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Movements of juvenile yellowfin tuna (*Thunnus albacares*) within the coastal FAD network adjacent to the Palau National Marine Sanctuary: Implications for local fisheries development

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ABSTRACT

Pacific Island nations and territories must build their capacity to harvest pelagic fishes to ensure domestic food security into the future. The Republic of Palau recently created the Palau National Marine Sanctuary, a Marine Managed Area that was intended to conserve marine resources and enhance local pelagic fisheries. However, the capacity of the nation's domestic fishery to exploit pelagic species must be built to meet these objectives and, to this aim, the development of a coastal network of Fish Attracting Devices (FADs) has been proposed. To inform the development of the nation's FAD program, we used acoustic telemetry to study the movements of yellowfin tuna (*Thunnus albacares*) within Palau's existing FAD network. Subadult yellowfin tuna (50 − 79 cm FL) remained within the FAD network for up to 175 days and young-of-the-year yellowfin tuna spent significantly more time in association with FADs in comparison to year-1 fish. A network analysis suggests that the Ngardmau and Peleliu FADs were the most important components of the current FAD network, and a mixed effects Poisson generalized linear model indicated that the residency of yellowfin tuna to these FADs was significantly related to mooring depth and distance from the reef. These results provide a description of yellowfin tuna movements within Palau's FAD network and recommendations to improve the nation's FAD program that are also applicable to other Pacific Island nations and territories that desire to improve domestic access to pelagic fish stocks.

1. Introduction

Fisheries resources are vital to food security and economic opportunity in the Pacific Islands (Zeller et al., 2006a; Bell et al., 2009; Gillett, 2009). Historically, coral reef species provided a major source of marine-derived protein to communities throughout the region (Zeller et al., 2006b; Friedlander, 2018), and in contemporary society, fresh fish continues to be a principal source of nutrition (Bell et al., 2009). Small-scale tropical fisheries were developed for coral reef species throughout the 20th century given the easy accessibility of nearshore waters and the limited capacity of Pacific Island communities to exploit pelagic fish stocks (Adams et al., 1996; Dalzell et al., 1996; Chapman, 2004; Kronen et al., 2006; Zeller et al., 2006a). However, the yields of many coral reef fisheries in the region are now declining due to overexploitation, human population growth, and climate change (Johannes, 1978; Barnett, 2010; Cinner et al., 2012; Houk et al., 2012; Bell et al., 2013). Consequently, future projections suggest that coral reef fisheries will only be able to meet local demand for fish in one third of Pacific Island countries and territories by 2030 (Bell et al., 2009), and it is predicted that tuna will constitute ~25 % of the fish consumed in the region by 2035 (Bell et al., 2015a). As a result of the increased reliance on tuna resources to fill the void in coral reef fisheries, Pacific Island nations and territories must build their capacity to harvest tuna and develop domestic pelagic fisheries to meet the demand for food security into the future (Bell et al., 2015a, b, 2018a).

The Republic of Palau is a small island nation in the western Pacific Ocean that is world-renowned for its biodiversity and marine life, but faces challenges achieving sustainable ecosystems in the 21st century (Golbuu et al., 2005; Jupiter et al., 2014; Wabnitz et al., 2018). Coral reef associated species have traditionally been a staple of the Palauan

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diet, but in recent years these species and their fisheries have been subject to increased pressure and have declined from their historical abundance (Johannes, 1981; Golbuu et al., 2005; Fitzpatrick and Donaldson, 2007). Research suggests that the reef fish populations in the northern reefs of Palau are overexploited, with the spawning potential ratios (SPRs) of many principle reef species being < 20 %, and some < 10 % (Prince et al., 2015). In addition to the threat to food security posed by deteriorating coral reef fisheries, these resources represent an important attraction to the nation's diving and eco-tourism industry, which contributes significantly to Palau's economy (Vianna et al., 2012; Wabnitz et al., 2018). If left unmanaged, the current level of fishing pressure, coupled with climate change and other disturbances, could be devastating to reef fish stocks and the socio-economic institutions their populations support (Bell et al., 2013; Wabnitz et al., 2018). Fortunately, the Republic of Palau has abundant tuna resources that have been historically fished by foreign fleets (Sisior, 2006; Dacks et al., 2020), and considering the status of its coral reef fisheries, the development of alternative domestic fisheries for pelagic species is needed to reduce the nation's dependence on its nearshore resources.

In 2015, the Republic of Palau passed the Palau National Marine Sanctuary (PNMS) act and the PNMS went into full effect in January 2020. The PNMS is a Marine Managed Area that includes a 475,669 km^2 no-take protected area, a 105,705 km^2 commercial fishing zone, and a 12,073 km^2 artisanal fishing zone (Fig. 1). Although the development of a domestic fishery in the PNMS could improve the ability of Palau's local pelagic tuna fisheries to provide a sustainable alternative to reef fisheries, the capacity of the nation's domestic fishery to access and exploit these resources must be built to meet the demand for fish and support food security (Gruby et al., 2017; Tolvanen et al., 2019; Dacks et al., 2020). Investment into locally-owned boats, cold storage and training in pelagic fisheries is needed to support these objectives (Dacks et al., 2020), and among these requirements, the development of a Fish Aggregation Device (FAD) program has been proposed as an important prerequisite for improving local access to pelagic resources in Palau and throughout the wider Pacific region (Bell et al., 2015b, a).

The use of FADs is wide-spread throughout the world's tropical oceans and is critical to the success of many tuna fisheries (Marsac et al., 2001; Sharp, 2011b). These devices are believed to enhance the success of small-scale local pelagic fisheries by reducing search time and holding pelagic species, such as yellowfin tuna (*Thunnus albacares*) within the ranges of small fishing vessels for extended periods of time (Sims, 1988; Friedlander, 1994; Pollnac and Poggie, 1997). Recent studies indicate that FAD development programs have contributed to increased catch rates and reduced fuel consumption for small-scale artisanal fishers in several Pacific Island nations and territories (Sharp, 2011b; Albert et al., 2014; Tilley et al., 2019), and it is suggested that their wide-spread application will be critical to maintaining access to tuna resources and food security for local communities in the Pacific Islands (Bell et al., 2015a, 2018b). However, there are many obstacles to the development of FAD fisheries, including developing local capacity (i.e., boats, safety equipment, knowledge of effective fishing techniques), fisher willingness to shift from reef to the pelagic fisheries, and determining the appropriate locations for FAD placement. Some of the major research questions include identifying the key features that improve the efficacy of a FAD in aggregating yellowfin tuna; knowledge that could help assist in selecting appropriate locations for FAD deployment (Bell et al., 2015b, 2018b).

FADs have been utilized in the coastal waters of Palau since the 1980s but their application was sporadic until Palau's Bureau of Marine Resources launched a coastal FAD project under the guidance of The Pacific Community (formerly the South Pacific Commission, SPC) in 2013, and at present FADs are deployed by both the government of Palau's Bureau of Marine Resources and the Palau Sport Fishing Association (Gillett and McCoy, 2019). The Republic of Palau is currently working on developing a strategic FAD plan to coordinate future FAD deployments, monitor, maintain and replace FADs after they have been lost. However, little is known about the movements of yellowfin tuna within the current FAD network, and the network's ability to keep mobile schools of yellowfin tuna within the range of local fishermen remains unknown. Acoustic telemetry has been successfully used to describe the movements of tuna and other pelagic species in association with FADs, and has the potential to describe the residency of tuna schools to an individual FAD and connectivity through Palau's FAD network (Ohta and Kakuma, 2005; Dagorn et al., 2007; Taquet et al., 2007; Govinden et al., 2013; Forget et al., 2015). This information would assist in the development of a local domestic fishery by providing managers in these agencies with data on the efficacy of the existing FADs and inform future FAD deployments. To this aim, the objectives of this study were to describe the movements of yellowfin tuna in Palau's coastal FAD network using passive acoustic telemetry to: 1) quantify their retention time within the FAD network; 2) evaluate the residency of yellowfin tuna to FADs; 3) ascertain the connectivity of yellowfin tuna to the various FADs; and 4) investigate relationships between FAD characteristics that might be attributed to increased effectiveness in aggregating yellowfin tuna and other pelagic fisheries resources. This knowledge is directly applicable to generating recommendations that will improve the nation's FAD program and is relevant to other Pacific Island nations and territories that wish to improve domestic access to pelagic fish stocks.

2. Methods

2.1. Study site

The Palauan coastal FAD network is located within the nation's Territorial Seas (i.e., State waters) that are within 22 km of the coast and encircled by the federally managed PNMS (Fig. 1). At the time of this study, the coastal FAD network consisted of four FADs located along the west coast of Palau's main island of Babeldaob and offshore from the states of Peleliu, Ngardmau, and Ngerchelong. This series of anchored FADs was located at distances from 5 − 9 km from the reef and in depths ranging from 414 − 1,000 m. These FADs were all built following SPC's Indian Ocean FAD design, and constructed from a series of buoys and skirt material (e.g., palm fronds, netting, or plastic binding straps) stung together on a 19 mm diameter nylon rope that is moored to the seabed with a concrete block (Gates et al., 1996; Chapman et al., 2005). These floating structures attract a wide range of pelagic species including yellowfin tuna, and are fished by the nation's artisanal and sportfishing groups (Gillett and McCoy, 2019).

2.2. Passive tracking

The long-term movements of yellowfin tuna in the coastal FAD network were studied with a passive acoustic monitoring array. Vemco VR2W acoustic receivers (308 mm x 73 mm, Amirix Inc., Bedford, NS, Canada), were deployed at the four FADs located along the west coast of Palau (Fig. 1). The VR2W acoustic receivers were attached to the main line of the FAD at a depth of 18 m, with a series of three alternating 80 kg tensile strength plastic cable ties and three stainless steel hose clamps, secured over a 19 mm diameter vinyl tube to protect the main line of the FAD from chafing. Following installation of the acoustic array, 30 sub-adult yellowfin tuna (50 − 79 cm FL) were captured with hook and line in the waters surrounding the FAD network and tagged with Vemco V-13 coded transmitters programmed to transmit an individual identification number at pseudorandom intervals ranging between 75–125 seconds for up to 561 days. During tagging operations, yellowfin tuna were brought on board the research vessel and placed supine in a padded V-shaped board with a hose circulating sea water over their gills. The tags were then surgically implanted into the coelomic cavity of yellowfin tuna through a 2-cm incision in the abdominal wall and closed with an interrupted suture (PDO 2/0,

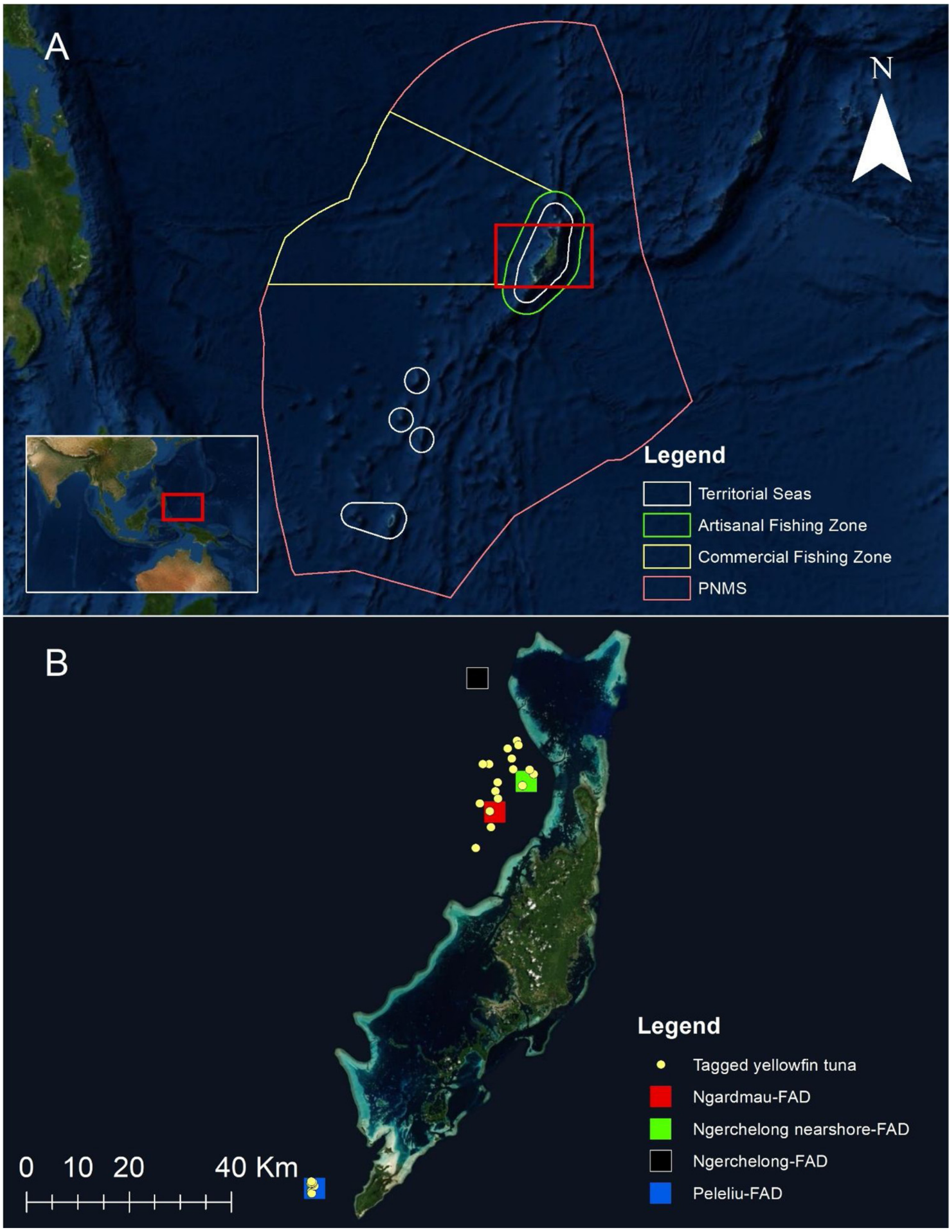

Fig. 1. A. Palau's Exclusive Economic Zone with locations of Territorial Seas, Artisanal Fishing Zone, Commercial Fishing Zone and the Palau National Marine Sanctuary (PNMS) indicated by colored polygons. B. Palau's main islands with colored squares indicating locations of FADs and yellow dots indicating locations of acoustic tagged yellowfin tuna. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

reverse cutting needle, Oasis, Glendora, CA). After surgery, all fish were measured (fork length, FL, to the nearest cm) and immediately released. The detection data from the VR2W acoustic receivers was retrieved and downloaded at 3-month intervals.

2.3. Statistical analyses

All statistical analyses were conducted using R and values are reported as means and one standard deviation, unless otherwise stated. To identify initial patterns of yellowfin tuna movement and behavior throughout the acoustic array, we generated abacus plots of individual detections at each FAD that indicate a date of arrival at a given location for each tagged fish. To test for differences in retention time within the coastal FAD network and residency to FADs between age classes, we pooled tagged fish by year class based on their fork length at time of capture and the growth characteristics of yellowfin tuna in the Western Pacific Ocean (Lehodey and Leroy, 1999). Yellowfin tuna < 60 cm FL were classified as young-of-the-year (YOY) and those from 60 to 100 cm FL were classified as year 1 (Y1).

2.3.1. Retention time within the FAD network and residency to FADs

To evaluate the retention time of yellowfin tuna within the coastal FAD network, we first determined the detection spans of tagged fish within the acoustic array (i.e., the number of days elapsed between first and last detection), then grouped the fish by age class as described above and generated survival curves for the two groups with the survfit function in the R package survival. We then tested for significant differences between the survival curves of each age class using Cox proportional hazards regression. To investigate differences in FAD residency between age classes, we calculated both the continuous residency time (CRT) and fine scale continuous residency time (FCRT) as described in Govinden et al. (2013), as the total amount of time (hrs)

Table 1
Tagging and detection summary data for yellowfin tuna tagged with V13 coded acoustic tags in the FAD complex surrounding the nearshore waters of the Palau's territorial seas.

Fish ID	Datetagged	FL(cm)	Date first detected	Date last detected	Detections	Days detected	Detection span (days)	FADs visited
THAL_1	10-Dec-17	61	29-May-18	1-Jul-18	21	4	33	2
THAL_2	10-Dec-17	61	23-Mar-18	23-Jul-18	98	13	122	3
THAL_3	15-Feb-18	53	15-Feb-18	15-Feb-18	2	1	0	1
THAL_4	15-Feb-18	54	16-Feb-18	27-Feb-18	20	4	11	2
THAL_5	15-Feb-18	50	16-Feb-18	16-Feb-18	9	1	0	1
THAL_6	15-Feb-18	53	17-Feb-18	19-Feb-18	10	3	2	2
THAL_7	15-Feb-18	54	13-Feb-18	7-Apr-18	409	9	53	3
THAL_8	15-Feb-18	53	15-Feb-18	2-May-18	2150	8	76	1
THAL_9	15-Feb-18	54	–	–	–	–	–	–
THAL_10	18-Feb-18	72	18-Mar-18	4-Aug-18	200	17	139	3
THAL_11	18-Feb-18	66	21-Feb-18	21-Feb-18	6	1	0	1
THAL_12	18-Feb-18	66	1-Apr-18	12-Aug-18	48	6	133	2
THAL_13	18-Feb-18	68	17-Mar-18	20-Mar-18	27	2	3	1
THAL_14	18-Feb-18	79	–	–	–	–	–	–
THAL_15	18-Feb-18	79	29-May-18	23-Jun-18	9	2	25	1
THAL_16	18-Feb-18	68	1-Apr-18	23-Sep-18	392	22	175	3
THAL_17	19-Feb-18	52	19-Feb-18	19-Feb-18	17	1	0	1
THAL_18	19-Feb-18	52	19-Feb-18	21-Apr-18	3674	17	61	2
THAL_19	19-Feb-18	55	19-Feb-18	11-Apr-18	1524	7	51	2
THAL_20	19-Feb-18	52	19-Feb-18	19-Jul-18	176	2	150	2
THAL_21	20-Feb-18	52	–	–	–	–	–	–
THAL_22	20-Feb-18	52	21-Feb-18	1-May-18	3352	17	69	2
THAL_23	20-Feb-18	63	22-Apr-18	21-Aug-18	80	14	121	3
THAL_24	22-Feb-18	56	22-Feb-18	31-May-18	2256	11	98	4
THAL_25	22-Feb-18	58	22-Feb-18	27-Mar-18	1778	5	33	3
THAL_26	22-Feb-18	56	22-Feb-18	24-Feb-18	576	2	2	1
THAL_27	22-Feb-18	54	22-Feb-18	1-Mar-18	182	4	7	1
THAL_28	22-Feb-18	54	22-Feb-18	11-Apr-18	4863	16	48	2
THAL_29	22-Feb-18	57	22-Feb-18	1-Mar-18	1030	5	7	3
THAL_30	22-Feb-18	56	22-Feb-18	27-Mar-18	1515	4	33	2

each transmitter equipped fish remained at a given FAD during each distinct residency event. For measures of CRT, a data frame consisting of arrival and departure times from each FAD was derived by conducting a residency search in the Vemco User Environment (VUE) program with a minimum residency threshold of two detections across a 24 -h period. For all detections that met these criteria, the total hours for each residency was calculated by taking the difference in elapsed time between first and last detection. Fine scale residency times were estimated following the same procedure as CRTs, however the residency threshold was set to two detections over a one-hour period (Govinden et al., 2013). Finally, to investigate differences in CRTs and FCRTs to the FADs by age class, we pooled yellowfin tuna CRT and FCRT residencies by fork length into the YOY and Y1 age classes and tested the survival curves of each age class with Cox proportional hazards regression following the same procedure described above.

2.3.2. Network analysis

Network analysis is an analytical methodology based in graph theory (Stehfest et al., 2013; Finn et al., 2014; Jacoby and Freeman, 2016; Griffin et al., 2019), used here to examine yellowfin tuna movements, connectivity, and space use across the coastal FAD network. To examine these features, we constructed a bipartite graph that links individual tuna movements to the FADs. Bipartite graphs are composed of two nodes, which in our study are the tagged yellowfin tuna and the individual FADs. The movements of tagged yellowfin tuna (i.e., visits) are represented as to-from arrows, called edges. Edge thickness indicates the relative number of movements to a FAD by an individual tuna on a logarithm scale. Further, the bipartite graph was plotted using the Fruchterman-Reingold force-directed layout algorithm (Fruchterman and Reingold, 1991). Implementing the bipartite graph with a Fruchterman-Reingold force-directed layout algorithm allowed us to examine differential space use patterns. This attraction-repulsion type algorithm orients the graph in a non-spatially explicit fashion and plots the nodes proportional to the weight of the edges connecting neighboring nodes (Tamassia, 2013). When nodes have strong attractions between one another (i.e., heavily weighted edges) they are grouped tighter together, alternatively, when nodes have weak connections (i.e., lightly weighted edges), they are increasingly isolated (Ledee et al., 2015; Jacoby and Freeman, 2016; Griffin et al., 2019). Thus, yellowfin tuna having many movements to certain nodes will be grouped closer together than nodes they rarely visited. In addition, individual yellowfin tuna nodes were color coded to represent age class and the relative size of the node indicates the log tracking duration proportionally to one another (i.e., larger size nodes have longer observed tracking durations).

Network fitting was implemented with the graph_from_data_frame function in the igraph package, and the network was summarized by node degree (i.e., the number of movements to and from each FAD), edge weight (i.e., the number of times this movement occurred for an individual fish) and the eigenvector centrality (i.e., how well a FAD serves as a corridor to other FADs in the network) of a FAD (Jacoby and Freeman, 2016). Finally, using network analysis, we examined the number of times individual yellowfin tuna movements overlapped at each FAD. We defined an "overlap interaction" between two tuna when their detections occurred within 30 min from one another on the same FAD. These overlap interactions were calculated for the entire dataset (i.e., both Y1 and YOY individuals) but the age classes were plotted separately on the logarithmic scale to examine potential differences.

2.3.3. FAD efficacy

We calculated the mean CRT to a given FAD and determined the total number of detections for each continuous 24 h residence (i.e. CRT) to investigate the efficacy of each FAD in aggregating yellowfin tuna and to identify potential characteristics that could be related to improved FAD performance. We then used this count of detections per-CRT as an index of FAD importance within the network, rationalizing that FADs having more detections during each residency event were being used more by juvenile yellowfin tuna. Since the dependent

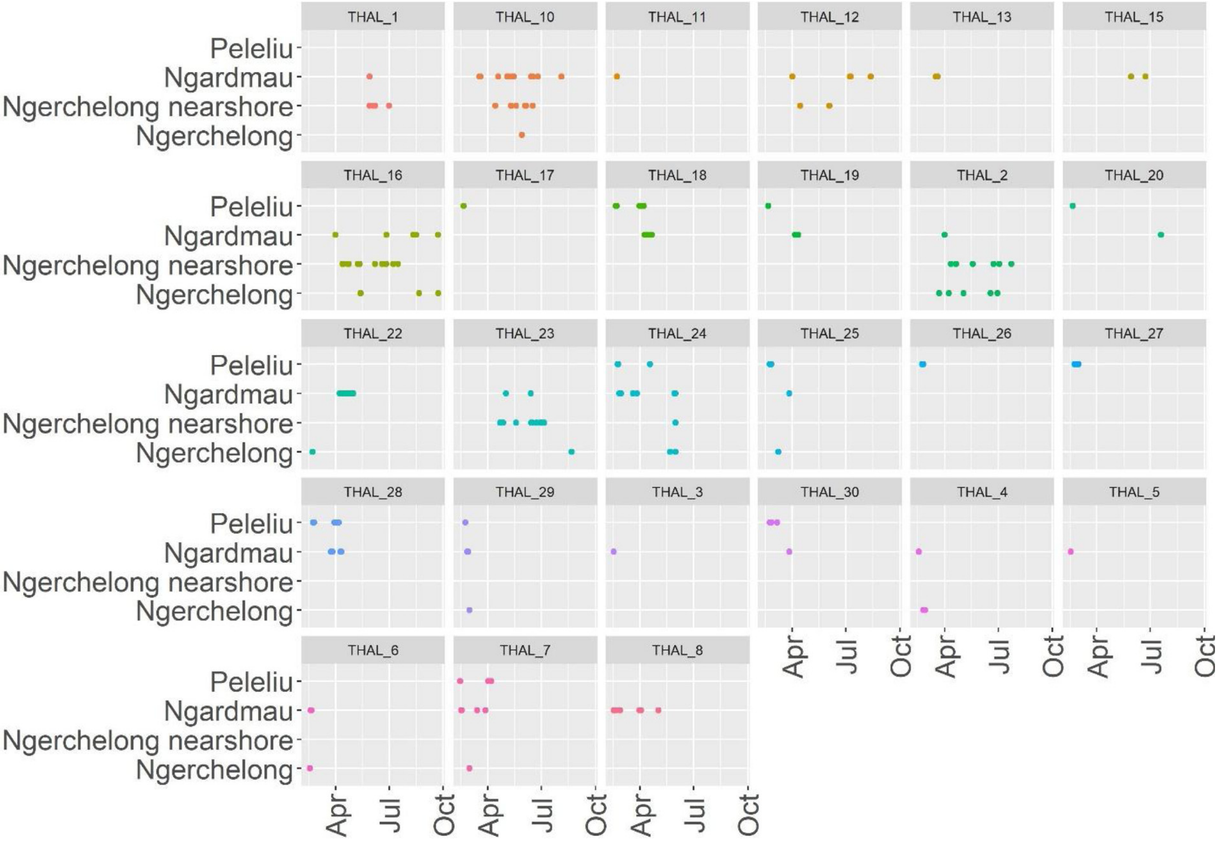

Fig. 2. Abacus plots of yellowfin tuna detection in Palau's coastal FAD complex from February 2018 to October 2018. Colored dots indicate detections of each fish at the FADs depicted in Fig. 1 (note that monitoring continued until July 2019).

variable was a count, we used a Poisson family generalized linear model and included individual ID as a random intercept given that counts were nested within individuals. The independent variables depth and distance from the reef were continuous but scaled so as to be centered around zero and the model was fit using the *glmer* function in the R package lme4 (Bates et al., 2015).

3. Results

Our analysis of yellowfin tuna detection data across the array indicated that 27 of the 30 sub-adult yellowfin tuna tagged with acoustic transmitters were detected during the study period providing a total of 24,436 detections (Table 1). A visual analysis of the movements of individual yellowfin tuna with abacus plots indicated that sub-adult yellowfin tuna regularly moved between the southernmost FAD at Peleliu and both the Ngardmau and Ngerchelong FADs located in the northwest corner of Palau's main island (Fig. 2). These movements demonstrate that schools of juvenile yellowfin tuna are capable of regularly traversing the FAD complex and can cover distances of 80 – 90 km within relatively short times periods (i.e., days to a week). Overall detection spans within the array ranged from 0 to 175 days (Fig. 3A), suggesting that these fish were retained within the FAD network for a period of up to 6 months. However, most detections occurred between February and April 2018 (Fig. 4). Despite a greater proportion of Y1 yellowfin tuna exhibiting prolonged overall detection spans in comparison to YOY individuals, these differences were not significant based on survival analysis (Table 2). In contrast, both CRTs and FCRTs were significantly different between the two age classes, with YOY spending significantly more time in association with the FADs (Fig. 3B and C; Table 2).

Network analysis revealed that the Ngardmau FAD had the highest degree (i.e., links) to yellowfin tuna, which demonstrates that this FAD had the greatest number of visits from individual fish (Table 3). The eigenvector centrality (i.e., how well a given FAD serves as a corridor to other FADs) was highest for the Ngardmau FAD (1.0), followed by Ngerchelong (0.56), Peleliu (0.46) and Ngerchelong nearshore (0.34), suggesting that the Ngardmau FAD is the most important corridor or stepping stone within the coastal FAD network (Table 3; Fig. 5). Using 30-minute detection windows, interactions of overlapping yellowfin tuna were highest at the Ngardmau and Peleliu FADs. There were no movements of Y1 fish to the Peleliu FAD, but Y1 yellowfin tuna movements overlapped at the Ngardmau, Ngerchelong, and Ngerchelong nearshore FADs (Fig. 5). YOY yellowfin tuna displayed higher levels of overlap at the Ngardmau and Peleliu FADs, indicating that these FADs were important for this age class (Fig. 6).

Residency spans of yellowfin tuna to individual FADs show that on average yellowfin tuna spent more time at the Peleliu FAD than the other FADs on the west side of Palau (Table 3). The Ngardmau and Ngerchelong nearshore FADs had the highest number of distinct residencies, indicating that tagged fish visited these FADs more frequently. This is likely attributed to northward movements in March and April 2018 of fish originally tagged at the Peleliu FAD. While present in the northwest region of Palau, yellowfin tuna frequently moved between the Ngardmau and Ngerchelong nearshore FADs. However, they spent more time at the Ngardmau FAD, with an average residency duration that is three times that of the Ngerchelong nearshore FAD (Table 3). In contrast, the Ngerchelong FAD had the lowest overall number of residencies and low average duration, suggesting that this FAD is less efficient at aggregating yellowfin tuna (Table 3). The mixed effects generalized linear model indicated that yellowfin tuna residency to the FADs was associated with FAD depth and distance from the reef. Yellowfin tuna detections in the FAD network increased significantly with FAD depth ($t = 61.54$, $P < 0.01$) and increasing distance from the reef ($t = 32.69$, $P < 0.01$).

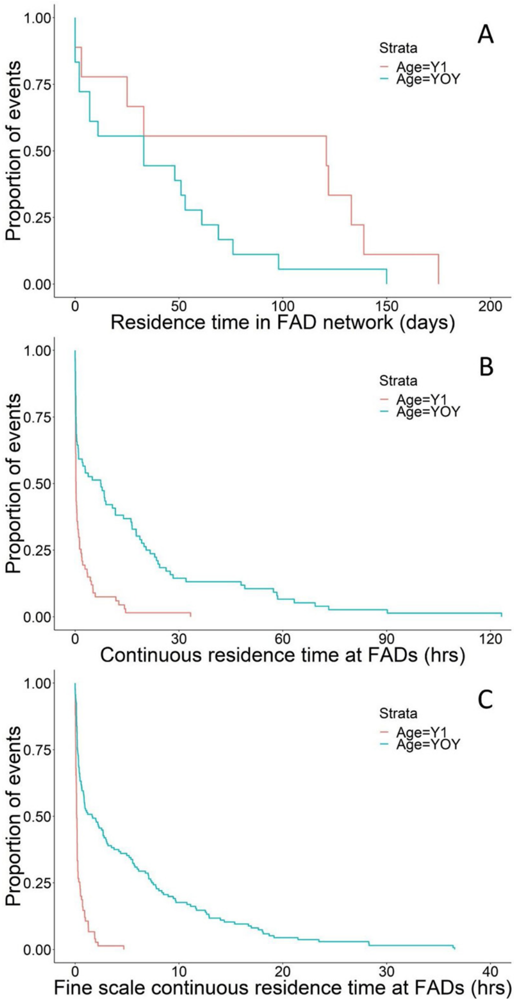

Fig. 3. Survival curves for the two age classes of yellowfin tuna within the coastal FAD network. A. Detection span within the entire FAD network in days, B. Continuous residency time (CRTs) in hrs, C. Fine scale continuous residency time (FCRTs) in hrs (green lines correspond to young-of-the-year (< 60 cm FL) and red lines correspond to year 1 (60-100 cm FL) age classes). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 2

Results of Cox proportional hazards regression on survival curves of young-of-the-year (YOY) and year 1 (Y1) yellowfin tuna and the corresponding descriptive statistics of their residencies (RT) indicating overall residency time in the FAD network in days. CRT indicates continuous residency time in hrs with a minimum of 2 detections per-24 h period and FCRT indicates fine scale continuous residency time in hrs with a minimum of 2 detections per-1 h period).

Test	N	p-value	exp(coef)	se(coef)	Min	Max	mean(± sd)
YOY RT	18	0.08	2.1910	0.4496	0	150	39 (67)
Y1 RT	9				0	175	83 (41)
YOY CRT	76	< 0.0005	0.3508	0.1893	0	123	16 (24)
Y1 CRT	67				0	33	2 (5)
YOY FCRT	136	< 0.0005	0.2484	0.1699	0	37	5 (7)
Y1 FCRT	75				0	4	0.4 (0.7)

4. Discussion

Case studies of fisheries development programs throughout the Pacific Islands suggest that the installation of FADs in coastal waters can improve access to pelagic fish and enhance food security in their surrounding communities (Sharp, 2011b; Albert et al., 2014; Tilley et al., 2019). However, FAD programs are not universally successful and the return on FAD investment can only be realized when the value of the fish acquired from FADs exceeds the costs associated with their deployment (Sharp, 2011a). To acquire the data required to evaluate FAD efficacy and improve FAD programs, fisheries management authorities should develop monitoring programs that collect fishery-dependent data such as catch per unit effort (CPUE) in their respective fisheries (Anderson and Gates, 1996; Bell et al., 2015b). However, given the isolated nature of rural fishing communities and limited human resources, many fisheries agencies in the Pacific Islands may be unable to survey FAD fishers (Gillett and McCoy, 2019). In consequence, fisheries-independent data, such as that provided in this study with acoustic telemetry, can inform FAD development and improve the success of the fisheries that depend on them.

The more time a yellowfin tuna spends at a FAD, the greater its vulnerability to capture, which in theory should result in increased CPUE of a FAD fishery (Itano and Holland, 2000). In this context, our findings on the residency of yellowfin tuna in the coastal FAD network are relevant to improving the success of Palau's domestic fishery. Our results suggest that both Y1 and YOY yellowfin tuna remain within the coastal waters of the PNMS for similar time periods. However, we found

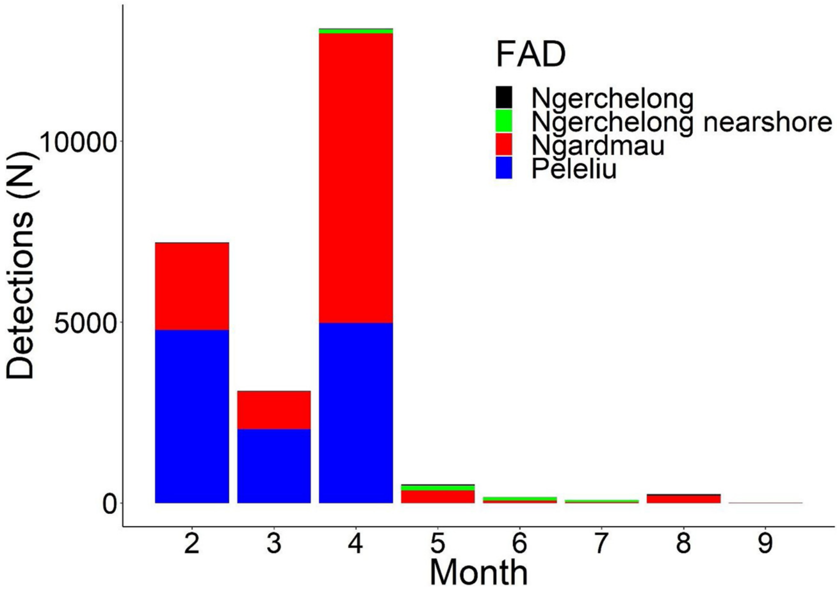

Fig. 4. Number of yellowfin tuna detections in the coastal FAD network per-month during 2018. Colors in stacked bars correspond to the number of detections at each FAD depicted in Fig. 1 (note, no detections were recorded after September 2018, although monitoring continued into July 2019). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 3
Characteristics of FADs in the coastal waters of Palau along with network statistics and summary of yellowfin tuna continuous residency times (CRTs) at the FADs (note, degree refers the number of links to yellowfin tuna and eigenvector centrality is a measure of how well a given FAD serves as a corridor to other FADs).

FAD	Year deployed	Distance from the reef (km)	Depth (m)	Degree	Eigenvector centrality	Number of CRTs	Min hrs. per-CRT	Max hrs. per-CRT	Average hrs. per-CRT (± SD)	Average detections per-CRT (± SD)
Ngardmau	2014	9	800	24	1.00	64	0.012	123.22	10.89 (22.70)	189(398)
Peleliu	2014	8	1,000	12	0.46	25	0.396	69.35	20.88 (21.54)	472(678)
Ngerchelong	2014	6	500	11	0.56	17	0.019	21.67	2.68 (5.73)	9(9)
Ngerchelong nearshore	2017	5	414	7	0.34	37	0.003	33.37	2.55 (6.25)	10(14)

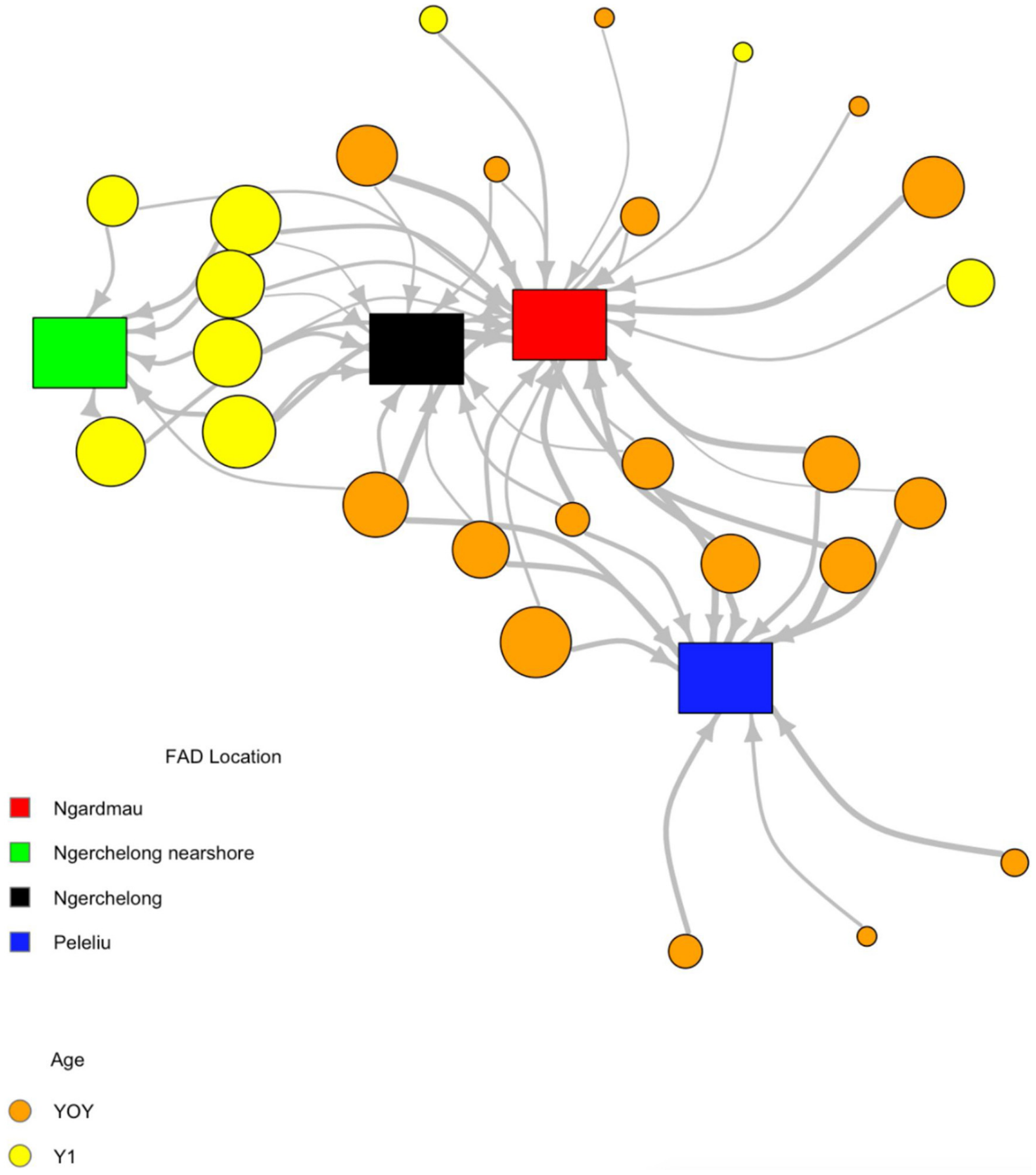

Fig. 5. Bipartite plot using the Fruchterman-Reingold force-directed layout algorithm of yellowfin tuna movements in Palau's coastal FAD network. Yellow dots represent Y1 yellowfin tuna with size of nodes proportional tracking duration, orange dots represent YOY yellowfin tuna with size of nodes proportional tracking duration, colored squares represent FADs depicted in Fig. 1 and grey lines indicate edges connecting the two nodes. Edges are scaled to their weight (i.e., the number of times this movement occurred for an individual fish). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

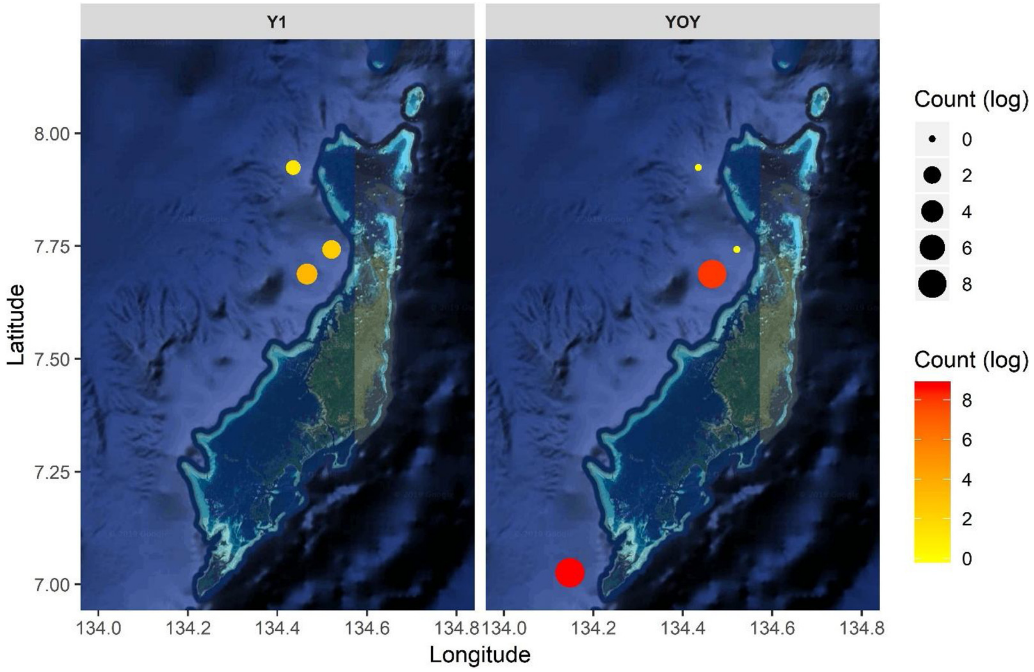

Fig. 6. Overlap of individual yellowfin tuna across each FAD using 30-minute detection windows. Number of overlap interactions are plotted on logarithmic scale and are separated by year 1 (Y1) and young-of-year (YOY) fish (note, both the size and color of the dots symbolizing each FAD correspond to the overall number of overlap interactions at each FAD with increasing symbol size corresponding to increased overlap and the color gradient yellow-orange-red corresponding to increased overlap). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

that yellowfin tuna exhibit decreased residency to the FADs within Palau's coastal network as they transition from the YOY to the Y1 age class, and these findings are consistent with the results of previous studies on yellowfin tuna FAD utilization throughout the Indo-Pacific, whose sample sizes ranged between 21–64 yellowfin tuna (Ohta and Kakuma, 2005; Dagorn et al., 2007; Robert et al., 2012; Govinden et al., 2013). Prior authors have hypothesized that this phenomenon could be related to changes in foraging habits of yellowfin tuna throughout their ontogeny, where larger tuna shift their diet from larval planktonic crustaceans to teleost fishes (Graham et al., 2007; Robert et al., 2012). Consequently, these changes may drive Y1 yellowfin tuna to be more mobile and less catchable around FADs. Regardless of the biological mechanism driving the inverse relationship between fish age and residency time, this finding has implications for the development of Palau's domestic fishery in that larger tuna (which maintain a higher market value) spend less time around FADs. This suggests that the development of a domestic export fishery may require other fishing methods to efficiently capture larger fish that are more marketable (Guillotreau et al., 2017). On the other hand, in the context of food security, the smaller YOY yellowfin tuna that strongly associate with Palau's FADs provide a readily accessible and catchable protein source that could meet the nutritional demands of the local population and improve food security, and to this aim, the maintenance of a FAD program is essential (Bell et al., 2015a, b, 2018b).

Our study was limited by the number of FADs that were deployed in Palau's coastal waters, as some Pacific Island nations and territories with well-developed FAD programs maintain upwards of 16–85 FADs at a given time and densities of 0.9 FADs per-1000 square km of coastal ocean (Gillett and McCoy, 2019). Nevertheless, we maintained complete receiver coverage of all the FADs that were present for the duration of the study and our results have important implications for the development of the nation's FAD program. Given the limited resources of the Palauan FAD program and those of many Pacific Island nations and territories, decisions must be made on which FADs should be replaced in the event of mooring failures or in communities without FADs the locations of new deployments must be selected. The results of our network analysis and the mean CRTs of yellowfin tuna at each FAD suggest that both the Ngardmau and Peleliu FADs were efficient at aggregating yellowfin tuna and should be given priority for continued deployment. These two FADs are the two deepest in the array and our results suggest that depth was an influential factor in the efficacy of Palau's FADs in aggregating yellowfin tuna. In contrast, the two Ngerchelong FADs were less efficient and should be relocated to deeper water. These findings in tuna residency with depth are consistent with those of Sharp (2011b), who found that in the Niuean FAD fishery, both CPUE and net revenue to fishers was higher when fishing offshore FADs, in comparison to inshore FADs (i.e., < 600 m). Furthermore, The SPC FAD manual suggests that FADs should be placed between 1,000–2,000 m to retain their effectiveness and minimize overall FAD costs (Gates et al., 1998).

In the context of developing small scale pelagic fisheries for Pacific Island nations and territories, although distance from the reef was a significant factor in the efficacy of the FADs in aggregating yellowfin tuna, there is a trade-off between depth and distance when selecting locations for FADs that are intended to be utilized by small scale fishers that have limited capacity to travel offshore. Accessibility is an important aspect to consider in the design of FAD programs that aim to shift the effort of artisanal fisheries from coral reefs to the pelagic sector and although FADs placed far from shore are likely to aggregate tuna effectively, increased fuel costs can reduce profits and safely issues associated with offshore fishing the can create barriers to fisher participation. Proximity to shore is an important safety consideration that could limit the ability of artisanal fishers to utilize the resources provided by FADs, especially in locations where local fishing communities use traditional canoes to access fishing grounds (Sharp, 2011b; Albert et al., 2014). Nevertheless, FADs must also be effective in aggregating tuna for fishers to profit from them and given the fact that the majority of Babeldaob and Palau's other central islands are characterized by a large inner lagoon with barrier reef, motorized boats are already being used to cover these large distances and access oceanic waters, making considerations for traditional canoe fishers are less of a concern. Our results and those of Sharp (2011b), suggest that FADs located in deeper water are more likely to aggregate yellowfin tuna for longer periods of time and would benefit the Palauan fishery more, even at the cost of slightly greater distance from shore. However, placing FADs at extreme distances from shore would prohibit their use by small-scale artisanal fishers and likely make the FADs more vulnerable to mooring failure due to increased wave exposure. We therefore suggest that if yellowfin tuna are the intended target of a anchored FAD fishery, the locations of new FAD deployments in the Palauan FAD network should be selected by finding the closest possible location to safe harbor with a minimum water depth of 1000 m, which in Palau, depending on bathymetry could be found within 6–9 km from the reef.

In addition to depth and distance, the SPC FAD manual suggests that the appropriate characteristics for the locations of FAD deployment, include flat bathymetry that is free from pinnacles, far from shelfs or drop-offs and excludes areas where oceanic waters are concentrated such as passageways between islands, so that currents are < 2 knots (Anderson and Gates, 1996; Gates et al., 1998). These locations should also be vetted through consultations with local fishers to ensure that the general direction in prevailing winds or other ocean conditions do not restrict access and make these locations prohibitive to fishing operations (Anderson and Gates, 1996; Gates et al., 1996, 1998; Chapman et al., 2005). Future research priorities for the development of Palau's coastal FAD program include implementing a monitoring program to evaluate the factors that lead to FAD longevity, such as its location, materials (i.e., rope, swivels, buoys, mooring type), attachment methods, and the amount of scope in the main line of a FAD in relation to its depth. A detailed record of these characteristics, along with regular monitoring would allow mangers to evaluate the performance of different FAD deployments overtime to improve their design and overall return on investment (Anderson and Gates, 1996; Gates et al., 1996). Furthermore, recent reviews of domestic fisheries development policies for Pacific Island nations and territories suggest, that FAD programs could be optimized by improving the ability of small scale fishers to forecast the presence of tuna in a FAD network (Bell et al., 2015b, 2018b). To this aim, echosounder buoys that are commonly used by tuna purse seine fisheries to provide information on the location and biomass of fish aggregating on drifting FADs (Lopez et al., 2014), could be deployed on anchored FADs within the Palauan FAD network, and regular updates on the location and tuna biomass associated with the FADs could be shared publicly via online fishers, forms to inform small-scale fishers of the presence of tuna. This technology could help improve safety, reduce uncertainty in catches associated with offshore FAD fishing, aid in the monitoring of FADs and FAD recovery in the event of mooring failure. Collectively these actions would likely improve the success of the nation's domestic FAD program by enhancing FAD efficacy, access, CPUE, and longevity.

Beyond attracting yellowfin tuna and creating CPUE hotspots, for a FAD program to reduce local dependence on nearshore resources, FADs must shift the effort of artisanal coral reef fisheries to the pelagic sector. Estimates of domestic fish landings in Palau are between 165–284 mt of pelagic fish and 865 mt of reef fish annually, suggesting that pelagic fisheries would have to increase threefold to completely replace coral reef fisheries (Wabnitz et al., 2018; Oleson et al., 2019; Dacks et al., 2020). Our study did not address this issue. However, recent surveys of Palau's fishing community suggest that many Palauan's are reluctant to shift their fishing effort offshore due to the increased risk of a lower reward associated with pelagic fisheries, and instead favor marginal but reliable yields obtained from coral reef fisheries (Oleson et al., 2019; Dacks et al., 2020). Local fishers stated that increased fuel costs, inadequate cold storage, and lack of a centralized market are obstacles to shifting their fishing effort from the reef to the pelagic (PICRC and COS. 2019). Yet, there is high demand for sustainable locally caught tuna by tourists visiting Palau and these surveys indicated that commercial fishers would be willing to target pelagic species provided these obstacles could be overcome (Oleson et al., 2019; PICRC and COS, 2019). Therefore, along with the development of a functioning network of FADs, the expansion of a small-scale domestic pelagic fishery may require subsidies for operational costs (i.e., gear, ice, and fuel) for small-scale fishers to take advantage of FADs and cope with the increased financial risk associated with offshore fishing (Bell et al., 2018b). Furthermore, investment into boats and safety equipment (i.e., radios, EPRBs, and GPS) should be a priority along with the FAD program to build the capacity of local fishing communities to reach more productive offshore fishing grounds (Bell et al., 2015b, 2018b). Ultimately, once these issues can be addressed a FAD program could be implemented along with reef fisheries conservation measures, such as commercial size limits, bag limits, and seasonal closures for key reef species to improve coral reef management, provide alternative resources and encourage participation in pelagic fisheries (Wabnitz et al., 2018).

In conclusion, the development of a coastal FAD program along with the implementation of the PNMS, has the potential to improve access to tuna and other pelagic species that could help Palauan's diversify their food security base. This research highlights the efficacy of the current FAD array and identifies water depth as an important factor to consider in future design, making the FADs both biologically effective and more easily accessible to small-scale fishing communities. We suggest that along with careful site selection of FAD deployment based on depth, minimum distance from shore, and the above mentioned site characteristics that reduce the risk of FAD failure, investment into building the capacity of local fishermen to efficiently and safely exploit these resources is critical to the long-term success of the Palauan coastal FAD program in supporting the development of the nation's domestic fisheries.

CRediT authorship contribution statement

Alexander Filous: Conceptualization, Formal analysis, Methodology, Project administration, Writing - original draft. **Alan M. Friedlander:** Conceptualization, Funding acquisition, Methodology, Writing - review & editing. **Lucas Griffin:** Formal analysis, Writing - original draft. **Robert J. Lennox:** Formal analysis, Writing - original draft. **Andy J. Danylchuk:** Writing - review & editing. **Geory Mereb:** Methodology, Writing - review & editing. **Yimnang Golbuu:** Conceptualization, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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