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# Population dynamics of roundjaw bonefish *Albula glossodonta* at a remote coralline Atoll inform community-based management in an artisanal fishery

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## Abstract

Fisheries management requires knowledge on the population dynamics of exploited stocks. To that end, the present study used a mark–recapture approach to characterise the population demographics of roundjaw bonefish *Albula glossodonta* (Forsskål) and their interaction with a data-limited fishery on Anaa Atoll in the Tuamotu Archipelago of French Polynesia. Over the course of the study, 2,509 bonefish were tagged and 12.3% were recaptured. The $L_\infty$ of bonefish was estimated at 71 cm fork length (FL) with a K of 0.17, based on changes in FL between capture events. Artisanal fish traps located in the migratory corridors of the atoll accounted for 94% of recaptures and these movements occurred during the waning moon. Fishing mortality increased as bonefish reach sexual maturity, recruiting to the trap fishery at age 4 with the onset of spawning behaviour. Bonefish abundance between ages 3 and 5 was estimated to be 29,079 individuals. This case study demonstrated the utility of mark–recapture in filling knowledge gaps that impede the management of data-limited fisheries. Ultimately, these results supported the creation of an Educational Managed Marine Area and the resurgence of *rahui* (seasonal closure) to manage this fishery.

**KEYWORDS**
French Polynesia, integrated Brownie–Petersen model, lagoon fisheries, Mark–recapture, spawning aggregations, traditional ecological knowledge

## 1  |  INTRODUCTION

Tropical reef fisheries present unique challenges to fisheries management (Johnson et al., 2013; Pauly, 1997). Although these fisheries are often small in scale, they are complex and employ an array of gear types to harvest diverse species assemblages to meet local demands for food production (Allison & Ellis, 2001; Jennings & Polunin, 1996; Jennings, Reynolds, & Polunin, 1999). In the Pacific Islands, the protein provided by these fisheries is critically important to food security, and science-based management is urgently needed to ensure current yields are sustainable (Bell et al., 2015, 2009). However, the remote communities in which these fisheries typically

occur are limited in their capacity to conduct research and stock assessments on the numerous species with distinct life histories that comprise their resource base. Consequently, these fisheries are largely data deficient and difficult to manage (Pauly, 1997; Pauly et al., 2002; Salas, Chuenpagdee, Seijo, & Charles, 2007). Furthermore, the rapid modernisation of harvesting technologies compounds the growing gap between resource extraction and management capacity (McClanahan, Castilla, White, & Defeo, 2009; McGoodwin, 1995; Ochiewo, 2004). Considering these challenges as well as the declining fisheries yields across the region, there is a strong case for the application of data-less marine management to these fisheries (Johannes, 1998). Nevertheless, this logical argument is often

overlooked by contemporary governance systems, where robust scientific evidence is essential to demonstrate the impending need for change in a socio-ecological system (Johannes, 1978; McClanahan et al., 2009).

To this end, data on the population dynamics of harvested species can be fundamental to the promotion of effective fisheries management (Beverton & Holt, 1957; Jennings, Kaiser, & Reynolds, 2009; Schaefer, 1954). Fortunately, although these fisheries are often data deficient, the communities in which they operate have in-depth traditional ecological knowledge on the populations of fish that sustain them and this information provides an important source of information to guide research and management, including movement patterns and historic baselines in natural resource abundance (Drew, 2005; Johannes, 1981; Johannes, Freeman, & Hamilton, 2008; Silvano & Valbo-Jørgensen, 2008; Valbo-Jørgensen & Poulsen, 2000). Nonetheless, this knowledge base can be enhanced by biological research to provide quantitative measures of the underlying processes behind this collective knowledge (Davis & Wagner, 2003; Poizat & Baran, 1997). Consequently, there is a need for the application of simple cost-efficient fishery tools to augment the traditional ecological knowledge of these communities and collect the data required to support the management of their fisheries.

Mark and recapture tagging studies are a relativity inexpensive and informative means of collecting fisheries data (Pine, Hightower, Coggins, Lauretta, & Pollock, 2012; Pine, Pollock, Hightower, Kwak, & Rice, 2003; Polacheck, Eveson, & Laslett, 2010). The external tags that are applied in such studies render marked fish recognisable to fishers and allow a fish to be uniquely identified (Pine et al., 2012, 2003). The practice of deploying and recovering marks in a fishery setting inherently engages members of fishing communities and enables the movements of fish to be monitored between recapture events, which can be used to describe the spatial distribution of a stock, timing and extent of movement, and sources of mortality (Kamikawa et al., 2015; Kohler & Turner, 2001; Larkin, Ault, Humston, Luo, & Zurcher, 2007). Growth rates can be estimated by measuring changes in individual fish length between capture events (Eveson, Laslett, & Polacheck, 2004; Eveson, Million, Sardenne, & Le Croizier, 2015; Francis, 1988; Gulland & Holt, 1959; Laslett, Eveson, & Polacheck, 2002; Pine et al., 2012), and there are a variety of methods to estimate the size of a given population from simple closed to advanced open population models (Ogle, 2016; Pine et al., 2012; Polacheck, Eveson, Laslett, Pollock, & Hearn, 2006; Polacheck et al., 2010; Schnabel, 1938). Furthermore, estimates of both fishing and natural mortality can be derived from mark–recapture, tag-return studies (Hoenig, Barrowman, Pollock, Brooks, et al., 1998; Hoenig, Barrowman, Pollock, Hoenig, et al., 1998; Jiang et al., 2007; Pine et al., 2003; Polacheck et al., 2006), which can provide an alternative to the estimation of these parameters from empirical equations (Beverton & Holt, 1959; Hoenig, 1983; Pauly, 1980) or measuring the stock structure of virgin fish populations and estimating total mortality in the scenario when fishing mortality is non-existent (Vetter, 1988). Finally, in addition to scientific data, conventional mark–recapture methods have proven to be successful in involving fishers in scientific research, promoting awareness of science and a conservation ethic in their respective communities (Kamikawa et al., 2015; Larkin et al., 2007). All the above suggests that conventional mark–recapture could be used to fill the knowledge gaps that impede the management of many small-scale tropical reef fisheries.

Roundjaw bonefish *Albula glossodonta* (Forsskål) (henceforth bonefish) are abundant in lagoons and shallow coastal ecosystems throughout Oceania, where spawning aggregation fisheries are of paramount importance (Adams et al., 2013; Allen, 2014; Beets, 2000; Friedlander et al., 2007). References to their lunar spawning behaviour are pervasive in the traditional ecological knowledge of fishers throughout the region (Allen, 2014; Johannes et al., 2008; Johannes & Yeeting, 2000), and like many coastal fishes, bonefish have been intensively harvested to support food security and small-scale economic commerce in isolated communities, rendering them a species of conservation concern (Adams et al., 2013; Allen, 2014; Beets, 2000; Friedlander et al., 2007; Wallace, 2015). Such is the case on Anaa Atoll in the Tuamotu Archipelago of French Polynesia, where bonefish is harvested during their spawning migrations by artisanal fish traps (Filous, Lennox, Coleman, et al., 2019). The traditional ecological knowledge of this community suggests that throughout the Austral autumn and winter, bonefish pre-spawning aggregations form during the full moon, followed by a spawning migration through the atoll's passageways to the open ocean throughout the waning moon. During these events, thousands of fish migrate to and from the ocean, through the main channel northwest of Tukuhora village where they are vulnerable to harvest by artisanal traps. Although the trap fishery has existed for centuries (Torrente, 2015), in recent decades both the proliferation in the number of fish traps and introduction of new technology (i.e. chicken wire) has increased its capacity to harvest the resource (Filous, Lennox, Clua, & Danylchuk, 2019).

The unregulated harvest of spawning aggregations has been shown to reduce the number of adults in a given population rapidly, diminish egg production, and lead to depression of stock status (Domeier, 2012; Sadovy & Domeier, 2005; Secor, 2015). As a consequence, analogous bonefish spawning aggregation fisheries have declined throughout the Pacific (Beets, 2000; Friedlander et al., 2007; Johannes & Yeeting, 2000; Ram-Bidesi, 2011). Owing to these regional population declines, the species is now listed as vulnerable by the International Union for the Conservation of Nature (Adams et al., 2012). Congruently, the traditional ecological knowledge of elder residents of Anaa Atoll indicates the abundance of this species has declined significantly from their historic baseline and suggests that these effects have manifested in the bonefish population. However, this sentiment is not universal among younger fishers; as during spawning events, the bonefish population is concentrated in a discrete place and time, creating a perception of an inexhaustible resource (Residents of Anaa Atoll, personal communication). This suggests that this fishery is hyper stable and, consequently, this shifting baseline in resource abundance obscures the ability of the local community to evaluate collectively the current status of the bonefish population, which is a widespread problem in spawning aggregation

fisheries (Erisman et al., 2011; Mcclenachan, Ferretti, & Baum, 2012; Pauly, 1995). In this context, data are urgently needed on the movement, growth, mortality and population abundance to support the management of this fishery.

Previous scientific studies indicate that *Albulids* exhibit site fidelity to shallow-water foraging habitats and their movements into these environments are controlled by fluctuations in tide, water temperature and the presence of predators (Cooke & Philipp, 2004; Danylchuk et al., 2007; Humston, Ault, Larkin, & Luo, 2005; Kamikawa et al., 2015; Larkin et al., 2007; Murchie et al., 2013). Less is known about the long-term movements of this genus, but several studies have demonstrated that the home range of bonefish is surpassed to undertake seasonal spawning movements to offshore waters with access to the pelagic environment (Adams et al., 2019; Boucek et al., 2018; Danylchuk et al., 2011; Danylchuk, Lewis, Jud, Shenker, & Adams, 2018; Perez, Schmitter-Soto, Adams, & Heyman, 2018). The traditional ecological knowledge regarding bonefish movement in Anaa Atoll is consistent with this hypothesis and suggests that significant portions of the atoll's bonefish population are required to traverse a bottleneck as they migrate through the passageways between their lagoon and pelagic habitats, where they are simultaneously vulnerable to the atoll's artisanal traps (Filous, Lennox, Clua, et al., 2019). This scenario provides an opportunity to fill knowledge gaps that exist in their biology and population demographics with mark and recapture techniques. To this aim, conventional mark–recapture was used to describe the harvest intensity, spatial and temporal movements of bonefish spawning migrations, somatic growth, natural mortality, fishing mortality and population size. Ultimately, the intent of this research was to complement the existing traditional ecological knowledge of this species and support community-based management of this fisheries resource.

## 2 | METHODS

Anaa is a small atoll (38 km$^2$) 350 km east of Tahiti in the Tuamotu Archipelago of French Polynesia (Figure 1). Bonefish are found throughout the lagoon, inhabiting both the fringing sand flats and deeper lagoon (3–8 m). The atoll's interior is divided by a natural land bridge that traverses the atoll from north to south forming what is locally known as the "Petit Lagoon" (smaller bisection along the north of the atoll) and "Grand Lagoon" (the larger southern bisection). The two segments of the lagoon are connected by two shallow passes on either side of the land bridge, allowing the movement of fish and other marine life between them. However, unlike most atolls in the Tuamotu Archipelago, Anaa is closed along the outer periphery and lacks a deep oceanic pass between its interior lagoon and outer reef. The reef crest forms a barrier around the atoll and there are a few shallow passageways in the reef that allow bonefish spawning aggregations to move between the lagoon and oceanic habitats that are situated in the northeast of the atoll, adjacent to Tukuhora village. An artisanal trap fishery targets the spawning

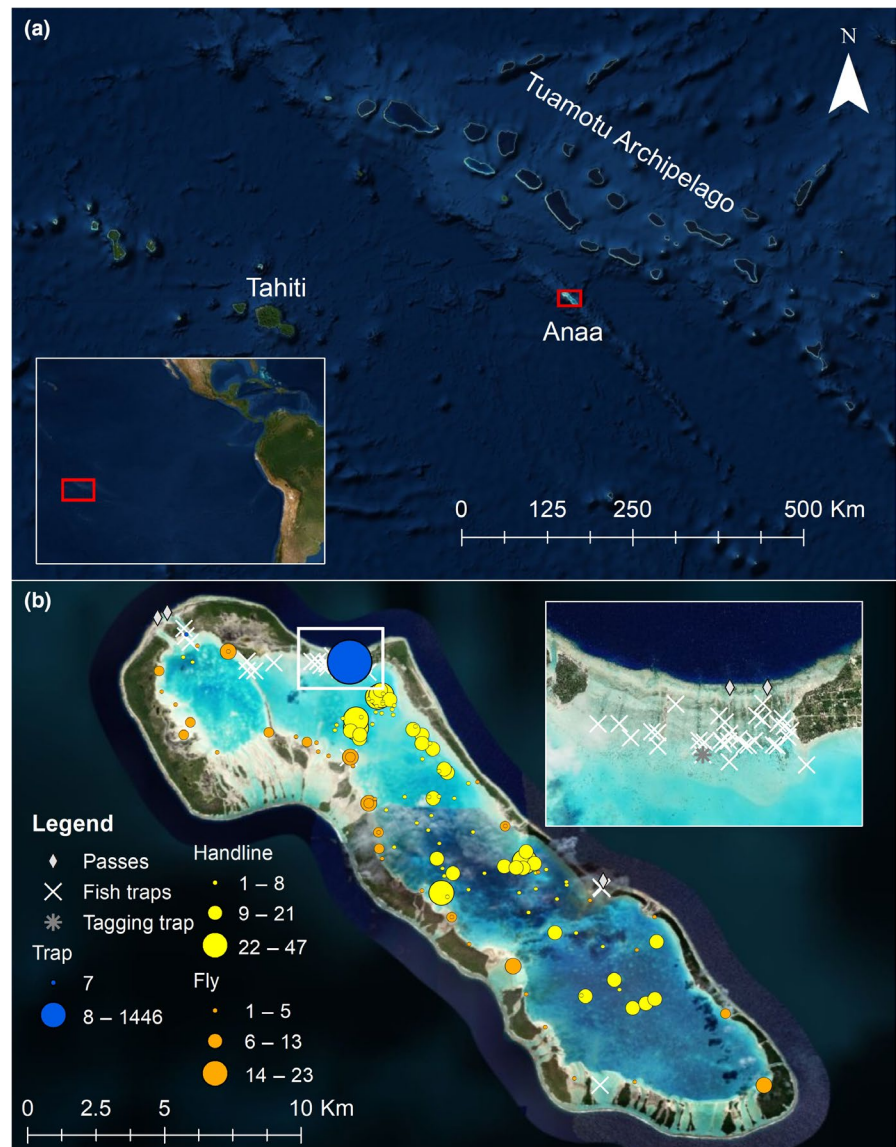migrations of bonefish that are funnelled through these critical migratory passages (Figure 1).

Prior to the commencement of tagging operations, permission to tag bonefish was requested from the community of Anaa Atoll, and they were solicited to share recapture information in the event a tagged fish was captured. A community-wide public meeting was held on 12 October 2015 and outreach materials that informed residents of the possibility of capturing a tagged bonefish were distributed in both French and Puamotu. These materials specified the information that should be collected in the event of a recapture including the date, fishing method, location, tag number, fork length (FL) and how to report this information. Posters and tag report cards were distributed at public places including the post office and the three stores in Tukuhora village. Furthermore, to facilitate the collection of recapture data, waterproof logbooks, pencils and tape measures were distributed to the head of households in families that operated private fish traps.

Bonefish were caught, tagged and released between 2016 and 2018 using three methods in three different habitat types including, fly-fishing along the atoll's fringing sand flats, traditional local hook and hand line (baited with hermit crab) in the deeper portions of the lagoon, and with an artisanal fish trap located in the migratory passage to the open ocean north of Tukuhora village (Figure 1). Upon initial capture, fish were placed in a purpose-built floating basket (40 × 80 cm) that allowed the fish to be tagged and measured without removing them from the water. Bonefish were measured for FL (nearest cm) and tagged with individually numbered, external, plastic dart tags (10 cm PDL, Hallprint, Australia) through the pterygiophores at the base of the dorsal fin. Each tag was printed with a unique four-digit number on the distal and proximal end, phone number and email address with instructions to report the date, tag ID, location and FL in the event of recapture. Finally, to investigate long-term tag shedding rates, a sub-sample of these fish was double tagged on both sides of the dorsal fin in the same manner described above. These double tagged fish were released and marked as such in the data base. During both tagging and recapture events, the date, capture method, location and FL of all tagged bonefish were recorded. During recapture events, all fish were examined for the presence of two tags and upon recovery of a fish that was originally double tagged, tag retention was evaluated.

### 2.1 | Statistical analyses

Size differences between bonefish tagged with the three gear types were tested with linear models using the lm() function and post hoc multiple comparisons were performed with Tukey's honestly significant difference (HSD) test with the glht() function in the multcomp package. Catch-per-unit-effort was calculated for each gear type by calculating the number of fish tagged/day, by a given gear. To estimate the extent and direction of bonefish movement between capture events, the original tagging and recapture locations of bonefish were plotted in Arc Geographic Information Systems (ESRI), and the

**FIGURE 1** Location of Anaa Atoll, the eastern most atoll in the Tuamotu archipelago of French Polynesia (a), and Anaa with scaled bubbles corresponding to the number of bonefish tagged and released at a given location. Orange bubbles indicate fish tagged with fly-fishing equipment, yellow bubbles indicate fish tagged with handlines and blue bubbles indicate bonefish tagged in the artisanal fish traps. White X's indicate the locations of artisanal fish traps, the grey asterix represents the location of the fish trap in which fish were tagged, grey diamonds represent locations of passageways in the reef crest used by spawning bonefish (b) [Colour figure can be viewed at wileyonlinelibrary.com]



minimum linear distance between the two locations over water was measured in km (Kamikawa et al., 2015; Larkin et al., 2007). Time at large was then calculated by taking the difference between the date of initial tagging and recapture. The relationship between time at large and size at release was described with linear regression using the lm() function. Additionally, biological samples were taken from both a sub-sample of fish captured during tagging operations in the lagoon and fish that were recaptured in the artisanal trap fishery. The FL (cm), weight (g), sex and gonad weight (g) of recaptured fish were recorded, and the gonadosomatic index (GSI) was calculated from the subsampled fish as:

$$GSI = \left( {GW}/{TW} \right) \times 100$$

where GW is total weight of both gonads (in g), and TW is the total body weight (in g) (Fontoura, Braun, & Milani, 2009). The GSI of bonefish recaptured in the artisanal fish traps was then compared to

bonefish subsampled during tagging events in the lagoon with the kruskal.test() function.

To describe the relationship between lunar phase and bonefish catches in the artisanal trap fishery, the lunar phase (full, waning, new, waxing) and illumination for each day of the study were acquired with the lunar.phase() and lunar.illumination() functions in the lunar package (Lazaridis, 2015). To test for differences in the number of bonefish caught between the moon phases, the total number of bonefish tagged and recaptured in the artisanal fish trap was pooled by monthly lunar phase and a negative binomial generalised linear model was used with the glm() function to test for significant differences in the number of bonefish captured across the four lunar phases. Post hoc multiple comparisons were then performed with Tukey's HSD test with the glht() function.

Growth parameters of recaptured bonefish were estimated with maximum likelihood following the methods of Francis (1988). For each fish that had a reported FL at recapture, its change in FL between capture events was estimated in cm FL per year. These

measurements were then fit to a von Bertalanffy growth model using the equation proposed by Fabens (1965):

$$\Delta L = (L_\infty - L_1)\left(1 - e^{-k\Delta T}\right)$$

where $\Delta L$ is the change in FL, $L_\infty$ is the maximum length, $L_1$ is the FL at the time of tagging, $K$ is the growth rate, and $\Delta T$ is the time at large between recaptures (Fabens, 1965).

Four potential models with different error structures including, constant, inverse linear, exponential decline and power decline were evaluated (Francis, 1988). Finally, Akaike Information Criterion (AIC) and likelihood ratio tests were then used to select the best model and its corresponding parameter estimates (Francis, 1988).

To assess mortality and population abundance, the integrated Brownie–Petersen mark–recapture model, developed by Polacheck et al. (2006), was used to estimate the rates of natural mortality and fishing mortality in the bonefish population from 2016 to 2018, as well as the initial year-class abundances of ages 3, 4 and 5 in 2016 (the first year of tagging). This method requires that fish from a given cohort are tagged in consecutive years (i.e. at consecutive ages), that they are caught in subsequent years, their recaptured tags returned, and that estimates of the number of fish from that cohort examined for tags (i.e. number of fish harvested) are available for each recapture year. Tagging the same cohort in multiple years allows for return rates over time from consecutive release events to be compared to provide separate estimates of fishing and natural mortality rates, via a Brownie model (Brownie, Anderson, Burnham, & Robson, 1985). While including catch data in the model allows for a Petersen-type estimate of initial cohort abundance to be obtained (Polacheck et al., 2006). The integrated Brownie–Petersen model involves a likelihood component for the tag-recapture data and another for the catch data (see Supporting Information S1 for details).

To apply the Brownie–Petersen model to this fishery, several data sources were required: the number of bonefish of a given age tagged and released prior to the start of each fishing season, the number of recaptures by age in subsequent years from these initial release events, an estimate of the number of fish of each age class harvested each year in the fishery (along with an estimated standard error), an estimate of the annual reporting rate ($\lambda$) for each year of the study, and finally an estimate of tag shedding frequency ($\phi$).

To meet the assumption of a fully mixed population, only bonefish tagged and released in the artisanal fish trap at the start of each fishing season and their corresponding recaptures were included in the analysis. To determine the number of bonefish of each age class harvested annually in the fishery, creel surveys were conducted from 2016 to 2018. Local fishermen were accompanied during monthly harvest events that coincided with bonefish spawning activity during the waning moon to record the number of bonefish captured and measure their FLs. After obtaining these FL frequency distributions, the age of fish harvested and tagged was determined by converting their FLs to age with the non-sex-specific von Bertalanffy growth parameters ($L_\infty$ = 76, K = 0.20, $t_0$ = −0.75) estimated from annual growth rings in otoliths (Filous, Lennox, Coleman, et al., 2019). The

natal year for each fish was then back calculated and each fish was placed into age cohorts. Age at recapture was estimated by adding their time at large to their estimated age at first capture (Polacheck et al., 2006).

The reporting rate ($\lambda$) was estimated for each year of the study by comparing the ratio of observed recaptures to reported recaptures. Local fishermen were accompanied during harvesting events to observe the total number of fish caught and the total number of marked fish recaptured. These events provided an estimate of the proportion of tagged fish in the population. However, when it was not possible to observe all catches, fishers were asked how many unobserved packets of fish were sold to obtain an estimate of their total catch size. Bonefish are sold as a packet of five fish strung together on a strip of tree bark. Therefore, the total size of the annual unobserved catch was estimated by multiplying the total number of packets sold by five. When unobserved tags were subsequently recovered and reported by community members, they identified the source of the fish. These recaptures were matched to their corresponding catches, and the overall annual reporting rate was estimated using:

$$\lambda = \frac{r_{reported}c_{observed}}{c_{reported}r_{observed}}$$

where is $\lambda$ = the reporting rate, $r_{observed}$ = total number of recaptures in observed catch, $c_{observed}$ = total number of fish in observed catch, $r_{reported}$ = total number of recaptures reported from unobserved catch, $c_{reported}$ = total number of fish in unobserved catch.

Tag shedding rates ($\phi$) were estimated by taking the number of double tagged bonefish recaptured in the artisanal fishery, evaluating the retention of both tags, and applying number of bonefish recovered with and without both tags to the model described by Seber and Felton (1981):

$$\varnothing = \frac{2(dt)}{2(dt) + st}$$

where $dt$ is the number of fish recovered with double tags, and $st$ is the number of fish recovered with a single tag that were originally double tagged (Seber & Felton, 1981).

These data were then input to the Brownie–Petersen model (see Supporting Information S1), and fitted assuming tagged fish are fully mixed in to the population, a constant coefficient of variation of 0.1 in annual catch estimates, the tag reporting rates and shedding rates are known without error, and the ages of fish at tagging are known accurately. Fishing mortality was allowed to vary by year and age, but natural mortality was assumed only to vary by age. In addition, since only two natural mortality parameters can be estimated in an experiment with three consecutive release years (Polacheck et al., 2006), natural mortality was constrained to be a linear function of age, parameterised in terms of natural mortality at the youngest and oldest ages in the model (ages 3 and 7, respectively). Brownie–Petersen model coding and implementation was completed in AD

Model Builder (Fournier et al., 2012). All other statistical analyses were conducted using R (v3.4.3), and all mean values are reported as the mean ± one $SD$ unless otherwise stated.

# 3 | RESULTS

Over the course of the study, 2,509 bonefish were tagged and re-leased with conventional dart tags (Figure 1) of which 1,447 were tagged in artisanal fish traps during their spawning migrations (54 ± 6 cm FL; min–max = 38–70 cm), 800 were tagged by hand-line in lagoon muds (40 ± 5 cm FL; min–max = 27–63 cm), and 262 were tagged with fly-fishing equipment (47 ± 7 cm FL; min–max = 32–75 cm) in the atoll's fringing sand flats (Figure 2; $r^2$ = 0.53, $F$ = 1,449, $p$ < 0.005). The mean number of bonefish captured per-day with the artisanal fish trap was 3 ± 15, 17 ± 17 with handlines and 2 ± 2 with fly-fishing equipment. As of 1 October 2018, 308 of the tagged bonefish (12.27%) were recaptured by five gear types, in-cluding speargun ($n$ = 1), handline ($n$ = 1), fly rod ($n$ = 3), gillnet ($n$ = 12) and artisanal fish trap ($n$ = 291). The time at large for these recap-tured fish ranged from 0 to 928 days, with a mean of 248 ± 187 days and artisanal fish traps located in the migratory corridors of the atoll accounted for 94% of all recaptured bonefish.

Of the bonefish recaptured in the present study, 72% were both tagged and recaptured in artisanal fish traps, yielding little spatial movement data between capture events. However, 10 of the 221 fish (4.5%) that were exclusively tagged and recaptured in fish traps were recaptured in traps located in different migratory passageways, demonstrating some intra-individual variation exists in the selection
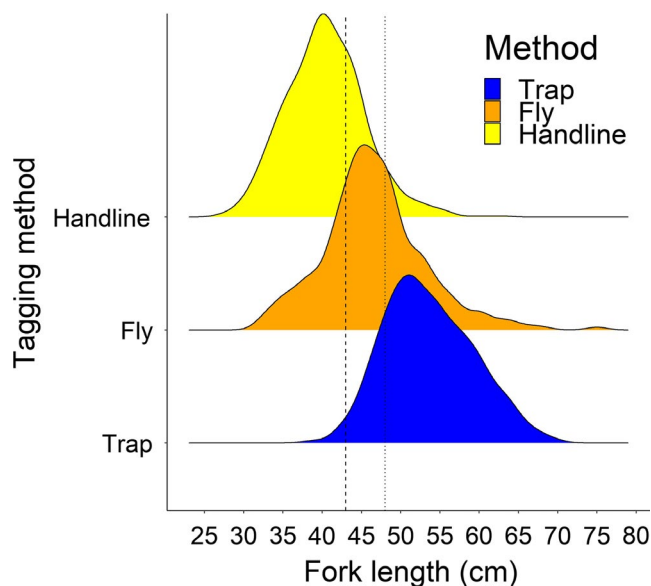


**FIGURE 2** Density distribution of the size of bonefish *Albula glossodonta* tagged with the three different fishing methods (Handline, Fly, and Trap). The dash dotted line represents the size at sexual maturity for male bonefish ($L_{50}$ = 43 cm FL), and the dotted line represents the size at sexual maturity for female bonefish ($L_{50}$ = 48 cm FL) [Colour figure can be viewed at wileyonlinelibrary.com]
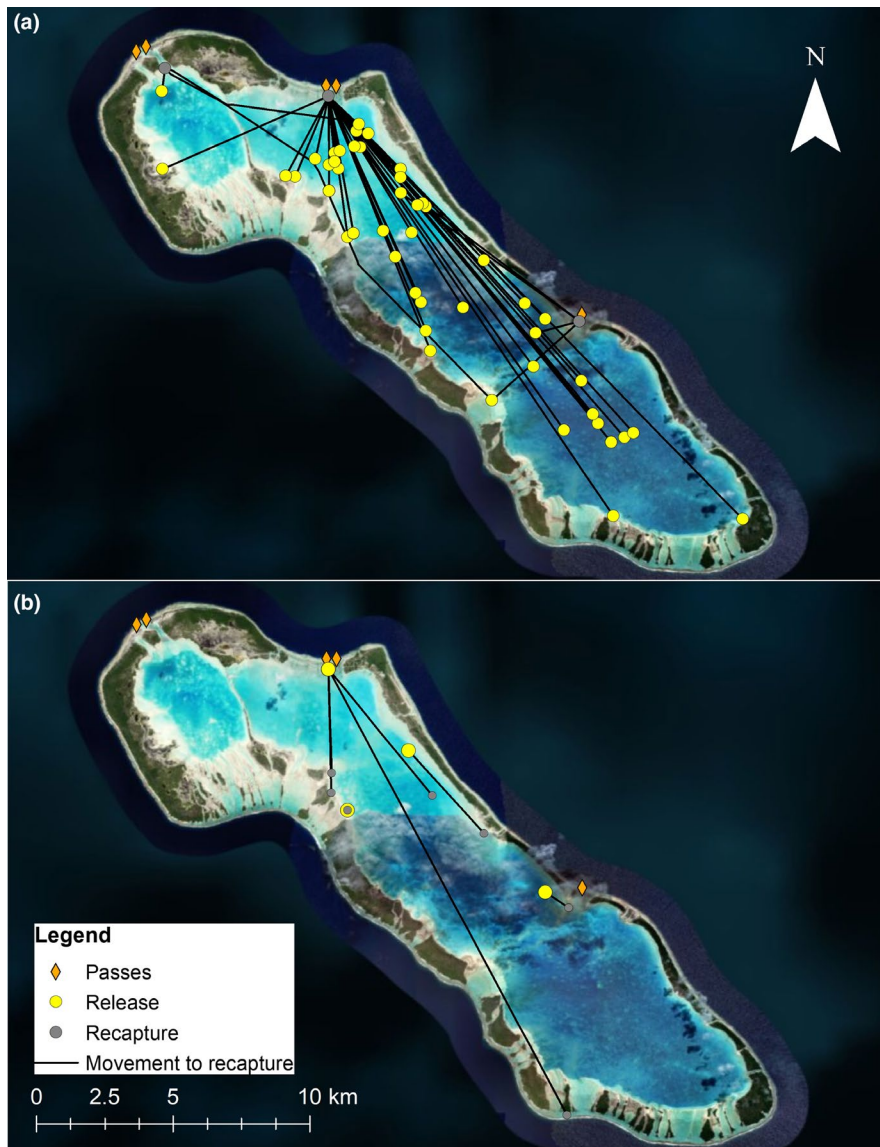
of movement corridors for spawning migrations. Bonefish that were initially captured and tagged with either handline or fly-fishing equipment in the outer reaches of the atoll were recaptured in all three movement corridors along the northeast perimeter of the atoll, suggesting a northward migration (Figure 3). However, the majority of these bonefish (92%) were recaptured in the passageway adjacent to Tukuhora village, whereas both the northernmost passageway at Verite and southern most passageway at Ongongo accounted for 4% of recaptures. The mean distance of these movements to and from the atoll's migratory passageways was 7.5 ± 5.4 km (min–max = 0.8–21.1 km), thus demonstrating connectivity between the atoll's two sub-lagoons (Figure 3). Only three of the recaptured bonefish were both captured and recaptured with methods other than fish traps. These movements were non-migratory, ranging between 0 and 4 km and likely reflective of foraging behaviour between the deep lagoon muddy locations and the shallow flats where they were subsequently recaptured (Figure 3). All of the tagged bonefish that were <40 cm FL exhibited times at large in excess of 500 days, while considerable variation in time at large was observed among fish that were larger than the size at sexual maturity at the time of tagging: 43 cm FL for males and 48 cm FL for females (Figure 4). This nega-tive relationship between days at liberty and size was significant, with smaller, immature fish exhibiting longer times at liberty than larger, reproductively mature adults ($r^2$ = 0.10, $F$ = 19.66, $p$ < 0.005). When recaptured in the artisanal fish traps, the GSI of both female and male bonefish was higher (female = 7.24 ± 4.06, male = 2.3 ± 1.7) than bonefish subsampled during tagging operations in the lagoon (female = 0.24 ± 0.21, male = 0.15 ± 0.08) and these differences were statistically significant in both sexes (female: $\chi^2$ = 18.209, $df$ = 1, $p$ < 0.005; male: $\chi^2$ = 9.5553, $df$ = 1, $p$ < 0.005).

The number of bonefish tagged and recaptured in the artisanal fish traps followed the lunar cycle, with peaks in tagging occurring during the waning moon phase between 58% and 78% lunar illumi-nation (Figure 5). Of the bonefish tagged in the artisanal fish trap, 87% were captured during the waning moon and the maximum number of bonefish tagged per-monthly moon phase was 295 with a mean of 79 ± 93. The negative binomial generalised linear model indicated that the difference in the number of bonefish captured be-tween the four lunar phases was statistically significant ($p$ < 0.005), with Tukey's HSD tests for multiple comparisons demonstrating that the number of bonefish captured during the waning moon was sig-nificantly greater than the three other lunar phases (Figure 5).

Change in FL and time-at-large data were available for 167 re-captured bonefish (Figure 6). The initial FLs of these recaptured fish ranged between 32 and 69 (50 ± 6) cm and time-at-large ranged from 1 to 928 (325 ± 172) days. Of the four models derived with these data, both the likelihood ratio tests and AIC suggest that the model with power decline variance was most appropriate (Supporting Information S2). With this model, the asymptotic length of a fish ($L_\infty$) was estimated to be 71 ± 1.4 SE cm FL with a growth parameter (K) of 0.17 ± 0.02 $SE$.

To obtain the required data elements for the integrated Brownie–Petersen model, first both reporting rates and tag

**FIGURE 3** Movements of bonefish *Albula glossodonta* originally tagged in the outer reaches of the atoll and recaptured in the artisanal fish traps, for simplicity the location of recapture is aggregated (a) and the movements of bonefish originally tagged in the artisanal fish traps and recaptured in the outer reaches of the atoll, along with the movements of bonefish tagged and recaptured by other gear types (b) [Colour figure can be viewed at wileyonlinelibrary.com]

shedding rates in the artisanal fishery were evaluated. The reporting rates for the 2016, 2017 and 2018 fishing seasons were estimated to be 0.89, 0.82 and 0.86, respectively (Table 1). Of the 100 double tagged fish originally released in the study, 19 were recaptured (19%) with times at large ranging from 2 to 254 (174 ± 80) days. All the recaptured double tagged fish retained both their tags, suggesting that tag shedding was minimal (φ = 0). However, it should be noted that broken tags were observed in 21 of the 2,409 fish (0.87%) that were originally tagged with a single tag. These fish with broken tags were generally at large for longer time periods, ranging from 61 to 928 (514 ± 174) days and their tags presumably broke as a result of algae build up. Despite being broken, their presence was easily detectible to fishers, as the tags broke at their distal end and in all cases, algae coated the remaining external portion of the tag. In these occasions, the tag ID number was recovered from the proximal end of the tag, and the tag anchor was firmly attached to the pterygiophores, suggesting that tag shedding was negligible.

After data filtering, 424 bonefish from ages 3 to 7 (which were tagged and released at the beginning of each year's fishing season) were included in the integrated Brownie–Petersen analysis (Table 1), and 76 (18%) of these fish were recaptured over the study period with times at large ranging from 1 to 853 days and a mean of 237 ± 188 (Figure 7). Finally, 3,068 fish from ages 3 to 7 were documented in the artisanal fishery over the course of the three fishing seasons and were included in this analysis (Table 1). The maximum likelihood estimates of natural mortality and their standard errors indicate that natural mortality is high in age-3 fish (0.64 ± 0.29) and declined as bonefish approach their asymptotic size at age 7 (0.001 ± 0.0004). Conversely, fishing mortality increases with age as bonefish grow and become fully recruited to the fishery, with age-3 fish experiencing little-to-no fishing mortality (0.02 ± 0.004). However, as bonefish reach sexual maturity at ages 4 and 5, fishing mortality increases by an order of magnitude (min–max = 0.10–0.16), reaching its peak (0.28 ± 0.05) in age-6 fish (Table 2). In 2016, the abundance of age-3 fish was estimated to be 13,773 ± 5,147 individuals, the abundance of age-4 fish
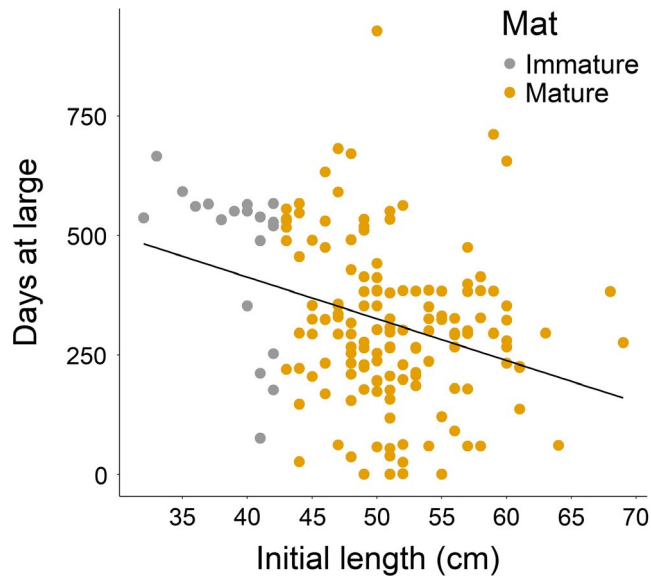
**FIGURE 4** Relationship in bonefish *Albula glossodonta* between the fork length (FL) at initial tagging and time at large (grey dots represent fish that were less than 43 cm (i.e., the size at maturity in males) and orange dots represent fish tagged at sizes greater than 43 cm FL) [Colour figure can be viewed at wileyonlinelibrary.com]
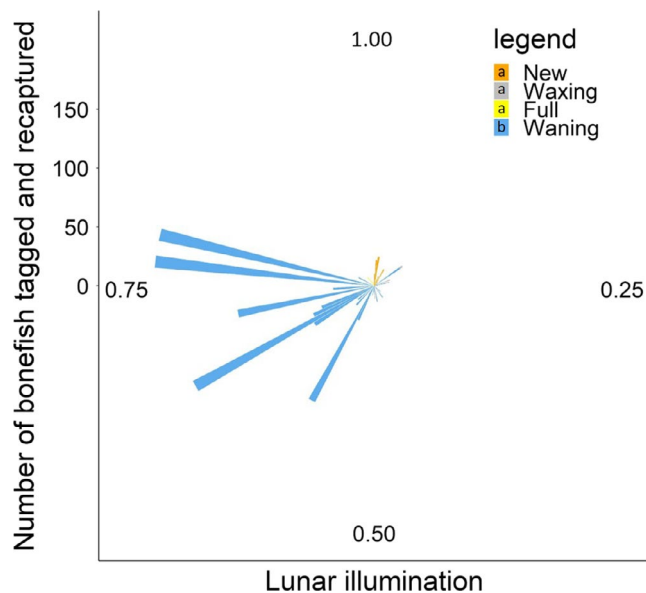


**FIGURE 5** Number of bonefish *Albula glossodonta* tagged and recaptured in the artisanal fish trap with the lunar illumination and corresponding lunar phase from 2017 to 2018. The number of bonefish tagged was significantly different between moon phases (*p* < 0.001). Tukey's HSD tests were used for unplanned multiple comparisons among lunar phase; lunar phases with the same letter are not significantly different (*α* = 0.05) [Colour figure can be viewed at wileyonlinelibrary.com]



**FIGURE 6** The change in length and time at large for recaptured bonefish *Albula glossodonta*. Note, bubble size and colour correspond to the initial size at tagging (L$_m$) [Colour figure can be viewed at wileyonlinelibrary.com]

of these age classes (suggestive of their rarity in the population). But given the majority of age-3 fish are sexually immature, the precipitous decline in the abundance of 4- and 5-year-old fish, and the twofold predicted increase in fishing mortality in age-6 + fish, the size of the spawning stock (i.e. fish actively involved in reproductive events) was likely well below this total abundance estimate (Table 2).

## 4 | DISCUSSION

This study documents the population dynamics of bonefish in the South Pacific using mark–recapture methods and provides vital information to the management of this species for Anaa Atoll. The overall recapture rate of 12.27% indicates that fishing mortality is extremely high in this fishery. To put these results into context, the mean time at large in Hawaii's Oio (bonefish) Tagging Project was 354 days, and 2.7% of these bonefish were recaptured over a period of 11 years (Kamikawa et al., 2015). Similarly, conventional tagging studies of bonefish *Albula vulpes* in the Atlantic, yielded recapture rates of 1.5%–6.6% over equivalent time periods (Boucek et al., 2018; Larkin et al., 2007; Perez et al., 2018). In contrast to these studies, the recapture rate of bonefish at Anaa Atoll is much higher and was obtained over a comparatively short time period (3 years). Prior to the present study, the highest observed recapture rate in a bonefish tagging project (6.6%) was reported by Perez et al. (2018), who also targeted spawning aggregations during tagging and recapture events. The aforementioned study highlighted the vulnerability of bonefish during this stage of their life. With this in mind, the rate of tag recovery at Anaa Atoll is nearly double that of Perez et al. (2018) and equivalent to the recapture rates reported in industrial tuna fisheries that range from 12% to 20% (Adam & Sibert, 2002; Fonteneau & Hallier, 2015), suggesting that this bonefish population is heavily exploited. The gear types responsible for recapturing bonefish demonstrate that although bonefish are harvested with multiple fishing methods at Anaa Atoll,

was estimated to be 9,934 ± 5,035 and the abundance of age-5 fish was estimated to be 5,372 ± 3,592, suggesting a total population size of 29,079 bonefish between 3 and 5 years old. The abundance of age-6 + bonefish was not predicted due to the small sample size
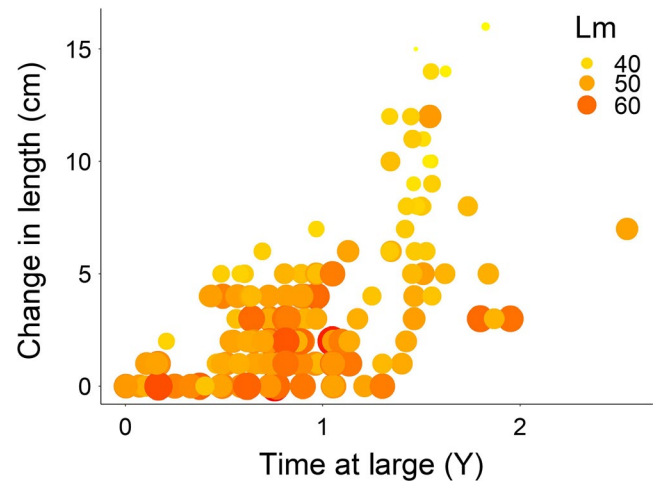
**TABLE 1** Tagging, recapture, and harvest data utilised in the integrated Brownie–Petersen model, to obtain estimates of natural mortality, fishing mortality and initial cohort abundance (in the year of first tagging) in the bonefish *Albula glossodonta* population of Anaa Atoll from 2016 to 2018
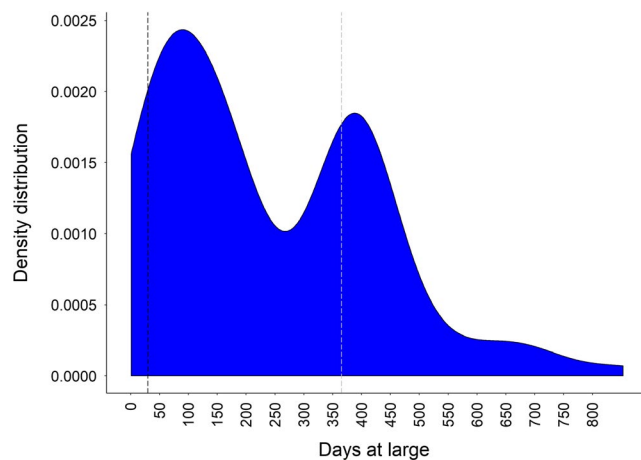
| Release data | | | | No. of tag-returns | | |
|---|---|---|---|---|---|---|
| Cohort | Release year | Release age | No. of releases | 2016 | 2017 | 2018 |
| 2011 | 2016 | 5 | 13 | 2 | 3 | 0 |
| | 2017 | 6 | 73 | | 10 | 12 |
| | 2018 | 7 | 40 | | | 5 |
| 2012 | 2016 | 4 | 40 | 1 | 2 | 2 |
| | 2017 | 5 | 95 | | 12 | 5 |
| | 2018 | 6 | 36 | | | 6 |
| 2013 | 2016 | 3 | 30 | 2 | 1 | 0 |
| | 2017 | 4 | 73 | | 5 | 6 |
| | 2018 | 5 | 24 | | | 2 |
| No. of fish harvested | | | | | | |
| Cohort | 2016 | 2017 | 2018 | | | |
| 2011 | 194 | 261 | 137 | | | |
| 2012 | 412 | 370 | 264 | | | |
| 2013 | 156 | 769 | 505 | | | |
| Reporting rate | 0.89 | 0.82 | 0.86 | | | |



**FIGURE 7** The density distribution of days at large for bonefish *Albula glossodonta* tagged and recaptured applied to the integrated Brownie and Petersen model (black dashed line represents the ≈30-day lunar cycle and grey dashed line represent the 360-day annual cycle) [Colour figure can be viewed at wileyonlinelibrary.com]

**TABLE 2** Maximum likelihood estimates of bonefish *Albula glossodonta* age-specific natural mortality (M), Fishing mortality (F) in the 2016 to 2018 fishing seasons and cohort abundance at initial tagging in 2016 with the associated standard errors in parenthesis derived from the integrated Brownie–Petersen model ($M_{(age3)}$ and $M_{(age5)}$ estimates apply to all three cohorts)

| Parameter | Cohort | | |
|---|---|---|---|
| | 2011 | 2013 | 2014 |
| $M_{(age\ 3)}$ | 0.64 (0.29) | | |
| $M_{(age\ 7)}$ | 0.001 (0.0004) | | |
| $F_{(age\ 3)}$ | - | - | 0.02 (0.004) |
| $F_{(age\ 4)}$ | - | 0.10 (0.02) | 0.14 (0.04) |
| $F_{(age\ 5)}$ | 0.14 (0.03) | 0.16 (0.04) | 0.16 (0.07) |
| $F_{(age\ 6)}$ | 0.28 (0.05) | 0.17 (0.05) | - |
| $F_{(age\ 7)}$ | 0.21 (0.23) | - | - |
| $P_1$ | Age 5 = 5,376 (3,592) | Age 4 = 9,934 (5,035) | Age 3 = 13,773 (5,147) |

artisanal fish traps place the highest level of fishing mortality on the population and should be the focus of management.

The size distributions of bonefish captured in the three different habitats suggest that juvenile bonefish reside in the deeper portion of the lagoon and recruit to the atoll's fringing flats as they approach the size of sexual maturity (i.e. 48 cm FL and 4 years of age for females and 43 cm FL and 3 years for males). Ontogenetic shifts in habitat use are common among marine fishes (Dahlgren & Eggleston, 2000; Gillanders, Able, Brown, Eggleston, & Sheridan, 2003; Gutiérrez, Hilborn, & Defeo, 2011). However, the rapid decline of larger fish (i.e. greater than the size of sexual maturity) in the size distributions of both fly and handline caught fish is likely due to

the elimination of the spawning stock by the artisanal trap fishery, as these older and larger fish are intensively harvested by this gear type and the size structure of the overall population is truncated as a result of fishing mortality (Beverton & Holt, 1957; Hsieh, Yamauchi, Nakazawa, & Wang, 2010). Similarly, the negative relationship between the initial size at tagging and days at large can be attributed to the maturation schedule of this species and the commencement of spawning behaviour, which increases their vulnerability to capture in the artisanal trap fishery.

An understanding of growth is critical to fisheries management and the parameters derived from the present study provide an

estimate of somatic growth that can be used to model and inform the management of bonefish fisheries throughout Oceania (Beverton & Holt, 1959; Maunder & Punt, 2013). The growth rate derived from tagging data at Anaa Atoll is equivalent to that estimated from tagging bonefish in Hawaii (K = 0.015/month, corresponding to 0.18/year). However, the $L_\infty$ value estimated for Anaa Atoll was smaller than the largest bonefish tagged (i.e. 75 cm FL). This inconsistency between the observed and predicted maximum size estimated by tagging may be a result of an underrepresentation of large fish (i.e. approaching their asymptotic length) that were recaptured in this study, a common limitation of mark and recapture growth studies in exploited populations (Francis, 1988; Gulland & Holt, 1959; Sainsbury, 1980).

Previous movement studies indicated that bonefish exhibit site fidelity to foraging habitats and depart these locations to migrate to offshore spawning locations (Adams et al., 2019; Boucek et al., 2018; Danylchuk et al., 2011, 2018; Humston et al., 2005; Murchie et al., 2013; Perez et al., 2018). However, where bonefish movement has been previously studied with conventional tagging, fishing (i.e. recapture) effort is primarily conducted on shallow sand flats where bonefish are customarily targeted with fly-fishing equipment. In that context, strong site fidelity was reported after times at large in excess of 1,000 days between recapture, suggesting that bonefish return to their flats after seasonal spawning events (Boucek et al., 2018; Kamikawa et al., 2015; Larkin et al., 2007). Yet, the open nature of these environments has made the spatial and temporal characteristics of spawning movements difficult to document with conventional mark–recapture. By contrast, the closed nature of Anaa Atoll and concentration of fishing effort in bonefish migratory corridors allowed this study to examine the spatial and temporal dynamics of bonefish spawning behaviour. Tag recoveries from the traps located in these migratory corridors indicate that bonefish travel long distances from their foraging habitats in all corners of the atoll to access these northern passes during their migrations to the outer reef, which is spatially consistent with long-distance movements observed in pre-spawning aggregations in the Atlantic (Boucek et al., 2018; Perez et al., 2018). Temporally, the peaks in the number of bonefish tagged and recaptured in the trap fishery coincide with the waning moon and indicate that the timing of movement towards offshore spawning locations overlaps with the gonad development observed in female bonefish across the lunar cycle (Filous, Lennox, Coleman, et al., 2019). Indeed, the GSI of bonefish recaptured in the trap complex was significantly higher than those subsampled during tagging events in the lagoon, which demonstrates that these movements are spawning-related. This supports the traditional ecological knowledge of the Pacific Islands, which suggests that bonefish leave their typical home ranges to make offshore movements in close association with the lunar cycle (Allen, 2014; Beets, 2000; Friedlander et al., 2007; Johannes & Yeeting, 2000).

The integrated Brownie–Petersen model performed well; nevertheless, the estimates derived from this model could be influenced by several sources of error. Firstly, the model assumes that the age at which fish are initially tagged is known without error (Polacheck

et al., 2006). Therefore, to reduce ageing bias, age and growth was modelled with unisex otolith-based parameter estimates, as they permit a more precise estimation of age at FL and are more reliable than the growth estimates obtained from the tagging data above. Secondly, tag shedding could also affect the models results, bur previous research indicated that tag retention of the 10-cm Hallprint PDL tag exceeded the comparatively limited time span of this study (Kamikawa et al., 2015; Larkin et al., 2007). Furthermore, there was no evidence of tag shedding in double tagged fish, only broken tags in a small number of single tagged fish, all of which did not render them unidentifiable to fishers. With this in mind, the error introduced by tag shedding was likely minimal. The estimation of the annual reporting rate is another potential source of error, but given that Anaa Atoll is a small, familiar community, and the majority of harvested fish were observed by the first author, the reporting rate was relatively high. Finally, a significant limitation in tagging experiments and their application to fisheries is the incomplete mixing of tagged and untagged components of a population and heterogeneity in capture probabilities due to the spatial-temporal distribution of sampling effort (Pine et al., 2003; Polacheck et al., 2006, 2010). However, by only including fish captured in the artisanal trap at the beginning of each spawning season, all fish were reproductively active (i.e. recruited to the trap fishery) and were vulnerable to capture over the remainder of their protracted spawning season suggesting that annual fishing mortality rate applied to all fish (Hoenig, Barrowman, Pollock, Brooks, et al., 1998; Hoenig, Barrowman, Pollock, Hoenig, et al., 1998; Pine et al., 2012). Furthermore, acoustic tracking suggests that after release, tagged fish return to the lagoon, mix with untagged fish and resume spawning activity, many of which rejoined spawning aggregations during the moon phase immediately following tagging (A. Filous, unpublished data). This in combination with the geographic isolation of Anaa Atoll, its closed nature, and the funnelled movements of the spawning stock through these passes to the open ocean during spawning events where and when sampling occurred, suggest that heterogeneity of capture probabilities due to the spatial distribution of fish and sampling effort was not a significant issue.

Fisheries models that take into account natural losses in a population of fish in comparison with fisheries losses are particularly sensitive to small changes in natural mortality estimates (Pascual & Iribarne, 1993; Vetter, 1988), and natural mortality is considered to be the most challenging parameter to estimate in wild fish populations (Hewitt & Hoenig, 2005; Hoenig, 1983; Kenchington, 2014; Pauly, 1980). Estimates of mortality from tag-return studies provide an alternative estimate to minimise uncertainty and improve the results of fisheries assessments in which natural mortality is a prerequisite (Hoenig, Barrowman, Pollock, Brooks, et al., 1998; Hoenig, Barrowman, Pollock, Hoenig, et al., 1998; Jiang et al., 2007; Pine et al., 2012, 2003; Polacheck et al., 2006). The estimates of fishing and natural mortality derived from the integrated Brownie–Petersen model suggest a pattern of mortality that is consistent with bonefish life history and the species interaction with the artisanal trap fishery at Anaa Atoll. The high natural mortality predicted in younger age

classes (i.e. age 3) could be reasonable because smaller bonefish are important prey items for sharks and other higher-level tropical predators (Newman, Handy, & Gruber, 2010). Furthermore, the predicted low level of natural mortality for age 7 fish is reasonable because bonefishes of the Genus *Albula* are long-lived and specimens of >20 years have been found in unfished populations (Ault, Humston, et al., 2007; Ault, Moret, et al., 2007; Filous, Lennox, Coleman, et al., 2019), suggesting that natural mortality is less intense as the species reaches its growth asymptote and presumably becomes less vulnerable to predation (Sogard, 1997). On the other hand, the estimates of fishing mortality suggest that fishing mortality is negligible in age-3 fish or less, and although some juvenile bonefish are captured in the artisanal trap fishery during high wind events, male and female bonefish are not fully recruited to the trap fishery until the age of 95% sexual maturity ($A_{95}$), 4 and 5 years, respectively (Filous, Lennox, Coleman, et al., 2019). The rapid and consistent increase in fishing mortality in age-4 + bonefish predicted by the integrated Brownie–Petersen model is consistent with this aspect of the species life history and its interaction with the artisanal trap fishery.

The estimation of population size is another critical component of fisheries stock assessment (Pine et al., 2012; Vélez-Espino et al., 2016). The bonefishes are schooling, soft-bottom-dwelling species that exhibit the life-history characteristics of intermediate strategists, suggesting that these species should be numerically abundant in their respective ecosystems (King & McFarlane, 2003). Yet, little quantitative information exists on the numeric abundance of bonefish populations throughout their worldwide distribution. In the Florida Keys (USA), the number of bonefish was estimated to be between 259,395 and 340,552 individuals in 2003–2005, using visual assessments made over a single day (Ault, Humston, et al., 2007; Ault, Moret, et al., 2007). However, at the time of the survey, local ecological knowledge suggested the population had declined by 90% since 1940 and their figures are not representative of the region's virgin population abundance (Ault et al., 2007; Ault, Moret, et al., 2007). Friedlander et al. (2007) estimated the effective population size of the relatively pristine bonefish population at Palmyra Atoll to be ≈2 million females, and four million individuals assuming a 1:1 sex ratio. Although this figure is based on genetics and is qualitative with numerous assumptions, it provides a reference to the theoretical carrying capacity of an ecosystem like Anaa Atoll (Friedlander et al., 2007). With this in mind, Anaa Atoll is approximately twice the size of Palmyra, thus underscoring the potential carrying capacity of Anaa Atoll and how large the population may have historically been. In comparison, the abundance estimates from the integrated Brownie–Petersen model indicate that the stock of bonefish between 4 and 5 years old is relatively small and was likely no greater than 15,310 individuals in 2016. Although the abundance of juvenile bonefish is unknown, these results suggest that the spawning stock (i.e. 4+ years) is likely a fraction of its historical abundance and supports the traditional ecological knowledge of Anaa Atoll's elder residents, which cited marked declines in the size of bonefish spawning aggregations over the past 30 years.

The lunar timing of bonefish spawning movements observed in the present study was also consistent with the traditional ecological knowledge of this community. Conversations with the atolls fishers suggest that a large proportion of the bonefish population synchronises their spawning movements when three nights of the waning half-moon known as, Ore Ore Mua (the day before the half), Ore Ore Roto (the actual half-moon), Ore Ore Muri (the day after the half-moon) coincide with an increasing southwest swell 2–4 m in height (Residents of Anaa Atoll, personal communication). Historically, when large numbers of bonefish were captured in the public traps, elder fishers would oversee the harvest to ensure each person took only what was needed to meet their family's requirements, until the rising ocean swells flooded the traps (over a period of several hours) and liberated the blockaded spawning aggregations. However, when the fishery was privatised in the 1980s, the proliferation of traps and introduction of chicken wire increased the capacity of this fishery to both capture and hold fish indefinitely (Residents of Anaa Atoll, personal communication). Analogous *Albula* fisheries throughout Oceania all show similar trends in response to intensified exploitation (Adams et al., 2013; Allen, 2014; Friedlander et al., 2007; Ram-Bidesi, 2011; Wallace, 2015). Historically, the number of bonefish harvested in the artisanal fish traps of Tarawa was estimated to be between one and five million fish per year (Johannes & Yeeting, 2000). However, the large-scale harvest of spawning aggregations led to declines in relative abundance of bonefish in the fishery from 44.6% to 7.5% over a period of 15 years (Beets, 2000). Similarly, the annual commercial landings of bonefish in Hawaii declined from 136,079 kg at the start of the 19th Century to 1,361 kg by the year 2002 (Friedlander et al., 2007; Friedlander, Nowlis, & Koike, 2015). Although the yields of these contemporary fisheries may be partially limited as a result of reduced fishing effort in response to past declines, these trends provide a historical context that suggest bonefish abundance can be reduced by orders of magnitude when heavily exploited and support the low population estimate obtained in the present study.

In conclusion, mark–recapture revealed numerous aspects of this data-limited fishery that augmented the traditional ecological knowledge of the community and provided information that was used to manage this fishery. The present work demonstrated that the bonefish spawning stock spatially and temporally synchronises its spawning movements and funnels through the migratory corridors in the north east of the atoll during the waning moon phase, where the bonefish are subjected to intense fishing mortality in the artisanal trap fishery. Furthermore, although these aggregations appear to be numerically abundant during their migrations, the present results indicate that the population size is not as large as conventionally believed and has likely been reduced to a fraction of its historical size, as suggested by the atoll's elder residents.

This body of evidence demonstrates that fish traps are the primary component of the artisanal fishery in need of management, and there are several potential options to enhance the sustainability of this fishery. Firstly, the high proportion of fish recaptured in the migratory corridor adjacent to Tukuhora village suggests a reduction in the overall

density of fish traps in this region would allow for the escapement of more fish during their migrations. Alternatively, if a permanent reduction in the total number of traps cannot be achieved, then short-term temporal closures during the waning moon phase (i.e. in which the traps are temporally deactivated) would also permit the escapement of spawning schools and reduce the fishing mortality on this population.

Ultimately, the data and recommendations for improving the sustainability of this fishery provided by this research were used by the local school to establish an Educational Managed Marine Area (EMMA), which overlaps with the bonefish migratory corridor adjacent to Tukuhora village. The local government approved a plan to manage this resource for future generations by instating a temporal rahui (i.e. closed season), where the artisanal fish traps are deactivated during the initial three months of the spawning season (www.radio1.pf/anaa-a-son-aire-marine-educative/).

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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