1998. The case for data less marine resource management: examples from tropical nearshore finfisheries. *Trends in Ecology and Evolution* 13:243–246.
- Johannes, R. E., and B. Yeeting. 2000. I-Kiribati knowledge and management of Tarawa's lagoon resources. *Atoll Research Bulletin* 489.
- Johnson, A. E., J. E. Cinner, M. J. Hardt, J. Jacquet, T. R. McClanahan, and J. N. Sanchirico. 2013. Trends, current understanding and future research priorities for artisanal coral reef fisheries research. *Fish and Fisheries* 14:281–292.
- Jokiel, P. L., K. S. Rodgers, W. J. Walsh, D. A. Polhemus, and T. A. Wilhelm. 2011. Marine resource management in the Hawaiian archipelago: the traditional Hawaiian system in relation to the western approach. *Journal of Marine Biology* 2011:1–16.
- Kamikawa, K. T., A. M. Friedlander, K. K. Harding, A. Filous, M. K. Donovan, and E. Schemmel. 2015. Bonefishes in Hawai'i and the importance of angler-based data to inform fisheries management. *Environmental Biology of Fishes* 98:2147–2157.
- Kenchington, T. J. 2014. Natural mortality estimators for information-limited fisheries. *Fish and Fisheries* 15:533–562.
- Kindsvater, H. K., M. Mangel, J. D. Reynolds, and N. K. Dulvy. 2016. Ten principles from evolutionary ecology essential for effective marine conservation. *Ecology and Evolution* 6:2125–2138.
- Lennox, R. J., A. Filous, S. C. Danylchuk, S. J. Cooke, J. W. Brownscombe, A. M. Friedlander, and A. J. Danylchuk. 2017. Factors influencing postrelease predation for a catch-and-release tropical flats fishery with a high predator burden. *North American Journal of Fisheries Management* 37:1045–1053.
- Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish Populations. *Fisheries Research* 56:125–131.
- Mace, P. M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* 51:110–122.
- McClanahan, T. R., H. Glaesel, J. Rubens, and R. Kiambo. 1997. The effects of traditional fisheries management on fisheries yields and the coral-reef ecosystems of southern Kenya. *Environmental Conservation* 24:105–120.
- Mullon, C., P. Freon, and P. Cury. 2005. The dynamics of collapse in world fisheries. *Fish and Fisheries* 6:111–120.
- Murawski, S. A., P. J. Rago, and E. A. Trippel. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. *ICES Journal of Marine Science* 58:1002–1014.
- Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenberg. 1995. Population dynamics of exploited fish stocks at low population levels. *Science* 269:1106–1108.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1997. Why do fish stocks collapse? The example of cod in Atlantic. *Ecological Applications* 7:91–106.
- Myers, R. A., and G. Mertz. 1998. The limits of exploitation: a precautionary approach. *Ecological Applications* 8(sp1):S165–S169.
- Nadon, M. O., J. S. Ault, I. D. Williams, S. G. Smith, and G. T. Dinardo. 2015. Length-based assessment of coral reef fish populations in the main and Northwestern Hawaiian Islands. *PLoS ONE [online serial]* 10(8):e01339601.
- Neil, A. L., C. Bene, S. J. Hall, E. H. Allison, S. Heck, and B. D. Ratner. 2007. Diagnosis and management of small-scale fisheries in developing countries. *Fish and Fisheries* 8:227–240.
- O'Farrell, M. R., and L. W. Botsford. 2006. The fisheries management implications of maternal-age-dependent larval survival. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2249–2258.
- Ogle, D. H., P. Wheeler, and A. Dinno. 2019. Fisheries stock analysis. R package version 0.8.25. Available: <https://github.com/droglenc/FSA>. (November 2019).
- Pascual, M. A., and O. O. Iribarne. 1993. How good are empirical predictions of natural mortality. *Fisheries Research* 16:17–24.
- Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* 10:430.
- Pauly, D. 1997. Small-scale fisheries in the tropics: marginality, marginalization, and some implications for fisheries management. Pages 40–49 in E. K. Pikitch, D. D. Huppert, and M. P. Sissenwine, editors. *Global trends: fisheries management*. American Fisheries Society, Symposium 20, Bethesda, Maryland.
- Pauly, D., V. Christensen, S. Guénette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. *Nature* 418:689–695.
- Prince, J. D., N. A. Dowling, C. R. Davies, R. A. Campbell, and D. S. Kolody. 2011. A simple cost-effective and scale-less empirical approach to harvest strategies. *ICES Journal of Marine Science* 68:947–960.
- Prince, J., S. Victor, and A. Hordyk. 2015. Length based SPR assessment of eleven Indo-Pacific coral reef fish populations in Palau. *Fisheries Research* 171:42–58.
- Reynolds, J. D., N. K. Dulvy, N. B. Goodwin, and J. A. Hutchings. 2005. Biology of extinction risk in marine fishes. *Proceedings of the Royal Society B: Biological Sciences* 272:2337–2344.
- Rowe, S., and J. A. Hutchings. 2003. Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology and Evolution* 18:567–572.
- Sadovy, Y. 2005. Trouble on the reef: the imperative for managing vulnerable and valuable fisheries. *Fish and Fisheries* 6:167–185.
- Sadovy, Y., and M. Domeier. 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs* 24:254–262.
- Sandin, S. A., J. E. Smith, E. E. Demartini, E. A. Dinsdale, S. D. Donner, A. M. Friedlander, T. Konotchick, M. Malay, J. E. Maragos, D. Obura, G. Paulay, M. Richie, F. Rohwer, R. E. Schroeder, S. Walsh, J. B. C. Jackson, N. Knowlton, and E. Sala. 2008. Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE [online serial]* 3(2):e1548.
- Sasikumar, G., K. S. Mohamed, P. Rohit, and G. Sampathkumar. 2015. Can an aggregation-fishery be responsible for recruitment overfishing? A case study on cuttlefish stock associated with moored fish aggregation devices (FADs). *Fisheries Research* 172:148–156.
- Schemmel, E., A. M. Friedlander, P. Andrade, K. Keakealani, L. M. Castro, C. Wiggins, B. A. Wilcox, Y. Yasutake, and J. N. Kittinger. 2016. The codevelopment of coastal fisheries monitoring methods to support local management. *Ecology and Society* 21(4):art.34.
- Secor, D. H. 2015. *Migration ecology of marine fishes*. Johns Hopkins University Press, Baltimore, Maryland.
- Smith, M. W., A. Y. Then, C. Wor, G. Ralph, K. H. Pollock, and J. M. Hoenig. 2012. Recommendations for catch-curve analysis. *North American Journal of Fisheries Management* 32:956–967.
- Stacey, P., and M. Taper. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2:19–29.
- Then, A. Y., J. M. Hoenig, N. G. Hall, and D. A. Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science* 72:82–92.
- Thorson, J. T., and M. H. Prager. 2011. Better catch curves: incorporating age-specific natural mortality and logistic selectivity. *Transactions of the American Fisheries Society* 140:356–366.

- Torrente, F. 2015. Ancestral fishing techniques and rites on Anaa Atoll, Tuamotu Islands, French Polynesia. *SPC Traditional Marine Resource Management and Knowledge Information Bulletin* 35:18–25.
- Usseglio, P., A. M. Friedlander, H. Koike, J. Zimmerhackel, A. Schuhbauer, T. Eddy, and P. Salinas-de-León. 2016. So long and thanks for all the fish: overexploitation of the regionally endemic Galapagos grouper *Mycteroperca olfax* (Jenyns, 1840). *PLoS ONE* [online serial] 11(10):e0165167.
- Vaughan, M. B., B. Thompson, and A. L. Ayers. 2017. *Pāwehe Ke Kai a'o Hā'ena*: creating state law based on customary indigenous norms of coastal management. *Society and Natural Resources* 30:31–46.
- Venturelli, P. A., B. J. Shuter, and C. A. Murphy. 2012. Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. *Proceedings of the Royal Society B: Biological Sciences* 276:919–924.
- Vetter, E. F. 1987. Estimation of natural mortality in fish stocks: a review. *U.S. National Marine Fisheries Service Fishery Bulletin* 86:25–43.
- Wallace, E. M. 2015. High intraspecific genetic connectivity in the Indo-Pacific bonefishes: implications for conservation and management. *Environmental Biology of Fishes* 98:2173–2186.
- Walsh, M. R., S. B. Munch, S. Chiba, and D. O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecology Letters* 9:142–148.
- Walters, C., and P. H. Pearse. 1996. Stock information requirements for quota management systems in commercial fisheries. *Reviews in Fish Biology and Fisheries* 6:21–42.
- Wilson, D. C., J. Raakjær, and P. Degnbol. 2006. Local ecological knowledge and practical fisheries management in the tropics: a policy brief. *Marine Policy* 30:794–801.
- Worm, B., R. Hilborn, J. K. Baum, T. A. Branch, J. S. Collie, C. Costello, M. J. Fogarty, E. A. Fulton, J. A. Hutchings, S. Jennings, O. P. Jensen, H. K. Lotze, P. M. Mace, T. R. McClanahan, C. Minto, S. R. Palumbi, A. M. Parma, D. Ricard, A. A. Rosenberg, R. Watson, and D. Zeller. 2009. Rebuilding global fisheries. *Science* 325:578–585.
- Zhou, S., S. Yin, J. T. Thorson, A. D. M. Smith, M. Fuller, and C. J. Walters. 2012. Linking fishing mortality reference points to life history traits: an empirical study. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1292–1301.