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Fisheries selectivity and annual exploitation of the principal species harvested in a data-limited artisanal fishery at a remote atoll in French Polynesia

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ABSTRACT

Artisanal fisheries are critically important to food security and economic opportunity in coastal communities throughout the developing world. However, the dynamics of these fisheries are poorly understood, and a basic understanding of the gear types and species harvested, is required to promote effective fisheries management. To this aim, we surveyed artisanal fishers at Anaa atoll from May 14th, 2016 to May 19th, 2017 and described the selectivity and exploitation of the fishery's dominant species. The harvested marine life included 98 species from 31 families, which were captured with seven gear types including artisanal fish traps, monofilament nets, spear guns, handlines, pole and line, hand, and harpoons. Bonefish (*Albula glossodonta*) were the most abundant species and comprised 25% of the overall catch, followed by *Chaetodon auriga*, *Kuhlia sandvicensis*, *Lutjanus fulvus*, and *Chanos chanos*. Artisanal fish traps and spearguns harvested a higher proportion of overexploited fishes, captured a more diverse range of species, and removed the most biomass from the atoll. An analysis of the size distribution of harvested fishes, with length-based catch curves, indicates that species with high natural mortality rates such as *Chanos chanos* and *Selar crumenophthalmus* were underexploited. While in contrast, slow growing, late maturing, and long-lived species such as *Naso lituratus* and *Epinephelus polyphekadion* were overexploited. The results of this research provided the community with the basis for making local management decisions regarding their fisheries resources, including the development of an Educational Managed Marine Area and a seasonal closure of the artisanal trap fishery to allow for movement, predominantly *A. glossodonta* during their offshore spawning migrations.

1. Introduction

Artisanal fisheries provide nutrition and mitigate the effects of poverty in coastal communities throughout the developing world (Ratner et al., 2007; Johnson et al., 2013). These critically important fisheries are defined by their small scale, utilization of traditional fishing methods, and contribution to local food security (Cochrane and Garcia, 2009). However, despite the limited capacity of artisanal fisheries, the overexploitation of their targeted species is commonplace and presents a major humanitarian and environmental challenge (Pauly, 1997; Allison et al., 2001; Worm et al., 2009). The preferential development of industrial fisheries, data deficiency, and the loss of traditional management infrastructure are often cited as reasons for the poor state of artisanal fisheries (Cycon, 1986; Mahon, 1997; Pauly, 1997). At present, co-management along with the promotion of leadership and social conscience of sustainable fisheries is proving to be a more effective approach to the management of artisanal fishing in remote communities (Jentoft, 2000; Gutiérrez et al., 2011; Kosamu, 2015; Freed et al., 2016; Romero Manrique de Lara and Corral, 2017).

The artisanal coral reef fisheries of Oceania exemplify this paradigm, as they are critical to food security, economic opportunity, and cultural practices throughout the region, but overfishing is pervasive across a gradient of human inhabitation (Friedlander and DeMartini, 2002; Newton et al., 2007; DeMartini et al., 2008; Sandin et al., 2008; Kronen et al., 2010). In the remote islands and atolls of French Polynesia, fish consumption is nearly double that of urban areas in the Pacific Islands, with artisanal fisheries providing the primary source of protein as well as a portion of expendable income for local inhabitants (South Pacific Commission, 1991; Dalzell et al., 1996; Gillett, 2000; Bell et al., 2009; Kittinger, 2013). Beyond protein and small scale commercial markets, these resources also have the potential to serve as a sustainable source of economic development in the form of ecotourism (Blamey, 2001; Bell et al., 2009; Barnett et al., 2016), and economic diversification is considered key to long-term success of artisanal

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fisheries (Allison et al., 2001). However, future projections suggest that coral reef fisheries will only be able to meet local demand for fish in 6 out of 22 Pacific Island countries and territories (Bell et al., 2009, 2015) and climate change is expected to accelerate declining fisheries yields (Cinner et al., 2012). The potential loss of ecosystem services provided by healthy fisheries undermines the capacity of these communities to persist into the future, making investment into research and management of tropical coral reef fisheries a priority for marine conservation (Holmlund and Hammer, 1999; Roberts et al., 2002; Palumbi et al., 2009).

Historically, Pacific Island societies maintained a rich tradition of marine resource conservation. These societies recognized the importance of the marine environment to their survival, their collective capacity to overexploit these limited resources, and developed intricate marine management systems to maintain healthy fisheries (Johannes, 1978b; 2002; Friedlander et al., 2014; Friedlander, 2018). In Eastern Polynesia, community based management actions taken to protect scarce or fragile resources were known as "*Rahui*" and involved strictly enforced conservation practices including customary marine tenure, closed areas or seasons, and prohibited take of certain species (Friedlander et al., 2013; Bambridge, 2016; Friedlander, 2018). However, the tradition of *Rahui* and many other customary management systems in the Pacific Region was lost with the introduction of westernized governments and currency based economies (Johannes, 1978b). The loss of traditional resource management systems was further complicated by the introduction of new fisheries technologies that enhanced both the capacity to harvest and preserve large quantities of marine life, such as boat engines, monofilament gillnets, commercially available hooks, freezers and freight transport between islands (Valdemarsen, 2001; Shomura, 2004). Despite their overwhelming importance, coral reef fisheries have proven difficult to conserve with contemporary top down fisheries management efforts because they constitute a diverse assemblage of species and life histories that are harvested with multiple gear types (Dalzell, 1996; Dalzell and Adams, 1996). Moreover, most communities that rely on artisanal fisheries cannot devote adequate resources for conventional stock assessment, management, and enforcement in order to ensure the long-term sustainability of their fisheries resources (Hughes et al., 2010; Fenner, 2012).

In response to declining fisheries under the status quo, there has been a cultural renaissance of community based management efforts throughout Oceania (Adams, 1998; Ruddle, 1998; Johannes, 2002; Friedlander et al., 2013; Friedlander, 2018). Community-based management has proven to be a more socially acceptable and biologically effective approach to artisanal fisheries management than the top-down approach used to manage industrialized fisheries in the Western world (Friedlander et al., 2003). These efforts have and continue to be based on the traditional ecological knowledge of local residents, but can be informed with scientific assessments and data driven management recommendations to facilitate effective community-based conservation actions (Aswani et al., 2007; Friedlander et al., 2014; Schemmel et al., 2016; Goodell et al., 2018).

Unfortunately, little formal data exist to help inform community-based conservation actions in remote islands, like that of Anaa atoll in the Tuamotu Archipelago, French Polynesia, and shifting baselines in resource abundance obscure perceptions on the current status of fisheries yields (Pauly, 1995). In these coral reef ecosystems, artisanal fisheries are typically characterized by unorganized groups of fishers who employ a wide range of gear types to harvest diverse fish assemblages (Saila and Roedel, 1979; Jennings and Polunin, 1996; Jennings et al., 1999) and the gear used to harvest fish have been shown to have specific impacts on these ecosystems and the sustainability of their respective fisheries (Dalzell, 1996; Jennings and Kaiser, 1998). Consequently, effective tropical fisheries assessment requires an understanding of the species harvested and dominant gear types (McClanahan et al., 2007; McClanahan and Cinner, 2008; McClanahan and Mangi, 2015). The purpose of our study was to assess the contemporary artisanal fishery on Anaa atoll by quantifying the extent of marine life harvested, diversity of species captured, the gear types used, and the exploitation status of its dominant species. This information was intended to support community-based management, by providing both informal and government authorities with an understanding of these dynamics in this previously undescribed fishery.

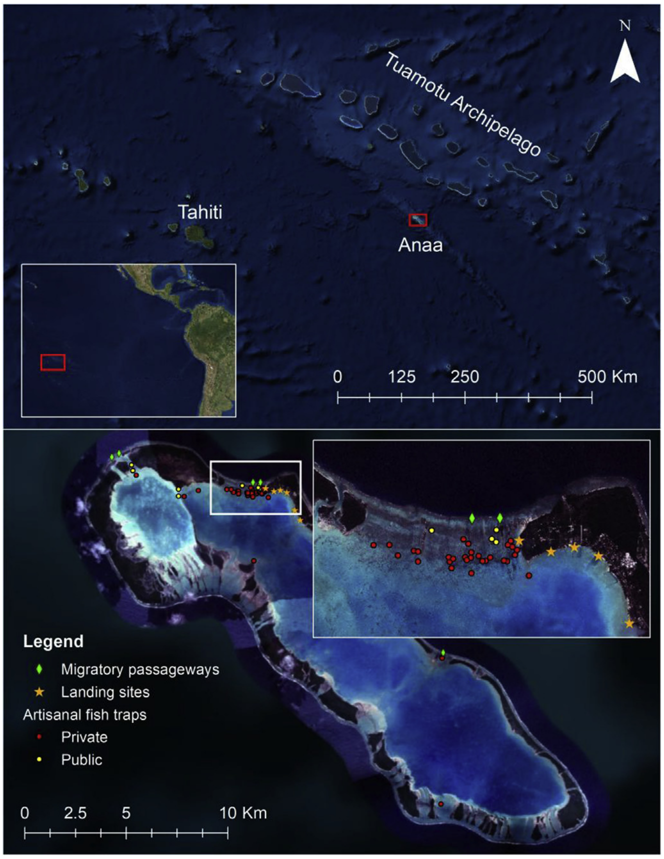

Fig. 1. Anaa atoll, with locations of artisanal fish traps and the locations of fisheries landing surveys around Tukuhora village (yellow circles indicate public traps, red circles indicate private traps, green diamonds indicate the locations of migratory passageways used by marine life and orange stars indicate landing sites). . (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2. Methods

2.1. Study site

Anaa is a small atoll (38 km^2) 350 km east of Tahiti, in the Tuamotu Archipelago of French Polynesia (Fig. 1). The atoll has one village, Tukuhora, with approximately 500 residents and at least five other abandoned settlements that were historically populated but are now impermanent dwellings for those harvesting copra, the island's principal economic export (ITSTAT, 1998). The land mass of Anaa is bordered by a coral reef that drops off into the open ocean (to depths of > 1000 m) and surrounds a shallow lagoon with 11 small islands known as "motu" and fringing sand flats. Unlike most atolls in the Tuamotu Archipelago, Anaa is closed and lacks a deep oceanic pass between its interior lagoon and outer reef. The reef crest forms a barrier around the atoll, and the few openings are characterized by small cuts in the reef crest and shallow back reef between motu. These openings are located along the atoll's eastern perimeter, but the majority of these breaks in the reef are situated in the Northeast of the atoll, adjacent to Tukuhora village (Fig. 1). There is limited tidal influence on the water movement in the lagoon and instead the water level is determined by the size and direction of the prevailing swell which can cause fluctuations in lagoon depth of several meters. The residents of Anaa are supplied by three different transport ships on rotation approximately once every 2–3 weeks. Residents can import and export food and other supplies to and from Tahiti, but the primary source of protein comes from artisanal fisheries harvest (Residents of Anaa atoll, personal communication).

2.2. Sampling of the artisanal fishery

To document the catch composition and fishing methods utilized to harvest marine resources in Anaa atoll, artisanal fishers were opportunistically surveyed in the marinas and landing sites at Tukuhora village from May 14th, 2016 to May 19th, 2017 (Fig. 1). During this time, we solicited local fishermen for the permission to sample their catches; all harvested fish were identified to the species level, counted, and measured in centimeters to their standard length (cm SL). In addition to measuring and identifying the harvested species, we determined and recorded the gear type used, fishing effort, number of fishers, location, and the habitat type from which the captured marine life was harvested through a dialogue with fishers. Artisanal fish traps locally known as *Kaua* are a prominent gear type in the atoll's fishery. In general, the traps are constructed from rocks and dead coral that are collected from the surrounding area and built into the shape of a spade. The traps function by re-shaping the natural habitat and funneling schooling fish into an enclosed section at the up current end of the trap (Fig. 2). The traps are located in choke points and back-reef habitats that serve as corridors between the lagoon and open ocean. These structures principally target fishes migrating between the two environments for reproduction or feeding and can only effectively fish when the water level in the lagoon is low as fish moving in the trap complex cannot traverse the shallow barrier of raised reef adjacent to the entrances of the oceanic passageways in the reef crest. Although, this gear type is passive, fishers increase their efforts during the waning moon phase to “splash fish”, for bonefish, using boats and personnel to drive schools into the traps, as described in Tarawa atoll (Johannes and Yeeting, 2000). To determine the number of fish traps in the lagoon, we conducted both ground and aerial surveys to enumerate the number of active and inactive traps. Then to estimate the area obstructed by artisanal fish traps in the atoll's principal movement corridor, we measured the linear distance between the end of each trap arm with georeferenced satellite imagery in Google Earth and added them together to obtain an estimate of the total linear distance obstructed by fish traps. The percentage of linear distance obstructed in the atoll's principal movement corridor was then calculated by dividing the value of total distance obstructed by the distance between either side of the landmasses surrounding Tukuhora village.

2.3. Statistical analysis

2.3.1. Species composition of the artisanal fishery

The species composition of the artisanal fishery was evaluated by calculating the number of a given species harvested by a given gear type and dividing this number by the total number of all the species in aggregate, that were taken by the gear. This metric provides the proportion of a given species in the overall catch and was used to assess the relative importance of each species in the entire artisanal fishery (all gear types) and across specific gear types to provide a measure of each species' contribution to a given sector of the artisanal fishery at Anaa atoll.

2.3.2. Relationships between gear types in fish assemblages

The catch composition of the artisanal fishery was analyzed by gear type to describe differences in the mean size of fish captured, catch per-unit effort (CPUE; kg/per-fisher/per-trip), species diversity, and mean trophic level among gear types. The mean standard length of harvested fish in each catch was calculated and we compared the mean standard length taken in catches made by the different gear types. Catch per-unit effort was determined in kilograms per fisherman per day by summing the total catch biomass in kilograms derived from applying species specific length-weight equations to the length measurements of harvested fish for a given catch and dividing it by the total number of fishers. The species diversity of catches made by each gear type was described with the Simpson's Index using the diversity function in the vegan package in R ((Oksanen et al., 2019); Equation (1)).

$$D = 1 - \sum p_i^2 \tag{1}$$

Equation (1): Simpson's Diversity index where D is an index of diversity ranging from 0 to 1 that signifies the probability that two randomly selected fish from a given catch will belong to a different species (1 = high diversity and 0 = low diversity) and p_i is the number of individuals belonging to each species divided by the total number of individuals in the sample (McClanahan and Mangi, 2015).

Finally, to estimate the trophic level targeted by the different gear types, the trophic level for each species was taken from FISHBASE (Froese and Pauly, 2000) and the mean trophic level of the catches made by each gear was then calculated (Equation (2)).

$$TL_k = \sum_{i=1}^{m} Y_{ik} TL / \sum Y_{ik} \tag{2}$$

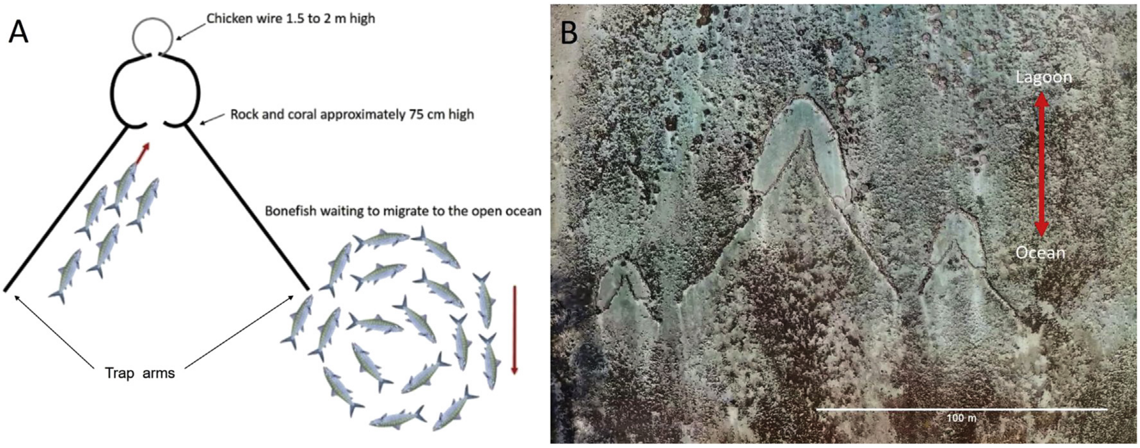

Fig. 2. Artisanal fish trap design and function at Anaa atoll (A), and areal image of fish traps in the atoll's principal migratory corridor between lagoon and oceanic habitats (B).

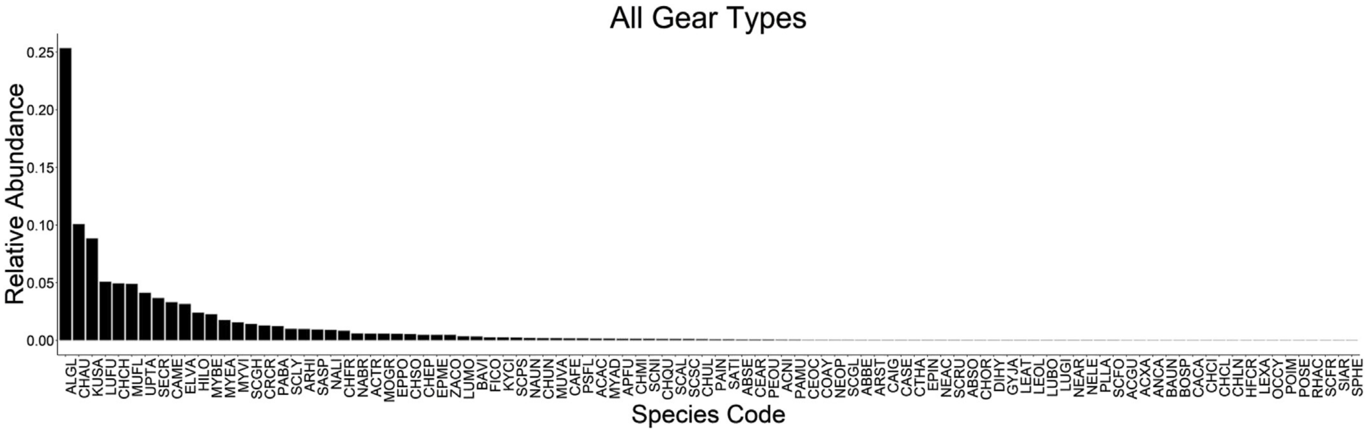

Fig. 3. The relative abundance (i.e., the proportion of a given species contribution to the overall catch) of the species harvested across all gear types in the artisanal fishery at Anaa atoll (see Table 1, for scientific names corresponding to four letter species codes).

Equation (2): Mean trophic level of fish species captured TL_k, where Y_{ik} is the catch of species i in gear k, TL is the trophic level of species i for m fish species (McClanahan and Mangi, 2015).

For all variables, differences among gear types were tested with linear models using the *lm* function in R. Post-hoc multiple comparisons were performed by the Tukey's honestly significant difference (HSD) test with the glht function in the multcomp package in R.

To visualize relationships in the degree of similarity among the species harvested and gear types, the catch data were ordinated by gear type using detrended correspondence analysis with the *decorana* function in the vegan package for R. This multivariate technique plots the species and the gears that harvested them in a two-dimensional space that reflects both the vulnerability of a given species to each gear and the similarity of the species assemblages that are harvested by the gear types. The closeness of a given species to a gear type in ordinated space indicates a higher selectivity of the species to that gear and the proximities between gear types reflect the similarity of fish assemblages harvested by those gears (McClanahan and Mangi, 2015). The top 25 percent of these species were then selected for plotting and further analysis using the *ordiselect* function in the goeveg package for R.

2.3.3. Fishing mortality and exploitation rates

To evaluate the exploitation rates of the atoll's principal fisheries species, both fishing and natural mortality were estimated and applied to the equation for fisheries exploitation following the methods of Caillart and Morize (1990). A literature review was conducted to acquire published estimates of the longevity ($t_{\max}$) for the top 25 species identified in the detrended correspondence analysis described above. Estimates of $t_{\max}$ were available for 10 of these species and their natural mortality rates were calculated with the Hoenig method, using the *M_empirical* function in TropFishR (Equation (3)).

$$\ln M = 1.46 - 1.01 \times \ln t_{max} \tag{3}$$

Equation (3): Hoenig estimate of tropical fish natural mortality as a function of life span, in which M is the estimated natural mortality rate and $t_{\max}$ is the longevity of the species (Hoenig, 1983).

The fishing mortality experienced by these 10-principal species was then estimated with length-based catch curves, a method of using regression inflection points to establish the timing of entry into a fishery and estimated the rate of mortality(Chapman and Robson, 1960). Standard lengths of each species were binned into 2-cm size classes and their length frequency distribution was log transformed. The peak in the catch curve (i.e., the mode of the length frequency distribution) for each species represents the length at which it is fully recruited to the fishery and the decline of individuals from the ensuing length-based cohorts to the last size class estimates the total (natural and fishing) instantaneous mortality (*Z*) experienced by the population. Linear regression was then used to estimate the slope of the catch curve and the instantaneous rate of total mortality (Z) for a given species. Fishing mortality (F) was then estimated for each species by deducting the natural mortality (M) and these results were then applied to the exploitation rate equation described by Gulland and Boerema (1973; Equation (4)).

$$E = \frac{F}{F + M} \tag{4}$$

Equation (4): Fish exploitation rate as a function of natural and fishing mortality. Where E is the estimated exploitation rate, M is the estimated natural mortality rate, and F is the estimated fishing mortality rate. Exploitation rates below 0.5 indicate the species is lightly exploited and exploitation values above 0.5 suggest that the species is heavily exploited and may be overfished (Gulland and Boerema, 1973; Caillart and Morize, 1990).

3. Results

3.1. Gear types and species composition of the artisanal fishery

We surveyed 258 catches from the artisanal fishery and sampled at total of 7519 fish and invertebrates during a one-year period at Anaa atoll. The harvested marine life included 98 different species from 31 families and were captured with seven gear types including artisanal fish traps (n = 3612), monofilament nets (n = 2291), spear guns (n = 804), handline (n = 342), pole and line (n = 178), hand (n = 149), and harpoons (n = 145). Fishing effort was distributed across five different habitats including, the back reef (52%), reef crest (21%), outer reef (9%), lagoon soft bottom (9%), lagoon hard bottom (4%), and inland saline ponds (4%). The most abundant species in the catch was short jaw bonefish (*Albula glossodonta*) contributing to 25% of the overall catch, followed by *Chaetodon auriga*, *Kuhlia sandvicensis*, *Lutjanus fulvus*, and *Chanos chanos*. Despite the overall high diversity of species captured in the fishery, together these top five species accounted for 54% of the total catch (Fig. 3). These dominant species were principally harvested with artisanal fish traps and monofilament gill nets.

Our survey identified 13 public fish traps throughout the atoll, but only four of these are regularly maintained. Fish from public traps are harvested on a first come first serve basis, with no limitations on what can be harvested by an individual person or family. It is illegal to sell fish harvested from the public traps, yet, the sale of fish captured in these public traps is common practice. In addition to the public traps, we identified approximately 36 private trap structures in the atoll and if all were activated (i.e., fitted with chicken wire) over 100% of the available linear distance in this movement corridor would be blocked

Fig. 4. Artisanal fishing at Anaa atoll. A spear fisher with his homemade spear gun and catch of *Sargocentron spiniferum, Myripristis sp.*, and *Epinephelus polyphekadion* (A), harpoon fishers with their home-made harpoons and catch of parrotfishes from the family *Scaridae* (B), net fishers deploying a monofilament gill net to encircle a school of *Selar crumenophthalmus* (C, note the location of the school highlighted by the red circle), trap fishers corralling *Albula glossodonta* into an artisanal fish trap (D, note the chicken wire cage material characteristic of a private trap), fishers collecting *Panulirus penicillatus* from the reef crest at night (E), and handline fishers targeting *Pseudobalistes flavimarginatus* and *Balistoides viridescens* from the back reef (F, note the captured fish being held in the rock pools indicated by the red circle). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

by artisanal fish traps. When active, these private traps are equipped with a chicken wire cage, supported by wood at the cod end of the trap. The mesh size of the chicken wire is 5 × 3.5 cm and the panels are 1.5 or 2 m in height, which enhances their ability to catch and hold fish at high water levels (Fig. 4). However, the cost of chicken wire and aproval by the Direction Des Resources Marines (DRM) limits the ability of people to utilize these traps and over the course of the study 8–12 private traps actively fished. Sixty-two different species were captured in the artisanal fish traps (Fig. 5), with the top five being *Albula glossodonta* (49%), *Mulloidichthys flavolineatus (8%), Upeneus taeniopterus (8%), Lutjanus fulvus (6%), and Chaetodon auriga* (5%).

Monofilament gill nets locally known as *Kope* range in dimensions from 25 to 100 m in length and 1–2 m in height with a stretched mesh of 3.5–12 cm. Nets are primarily used on soft bottom habitats or on the reef crest and net selection is generally determined by the target species and habitat type, but the most commonly used net dimensions are 50 m long x 1.5 m high. On the reef crest, a stretched mesh of 6.5 cm is used to target smaller fish such as flag tails (*Kuhlia sandvicensis*) and 10 cm stretched mesh is used to catch a variety of parrotfish species from the family *Scaridae*. Occasionally, larger fish such as bluefin trevally (*Caranx melampygus*), bonefish (*Albula glossodonta*) and adult milkfish (*Chanos chanos*) are targeted with 12 cm mesh, while 5 cm stretched mesh is used to target smaller fish such as scad mackerel (*Selar crumenophthalmus*) in the lagoon or juvenile milkfish harvested from inland saline ponds. These nets are most commonly fished in a surround net fashion, where the net is deployed to encircle the targeted fish; however, nets are sometimes set passively (Fig. 4). Over the course of the study 30 different species were taken with monofilament nets (Fig. 5) and the top five included *Kuhlia sandvicensis* (27%), *Chaetodon auriga* (23%), *Chanos chanos (16%)*, *Selar crumenophthalmus (12%),* and *Ellochelon vaigiensis* (7%).

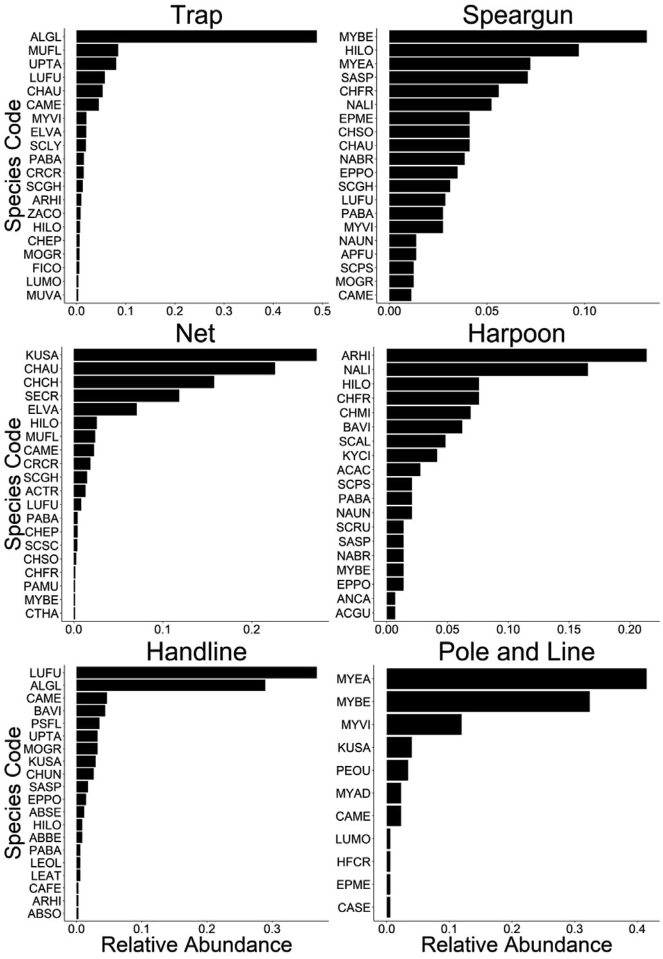

Fig. 5. The relative abundance (i.e., the proportion of a given species contribution to the overall catch) of the top 20 species harvested by each gear type in the artisanal fishery at Anaa atoll (see Table 1, for scientific names corresponding to four letter species codes).

Harpoons locally known as *Kauri* are custom made from a cut tree. The tapered wood is approximately 2.8 m long with three 30–35 cm long x 8 mm diameter iron rebar prongs that are fastened to the head of the spear with heavy nylon or cord. The harpoon is thrown at fish from above water while walking along the reef crest (Fig. 4). A total of 30 species were harvested with harpoons, the majority of which are large herbivores (Fig. 5) with the top five being *Arothron hispidus (21%)*, *Naso lituratus* (17%), *Hipposcarus longiceps* (8%), *Chlorurus frontalis* (8%), and *Chlorurus microrhinos* (7%). Harpoon fishing is predominantly opportunistic, and fishers harvest whatever species is encountered along the reef crest. However, the harpoon fishery for *Arothron hispidus* is a directed fishery where fishers wait at specific locations that serve as choke points for migrating pufferfish between the lagoon and ocean during the new moon phase.

Spear fishing locally known as *Pupuhi* is practiced throughout the atoll's inner lagoon hard bottom habitats and outer reef and fishers commonly use this method to target reef associated species during both day and night (Fig. 4). Locally and commercially made spear guns ranging in 1–1.8 m in spear shaft length are used to harvest marine life. Inside the lagoon, 1 m spear guns are used on hard bottom and coral outcrops, while on the outer reef larger guns ranging from 1.5 or 1.2 m in length are used. The largest guns are 1.8 m and rigged with a buoy for larger fish. Over the course of the study we documented 58 different species that were harvested with spearguns (Fig. 5), the top five of which include *Myripristis berndti* (13%), *Hipposcarus longiceps* (10%), *Myripristis earlei* (7%), *Sargocentron spiniferum* (7%), and *Chlorurus frontalis* (6%).

Handline fishing locally known as *Kanehu* is practiced in the lagoon on hard or soft bottom inner lagoon habitats (Fig. 4). The most common baits include hermit crabs, swimmer crabs and octopus. Over the course of the study 23 different species were harvested with handlines (Fig. 5), with the top five being *Lutjanus fulvus* (37%), *Albula glossodonta* (29%), *Caranx melampygus* (5%), *Balistoides viridescens* (4%), *and Pseudobalistes flavimarginatus* (3%). Bamboo pole and line is used on the reef crest at night and 11 different species were harvested with this method, but artisanal fishers primarily target nocturnally active soldierfishes from the genus *Myripristis* (Fig. 5). The top five species taken by pole and line include *Myripristis earlei* (41%), *Myripristis berndti* (32%), *Myripristis violacea* (12%), *Kuhlia sandvicensis* (4%), and *Pempheries oualensis* (3%). Finally, in addition to teleost fishes, fishers gather lobsters (*Panulirus penicillatus*) and other marine invertebrates (*Turbo sp., Tridacna sp.*) by hand in a practice known as *Kuhi-Rima*. These invertebrates are collected from the reef crest or by diving on the seaward side of the reef at night (Fig. 4). Lobsters are sold by the kilogram to commercial markets in Tahiti or sent to friends and family during the holidays or other special events.

3.2. *Differences in gear types*

Our investigation into size differences of fish harvested with each gear type demonstrates that the gear types can be separated into two groups based on the sizes of fish targeted. Smaller fishes are harvested by spearguns (22.27 ± 3.45 cm), nets (22.9 ± 7.7 cm) and pole and line (18.6 ± 3.8 cm). This trend is driven by the high abundance of soldierfishes (*Myripristis sp.*) taken by spear fishing, pole and line, and the large numbers of small fish taken by monofilament gill nets such as, *Chanos chanos*, *Selar crumenophthalmus,* and *Chaetodon auriga*. In contrast, the largest fish are taken by fish traps (34.9 ± 11 cm), handlines (30.8 ± 9.2 cm) and harpoons (33.3 ± 7.4 cm), as large numbers of bonefish are harvested by traps and handlines and harpoon catches are dominated by longer fish such as *Arothron hispidus* and large herbivorous reef fishes ($F = 16.34$, $P < .005$; Fig. 6). The atoll's artisanal fish traps yielded the highest average biomass at 9.3 ± 10.9 kg/fisher trip. The high average is due to the large catches of bonefish, which occur across a period of three days during the waning moon phase and can exceed 200 adults per trap. Catches with this gear type are inconsistent and characterized by small catches of assorted species and monthly large catches of bonefish associated with migratory events, hence a large standard deviation. The other gear types, monofilament gill nets (3.7 ± 3.5 kg), spear gun (3.1 ± 2.9 kg), harpoon (1.8 ± 1.5 kg), pole and line (1.8 ± 1.2 kg), and handlines (1.4 ± 1.0 kg) typically yield smaller but more consistent catches. Mean biomass harvested per-fisher was significantly greater between traps and the other gear types used in the fishery ($F = 13.08$, $P < .005$, Fig. 6). Catches made with spearguns were most diverse (0.76 ± .17), followed by pole and line (0.52 ± .3), harpoon (0.42 ± .33), trap (0.38 ± .33), handline (0.29 ± .26) and net (0.19 ± .25). These differences were significant ($F = 13.2$, $P < .005$), with Tukey multiple comparisons indicating that the mean species diversity harvested with spear guns, was significantly greater than the other gear types used in the fishery (Fig. 6). Mean trophic level of the catches in each gear type ranged from 3.2 to 3.5 and no significant differences existed in the trophic levels harvested between the different gear types (Fig. 6).

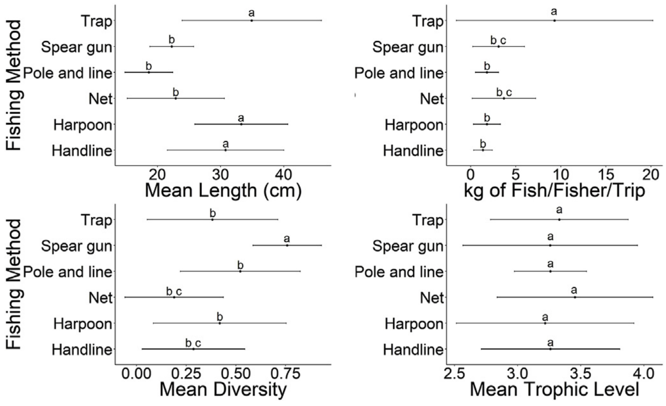

Fig. 6. The mean standard length, biomass harvested per-fisher, diversity, and trophic level taken by each gear type (trap, spear gun, pole and line, net, harpoon and handline) harvested in the artisanal fishery at Anaa atoll. Different letters indicate significant differences between gear types based on Tukey-Kramer HSD multiple comparisons with a P value < .05 and error bars are standard deviations from the mean.

The DCA analysis separated the gear types into four groups, based on their selectivity for similar species in this mixed gear fishery. The first ordinated group was comprised of pole and line, spear gun, and harpoon. Group two consisted of traps and handlines. Group three and four, monofilament gill nets and collecting by hand, respectively are singular gear types that stood apart from the other gears due to the distinctiveness in harvested species (Fig. 7). The clustering of group one is driven by the abundance of soldierfishes (*Myripristis sp.*) and other hard bottom species such as parrotfishes and surgeon fishes that dominate the reef crest and outer reef habitats where these three gear types are commonly used. Traps and handlines selected a combination of both soft and hard bottom lagoon species. For example, bonefish is a soft bottom species and is principally harvested by fish traps during their spawning migrations between the lagoon and outer reef spawning habitats, however, they are also targeted with handlines in the lagoon. Furthermore, *Lutjanus fulvus* is a hard bottom species that is specifically targeted with handlines on coral outcrops and other hard bottom structures in the lagoon but are also captured in the fish traps during their migrations to oceanic spawning habitats. Nets are principally used to capture smaller species that aggregate in large groups such as juvenile *Chanos chanos* inside of inland saline ponds, *Selar crumenophthalmus, Kuhlia sandvicensis,* fishes of the family *Mugilidae and Scaridae*. Finally, hand collecting is often used to harvest invertebrates with the principal species begin lobsters (*Panulirus penicillatus*) and incidental take of sleeping parrotfishes (Fig. 7).

3.3. *Fishing mortality and exploitation rates*

Longevity data were available to assess the natural mortality rates of 10 of the top 25 percent of species harvested. The natural mortality rates we estimated with the Hoenig fish equation ranged from a maximum of 1.42 in *Selar crumenophthalmus* to a minimum of 0.11 in *Naso lituratus* (Table 2). The majority of short-lived species are underexploited, and long-lived species are overexploited. The exploitation rate of four species *Selar crumenophthalmus* (−0.7), *Chanos chanos* (−0.79), *Hipposcarus longiceps* (−0.77), and *Scarus ghobban* (0.37) fell below the threshold of 0.50 and can be considered underexploited. The exploitation rates of both *Naso brevirostris* (0.46) and *Mulloidichthys flavolineatus* (0.51) are close to the fully exploited threshold and finally, the exploitation rates of *Naso lituratus* (0.82), *Lutjanus fulvus* (0.9), *Epinephelus polyphekadion* (0.74) and *Albula glossodonta* (0.69) are all overexploited (Table 2, Fig. 8). Other species of ecological significance that are opportunistically harvested in this fishery but not numerically abundant, include the threatened species *Cheilinus undulatus* which was frequently harvested with spear guns, handlines and harpoons, 14 of which were documented in the catch throughout the duration of this study (Lennox et al., 2019).

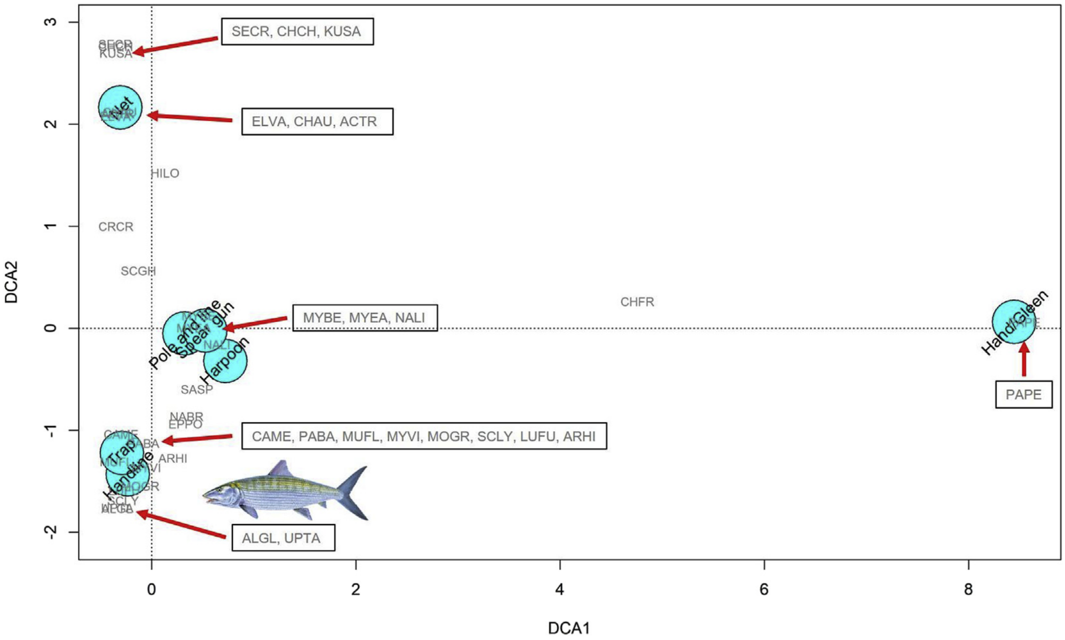

Fig. 7. The detrended correspondence analysis (DCA) plot of the seven gear types and the top 25% of species harvested on Anaa atoll (the turquoise bubbles correspond to gear types and the four-letter species codes correspond to the species harvested). The closeness of a given species to a gear type indicates a higher selectivity of the species to that gear and the proximities between gear types reflect the similarity in fish assemblages harvested by those gears (see Table 1, for scientific names corresponding to four letter species codes, note PAPE is *Panulirus penicillatus*).

4. Discussion

Coral reefs are fragile marine systems that are disproportionally vulnerable to fisheries exploitation (Pauly et al., 2002; Roberts et al., 2002; Bellwood et al., 2004). These fisheries are often low in productivity, high in species diversity (Sale, 2018), contain a complex array of life histories, and provide the primary source of protein for the indigenous communities of remote islands (Bohnsack, 1996; Cisneros-Montemayor et al., 2016). Like many remote communities in Oceania, artisanal fishing on coral reefs is essential to life on Anaa, and for centuries the inhabitants of this atoll have employed an array of fishing technologies to subsist off this ecosystem's marine resources (Torrente, 2015). Historically, *Rahui* and other ceremonial practices regulated harvest and rudimentary fishing equipment made the large-scale overexploitation of these resources uncommon. Prior to modernization of Anaa's fisheries, nets were made of woven coconut palms, hooks were made from shells, and fishers often worked in groups harvesting only enough fish that could be eaten or shared among community members (Torrente, 2015). However, our results indicate that although many of these traditional fishing techniques are still in practice today, these practices and gear types have evolved with the advent of new technologies and these changes along with the loss of customary management may have altered the historical balance between sustenance and sustainability, as occurred in many other analogous island communities (Johannes, 1998; Friedlander, 2018). We observed seven main gear types that are commonly used in the atoll's contemporary fisheries, several of which are traditional methods that have been modified. Changes to these gear types include the proliferation in the number of rock traps, addition of chicken wire to the traps, replacement of woven nets with monofilament gill nets, and the introduction of underwater spear fishing equipment; these advances have undoubtedly increased the efficacy of these gear types in harvesting marine resources (Eigaard et al., 2014). This coupled with the ability to preserve and export large amounts of fish off island markets has built the capacity of the community to exploit their resources (Brewer et al., 2013) without complementary maintenance of resource management systems (Johannes, 1978b).

Our results demonstrate that fishing is practiced throughout the atoll's marine ecosystems and we recorded 98 species taken for human consumption suggesting that fishing mortality influences nearly all levels of this ecosystem. The only species that are not regularly harvested for consumption are sharks, rays and large *Lutjanus bohar* from the outer reef due to a high incidence of ciguatera poisoning in this species (Residents of Anaa atoll, personal communication). However, despite the diverse assemblage of marine life capable of providing sustenance to the atoll's inhabitants, the fishery is dominated by a few key species, many of which are overexploited based on estimates from the catch curves. The middle trophic level species assemblages captured by all the gear types may be reflective of historic overfishing of the atoll's reefs (Jackson et al., 2001), reducing the abundance of larger predatory species and shifting contemporary fisheries harvests toward catches dominated by lower trophic levels, a common trend in coral reef fisheries (Jennings and Polunin, 1996; Pauly et al., 1998). These results are similar to those of artisanal fisheries in East Africa, with diverse species assemblages and a handful of principal species that provide a backbone to the fishery (McClanahan and Mangi, 2015).

Although nearly all fish are harvested opportunistically, fishers choose their method based on the desired target species and there is limited overlap in the species composition taken by the different gear types. The overlap that does exist between gears is most likely attributed to the habitats in which these gear types are used. Pole and line, spear gun, and harpoons are all used on hard bottom coral reef habitats and therefore, harvest similar fish assemblages. Spear fishers principally target soldierfishes from the genus *Myripristis* and parrotfishes from the family *Scaridae* but take the highest species diversity, as this method allows fishers to actively pursue and target an array of species, that would otherwise be uncatchable with hook and line or nets in hard bottom habitats. Furthermore, spearfishing is often practiced at night making nocturnally inactive reef fishes from the families *Scaridae* and *Acanthuridae* extremely vulnerable to this gear (Hamilton et al., 2012; Ford et al., 2016). Spearfishing has been shown to have significant impacts on the trophic structure, biodiversity, and size of targeted species in analogous fisheries (Cinner et al., 2009a; Frisch et al., 2012; Bejarano et al., 2013; Sbragaglia et al., 2018) and is considered a Pacific

Table 1
The species harvested in the artisanal fishery at Anaa atoll and their corresponding four-letter codes (note, the I and T signify the Puamotu name of a given parrotfish species in its initial or terminal phase respectively).

Species	Scientific name	Family	Puamotu name	N	Relative abundance
ALGL	*Albula glossodonta*	*Albulidae*	Kiokio	1868	0.25
CHAU	*Chaetodon Auriga*	*Chaetodontidae*	Koria	743	0.1
KUSA	*Kuhlia sandvicensis*	*Kuhliidae*	Ahore	652	0.09
LUFU	*Lutjanus fulvus*	*Lutjanidae*	Magu magu	376	0.05
CHCH	*Chanos chanos*	*Chanidae*	Pati	365	0.05
MUFL	*Mulloidichthys flavolineatus*	*Mugilidae*	Vete	361	0.05
UPTA	*Upeneus taeniopterus*	*Mullidae*	Nako	305	0.04
SECR	*Selar crumenophthalmus*	*Carangidae*	Komene	271	0.04
CAME	*Caranx melampygus*	*Carangidae*	Paaihere	245	0.03
ELVA	*Ellochelon vaigiensis*	*Mugilidae*	Hopiro	233	0.03
HILO	*Hipposcarus longiceps*	*Scaridae*	Kukina	177	0.02
MYBE	*Myripristis berndti*	*Holocentridae*	Peti	168	0.02
MYEA	*Myripristis earlei*	*Holocentridae*	Peti	131	0.02
MYVI	*Myripristis violacea*	*Holocentridae*	Peti	115	0.02
SCGH	*Scarus ghobban*	*Scaridae*	Titeketeke(I)/Homo homo(T)	105	0.01
CRCR	*Crenimugil crenilabis*	*Mugilidae*	Kanae	96	0.01
PABA	*Parupeneus barberinus*	*Mullidae*	–	91	0.01
SCLY	*Scombromoides lysan*	*Scombridae*	Rai	74	0.01
ARHI	*Arothron hispidus*	*Tetraodontidae*	Hue	73	0.01
SASP	*Sargocentron spiniferum*	*Holocentridae*	Ruke ruke	70	0.01
NALI	*Naso lituratus*	*Acanthuridae*	Ume tarei	67	0.01
CHFR	*Chlorurus frontalis*	*Scaridae*	Noga	62	0.01
NABR	*Naso brevirostris*	*Acanthuridae*	Tatihi	45	0.01
ACTR	*Acanthurus triostegus*	*Acanthuridae*	Akega	43	0.01
MOGR	*Monotaxis grandoculis*	*Lethrinidae*	Mu	43	0.01
EPPO	*Epinephelus polyphekadion*	*Serranidae*	Kito	42	0.01
CHSO	*Chlorurus sordidus*	*Scaridae*	Pakoti	40	0.01
ZACO	*Zanclus cornutus*	*Zanclidae*	Panapana	36	0
CHEP	*Chaetodon ephippium*	*Chaetodontidae*	Tovi	36	0
EPME	*Epinephelus merra*	*Serranidae*	Veve	36	0
LUMO	*Lutjanus monostigma*	*Lutjanidae*	Tero	26	0
BAVI	*Balistoides viridescens*	*Balistidae*	Oiri	25	0
FICO	*Fistularia commersonii*	*Fistulariidae*	–	20	0
KYCI	*Kyphosus cinerascens*	*Kyphosidae*	Nenue	19	0
SCPS	*Scarus Psittacus*	*Scaridae*	Tokati	18	0
NAUN	*Naso unicornis*	*Acanthuridae*	Ume	15	0
CHUN	*Cheilinus undulates*	*Labridae*	Tapiro	14	0
MUVA	*Mulloidichthys vanicolensis*	*Mugilidae*	Vete	14	0
PSFL	*Pseudobalistes flavimarginatus*	*Balistidae*	Oiri	13	0
CAFE	*Carangoides ferdau*	*Carangidae*	–	13	0
ACAC	*Acanthurus achilles*	*Acanthuridae*	Pakurakura	12	0
MYAD	*Myripristis adusta*	*Holocentridae*	Peti	12	0
CHMI	*Chlorurus microrhinos*	*Scaridae*	Tegatega	11	0
APFU	*Aphareus furca*	*Lutjanidae*	–	11	0
SCNI	*Scarus niger*	*Scaridae*	–	11	0
SCSC	*Scarus schlegeli*	*Scaridae*	–	10	0
CHQU	*Chaetodon quadrimaculatus*	*Chaetodontidae*	Koria	10	0
SCAL	*Scarus altipinnis*	*Scaridae*	Kutu (I)/Gavere (T)	10	0
CHUL	*Chaetodon ulietensis*	*Chaetodontidae*	Koria	9	0
PAIN	*Parupeneus insularis*	*Mullidae*	Kaveti veti	8	0
SATI	*Sargocentron tiere*	*Holocentridae*	Ruke ruke	8	0
ABSE	*Abudefduf sexfasciatus*	*Pomacentridae*	Katimu	6	0
CEAR	*Cephalopholis argus*	*Serranidae*	Roi	6	0
PEOU	*Pempheries oualensis*	*Pempheridae*	–	6	0
PAMU	*Parupeneus multifasciatus*	*Mullidae*	Kaveti	5	0
ACNI	*Acanthurus nigricans*	*Acanthuridae*	Mito	5	0
CEOC	*Cetoscarus ocellatus*	*Scaridae*	–	4	0
NEOP	*Neoniphon opercularis*	*Holocentridae*	–	4	0
SCGL	*Scarus globiceps*	*Scaridae*	–	4	0
COAY	*Coris aygula*	*Labridae*	Marari	4	0
CTHA	*Ctenochaetus hawaiiensis*	*Acanthuridae*	–	3	0
SCRU	*Scarus rubroviolaceus*	*Scaridae*	–	3	0
NEAC	*Negaprion acutidens*	*Carcharhinidae*	Arava	3	0
ABBE	*Abudefduf septemfasciatus*	*Pomacentridae*	Katimu	3	0
ARST	*Arothron stellatus*	*Tetraodontidae*	–	3	0
CAIG	*Caranx ignobilis*	*Carangidae*	–	3	0
CASE	*Caranx sexfasciatus*	*Carangidae*	–	3	0
EPIN	*Epibulus insidiator*	*Labridae*	–	3	0
NELE	*Neomyxus leuciscus*	*Mugilidae*	–	2	0
NEAR	*Neoniphon argentus*	*Holocentridae*	–	2	0
SCFO	*Scarus forsteni*	*Scaridae*	–	2	0
ABSO	*Abudefduf sordidus*	*Pomacentridae*	Katimu	2	0
CHOR	*Chaetodon ornatissimus*	*Chaetodontidae*	Koria	2	0

(*continued on next page*)

Table 1 (*continued*)

Species	Scientific name	Family	Puamotu name	N	Relative abundance
LEOL	*Lethrinus olivaceus*	*Lethrinidae*	Meko	2	0
LUBO	*Lutjanus bohar*	*Lutjanidae*	Mero mero	2	0
GYJA	*Gymnothorax javanicus*	*Muraenidae*	Puhi	2	0
LEAT	*Lethrinus atkinsoni*	*Lethrinidae*	Tamure	2	0
LUGI	*Lutjanus gibbus*	*Lutjanidae*	Teae	2	0
PLLA	*Plectropomus laevis*	*Serranidae*	Tonu	2	0
DIHY	*Didon hystrix*	*Diodontidae*	Totara	2	0
ACXA	*Acanthurus xanthopterus*	*Acanthuridae*	–	1	0
ANCA	*Anampses caeruleopunctatus*	*Labridae*	–	1	0
BAUN	*Balistapus undulates*	*Balistidae*	–	1	0
CACA	*Calotomus carolinus*	*Scaridae*	–	1	0
HFCR	*Heteropriacanthus cruentatus*	*Priacanthidae*	–	1	0
LEXA	*Lethrinus xanthochilus*	*Lethrinidae*	–	1	0
OCCY	*Octopus cyanea*	*Octopodidae*	–	1	0
POIM	*Pomacanthus imperator*	*Pomacanthidae*	–	1	0
SCFR	*Scarus frentaus*	*Scaridae*	–	1	0
ACGU	*Acanthurus guttatus*	*Acanthuridae*	Kikito	1	0
RHAC	*Rhinecanthus aculeatus*	*Balistidae*	Kokiri	1	0
CHCI	*Chaetodon citrinellus*	*Chaetodontidae*	Koria	1	0
CHLN	*Chaetodon lunulatus*	*Chaetodontidae*	Koria	1	0
SIAR	*Siganus argenteus*	*Siganidae*	Marava	1	0
POSE	*Polydactylus sexfilis*	*Polynemidae*	Moi	1	0
SPHE	*Sphyraena helleri*	*Sphyraenidae*	Ono	1	0
BOSP	*Bothus pantherinus*	*Bothidae*	Patiki	1	0
CHCL	*Cheilinus chlorourus*	*Labridae*	Topiropiro	1	0

wide management challenge (Gillett and Moy, 2006). Net fishing harvests primarily smaller schooling fishes and is lowest in species diversity as nets are most often fished actively, targeting aggregations of a single species. Net fishing on Anaa is different to many other tropical fisheries where nets are frequently fished passively and unbiased to the species taken provided a fishes body is larger than the mesh size (Dalzell, 1996; Remesan and Meenakumari, 2009). The proximity of traps and handlines in the DCA indicates that these two gear types harvest similar species but at different stages of their life cycle, as fish traps primarily capture sexually mature fishes during their reproductive migrations between the lagoon and oceanic habitats.

A principal tenet of sustainable fisheries is to let fish grow to the size of sexual maturity before harvesting them, suggesting that in theory, harvesting fishes captured in the trap fishery could be sustainable (Froese, 2004). However, in practice, the large scale harvest of spawning aggregations is rarely sustainable (Sadovy and Domeier, 2005; De Mitcheson and Erisman, 2012), and sufficient escapement of spawning fish and the preservation of mega-spawners is essential to permit successful reproductive events (Berkeley et al., 2004; Hixon et al., 2014). This suggests that fishing by handline is a more sustainable method as similar species are targeted, but the spawning aggregations of these species are not affected. Traps, nets and spear guns provide the highest biomass and are the primary methods of fish acquisition for the islands small scale commercial markets. While in contrast, handline, harpoon and pole and line method is typically used to provide nutrition while working away from the village. These results are comparable to that of Chauvet and Galzin (1996) who found traps account for 90% of the total fisheries harvest exported from the Tuamotu archipelago, while other gear types were primarily used for sustenance (Chauvet and Galzin, 1996).

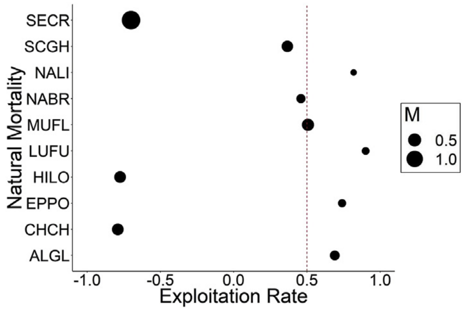

Fig. 8. The exploitation rate and corresponding rate of natural mortality for 10 species harvested in the artisanal fishery at Anaa atoll. The location on the x-axis is indicative of the exploitation rate, size of the bubble corresponds to their rate of natural mortality and the red dotted line signifies the 0.5 threshold between under and over exploited fisheries (see Table 1, for scientific names corresponding to four letter species codes). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Longevity, mortality and exploitation estimates of ten key species in the artisanal fishery at Anaa atoll (see Table 1, for scientific names corresponding to four letter species codes, note that estimates of mortality are rounded to the nearest hundredth).

Species	Longevity (T_{max})	Natural mortality (M)	Total mortality (Z)	Fishing Mortality (F)	Exploitation rate (E)	T_{max} citation
LUFU	34	0.12	1.23	1.11	0.9	Shimose and Nanami (2014)
SCGH	13	0.32	0.51	0.19	0.37	Froese and Pauly (2000)
MUFL	10.8	0.39	0.79	0.4	0.51	Mehanna et al. (2018)
HILO	12	0.35	0.2	−0.15	−0.77	Choat and Robertson (2002)
NABR	25	0.17	0.31	0.14	0.46	Choat and Robertson (2002)
EPPO	31	0.13	0.52	0.38	0.74	Froese and Pauly (2000)
CHCH	12	0.35	0.2	−0.15	−0.79	Bagarinao (1991)
ALGL	20	0.21	0.68	0.47	0.69	Ault et al. (2007)
NALI	39	0.11	0.58	0.48	0.82	Choat and Robertson (2002)
SECR	3	1.42	0.84	−0.58	−0.7	Froese and Pauly (2000)

Artisanal fish traps yielded the largest catches, a finding that is consistent with the observations of comparative fisheries throughout the archipelago (Caillart and Morize, 1990; Chauvet and Galzin, 1996). These large structures fish passively, targeting 62 species of fish that move within the trap complex and are a persistent source of fishing mortality in this ecosystem. Our results indicate that nearly all of the atoll's fish traps are located along a 2 km stretch of back reef, adjacent to Tukuhora village and harvested 48% of the fish in our survey. This area is immediately adjacent to four significant cuts in the reef crest and local ecological knowledge suggests that it is the primary passageway for fish movement into and out of this closed atoll. In a similar fishery at Rangiroa atoll, Chauvet and Galzin (1996) found that the number of traps often exceeded the maximum sustainable yield, and the fishery conformed to a Fox-type surplus production (Fox, 1970), with a maximum economic yield of 10 traps, well below the predicted maximum sustainable yield of 53 (Chauvet and Galzin, 1996). This suggests that high densities of fish traps do not increase economic benefits to fishers, but rather reduces individual catches and marginalizes profits allowing the symptoms of both biologic and economic overfishing to proliferate. Unlike in open atolls in which traps are built parallel to the walls of oceanic passes (Caillart and Morize, 1990), fish traps on Anaa are built perpendicular to the access points of the closed atoll, greatly restricting movement between habitats; indeed if all are activated, 100% of the linear distance between the landmass is obstructed by these manmade structures. Most coral reef species utilize a combination of these subecosystems throughout their ontogenetic development (Gillanders et al., 2003) and the current intensity of trapping likely severs the circulation of fish movement in the atoll, prohibiting the movement of adults and limiting the reproductive success of species that migrate from lagoon to pelagic environments for spawning (Johannes, 1978a). Ultimately, the intense fishing pressure on this critical passageway may severely reduce the productivity and biomass of the atoll's inter-lagoon habitats. Furthermore, local ecological knowledge suggests the effect of reduced herbivory is manifesting in this region, as localized algae blooms occur regularly in the trap complex (Residents of Anaa atoll, personal communication); many of the species harvested in the trap fishery are herbivores and those that enter this region of the atoll are serially removed. The ecological release of macro algae is well documented with the loss of herbivory in coral reefs and this persistent source of mortality on this functional group likely influences the trophic structure of this micro-ecosystem (Hughes, 1994; Mumby et al., 2006; Bellwood et al., 2012).

The exploitation rate of the species harvested at Anaa atoll is predictable from their rates of natural mortality (Jennings et al., 1998; Reynolds et al., 2001). Fishes with high natural mortality such as *Chanos chanos* and *Selar crumenophthalmus* were all classified as underexploited, even though they are heavily fished in the artisanal fishery. *Chanos chanos* was the fifth most abundant species in the catch and although adults are occasionally harvested with large gill nets and fish traps, the species is predominantly harvested as juveniles in inland saline ponds. The ability of this species to withstand intense fishing pressure in the juvenile stage of its life cycle without recruitment overfishing is likely due to their innate ability to withstand environmental stochasticity and high juvenile mortality rates in the event of pond desiccation (Bagarinao, 1991). In contrast, over exploited species such as *Naso lituratus* and *Epinephelus polyphekadion* are all characterized as slow growing, late maturing, long lived species with life histories that are incompatible to large scale harvest (Choat and Axe, 1996; Reynolds et al., 2001; Sadovy de Mitcheson et al., 2013). Although these species represent a very small component of the overall catch, being ranked at 21 and 26 respectively with a relative abundance of less than 1%, these species are overexploited.

Although tropical reef fisheries in this region are data limited, our results demonstrate that life history traits such as T_{max}, can be predictive of a species response to exploitation and help identify priority species during the initial evaluation of lagoon fisheries in the Tuamotus and other reef fisheries throughout Oceania (Jennings et al., 1998, 1999; Taylor et al., 2014). However, our analysis was limited by the lack of available life history parameters (i.e., age, growth and reproduction) of these tropical species and as a result we had to use longevity data from the literature as well as length-based catch curves in lieu of age, which is less robust and may introduce a source of bias to our results. Never the less, in data limited scenarios “borrowed” life history parameters can be informative (Prince et al., 2014), and our results provide an initial assessment of this multispecies fishery that would otherwise be undescribed. With this in mind, further research is urgently needed to identify the age and growth characteristics of these species in the pristine atolls of the Tuamotu Archipelago in order to obtain baseline biological information such as T_{max} and von Bertalanffy growth parameters with which the exploited status of fish populations can be determined (Taylor et al., 2014).

The natural mortality rate of the atoll's principal fisheries resource, *Albula glossodonta,* falls between the two extremes, suggesting that the species is a good candidate for exploitation. The atoll's shallow lagoon provides ideal habitat for this soft bottom species and its closed nature makes their predictable spawning aggregations easily targetable by fishers, however, as noted above, the trap complex through which bonefish migrate for reproduction has become nearly unpassable and the large-scale harvests of this species during their spawning migrations induces a critically high level of fishing mortality. The overexploited status of the bonefish population is concerning, as the results of this study indicate that although the fishery at Anaa atoll is comprised of multiple species, *Albula glossodonta*, accounts for nearly a quarter of the atoll's overall fishery productivity. Bonefish are sold per packet of five fish for 1000 CFP (~ 10 USD) and during spawning events, large pulses in catch provide a significant source of income to artisanal fishers. Furthermore, the proximity of the village to the main passageways used by migrating bonefish facilitates the harvest of this resource as their spawning aggregations congregate near the atoll's demographic centre making the effort expended to harvest this high yield resource minimal (Allen, 2014). Similar *Albula* fisheries have declined throughout the Pacific (Beets, 2000; Johannes and Yeeting, 2000; Friedlander et al., 2007; Adams et al., 2014) and an unmanaged trap fishery has the potential to collapse the island's principal fisheries resource, threating food security and economic opportunity presented by small scale commercial markets and recreational fly-fishing tourism (Holmlund and Hammer, 1999). Given its importance, further research is urgently needed into the life history, movement patterns, and exploitation of this atoll's bonefish resource to obtain an improved understanding of this stock's conservation status.

The management of both local and outside demands on Anaa atoll's coral reef fisheries is essential to sustain long-term fishery yields, as the recovery of these ecosystems after degradation is slow and often unachievable (Bohnsack, 1996). Although we were unable to quantify the proportion of harvested marine resources exported off island, the practice of sending fish to Tahiti is commonplace (A.F, personal observation) and the magnitude is likely a significant contribution to this fishery and an important component of this socio ecological system (Kittinger et al., 2015; Grafeld et al., 2017). This work demonstrates that both artisanal traps and spearfishing harvest a higher proportion of overexploited fishes, take fish assemblages that are more diverse and remove the most biomass from the atoll. Consequently, the management of these two gear types is critically needed and if single-species management is the conservation target, a combination of gear and life history-based management, such as bag limits and size limits, could be an effective tool in regulating the harvest of selected species or assemblages in this atoll (Cinner et al., 2009a). However, the multispecies nature of the fishery suggests that an ecosystem based management approach may be the best way to manage this atoll's fisheries (Slocombe, 1993; Pikitch et al., 2004) and is most likely to be consistent with the customary marine management practices like that of the Rahui in eastern Polynesia (Cinner et al., 2009b; Bambridge, 2016).

A step towards ecosystem-based management of this dynamic fishery could be taken by managing the total number of artisanal fish traps to ensure that there is adequate space or a time period to allow for movement and reproduction of fishes through the atoll's principal migratory passage. This action would both improve the sustainability of the *Albula* fishery and have an umbrella effect as it would open the gateway to the atoll for these biologic processes in multiple species. Ultimately, this work supported local fisheries management at Anaa atoll, as the community established an Educational Managed Marine Area (EMMA) that overlaps with the bonefish migratory corridor adjacent to Tukuhora village (http://www.aires-marines.com/content/view/full/16746) and ratified a Rahui in this migratory corridor (i.e., a three month seasonal closure to fishing) during March, April and May, the peak of the bonefish spawning season (https://www.radio1.pf/anaa-a-son-aire-marine-educative/). To this end, the results of this study provided local conservation efforts and management authorities with a description of the species of fish harvested, gear selectivity and exploitation rates in this previously undocumented fishery and delivered a basis for designing effective community-based conservation strategies to preserve the ecosystem services and food security provided by the atoll's fisheries.

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