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Fidelity of yellowfin tuna to seamount and island foraging grounds in the central South Atlantic Ocean

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ABSTRACT

The yellowfin tuna (*Thunnus albacares*) is a widely distributed, migratory species that supports valuable commercial fisheries throughout their range. Management of migratory species requires knowledge of movement, mixing and key life history parameters such as growth rate, natural and fisheries mortality. Current management is based on the assumptions that the species is highly migratory and populations are well mixed, but these assumptions have been questioned by recent studies. Since November 2015, yellowfin tuna have been tagged with conventional, archival and pop-up satellite tags (PSAT) in the South Atlantic Ocean around St Helena, with the goal of better understanding their movement patterns and ecology in this region. Conventional tags were attached to 4049 yellowfin tuna (size range 24–158 cm fork length, FL), PSAT tags were deployed on 15 yellowfin in inshore St Helena waters (size range 95–138 cm FL) and 7 yellowfin (size range 125–140 cm FL) at Cardno Seamount, and archival tags were deployed on 48 yellowfin tuna in inshore St Helena waters (size range 69–111 cm FL). Most yellowfin tuna remained within 70 km of their release location, suggesting a degree of retention to the region. Although displacement of yellowfin was generally low, the furthest distance travelled between release and recapture location was 2755 km, with other tuna also displaying large-scale movements. Tagging revealed connections between inshore regions and seamounts, as well as links between St Helena waters and key fishing regions and putative spawning grounds in the Gulf of Guinea.

1. Introduction

The yellowfin tuna (*Thunnus albacares*) is a cosmopolitan species with high fecundity, and a distribution across tropical and subtropical oceans (FAO, 2020). Global annual commercial landings averaged 1.4 million tonnes between 2015 and 2018, the second highest landings by weight of any tuna species, accounting for approximately one quarter of the total catch of all tuna combined (FAO, 2020). Its global distribution and accessibility in surface waters (Schaefer et al., 2014) makes yellowfin a commercially important species for many communities, particularly small island developing states and other remote islands. However, there is currently a lack of knowledge on the ontogenetic and seasonal changes in behaviour and connectivity of stocks across several regions, including the North and South Atlantic.

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The International Commission for the Conservation of Atlantic Tunas (ICCAT) is responsible for the management of the yellowfin tuna stock in the Atlantic (ICCAT, 2019a). Current international management treats all Atlantic yellowfin tuna as a single stock (ICCAT, 2019a) despite recent tagging and biomarker work in other oceans indicating widespread population structure (Leroy et al., 2015; Moore et al., 2020; Pecoraro et al., 2017; Schaefer et al., 2011; Wu et al., 2010). Understanding the nature and degree of mixing between populations is therefore crucial for effective management; several tools including tagging, genetics, biomarkers and the analysis of landings data can be used to develop greater understanding of movement and population interchange (Pecoraro et al., 2017).

Tag release and recapture experiments using conventional tags have provided valuable information on movements and stock structure of tuna and billfish species (Bayliff, 1993). Data from such conventional tagging studies have been used to better understand growth rates, stock size, and connectivity between regions. More recently, electronic archival tags provided a more detailed understanding of spatio-temporal movements, behaviour (Block et al., 2005) and fisheries mortality (Kurota et al., 2009; Block et al., 2019). Archival tags provide a means of obtaining high-resolution data sampled over prolonged periods of time (sometimes over periods of several years). This information has been used to increase knowledge of tuna behaviour, including the environmental drivers of movement and habitat utilisation (Schaefer et al., 2007a) and more recently to help inform tuna management including integration into stock assessments (Sippel et al., 2015). Combining conventional and electronic tagging allows for the assessment of broadscale movements with large sample sizes (conventional tags), as well as finer scale assessments of daily movements and vertical behaviour (electronic tags).

The yellowfin tuna is considered a highly migratory species, yet recent studies using tagging, biomarkers, and genetics have revealed potential yellowfin population structure in several ocean basins (Anderson et al., 2019; Appleyard et al., 2001; Graham et al., 2010; Richardson et al., 2018; Schaefer et al., 2007b; Ward et al., 1997). Studies exploring the movements and behaviour of yellowfin tuna with archival tags off the coast of California indicated higher site fidelity or residency than expected for a highly migratory pelagic species, with 95% of yellowfin in two studies remaining within 1667 km or 1358 km of their release location (Schaefer et al., 2007a; Schaefer et al., 2011, respectively). Regional fidelity to release locations has also been identified in the central and western Pacific Ocean (Sibert and Hampton, 2003), with other studies linking retention to specific features, including Fish Aggregating Devices (FADs), seamounts, and islands (Dagorn et al., 2007; Filous et al., 2020; Itano and Holland, 2000; Robert et al., 2012). FADs attract marine species including tuna and are used as a tool in global tuna fisheries (Guillotreau et al., 2011), with tuna shown to be one of the first species to colonise virgin FADs (Orue et al., 2019). The mechanism that drives such associations are still unclear (Hall et al., 1992), but are known to be affected by productivity and specific features of the FADs (Lopez et al., 2017). Retention around seamounts and islands may be linked to seasonal increases in food availability driven by upwellings (Pitcher et al., 2007; Sergi et al., 2020). Such site fidelity (or philopatry) contradicts conventional views of yellowfin tuna as a 'highly migratory species' and indicates that, although widely distributed, yellowfin may have subpopulations that calls into question the validity of current single stock assumptions. Studies of yellowfin tuna migratory behaviour in the Atlantic have, to date, been limited and developing a better understanding of spatial movements and migration is therefore valuable to future stock assessments.

St Helena is a small remote island in the tropical South Atlantic (15.965 ^{o}S, 5.7089 ^{o}W) with an EEZ that encompasses ~450,000 km^2 of open ocean. Yellowfin tuna are caught throughout the year in waters close to the island as well as at the offshore Bonaparte and Cardno seamounts (Fig. 1). The local artisanal fishery catches between 100 and 400 tonnes of yellowfin tuna per year using pole & line methods making yellowfin an important resource to the St Helena economy (Collins, 2017). The aim of this study is to identify the migratory patterns of yellowfin tuna caught at important fishing grounds in St Helena's Exclusive Economic Zone (EEZ), including the investigation of potential ontogenetic differences in their movement patterns and behaviour.

2. Methods

2.1. Study area

There are three key tuna fishing areas in St Helena's EEZ: inshore regions (within 30 miles of land), Bonaparte Seamount to the north west of St Helena and Cardno Seamount to the north of St Helena (Fig. 1), just inside the 200 nautical mile EEZ boundary. Inshore regions include both fishing grounds on an anchored FAD (15.961^{o}S, 5.778^{o}W) and on free schools within 30 miles of land. Conventional tags were deployed at all fishing areas, and electronic tags (archival and PSAT) were deployed inshore and at Cardno Seamount.

2.2. Landings

All boats operate from one port within St Helena's EEZ, and all commercially caught fish are landed at the St Helena Fisheries Corporation processing plant. The gilled and gutted weight of all fish (combined weights, but also individual weights where possible), were collected from landings data between 2015 and 2019. Landed fish were randomly sampled on a regular basis (monthly) to determine the size (length and weight) of the exploited population. Fish were measured (fork length) to the nearest cm below (i.e. a fish of 81.6 cm is recorded as 81 cm). The target was to sample 200 fish per month from each of the three fishing areas (inshore, Bonaparte Seamount and Cardno Seamount).

2.3. Tags

Three tag types were deployed on yellowfin tuna: conventional tags, archival tags and pop-up satellite (PSAT) tags. For all tag types yellowfin were caught using hook-and-line methods using barbless circle hooks with live mackerel (*Scomber colias*) or *Decapterus* sp. as bait.

Conventional tagging was conducted between November 2015 and June 2019 ($n = 4049$) focused on inshore regions ($n = 2364$; 58% of total tagged), Bonaparte Seamount ($n = 796$; 20% of total tagged) and Cardno Seamount ($n = 889$; 22% of total tagged). PSAT tags were deployed on yellowfin in inshore waters in November 2016 ($n = 12$), and December 2018 to January 2019 ($n = 10$). Internal archival tags were deployed on yellowfin in inshore waters in March 2018 ($n = 48$) (Table 1). Of the 22 PSATs deployed (all on yellowfin tuna $> L_{50}$; 86 cm), a state-space model (SSM) was used to estimate daily geolocated positions for tags which transmitted sufficient data ($n = 13$) (GPE3, https://static.wildlifecomputers.com/Location-Processing-UserGuide.pdf).

Conventionally tagged tuna were released with Hallprint plastic dart tags ($N = 4049$) on one or both sides of the second dorsal fin. Tags were applied with manufacturer supplied applicators, which were cleaned between tagging events.

Tuna tagged with archival devices ($n = 48$) were released with Cefas Technology Limited (https://www.cefastechnology.co.uk) G5 tags (with a conventional tag attached). Each G5 tag was inserted into the intracoelomic cavity. Prior to tagging, tuna were first anaesthetised by placing the fish in a tank containing 0.4 ml/l solution of 2-phenoxyethanol. Once they had lost equilibrium they were transferred to a wetted V-shaped sponge, with the ventral surface facing up. A small (approx. 3 cm) incision was made on the ventral wall (roughly 3 cm anterior to the anus and off the midline of the fish) using a curved scalpel blade and the tag was inserted through this incision into the intracoelomic cavity leaving a trailing conventional tag on the outside of the body. Local analgesia (1 mg/ml of lidocaine hydrochloride in saline) was then applied into the intracoelomic cavity and the wound was closed using the cross-stitch method. Tags were programmed to record depth and temperature at 1 min resolution. Archivally tagged tuna were also double tagged with conventional tags on each side of the second dorsal fin.

Tuna were tagged with PSAT tags (Wildlife Computers, Redmond, WA), model MiniPAT (n = 22) using standard methods (Schaefer et al., 2007a). Tags were programmed to record depth, temperature, light and acceleration, with the resolution dependent on the programmed time of tag deployment. For PSAT tagging, once on the vessel, a saltwater hose was immediately inserted into the fish's mouth to oxygenate the gills and a soft cloth soaked in a protective solution (PolyAqua®) placed over the eyes. Fish were sampled for genetics (fin clip from the second dorsal fin) and stable isotope analysis (muscle biopsy), measured for curved fork length (CFL), and the PSAT tag was inserted into the dorsal musculature behind the first dorsal fin using a short tagging pole fitted with a tagging applicator tip. Tags were secured externally using one titanium dart connected directly to the PSAT tag and a second titanium dart connected to a loop around the tag (Lawson et al., 2010a,b). Tag and loop leaders were made with 180 kg breaking strain monofilament covered with aramide braided cord for abrasion resistance and covered by a layer of heat shrink wrap. Tag tips were custom titanium darts. Yellowfin tuna were landed, sampled, tagged, and released within 1–2 min of capture.

A reward of between £5 and £10 was paid for fish returned with just conventional tags, and £100 for fish returned with archival or PSAT tags (payments in GBP). Information about the recovery location and size of the fish were recorded when possible. For landed fish, additional information (sex, maturity) and biological samples (stomach contents and otoliths), were also taken.

2.4. Analytical methods

2.4.1. Maturity

Yellowfin tuna maturity at release was estimated based on data from other 'size at maturity' studies (Grande et al., 2014; Itano and Holland, 2000; Marsac et al., 2006; Schaefer, 1998). Gear selectivity may reduce numbers of mature fish within samples, with ontogenetic vertical stratification of individuals in different reproductive states (Suzuki,

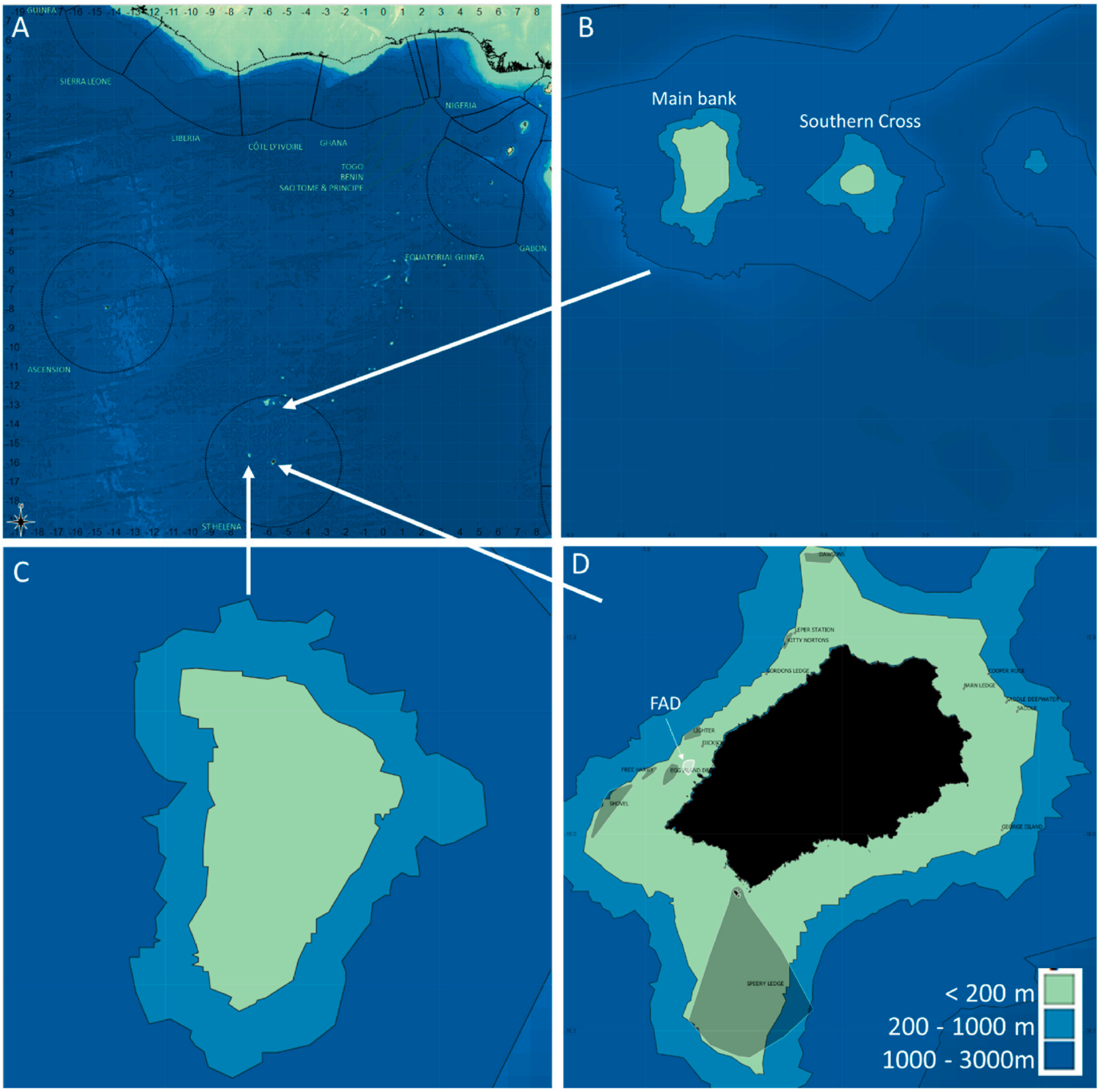

Fig. 1. The St Helena Exclusive Economic Zone (EEZ) highlighting the key fishing grounds (A) of Cardno Seamount (B), Bonaparte Seamount (C) and inshore (D). The inshore fishing region highlights the location of the anchored Floating Aggregation Device (FAD) in white and the island (black). Bathymetry from the General Bathymetric Chart of the Oceans, GEBCO (ca. 1 km grid size), Schenke (2016).

Table 1

PSAT and archival tag release and recovery information for yellowfin tuna (Thunnus albacares) tagged in the St Helena EEZ, South Atlantic Ocean. Length as Standard Fork Length (SFL). Reasons for PSAT returns specified as caught (CT), pinbreak (PB), tagging mortality (TM), predation (PR), tags popped on time (PO), no communication (NC) and unknown (UK). All recovered archival tags were recaptured by fishermen (CT).

Tag Type	ID	Release information				Pre-set pop date	Pop date/recapture information					Time at lib. (days)	Distance (km)	Recovered	Depth (max)
		Date	Lon (°)	Lat (°)	SFL (cm)		Date	Lon (°)	Lat (°)	Length (cm)	Reason				
Sat. (inshore)	1116003	November 19, 2016	−5.82	−15.98	125	August 16, 2017	January 06, 2017	−5.76	−16.08	–	UK	48	12	N	336
	1116004	November 21, 2016	−5.75	−16.11	101	May 20, 2017	January 04, 2017			–	CT	45	–	Y	476
	1116005	November 21, 2016	−5.75	−16.11	101	February 19, 2017	November 28, 2016	−6.33	−16.16	–	UK	7	61	N	552
	1116006	November 21, 2016	−5.75	−16.11	95	December 21, 2016	February 28, 2017	−5.67	−16.02	–	TM	99	13	Y	–
	1116007	November 21, 2016	−5.75	−16.11	138	August 18, 2017	–	–	–	–	NC	–	–	N	–
	1116008	November 21, 2016	−5.75	−16.11	131	May 20, 2017	–		–	–	NC	–	–	N	–
	1116009	November 21, 2016	−5.75	−16.11	119	November 21, 2017	July 11, 2017	−5.71	−15.92	–	CT	232	21	Y	488
	1116010	November 21, 2016	−5.75	−16.11	128	August 18, 2017	August 25, 2017	−6.32	−15.85	–	PO	277	67	N	–
	1116011	November 21, 2016	−5.75	−16.11	122	February 19, 2017	–	–	–	–	NC	–	–	N	–
	1116012	November 21, 2016	−5.75	−16.11	128	December 21, 2016	December 22, 2016	−5.67	−16.05	–	PO	31	11.	N	–
	1116013	November 22, 2016	−5.75	−16.11	104	November 22, 2017	December 08, 2016	−6.05	−16.02	–	UK	16	33	N	–
	1116014	November 22, 2016	−5.75	−16.11	104	November 22, 2017	December 15, 2016	−6.07	−16.09	–	PR	23	34	N	–
	83841	January 13, 2019	−5.76	−16.06	118	November 09, 2019	November 10, 2019	−5.83	−16.07	–	PO	301	8	N	288
	83843	January 13, 2019	−5.76	−16.06	115	December 09, 2019	February 18, 2019	−11.3	−22.77	–	UK	36	–	N	1024
	83844	January 13, 2019	−5.76	−16.06	101	January 08, 2020	January 20, 2019	−6.10	−16.30	–	PR	7	–	N	280
Sat. (offshore)	83818	December 12, 2018	−5.73	−12.92	134	April 11, 2019	March 24, 2019	−6.01	−12.83	–	PO	102	32	N	389
	83839	December 12, 2018	−5.73	−12.92	136	October 08, 2019	April 08, 2019	−5.79	−12.95	–	PB	117	7	N	528
	163243	December 12, 2018	−5.73	−12.92	130	April 11, 2019	–	–	–	–	NC	–	–	N	–
	83823	December 10, 2018	−6.02	−12.87	140	September 06, 2019	–	–	–	–	NC	–	–	N	–
	83821	December 10, 2018	−6.02	−12.87	130	August 07, 2019	April 25, 2019	−6.04	−12.87	–	NC	–	–	N	–
	83842	December 10, 2018	−6.02	−12.87	125	November 05, 2019	April 12, 2019	−6.03	−12.87	129	CT	123	1	Y	–
	163261	December 10, 2018	−6.02	−12.87	126	April 09, 2019	April 22, 2019	–	–	–	PO	133	–	N	440
Archival (inshore)	A14757	March 22, 2018	−5.81	−15.98	67	–	April 24, 2018	–	–	69	CT	33	–	Y	547
	A14764	March 22, 2018	−5.789	−15.97	80	–	April 25, 2018	–	–	85	CT	34	–	Y	540
	A14766	March 23, 2018	−5.79	−15.97	78	–	April 20, 2018	−5.64	−15.92	82	CT	28	17	N	–
	A14770	March 23, 2018	−5.79	−15.97	77	–	May 07, 2018	−5.94	−15.98	86	CT	45	16	N	–
	A14772	March 23, 2018	−5.79	−15.97	79	–	May 07, 2018	−5.94	−15.98	84	CT	45	16	N	–
	A14774	March 23, 2018	−5.79	−15.97	75	–	May 03, 2018	−5.94	−15.98	80	CT	41	16	Y	1014

(*continued on next page*)

Table 1 (*continued*)

Tag Type	ID	Release information				Pre-set pop date	Pop date/recapture information					Time at lib. (days)	Distance (km)	Recovered	Depth (max)
		Date	Lon (°)	Lat (°)	SFL (cm)		Date	Lon (°)	Lat (°)	Length (cm)	Reason				
	A14775	March 23, 2018	–5.79	–15.97	79	–	January 10, 2019	–5.83	–16.01	111	CT	293	6	Y	452
	A14778	March 23, 2018	–5.79	–15.97	79	–	April 13, 2018	–5.94	–15.98	80	CT	21	16	Y	243
	A14779	March 23, 2018	–5.81	–15.98	77	–	May 11, 2018	–	–	–	CT	49	–	Y	603
	A14780	March 21, 2018	–5.81	–15.98	72	–	May 19, 2018	–	–	81	CT	59	–	Y	581
	A14781	March 22, 2018	–5.81	–15.98	78	–	November 27, 2018	–5.81	–15.98	110	CT	250	2	Y	561
	A14784	March 21, 2018	–5.79	–15.97	82	–	May 14, 2018	–	–	–	CT	54	–	Y	382
	A14788	March 23, 2018	–5.81	–15.98	74	–	April 25, 2018	–	–	78	CT	33	–	Y	494
	A14795	March 21, 2018	–5.81	–15.98	85	–	June 19, 2018	–	–	96	CT	90	–	Y	464
	A14798	March 22, 2018	–5.80	–15.97	77	–	May 30, 2018	–5.73	–15.87	85	CT	69	15	Y	409
	A14799	March 22, 2018	–5.81	–15.98	79	–	November 11, 2018	–	–	–	CT	234	–	Y	422
	A14808	March 23, 2018	–5.79	–15.97	82	–	June 12, 2018	–	–	95	CT	81	–	Y	431

1994), so L_{50} was taken from studies involving feeding independent gear (purse seiners), and represents the length at first maturity. The size at L_{50} for purse-seine caught yellowfin ranges from 69 cm to 108 cm (92 cm for females and 69 cm for males (Schaefer, 1998); 107.9 cm for females (Itano and Holland, 2000); 77.8 cm for females (Grande et al., 2014), and 104 cm for females (Marsac et al., 2006)). Here, juvenile and adult fish are defined as individuals $<L_{50}$ and $>L_{50}$, respectively, based on an L_{50} of 86 cm (straight fork length, SFL).

2.4.2. *Length-frequency processing*

Length-frequency plots were analysed using the mclust package in R (version 3.6.1) (Scrucca et al., 2016). An optimal mixture model was used to produce a density estimate for each cohort in each fishing area (inshore, Bonaparte and Cardno) and month (Fraley and Raftery, 2002). A non-parametric bootstrap estimation of the standard errors and percentile bootstrap confidence intervals was made for the mixture model, providing the Maximum Likelihood Estimators (MLEs) for each distribution (which is reflective of the modal lengths for each yellowfin tuna cohort by month).

2.4.3. *Horizontal movements*

For tuna tagged with PSATs, raw location data were processed through Wildlife Computers Global Position Estimator Version 2 (proprietary software) to produce daily longitude estimates. Sea surface temperature (SST) based latitudes were then generated by matching the longitudes and tag recorded temperatures to remotely sensed SSTs (Teo et al., 2004). A Bayesian state-space model (SSM) refined the position estimates into most probable daily tracks for the individual yellowfin tuna (Block et al., 2011; Wilson et al., 2015), and the distance between each was calculated (referred to as daily distance travelled). Total distance travelled was calculated as the sum of daily distance travelled. For tuna tagged with conventional tags, straight-line distance (km) between release and recapture locations was calculated and used as an index of distance travelled.

Site fidelity was defined as fish travelling less than 50 km from their release location. Thus, all recoveries (independent of time at liberty) were used to assess site fidelity of yellowfin tuna.

2.4.4. *Growth*

Exclusion of anomalies and error corrections were applied to the tagging and cohort MLEs prior to processing for growth rate estimates. Tagged data had the following corrections or exclusions:

- Curved fork length (CFL) measures were converted to standard fork length (FL);
- To eliminate extreme outliers from the analysis (most likely due to measurement error), the highest and lowest 5% of growth rate estimates were excluded (resulting in the exclusion of 23 tuna)

For growth rates estimated from cohort modal frequency progression (MLEs), a number of biases can be assumed, with the following corrections:

- As tuna growth slows at maturity, quantification of growth rate above size at maturity is not possible, as multiple cohorts will be a similar length;
- Size-selection by the fishery means that there will be a skew towards larger individuals at the smallest size classes, for example any fish deemed too small (<60 cm) were typically released by fishers.

Therefore, growth rate estimates were used from all tag data returns (GR_{tag}) but only tuna sampled at the mid-range of sizes (50 cm–150 cm) were used for growth rate estimates from MLEs (GR_{szf}).

Growth rates were estimated from GR_{tag} and GR_{szf} as:

$$GR_{tag} = (L_{rec} - L_{rel}) / TaL$$

$GR_{szf} = (L_{t2} - L_{t1})/1$ month

Where, L_{rec} is FL at recapture (cm), L_{rel} is yellowfin FL at release, TaL is the time at liberty in months, L_{t1} is yellowfin FL in a given month and, L_{t2} is yellowfin FL a month after L_{t1}.

3. Results

3.1. Landings

Length-frequency plots for landed yellowfin tuna allowed individual cohorts to be distinguished through each year of sampling (Fig. 2). The mean size of fish at capture indicates that larger individuals were caught with increasing distance from St Helena, with average FLs (mean ± SD) of 71 ± 13 cm inshore (72 ± 13 cm at the FAD and 69 ± 13 cm on free schools), 81 ± 14 cm at Bonaparte Seamount, and 96 ± 24 cm at Cardno Seamount (Fig. 2A).

3.2. Tagging release and recovery

Between November 02, 2015 and June 02, 2019, 182 tuna-fishing events occurred within St Helena's EEZ (Fig. S1). Of the 4049 yellowfin tuna conventionally tagged, 764 tags have been recovered (19%; Table 2). Twenty-two archival tags have also been recovered (46%) from recaptured fish, and 3 PSAT tagged yellowfin tuna were recaptured (14%).

The sizes of conventionally tagged yellowfin ranged from 42 to 158 cm FL, averaging 70.5 cm (±13.2 cm SD), 80.8 cm (±14.1 cm SD) and 95.9 cm (±23.6 cm SD) for tuna tagged inshore, and at Bonaparte and Cardno seamounts, respectively. The size of the recovered yellowfin tuna ranged from 56 to 150 cm FL, averaging 84.8 cm (±10.7 cm SD), 101.1 cm (±17.1 cm SD) and 112.3 cm (±21.4 cm SD) for tuna recovered inshore, at Bonaparte and Cardno seamounts, respectively.

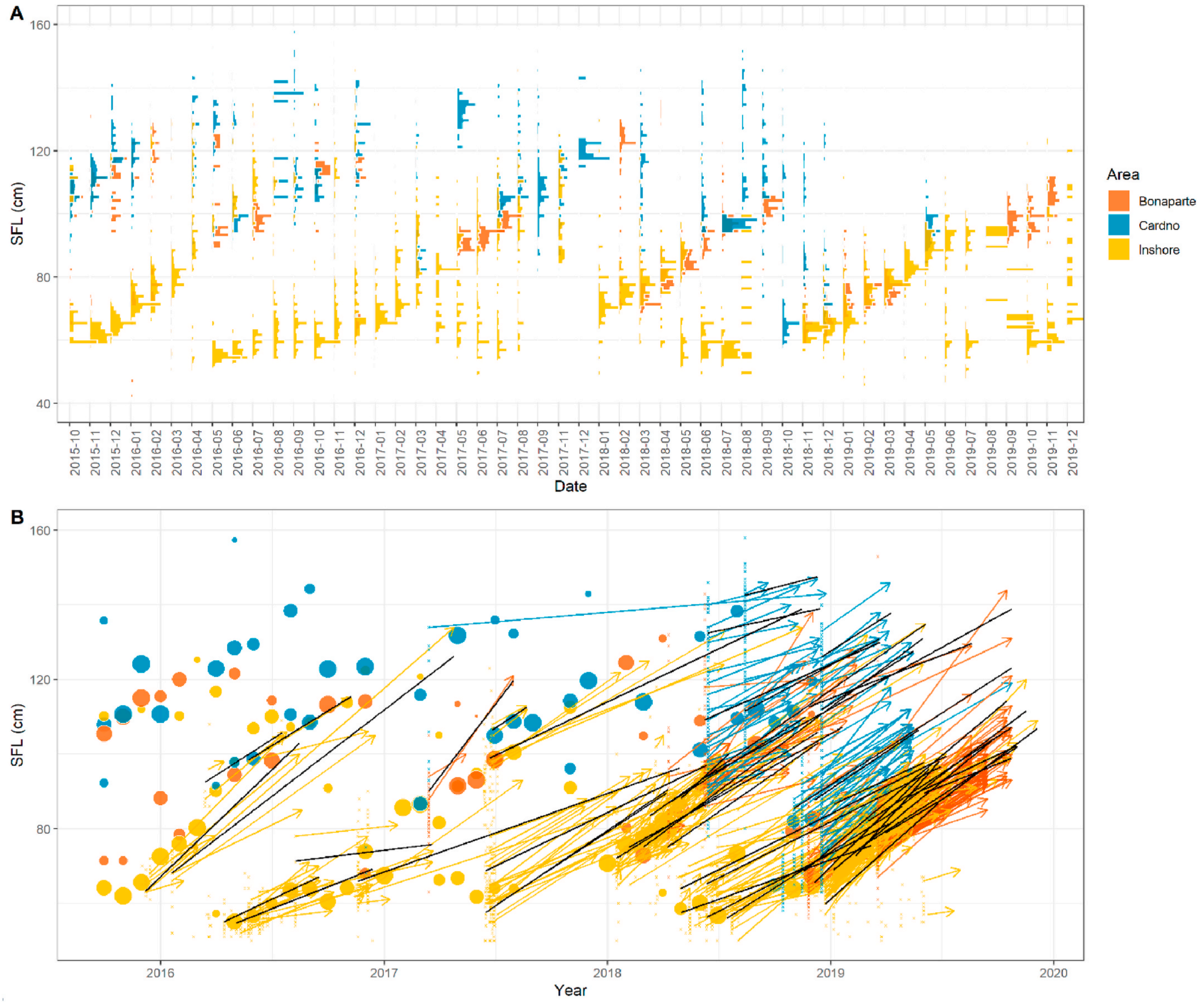

Fig. 2. A. Length frequency distribution of landed yellowfin tuna (*Thunnus albacares*) from inshore regions, Bonaparte Seamount and Cardno Seamount in the St Helena EEZ, South Atlantic Ocean. B. Cohort analysis of landed yellowfin tuna from inshore regions, Bonaparte Seamount and Cardno Seamount. Filled circles reflect the Maximum Likelihood Estimator for each month and region. Circle colour is the tuna release location, circle size is the relative proportion of individuals within the cohort by month and landing location from the MLE analysis. Coloured arrows representing the conventional tagged-yellowfin tuna length at release and length at recapture. The black lines reflect linear models of MLE for unique cohorts by month of release. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Numbers of yellowfin tuna (*Thunnus albacares*) tagged and released each year with conventional tags in waters around St Helena island, Bonaparte Seamount, and Cardno Seamount, in the South Atlantic Ocean.

Year	Released	Recapture				% recovered
		2016	2017	2018	2019	
2015	30	9	0	0	0	30%
2016	537	33	41	1	0	14%
2017	371	0	23	22	0	12%
2018	1858	0	0	197	128	17%
2019	1253	0	0	0	311	25%
Total	4049	42	64	220	439	19% (mean)

Conventionally tagged yellowfin tuna were at liberty between 2 and 650 days (mean = 87 days ± 84 days SD). Archivally tagged yellowfin were at liberty between 21 and 440 days (mean = 132 days ± 140 days SD). Of the PSAT returns, five tags popped-off on their pre-programmed release dates, six did not report at all, and the other 11 popped-off early for a variety of reasons (Table 1). One was due to tagging mortality (Tag ID# 1116006), two were consumed by predators (Tag ID#1116014 presumably by a shark, and Tag ID# 83844 on first day at liberty), and the other three were recaptured by fisherman (Tag ID# 1116004, Tag ID# 1116009 and Tag ID# 83842). The cause of the early release of the remaining five tags could not be determined. One of the tags that popped-off on time (Tag ID# 1116010) had large gaps in the data, possibly due to biofouling of the device a few months into the deployment.

3.3. *Site fidelity*

Cohort maximum likelihood estimators (MLEs) for each month and year since November 2015 (Fig. 2B) suggest that yellowfin tuna were recruited to the fishery between February and March. These tuna remained inshore and subsequently appear in landings at Bonaparte Seamount in March/April the following year, followed by Cardno Seamount in May/June, though timings varied between years (Fig. 2B).

For conventionally tagged fish, recapture rates by year ranged from 12% (2017) to 30% (2015) with an average recapture rate of 19% overall (Table 2). The maximum time a liberty for all conventionally tagged yellowfin tuna was 526 days for a tuna released and recovered from the inshore region (Fig. S2). Recapture rates by release location were 30% for fish released on the anchored FAD, 25% for fish released inshore in free schools and 9% for fish released on seamounts.

3.4. *Residency of juveniles*

The majority of yellowfin tuna were recaptured on the grounds on which they were released (Table 3). For yellowfin tuna released at sizes $< L_{50}$, recaptures on the same grounds were 99%, 85%, and 63% for fish released inshore (n recaptured = 317), at Cardno Seamount ($n = 22$), and at Bonaparte Seamount ($n = 5$), respectively. Mixing was observed between inshore regions and Bonaparte Seamount (<1% and 38% for inshore and Bonaparte released fish, respectively), with movements between inshore and Bonaparte Seamount occurring between February and April (Table 3). Fish released at Cardno and recaptured at $< L_{50}$ (n recaptured = 4) were all recaptured outside St Helena's EEZ, noting that all migratory individuals were released at sizes <70 cm (Fig. 3); these four juveniles were recaptured in waters outside the EEZ in January and February of the following year (Table 4, Fig. 4).

3.5. *Residency of adults*

For fish recaptured at sizes $> L_{50}$ (adults), the rates of recapture on the same grounds as release were 95%, 97% and 91% for inshore ($n = 42$), Bonaparte ($n = 32$) and Cardno ($n = 60$), respectively (Table 3). A small number of adult yellowfin tuna showed connectivity between regions. Two fish from inshore regions were recaptured at Bonaparte, and one from Bonaparte was recaptured at Cardno (Table 4 and Fig. 4). Connectivity to regions outside St Helena's EEZ were also apparent for adult yellowfin, with one inshore and four Cardno released fish recaptured outside St Helena's EEZ (Tables 3 and 4; Fig. 4). Recaptures outside St Helena's EEZ occurred between December and April. See Fig. S3 for all tracks.

The average PSAT attachment time for yellowfin tuna was 100 days (Table 1). Daily position estimates from yellowfin tuna tagged inshore ($n = 9$) indicates that all of the PSAT-tagged yellowfin tuna remained within the EEZ, to the southwest of the island, from November–December. In December, for yellowfin tuna with PSATs still attached ($n = 4$), one tuna remained inshore to the east of St Helena (Tag ID#1116004) and three went into deeper waters to the north and south of St Helena, one of which then moved inshore where it was recaptured (Tag ID#1116009). One yellowfin tuna at liberty between June and August spent time in waters around Cardno Seamount before returning south to inshore waters close to St Helena (Tag ID#83841). Most yellowfin tuna that were PSAT-tagged at Cardno Seamount remained in close proximity to the seamount throughout the year (Tag ID#s 163261, 83842, 83821, 83818). One individual migrated south, past St Helena island in January, before returning northward to the seamount in March (Tag ID#83839).

The average monthly displacement for all conventionally tagged fish was 85 km (23 km for inshore, 27 km for Bonaparte and 272 km for Cardno released fish (Fig. S4). The minimum speed for conventionally tagged long-distance migrators was 20 km d^{-1} for a fish released at Cardno and recaught 81 days later outside St Helena's EEZ (Tag ID# ATP0135385, Table 4).

3.6. *Growth*

Growth rates were estimated from tagging data and size frequency distributions (Fig. 5) and indicate that yellowfin tuna <60 cm had average monthly growth rates of 2.91 ± 1.94 cm month^{-1} ($n = 26$) and 4.45 ± 2.14 month^{-1} ($n = 12$) for GR_{tag} and GR_{szf}, respectively. Yellowfin tuna 60–80 cm had an average monthly growth rate of 3.38 ± 1.71 cm month^{-1} ($n = 98$) or 4.38 ± 2.35 cm month^{-1} ($n = 43$) for GR_{tag}

Table 3
Proportion of yellowfin tuna *(Thunnus albacares)* tagged in the St Helena EEZ, South Atlantic Ocean, recaptured by region (waters around St Helena ('Inshore'); Bonaparte Seamount; Cardno Seamount) and recapture size. Months of corresponding recaptures outside release areas shown in parentheses.

Release area	Recapture Size	Recapture Number	Recapture area			
			Inshore	Bonaparte	Cardno	Outside EEZ
Inshore	<L50	319	99%	<1% (Feb)	0%	<1% (Dec)
	>L50	44	95%	5% (Jul, Nov)	0%	0%
Bonaparte	<L50	8	38% (Feb, Mar, Apr)	62%	0%	0%
	>L50	33	0%	97%	3% (Apr)	0%
Cardno	<L50	26	0%	0%	85%	15% (Jan, Feb)
	>L50	66	1% (Apr)	0%	91%	8% (Dec, Feb, Mar, Apr)

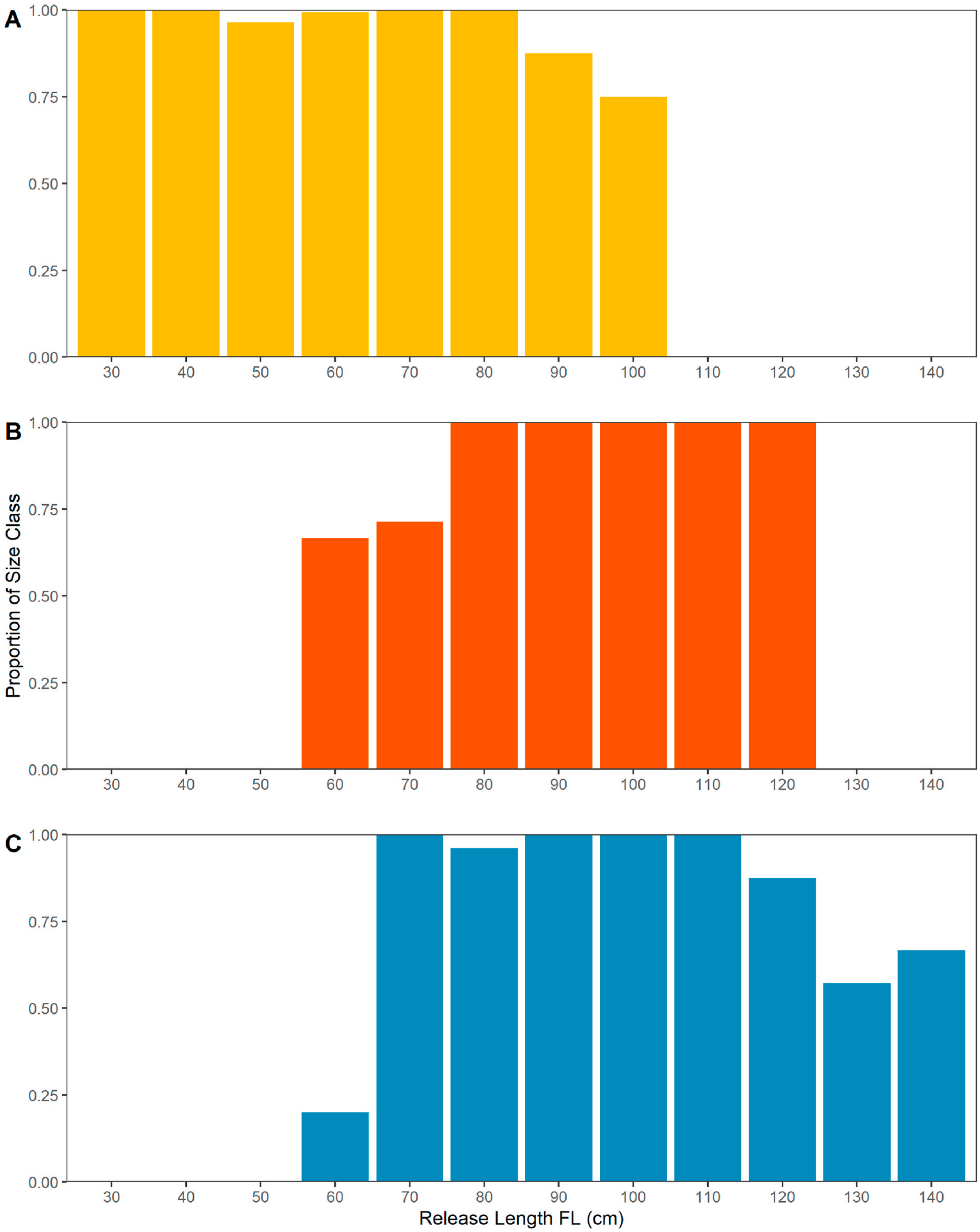

Fig. 3. Proportion of conventionally tagged yellowfin tuna (*Thunnus albacares*) in the St Helena EEZ, South Atlantic Ocean, that were resident by yellowfin tuna size-at-release and by release location: inshore (A), Bonaparte Seamount (B) and Cardno Seamount (C). Yellowfin tuna were classified as resident if they remained at their release ground (within 50 km).

and GR_{szf}, respectively. Yellowfin tuna >80 cm had average monthly growth rates of 2.95 ± 1.74 cm $month^{-1}$ (n = 77) and 4.60 ± 2.35 cm $month^{-1}$ (n = 93) for GR_{tag} and $GR_{szf,}$ respectively.

4. Discussion

This study provides evidence of seasonal residency and site fidelity in yellowfin tuna in South Atlantic Ocean waters around the island of St Helena. Both juvenile and adult yellowfin tagged in St Helena's EEZ displayed site fidelity, with recaptures up to 650 days after release. We hypothesise that St Helena is used as a feeding ground for sub-adult fish and following maturation, these fish migrate to spawning grounds (potentially the shelf waters of the Gulf of Guinea).

Similar behaviour by yellowfin tuna, albeit with a much smaller sample size, has been observed around Ascension Island (Richardson et al., 2018), 1300 km NE of St Helena. Remote volcanic islands and

Table 4

Release location, fork length, and distance travelled for yellowfin tuna (Thunnus albacares) recaptured after longer migrations (>70 km) from their release location in the St Helena EEZ, South Atlantic Ocean: waters around St Helena Island (‘Inshore’), Bonaparte Seamount, and Cardno Seamount.

Release Area	Recapture Area	Tag ID	Release date	Release fork length (cm)	Recapture fleet	Recapture gear	Recapture date	Recapture fork length (cm)	Time at lib.	Distance travelled (km)	Min. Km d^{-1}
Inshore	Bonaparte	GBS000137	May 24, 2016	98	St Helena	Bait boat	November 08, 2016	115	168	132	0.8
	Bonaparte	GBS001669	June 23, 2017	104	St Helena	Bait boat	July 13, 2017		20	126	6.3
	Outside	GBS000567	June 16, 2017	60	EU Spain	Purse seiner	December 15, 2017	73	182	2023	11.1
Bonaparte	Inshore	ATP0135684	November 26, 2018	68	St Helena	Bait boat	08/042019	89	133	130	1.0
	Inshore	ATP0135798	November 26, 2018	71	St Helena	Bait boat	March 19, 2019	72	113	126	1.1
	Inshore	ATP0136047	November 26, 2018	79	St Helena	Bait boat	February 24, 2019	84	90	135	1.5
	Cardno	GBS001139	March 15, 2017	86	St Helena	Bait boat	April 01, 2017		17	321	18.9
Cardno	Inshore	ATP0136747	December 17, 2018	122	St Helena	Bait boat	April 23, 2019	89	127	327	2.6
	Outside	ATP0135368	October 15, 2018	65	El Salvador	Purse seiner	January 08, 2019	65	85	593	7.0
	Outside	ATP0135381	October 15, 2018	66	El Salvador	Purse seiner	February 04, 2019	65	112	249	2.2
	Outside	ATP0135385	October 15, 2018	64	Ghana	Purse seiner	January 04, 2019	63	81	1595	19.7
	Outside	ATP0135394	October 15, 2018	65	Curaçao	Purse seiner	January 25, 2019	65	102	1572	15.4
	Outside	GBS001307	March 15, 2017	134	–	–	December 25, 2018	143	650	1722	2.6
	Outside	ATP0162962	June 14, 2018	142	Curaçao	Purse seiner	February 03, 2019	144	234	1769	7.6
	Outside	ATP0135472	August 14, 2018	141	Guatemala	Purse seiner	March 09, 2019	147	207	1309	6.3
	Outside	ATP0135588	August 14, 2018	136	Guatemala	Purse seiner	April 17, 2019	139	246	2755	11.2

seamounts are known to produce local upwellings and this has been linked to aggregation of pelagic prey and predators (e.g. Sergi et al., 2020; Clark et al., 2010). Bathymetric forcing and elevated primary productivity (Barlow et al., 2002), associated with St Helena and the seamounts are thought to provide richer feeding grounds than the open ocean and hence retain yellowfin tuna until they migrate for reproduction. However, as shown here, a high proportion of tagged individuals remained close to their release locations independent of size, a finding that reinforces the importance of natural aggregating features (such as seamounts and islands) to yellowfin tuna. Further, the tendency to remain within St Helena’s EEZ highlights that local fisheries exploiting this resource are relying on a yellowfin population that might be highly resident once they have recruited to the region.

4.1. Evidence for site fidelity

Site fidelity is the tendency of an organism to return to areas repeatedly, including regions for feeding, breeding, and/or spawning. Site fidelity has been demonstrated in many pelagic fish (Guttridge et al., 2017), including tunas (Block et al., 2011). In this study, most yellowfin tuna were recovered close to their release location (within 50 km), with PSAT-tagged yellowfin tuna remaining within 70 km of their release location. While in some cases this was due to short duration tag recoveries, the mean time at large was 100 days and it is highly likely the fish were remaining within the EEZ for foraging purposes. For conventionally tagged yellowfin tuna, few larger scale movements were observed.. The maximum distance travelled was 2755 km by a yellowfin tagged at Cardno Seamount which was recaptured in the Gulf of Guinea after 246 days.

Based on fisheries landings data, larger yellowfin tuna were generally caught with increased distance from St Helena (Fig. 2), and this pattern was reinforced by yellowfin size patterns in conventional tag recoveries. Fish released inshore and at the closer Bonaparte Seamount had high site fidelity, with more than 95% of juveniles and adults recaptured in inshore waters or at Bonaparte. Of the individuals that showed longer distance migrations, smaller individuals released at Bonaparte were shown to migrate towards St Helena to inshore waters, and larger individuals released inshore migrated away from St Helena to Bonaparte (Fig. 4).

At Cardno Seamount there was also high site fidelity (more than 85% of juveniles and adults were recaptured at Cardno), though this region showed the highest rates of emigration from the tagging region by small individuals (15% of fish $< L_{50}$ recaptured at more than 50 km from Cardno). The higher migratory potential of small yellowfin tuna released at Bonaparte and Cardno seamounts may be linked to increased foraging competition with larger tuna at these seamounts compared to inshore, as yellowfin in the region have been shown to feed on similar prey independent of size (Laptikhovsky et al., 2020).

Differences in recapture rate were also observed between FAD-associated and free-schooling yellowfin tuna in inshore regions. Yellowfin tuna released at the inshore FAD had a slightly higher recovery rate compared to releases on free schools. In addition to the island effect the increased recovery on the FAD may indicate that these regions result in a higher vulnerability to local fishing pressure. Noting that residency times at FADs can vary depending on local conditions (Robert et al., 2013).

Site fidelity was also indicated by daily position estimates from electronically tagged individuals as well as the size-frequency of landings by month which showed distinct cohorts in landings data. Stable isotope analysis (SIA) of yellowfin tuna and prey carried out in the EEZ may lend further insight into residency and recruitment dynamics; preliminary analyses indicate that whilst a large contingent of yellowfin tuna appear to be resident, some larger tuna were more likely to be migrants based on an isotopic signature reflective of a different region

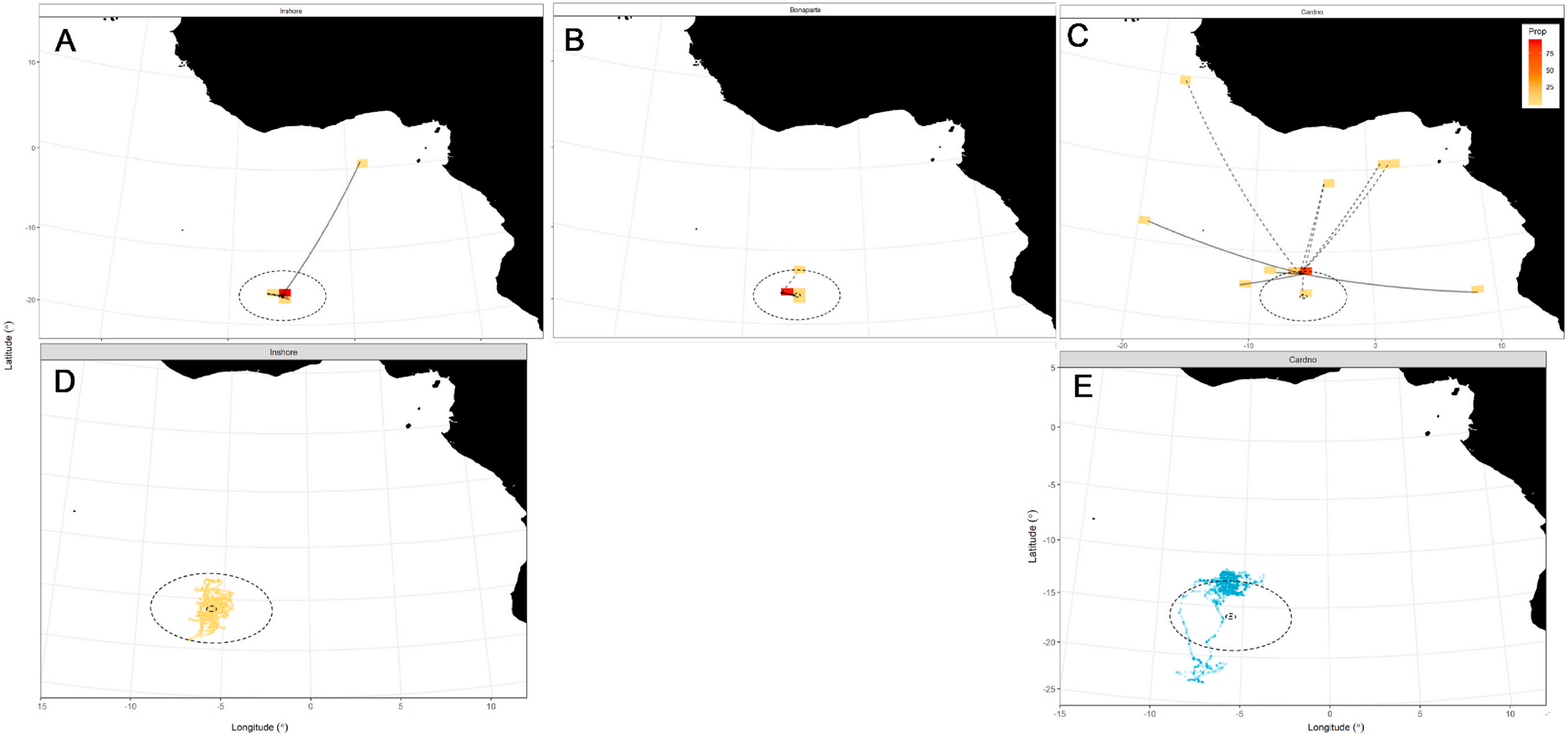

Fig. 4. A-C. Release and recapture locations for conventionally tagged yellowfin tuna (*Thunnus albacares*) at St Helena EEZ, South Atlantic Ocean, released at three locations: inshore (A), Bonaparte Seamount (B) and Cardno Seamount (C). Lines show whether fish were recaptured at sizes < L_{50} (solid lines) and >L_{50} (dashed lines). Grid cell colour reflects the proportion (%) of individuals recaptured within each cell (see Legend). (D & E). Show state space model (SSM) daily position estimates for PSAT-tagged tuna released inshore (D: yellow) and at Cardno Seamount (E: blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

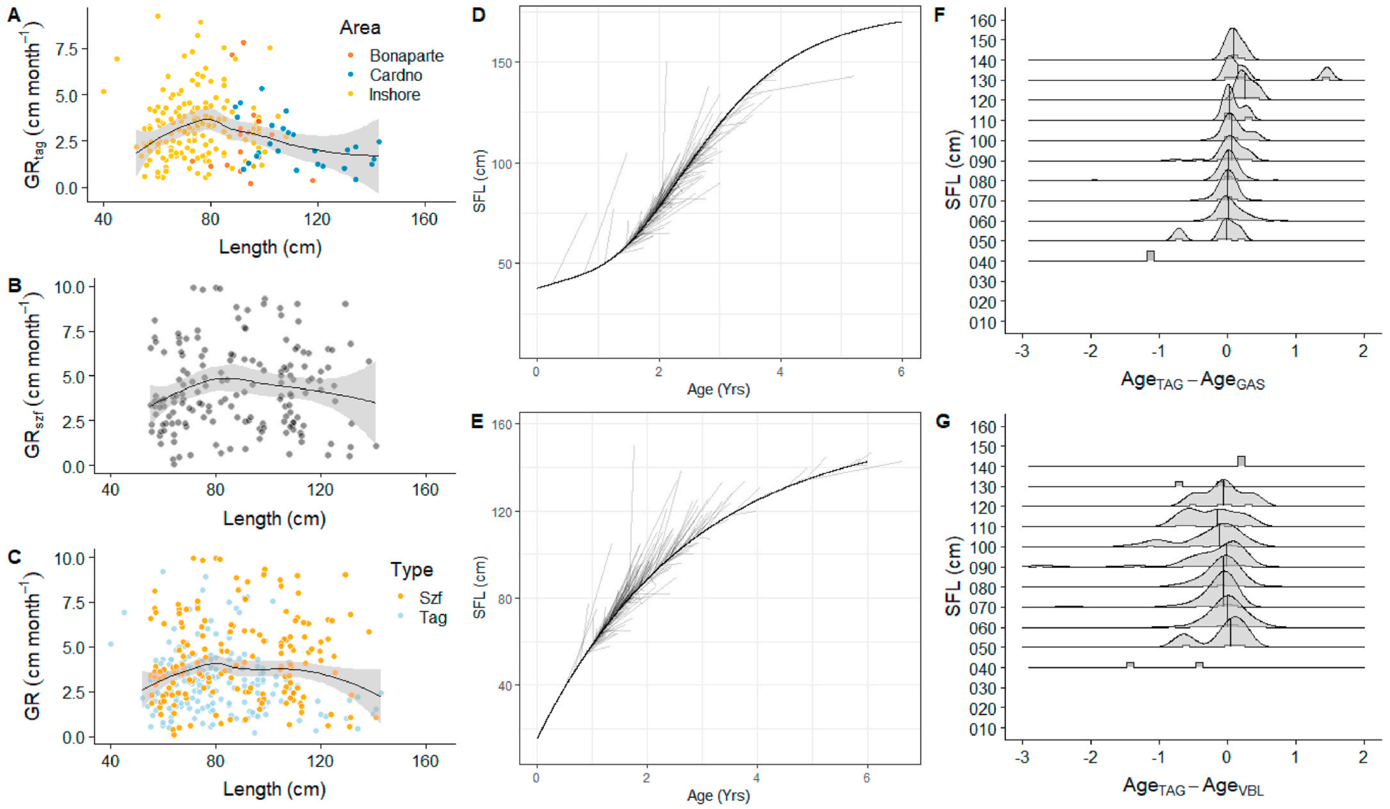

Fig. 5. (A) Growth rates of yellowfin tuna (*Thunnus albacares*) estimated from tag release/recapture data: GR_{tag}, (B) modal progression from size-frequency: GR_{szf} and (C) both growth rate estimates combined (GR). Size at release and recapture plotted using (D) the Gascuel curve and (E) von-Bertalanffy curve, with corresponding differences between age estimates from (F) size at recapture versus the Gascuel curve and (G) size at recapture versus the con-Bertalanffy curve.

than the St Helena EEZ (Madigan et al. unpublished data). Since SIA provides estimates of retrospective movement, complementary to the prospective data provided by tagging, this approach may be used to identify the sizes at which yellowfin tuna recruit to St Helena waters, and the potential source regions for yellowfin tuna in the St Helena EEZ.

The apparent fidelity of yellowfin tuna within St Helena's EEZ to their release locations seems to be a common phenomenon in tropical tunas (Fonteneau and Hallier, 2015; Fuller et al., 2015; Ohta and Kakuma, 2005). Previous studies indicate retention and localised movements in association with FADs, seamounts, and islands (Dagorn et al., 2007; Filous et al., 2020; Itano and Holland, 2000; Robert et al., 2012). Itano and Holland (2000) reported high recovery rates from yellowfin tuna caught at FADs and natural aggregation points (seamounts and islands) compared to free schools. Dagorn et al. (2007) and Robert et al. (2012) indicated retention times around island FADs of up to 150 days and 221 days, respectively, with an increased retention time for smaller tuna (Robert et al., 2012). Similar retention times (175 days) were also found for yellowfin tuna around island FADs in Palau's EEZ (Filous et al., 2020).

In this study, conventionally tagged tuna were recovered within St Helena's EEZ up to 526 days from release (Fig. S2), with retention to the region reinforced by electronically tagged juvenile and adult yellowfin tuna remaining close to or within the EEZ for up to 301 days after release. The electronic tag returns show higher levels of retention compared to previous studies in the Pacific (Dagorn et al., 2007; Filous et al., 2020). Although the relative fishing effort within and outside St Helena's EEZ will have an effect on recapture rate, the evidence of retention in this study is clear. The local St Helena fishing fleet have a centralised landing point and are closely involved in the tagging release and recovery operations within the EEZ. Recoveries outside have been by purse seiners (Table 4), with no recoveries from other gears (for example long liners or bait boats), which reflects the dominant fishing gear used to target yellowfin tuna in the central and southern East Atlantic (ICCAT, 2019b).

The continuation of the tagging programme will help to shed light on retention of yellowfin tuna with increasing size and time at liberty. For example, at present there is no evidence that yellowfin tuna spawn within St Helena's EEZ, so the retention is likely linked to food availability within the territory resulting from enhanced local nutrients around oceanic islands (James et al., 2020), which can be linked to positive effects on higher trophic levels (Pitcher et al., 2007).

The local biomass of yellowfin tuna fished at St Helena is part of a larger Atlantic stock. Tagging studies and analysis of catch length distributions has established that yellowfin tuna are present in St Helena waters at ~50 cm and remain for around two years (Fig. 2). After two years tag returns decline to almost zero and catches of yellowfin tuna above 130 cm are scarce. These trends imply that yellowfin tuna move beyond the waters surrounding St Helena once mature, with tag returns shifting towards the Gulf of Guinea and the central Atlantic.

Site fidelity within St Helena waters can be linked to the productivity of the local biomass in terms of its rate of turnover resulting from immigration ("recruitment") and emigration. Therefore, the sustainability of the residential population will rely on both recruitment and retention of the small fish, and periodic recruitment of large fish. The influence of distal source populations to yellowfin tuna within the EEZ is unknown, but it can be assumed that fishing pressure on this source population will affect the local population.

4.2. Speeds and distances

The average monthly displacement for conventionally tagged fish in the present study was 98 km between tag release and recovery positions, with greatest distances for fish released at Cardno Seamount (2755 km). The average monthly displacement is relatively low compared to average monthly displacement for yellowfin tuna released in the Atlantic Ocean (2915 km), the Indian Ocean (1413 km) and western Pacific Ocean (1320 km) which indicates an average displacement of 1706 km when all yellowfin tuna are combined across oceans (Fonteneau and Hallier, 2015). The lower average monthly displacements found here reinforces the hypothesis of potentially higher residency of yellowfin in the study region. However, findings of lower monthly displacement in tagged yellowfin tuna could also be linked to relatively short times (<21 months) compared to other studies in the Atlantic. For example, Fonteneau and Hallier (2015) report a yellowfin recaptured after 9.1 years at liberty. Future potential tag recoveries from yellowfin tagged as part of this study, as well as additional tagging in the St Helena EEZ, could provide the data necessary to evaluate the degree to which site fidelity explains such average monthly displacement discrepancies.

Whilst overall displacement between release and recapture locations cannot adequately represent monthly (or daily) displacement rates, displacement rates can be placed in the context of published swimming rates. Previous studies on bluefin tuna (*Thunnus thynnus*) swimming performance indicate that bluefin can achieve routine swimming speeds of 1.5 m s^{-1} (Gleiss et al., 2019) or between 1.4 and 1.7 m s^{-1} (Brill et al., 2002), compared to a maximum observed rate of 0.23 m s^{-1} (20 km d^{-1}) in the present study. The minimum estimated speed of conventionally tagged yellowfin within the present study showed that three individuals travelled in excess of 15 km d^{-1}, showing that 20 km d^{-1} is achievable.

4.3. *Long distance movements*

Several yellowfin tuna show links to regions outside of St Helena's EEZ. Four large yellowfin released at Cardno were recaptured in the Gulf of Guinea, whilst a small yellowfin, released in the Gulf of Guinea as part of the ICCAT AOTTP Programme, was recaptured within St Helena's EEZ. Though numbers showing these movements are small, it may suggest that a component of the population around St Helena may originate from the Gulf of Guinea and return to these key yellowfin spawning grounds once they have reached maturity. This would suggest that St. Helena is important as a foraging region for this large yellowfin stock. Given the accessibility to yellowfin for tagging in St Helena coastal waters, there is potential to deploy more archival tags to investigate longer journeys and elucidate linkages between different life stages. In Atlantic Bluefin tuna, archival tags have recorded up to 6 years consecutively indicating the technology is ready for long duration tags (Block, pers. Comm). A similar pattern has been noted in the work of Fonteneau and Hallier (2015) where a large yellowfin released off the east coast of America was recovered in the Gulf of Guinea.

4.4. *Growth*

Over the past few decades, yellowfin growth studies have supported a two-stanza growth model with a significant change in growth rate between juveniles and adults (Fonteneau and Chassot, 2013). The first phase indicates a slow growth rate (around 1.5 cm–2 cm $month^{-1}$) until they reach 60–70 cm (Dortel et al., 2015; Eveson et al., 2015; Fonteneau and Chassot, 2013), with a second faster growth phase (about 4 cm $month^{-1}$) until yellowfin are $>$ 75 cm. At sizes >75 cm, growth rate decreases to around 3 cm $month^{-1}$ (Fonteneau and Chassot, 2013).

In the present study, growth rate estimates were obtained from tag data (GR_{tag}) and from modal progression of size-frequency data (GR_{szf}). GR_{tag} estimates indicate an average growth rate of 2.91 cm $month^{-1}$ for tuna below 60 cm, 3.34 cm $month^{-1}$ for fish between 60 and 80 cm, and 2.91 cm $month^{-1}$ for fish above 80 cm. GR_{szf} was estimated at 4.38 cm $month^{-1}$ for fish between 60 and 80 cm. Therefore, growth rates are similar to previously reported values for fish above 60 cm, though the smaller sizes have higher growth rate estimates.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2021.103513.

References

Anderson, G., Lal, M., Hampton, J., Smith, N., Rico, C., 2019. Close kin proximity in yellowfin tuna (*Thunnus albacares*) as a driver of population genetic structure in the tropical western and central Pacific Ocean. Front. Mar. Sci. 6 https://doi.org/10.3389/fmars.2019.00341.

Appleyard, S., Grewe, P., Innes, B., Ward, R., 2001. Population structure of yellowfin tuna (*Thunnus albacares*) in the western Pacific Ocean, inferred from microsatellite loci. Mar. Biol. 139, 383–393. http://link.springer.com/10.1007/s002270100578.

Barlow, R.G., Aiken, J., Holligan, P.M., Cummings, D.G., Maritorena, S., Hooker, S., 2002. Phytoplankton pigment and absorption characteristics along meridional transects in the Atlantic Ocean. Deep Sea Res. Oceanogr. Res. Pap. 49, 637–660.

Bayliff, W., 1993. An indexed bibliography of papers on tagging of tunas and billfishes. Inter-Am. Trop. Tuna Comm. Special Report No. 8, 91pp.

Block, B.A., Teo, S.L.H., Walli, A., Boustany, A., Stokesbury, M.J.W., Farwell, C.J., Weng, K.C., et al., 2005. Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434, 1121–1127. http://www.nature.com/articles/nature03463.

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., et al., 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475, 86–90. http://www.nature.com/articles/nature10082.

Block, B.A., Whitlock, R., Schallert, R.J., Wilson, S., Stokesbury, M.J.W., Castelton, M., Boustany, A., 2019. Estimating natural mortality of Atlantic bluefin tuna using acoustic telemetry. Sci. Rep. 9, 4918.

Brill, R., Lutcavage, M., Metzger, G., Bushnell, P., Arendt, M.D., 2002. Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus thynnus*), in relation to oceanographic conditions of the western North Atlantic, determined with ultrasonic telemetry. Fish. Bull. 100, 155–167.

Clark, M.R., Rowden, A.A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K.I., Rogers, A.D., O'Hara, T.D., White, M., Shank, T.M., Hall-Spencer, M., 2010. The ecology of seamounts: structure, function, and human impacts. Annu. Rev. Mar. Sci. 2, 253–278.

Collins, M.A., 2017. South Atlantic overseas territories commercial fisheries management review: St Helena. An independent report by marecol. Commissioned by RSPB. https://www.rspb.org.uk/globalassets/downloads/documents/conservation-projects/ukots-hidden-treasures/2017/st-helena-fisheries-detailed-report-2017.pdf.

Dagorn, L., Holland, K.N., Itano, D.G., 2007. Behavior of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna in a network of fish aggregating devices (FADs). Mar. Biol. 151, 595–606. https://doi.org/10.1007/s00227-006-0511-1.

Dortel, E., Sardenne, F., Bousquet, N., Rivot, E., Million, J., Le Croizier, G., Chassot, E., 2015. An integrated Bayesian modelling approach for the growth of Indian Ocean yellowfin tuna. Fish. Res. 163, 69–84.

Eveson, J.P., Million, J., Sardenne, F., Le Croizier, G., 2015. Estimating growth of tropical tunas in the Indian Ocean using tag-recapture data and otolith-based age estimates. Fish. Res. 163, 58–68. https://www.sciencedirect.com/science/article/abs/pii/S016578361400188X.

FAO, 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in Action. Rome. https://doi.org/10.4060/ca9229en.

Filous, A., Friedlander, A.M., Griffin, L., Lennox, R.J., Danylchuk, A.J., Mereb, G., et al., 2020. Movements of juvenile yellowfin tuna (*Thunnus albacares*) within the coastal

FAD network adjacent to the Palau National Marine Sanctuary: implications for local fisheries development. Fish. Res. 230, 105688. https://doi.org/10.1016/J.FISHRES.2020.105688.

Fonteneau, A., Chassot, E., 2013. An overview of yellowfin tuna growth in the Atlantic ocean: von Bertalanffy or multistanza growth? Collect. Vol. Sci. Pap. ICCAT 69, 2059–2075.

Fonteneau, A., Hallier, J.-P., 2015. Fifty years of dart tag recoveries for tropical tuna: a global comparison of results for the western Pacific, eastern Pacific, Atlantic, and Indian Oceans. Fish. Res. 163, 7–22.

Fraley, C., Raftery, A.E., 2002. Model-based clustering, discriminant analysis, and density estimation. J. Am. Stat. Assoc. 97, 611–631. http://www.tandfonline.com/doi/abs/10.1198/016214502760047131.

Fuller, D.W., Schaefer, K.M., Hampton, J., Caillot, S., Leroy, B.M., Itano, D.G., 2015. Vertical movements, behavior, and habitat of bigeye tuna (*Thunnus obesus*) in the equatorial central Pacific Ocean. Fish. Res. 172, 57–70. https://www.sciencedirect.com/science/article/abs/pii/S0165783615300047.

Gleiss, A.C., Schallert, R.J., Dale, J.D., Wilson, S.G., Block, B.A., 2019. Direct measurement of swimming and diving kinematics of giant Atlantic bluefin tuna (*Thunnus thynnus*). Roy. Soc. Open Sci. 6 (5), 190203.

Graham, B.S., Koch, P.L., Newsome, S.D., McMahon, K.W., Aurioles, D., 2010. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: Isoscapes, pp. 299–318. http://link.springer.com/10.1007/978-90-481-3354-3_14.

Grande, M., Murua, H., Zudaire, I., Goñi, N., Bodin, N., 2014. Reproductive timing and reproductive capacity of the Skipjack Tuna (*Katsuwonus pelamis*) in the western Indian Ocean. Fish. Res. 156, 14–22. https://linkinghub.elsevier.com/retrieve/pii/S0165783614001453.

Guillotreau, P., Salladarré, F., Dewals, P., Dagorn, L., 2011. Fishing tuna around Fish Aggregating Devices (FADs) vs free swimming schools: skipper decision and other determining factors. Fish. Res. 109, 234–242. https://doi.org/10.1016/J.FISHRES.2011.02.007.

Guttridge, T.L., Van Zinnicq Bergmann, M.P.M., Bolte, C., Howey, L.A., Finger, J.S., Kessel, S.T., Brooks, J.L., et al., 2017. Philopatry and regional connectivity of the great hammerhead shark, *Sphyrna mokarran* in the U.S. And Bahamas. Front. Mar. Sci. 4, 00003. http://journal.frontiersin.org/article/10.3389/fmars.2017.00003/full.

Hall, M., Lennert-Cody, C., Garcia, M., Arenas, P., 1992. Characteristics of floating objects and their attractiveness for tunas. In: Scott, K., Bayliff, M.D., Lennert-Cody, W.H., Schaefer, C.E. (Eds.), Proceedings of the International Workshop on the Ecology and Fisheries for Tunas Associated with Floating Objects, February 11–13, 1992, Inter-American Tropical Tuna Commission Special Report, pp. 396–446. La Jolla, California.

ICCAT, 2019a. Report for Biennial Period, 2018-19 PART I, vol. 2, 2018.

ICCAT, 2019b. Report of the 2019 ICCAT Yellowfin Tuna Stock Assessment Meeting.

Itano, D.G., Holland, K.N., 2000. Movement and vulnerability of bigeye (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) in relation to FADs and natural aggregation points. Aquat. Living Resour. 13, 213–223. http://www.alr-journal.org/10.1016/S0990-7440(00)01062-7.

James, A.K., Washburn, L., Gotschalk, C., Maritorena, S., Alldredge, A., Nelson, C.E., Hench, J.L., et al., 2020. An island mass effect resolved near Mo'orea, French polynesia. Front. Mar. Sci. 7, 00016. https://www.frontiersin.org/article/10.3389/fmars.2020.00016/full.

Kurota, H., McAllister, M.K., Lawson, G.L., Nogueira, J.I., Teo, S.L.H., Block, B.A., 2009. A sequential Bayesian methodology to estimate movement and exploitation rates using electronic and conventional tag data: application to Atlantic bluefin tuna (*Thunnus thynnus*). Can. J. Fish. Aquat. Sci. 66 (2), 321–342.

Laptikhovsky, V., Naulaerts, J., Clingham, E., Collins, M.A., Cranfield, M., Henry, L., et al., 2020. Comparative feeding strategies of yellowfin tuna around St Helena and adjacent seamounts of the South Atlantic Ocean. J. Appl. Ichthyol., jai. 14122 https://doi.org/10.1111/jai.14122.

Lawson, G.G.L., Castleton, M.M.R., Block, B.A., 2010a. Movements and diving behavior of Atlantic bluefin tuna *Thunnus thynnus* in relation to water column structure in the northwestern Atlantic. Mar. Ecol. Prog. Ser. 400, 245–265. http://www.int-res.com/abstracts/meps/v400/p245-265/.

Lawson, G.G.L., Castleton, M.M.R., Block, B.A., 2010b. Movements and diving behavior of Atlantic bluefin tuna *Thunnus thynnus* in relation to water column structure in the northwestern Atlantic. Mar. Ecol. Prog. Ser. 400, 245–265. https://doi.org/10.3354/meps08394.

Leroy, B., Nicol, S., Lewis, A., Hampton, J., Kolody, D., Caillot, S., et al., 2015. Lessons learned from implementing three, large-scale tuna tagging programmes in the western and central Pacific Ocean. Fish. Res. 163, 23–33. https://doi.org/10.1016/J.FISHRES.2013.09.001.

Lopez, J., Moreno, G., Lennert-Cody, C., Maunder, M., Sancristobal, I., Caballero, A., et al., 2017. Environmental preferences of tuna and non-tuna species associated with drifting fish aggregating devices (DFADs) in the Atlantic Ocean, ascertained through Fishers' echo-sounder buoys. Deep Sea Res. Part II Top. Stud. Oceanogr. 140, 127–138. https://doi.org/10.1016/J.DSR2.2017.02.007.

Marsac, F., Potier, M., Peignon, C., Lucas, V., Dewals, P., Fonteneau, A., Pianet, R., et al., 2006. Updated biological parameters for Indian Ocean yellowfin tuna and monitoring of forage fauna of the pelagic ecosystem, based on a routine sampling at the cannery in Seychelles. IOTC-2006-WPTT- 9, 14.

Moore, B.R., Bell, J.D., Evans, K., Farley, J., Grewe, P.M., Hampton, J., et al., 2020. Defining the stock structures of key commercial tunas in the Pacific Ocean I: current knowledge and main uncertainties. Fish. Res. 230, 105525. https://doi.org/10.1016/J.FISHRES.2020.105525.

Ohta, I., Kakuma, S., 2005. Periodic behavior and residence time of yellowfin and bigeye tuna associated with fish aggregating devices around Okinawa Islands, as identified with automated listening stations. Mar. Biol. 146, 581–594. http://link.springer.com/10.1007/s00227-004-1456-x.

Orue, B., Lopez, J., Moreno, G., Santiago, J., Soto, M., Murua, H., 2019. Aggregation process of drifting fish aggregating devices (DFADs) in the Western Indian Ocean: who arrives first, tuna or non-tuna species? PloS One 14, e0210435. https://doi.org/10.1371/journal.pone.0210435.

Pecoraro, C., Zudaire, I., Bodin, N., Murua, H., Taconet, P., Diaz-Jaimes, P., Cariani, A., et al., 2017. Putting all the pieces together: integrating current knowledge of the biology, ecology, fisheries status, stock structure and management of yellowfin tuna (*Thunnus albacares*). Rev. Fish Biol. Fish. 27, 811–841. http://link.springer.com/10.1007/s11160-016-9460-z.

Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S., 2007. In: Seamounts: Ecology, Fisheries & Conservation. Blackwell Publishing Ltd, Oxford, UK. https://doi.org/10.1002/9780470691953.

Richardson, A.J., Downes, K.J., Nolan, E.T., Brickle, P., Brown, J., Weber, N., Weber, S. B., 2018. Residency and reproductive status of yellowfin tuna in a proposed large-scale pelagic marine protected area. Aquat. Conserv. Mar. Freshw. Ecosyst. 28, 1308–1316. https://doi.org/10.1002/aqc.2936.

Robert, M., Dagorn, L., Deneubourg, J.L., Itano, D., Holland, K., 2012. Size-dependent behavior of tuna in an array of fish aggregating devices (FADs). Mar. Biol. 159, 907–914. https://doi.org/10.1007/s00227-011-1868-3.

Robert, M., Dagorn, L., Filmalter, J., Deneubourg, J., Itano, D., Holland, K., 2013. Intra-individual behavioral variability displayed by tuna at fish aggregating devices (FADs). Mar. Ecol. Prog. Ser. 484, 239–247. https://doi.org/10.3354/meps10303.

Schaefer, K.M., 1998. Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Inter-Am Trop. Tuna Comm. Bull. 21, 205–221.

Schaefer, K.M., Fuller, D.W., Block, B.A., 2007a. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. Mar. Biol. 152, 503–525. http://link.springer.com/10.1007/s00227-007-0689-x.

Schaefer, K.M., Fuller, D.W., Block, B.A., 2007b. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. Mar. Biol. 152, 503–525. http://link.springer.com/10.1007/s00227-007-0689-x.

Schaefer, K.M., Fuller, D.W., Block, B.A., 2011. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the Pacific Ocean off Baja California, Mexico, determined from archival tag data analyses, including unscented Kalman filtering. Fish. Res. 112, 22–37. https://www.sciencedirect.com/science/article/pii/S016578361100275X.

Schaefer, K.M., Fuller, D.W., Aldana, G., 2014. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in waters surrounding the Revillagigedo Islands Archipelago Biosphere Reserve, Mexico. Fish. Oceanogr. 23, 65–82. https://doi.org/10.1111/fog.12047.

Schenke, H., 2016. General bathymetric Chart of the Oceans (GEBCO). In: Harff, J., Meschede, M., Petersen, S., Thiede, J. (Eds.), Encyclopedia of Marine Geosciences. Encyclopedia of Earth Sciences Series. Springer, Dordrecht.

Scrucca, L., Fop, M., Murphy, T.B., Raftery, A.E., 2016. Mclust 5: clustering, classification and density estimation using Gaussian finite mixture models. The R Journal 8, 289–317. http://www.ncbi.nlm.nih.gov/pubmed/27818791.

Sergi, S., Baudena, A., Cotte, C., Ardyna, M., Blain, S., d'Olividio, F., 2020. Interaction of the Antarctic Circumpolar Current with seamounts fuels moderate blooms but vast foraging grounds for multiple marine predators. Front. Mar. Sci. 7, 416.

Sibert, J., Hampton, J., 2003. Mobility of tropical tunas and the implications for fisheries management. Mar. Pol. 27, 87–95. https://www.sciencedirect.com/science/article/pii/S0308597X0200057X.

Sippel, T., Paige Eveson, J., Galuardi, B., Lam, C., Hoyle, S., Maunder, M., et al., 2015. Using movement data from electronic tags in fisheries stock assessment: a review of models, technology and experimental design. Fish. Res. 163, 152–160. https://doi.org/10.1016/J.FISHRES.2014.04.006.

Suzuki, Z., 1994. A review of the biology and fisheries for yellowfin tuna, *Thunnus albacares*, in the western and central Pacific Ocean. FAO Fish. Tech. Pap. 336, 108–137.

Teo, S.L.H., Boustany, A., Blackwell, S., Walli, A., Weng, K.C., Block, B.A., 2004. Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. Mar. Ecol. Prog. Ser. 283, 81–98.

Ward, R.D., Elliott, N.G., Innes, B.H., Smolenski, A.J., Grewe, P.M., 1997. Global population structure of yellowfin tuna, *Thunnus albacares*, inferred from allozyme and mitochondrial DNA variation. Fish. Bull. 95, 566–575. https://www.st.nmfs.noaa.gov/spo/FishBull/953/ward.pdf.

Wilson, A.D.M., Brownscombem, J.W., Krause, J., Krause, S., Gutowsky, L.F.G., Brooks, E.J., Cooke, S.J., 2015. Integrating network analysis, sensor tags, and observation to understand shark ecology and behavior. Behav. Ecol. 26, 1577–1586.

Wu, G.C.-C., Chiang, H.-C., Chou, Y.-W., Wong, Z.-R., Hsu, C.-C., Chen, C.-Y., Yang, H.-Y., 2010. Phylogeography of yellowfin tuna (*Thunnus albacares*) in the western pacific and the western Indian oceans inferred from mitochondrial DNA. Fish. Res. 105, 248–253. https://www.sciencedirect.com/science/article/abs/pii/S0165783610000792.