Vol. 664: 165–182, 2021
https://doi.org/10.3354/meps13654

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 15

Ontogenetic shifts in home range size of a top predatory reef-associated fish (*Caranx ignobilis*): implications for conservation

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ABSTRACT: Defining the home range of vulnerable species is critical for designing effective spatial management strategies. However, animal home ranges often change with ontogeny, and quantifying the associated temporal and spatial changes is particularly challenging for mobile marine species. Here, we investigated how the space use of a top predatory reef-associated fish (giant trevally *Caranx ignobilis*) scales with body size. Fish were tagged with acoustic transmitters and passively tracked for >3 yr at a tropical island and atoll in the Republic of Seychelles. A sheltered atoll environment was critical for juvenile fish (<60 cm fork length, FL) that exhibited a shift in home range location and area as they matured into adults. Small (60–100 cm FL) and large (>100 cm FL) adult fish appeared to favour shallow coral reefs and associated reef drop offs whilst sharing a similar core home range location. Large adult fish utilized a greater diversity of habitat types and had significantly ($p < 0.05$) greater annual dispersal distances (mean = 35.29 km, max = 91.32 km) than small adults (mean = 13.72 km, max = 21.55 km). Additionally, the home range of large adults (mean = 209.74 km^2) was significantly ($p < 0.05$) larger than that of juveniles (mean = 38.73 km^2) and small adults (77.32 km^2) and there was a significant ($p = 0.02$) relationship between fish length and home range size. Furthermore, tagged fish took up to 34 mo (mean = 18.54 mo) to utilize the full extent of their home range. The habitat shift and expansion in home range size throughout ontogeny should be taken into account when designing effective spatial management plans for *C. ignobilis*.

KEY WORDS: Giant trevally · Body size · Spatial management · Marine protected area · Acoustic telemetry · Western Indian Ocean · Seychelles · Fisheries management

1. INTRODUCTION

A home range may be defined as the common area an animal repeatedly uses and has implications for important ecological processes that the animal needs to survive (Börger et al. 2008). Defining and protecting the home range is critical for the effective design of spatial management initiatives for vulnerable populations (Kramer & Chapman 1999, Moffitt et al. 2009, Hooker et al. 2011). However, home ranges of

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Publisher: Inter-Research · www.int-res.com

animals are not static, and can change with ontogeny due to shifting demands associated with energetic budgets and reproduction (Börger et al. 2008). Typically, there is a linear increase in home range size with increasing body size and mass, which is driven by the need to acquire additional resources to support the increased metabolic requirements of a larger body (Jetz et al. 2004). The relationship between home range and body size may be further complicated by various factors such as predation risk, diet shifts, habitat shifts, reproduction, and the need to maximise food availability (McNab 1963, Kimirei et al. 2013).

Many fish species undergo substantial ontogenetic change between their larval and adult stages, yet the long-term (>1 yr) spatial dynamics of home range shifts throughout these ontogenetic stages remain poorly understood for mobile species because they cannot be observed directly (Welsh et al. 2013). Given that many large, mobile fishes are also top predators that play key ecological roles within the various communities that they inhabit, an understanding of their habitat use and movement patterns is significant from both management and ecological perspectives. Such species may facilitate links between ecological processes across various habitats with increasing frequency as they grow and become increasingly mobile (Gaines et al. 2007, Papastamatiou et al. 2015). Understanding the relationship between body size and home range size in reef-associated predatory fish can therefore provide important insights into their movement behaviour as well as allow for improved conservation for vulnerable, ecologically and economically important species.

The giant trevally *Caranx ignobilis* is a large and mobile top predatory reef-associated fish distributed throughout the tropical and sub-tropical Indo-Pacific. Individuals can reach a maximum weight of 80 kg, total length of 1.7 m (Froese & Pauly 2009) and an age of at least 25 yr (Sudekum et al. 1991, Andrews 2020). Fifty percent maturity is reached after 3–3.5 yr, at 60–65 cm fork length (FL), and they are gonochoristic broadcast spawners that may form aggregations in early summer to spawn (von Westernhagen 1974, Claydon 2004, Daly et al. 2019). Giant trevally are apex predators that prey on a wide variety of fish species as well as squid and crustaceans (Sudekum et al. 1991, Froese & Pauly 2009, Mann 2013, Glass et al. 2020). Juveniles often settle into nursery areas such as sheltered bays, estuaries or atolls where they remain up to a length of at least 40–55 cm FL (Blaber & Cyrus 1983). Thereafter, they may move into deeper, reef-associated habitats, although the drivers of this behavioural and habitat shift remain unclear. It is postulated that this habitat shift may to be related to the onset of sexual maturity and the increased energetic demands of a larger body size (Blaber & Cyrus 1983, Smith & Parrish 2002, Wetherbee et al. 2004, Leis et al. 2006). Giant trevally are also an iconic fishery species and are prized by recreational anglers worldwide (Friedlander 2005). In the waters of Seychelles, giant trevally are part of the high value catch-and-release fishery, which forms a critical part of the Outer Island tourism sector for the Republic.

The aim of this study was to describe ontogenetic home range scaling in giant trevally. We employed passive acoustic telemetry techniques to investigate the long-term (>3 yr) movement patterns of giant trevally of varying sizes on the Amirante Bank in the Republic of Seychelles, Western Indian Ocean. We hypothesised that dispersal, habitat connectivity and home range size would increase with body size. The findings of this study will aid in developing recommendations for guiding effective spatial conservation management planning for giant trevally.

2. MATERIALS AND METHODS

2.1. Study site

This study took place at D'Arros Island and St. Joseph Atoll located on the Amirante Bank in the Republic of Seychelles, Western Indian Ocean (Fig. 1). The Amirante Bank is a shallow (typically <40 m deep) plateau consisting of 11 low-lying sand cay islands with a total land area of 11.5 km^2 (Stoddart et al. 1979). D'Arros Island and St. Joseph Atoll make up 3.03 km^2 of land and are separated by a channel approximately 900 m wide and 70 m deep. St. Joseph Atoll consists of a deep lagoon (mean 4 m depth) surrounded by fringing sand and sea grass flats that completely cuts off access to the outer reef on extreme low tides (Stoddart et al. 1979). The islands contain a diversity of marine habitat types from the atoll lagoon and sand flats to sea grass beds (primarily *Thalassodendron ciliatum*), to shallow coral reef crests and deeper reef drop-offs, and are home to a diverse fish community (Daly et al. 2018). The climate in Seychelles is tropical and dominated by 2 main seasons. The cooler, drier southwest monsoon season occurs between May and November, and the warmer, wetter northwest monsoon season occurs between December and March (Stoddart et al. 1979).

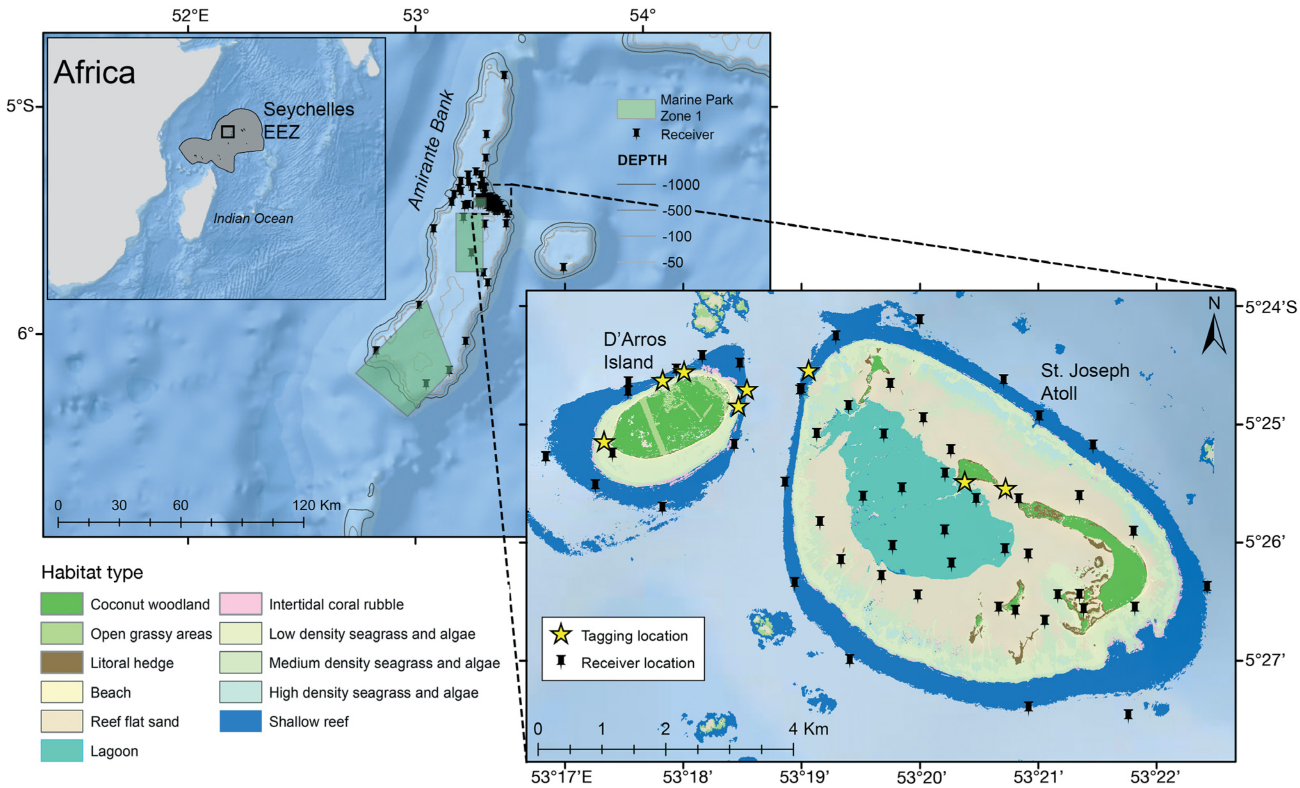

Fig. 1. D'Arros Island and St. Joseph Atoll in the Amirante Islands, Republic of Seychelles. Seventeen giant trevally were fitted with acoustic transmitters and passively monitored between 2016 and 2019 using an array of 89 acoustic receivers located throughout the Amirante Bank. Shaded blue surrounding shallow reef habitat represents deep water (>3 m deep). EEZ: exclusive economic zone

In 2020, the Republic of Seychelles gazetted a series of new Marine National Parks (Republic of Seychelles Official Gazette No. 5) throughout the Seychelles Archipelago. This included 3 Zone 1 Parks on the Amirante Bank, namely (1) D'Arros Atoll Marine National Park (park includes D'Arros Island, but not St. Joseph Atoll); (2) D'Arros to Poivre Atolls Marine National Park; and (3) Amirante South Marine National Park (shown in Fig. 1 in order from north to south, respectively). In total, these marine national parks constitute an area of approximately 1732 km^2, within which activities such as commercial fishing are regulated (specific regulations yet to be confirmed at time of writing). Additionally, the entire Amirante Bank falls within a designated Area of Outstanding Natural Beauty (Zone 2 Protected Area), within which no commercial fishing by foreign vessels is permitted (regulations yet to be finalized) (Seychelles Official Gazette No. 5).

Habitat maps were created in ArcGIS 10.2 using supervised image classification of 2 m 8-band MS 16-bit orthorectified WorldView-2 high-resolution satellite images from LAND INFO Worldwide Mapping (http://www.landinfo.com/). Supervised image classification was digitized using the image classification toolbar, and training samples were validated on the ground and using spectral scatterplot visual inspection. Habitats were classified into 13 categories (of which 11 are presented for the purposes of this study) using the maximum likelihood classification with a rejected fraction of 0 and an equal *a priori* probability weighting. Habitat maps were created by n + p biologists (www.nplusp.ch) and copyrighted by the Save Our Seas Foundation.

2.2. Fish tagging and monitoring

Between 27 April and 7 September 2016, 17 giant trevally were fitted with Vemco acoustic coded transmitters (Table 1). Fish were captured using standard rod and line tackle and brought onboard a research vessel where they were submerged in a water trough, ventral side up, for the duration of the tagging procedure. Fish <60 cm FL were surgically implanted with Vemco V13 1L (nominal delay 120 s,

Table 1. Tagging and detection summary for giant trevally fitted with acoustic transmitters. Fish were assigned to 3 size classes based on the measured fork length at the time of capture. Asterisks indicate individuals likely to have suffered post-release mortality. The residency index was calculated as: (total number of days detected)/(number of days monitored) × 100. NA: not assessed

Fish ID	Fork length (cm)	Initial size class	Release date (d/mo/yr)	No. detections	No. unique receivers	Days detected	Days monitored	Residency index (%)
1*	40.5	Juvenile	27/04/2016	100430	1	567	595	NA
2*	42.5	Juvenile	03/05/2016	151	5	3	3	NA
3	45.0	Juvenile	04/05/2016	9979	36	425	914	46.50
4*	47.0	Juvenile	05/05/2016	115	6	12	12	NA
5	72.5	Small Adult	05/05/2016	10282	30	671	1225	54.78
6	77.0	Small Adult	07/05/2016	5356	36	404	707	57.14
7	86.0	Small Adult	09/05/2016	6012	21	755	1252	60.30
8	89.0	Small Adult	09/05/2016	3886	22	370	629	58.82
9	90.0	Small Adult	09/05/2016	21139	24	817	1251	65.31
10	92.0	Small Adult	09/05/2016	13153	27	771	1259	61.24
11	93.0	Small Adult	11/05/2016	7266	29	814	1246	65.33
12	93.0	Small Adult	12/05/2016	5615	29	751	1227	61.21
13	101.0	Large adult	12/05/2016	130	16	18	25	72.00
14	103.0	Large adult	04/05/2016	9764	20	280	314	89.17
15	103.0	Large adult	07/09/2016	5579	25	634	797	79.55
16	105.0	Large adult	07/09/2016	2737	22	210	224	93.75
17	120.0	Large adult	14/07/2016	11532	32	1046	1239	84.42
Mean	82.32			12536.82	23	502.82	759.82	67.82
SD	24.59			23279.10	11	319.37	491.58	13.496

expected battery life 1582 d) acoustic transmitters while larger fish were implanted with Vemco V16 transmitters (nominal delay 60 s, expected battery life 3650 d). All transmitters were sterilized with surgical sterilant prior to the procedure and were implanted into the peritoneal cavity of each fish through a 2 cm long incision, which was subsequently sutured closed with 2 independent stiches using a braided silk suture. The incision was then coated with an anti-septic powder forming an adhesive gel prior to releasing the fish. The entire capture and tagging procedure typically lasted <15 min.

Tagged fish were monitored using an underwater acoustic receiver array consisting of 89 Vemco VR2W receivers located throughout the Amirante Bank (Fig. 1). Receivers were deployed year round throughout the study period and serviced annually (see Lea et al. 2016 for details). Receivers were attached to a buoyed rope anchored to the reef or mooring block or (for receivers located on sand and seagrass flats less than 2 m deep) fitted inside a cinder block placed on the substrate. Range tests conducted at the study site showed that the mean ± SD detection range for deployed tags was 165 ± 33 m (Lea et al. 2016), with limited overlap in detection range between neighbouring receivers. Downloaded detection data from receivers were imported into a database of known receiver and tag deployments and assigned to the appropriate receiver location. Detections were checked for duplicates and all timecodes were corrected for linear clock drift based on the internal receiver clock and the PC clock, as recommend by Vemco (see supplementary material in Lea et al. 2020 for additional details).

2.3. Fish size classes

Tagged giant trevally were assigned into 1 of 3 size classes: juveniles (<60 cm FL), small adults (60–100 cm FL) and large adults (>100 cm). Fish were categorized as small adults based on the length at which 50% of fish are sexually mature (Sudekum et al. 1991) and as large adults (>100 cm) based on the median length between sexual maturity and maximum reported size. Throughout the study period, the growth of tagged individuals was also taken into consideration. The size class of tagged fish was estimated on an annual basis and a new size class assigned in accordance with the growth curve derived by Sudekum et al. (1991) (see Table A1 in the Appendix for reference). It was assumed that giant trevally in the tropical waters of Seychelles grow at comparable rates to those in the similar tropical Hawaiian marine environment where Sudekum et al. (1991) conducted their growth study; however, further investigation will be required to confirm this assumption. Estimates of fish length post-tagging are therefore used only as a proxy within the present study to compare the relative space use of these fish, and caution should be used when applying our data to populations of giant trevally in different locations.

2.4. Summary statistics

For each tagged fish, we calculated the number of detections recorded, the number of unique receivers that tagged fish were recorded on, the total number of days detected and the number of days at liberty (from tagging date to last detection date). Of the 17 fish that were tagged, we presumed 3 juvenile fish suffered post release mortality, as their respective tags either pinged continuously from the same position with detections on only 1 receiver (Fish ID 1 logged 100 430 continuous detections on a single receiver over 567 d) or detections were temporally and spatially limited (Fish ID 2 and 4 were only detected for 3 and 12 d, respectively on 5 and 6 nearby receivers). Based on assumptions of post release mortality for acoustically tagged fish (stationary horizontal movement and ceased detections), we removed these fish from further data analyses in this study (Klinard & Matley 2020). For the remaining 14 tagged fish, a residency index was then calculated to examine the percentage of time each tagged individual spent within close proximity to the receiver array throughout the entire study period. This was achieved by dividing the total number of days detected by the number of days at liberty and multiplying by 100 for each fish.

2.5. Habitat connectivity

Network plots were used to visualise the habitat connectivity of the 3 assigned size classes (juvenile, small adult and large adult) of tagged giant trevally. Networks were plotted for each size class overall, and individuals were assigned to the appropriate size class annually based on their calculated growth. Plots were constructed in ArcMAP 10.6 (ESRI), with nodes representing detection frequency and edges representing sequential detections occurring between receiver pairs. Edge weights were adjusted to account for the number of tagged individuals within each size class per year to provide standardized and comparable counts across classes, and final values are presented as a percentage of the total.

2.6. Dispersal distance

Measures of dispersal distance and activity space were used to investigate the spatial ecology of tagged fish. These metrics were calculated for each tagged giant trevally using functions provided in the 'Animal Tracking Toolbox' extension to the package 'VTrack' (Campbell et al. 2012) in the R statistical environment (version 3.4.1), as described by Udyawer et al. (2018). The 'step dispersal' reflected the distances travelled by individuals between subsequent detections in the receiver array, and were calculated using the function 'dispersalSummary'. Step dispersal was calculated for each tagged individual relative to its size class at the time of tagging (i.e. as per Table 1). The dispersal distances of small and large adults were tested for significant differences using a *t*-test.

2.7. Home range size and time to maximum occupancy

Prior to quantifying home range sizes, short-term centres of activity (COAs) that represented the average position of each fish per hour of the study were calculated (Simpfendorfer et al. 2002). The use of COAs accounted for the temporally variable tag transmissions and the spatial biases caused by receiver locations (Udyawer et al. 2018). Home ranges were examined using 3 activity space metrics: (1) total area of occupancy, which was taken to be the full area of calculated minimum convex polygons (MCPs); (2) core home range area, which was defined as the area in which individuals spent more than 50% of their time based on Brownian bridge movement models; and (3) the extent of activity space, which was defined as the area in which individuals spent 95% of their time based on Brownian bridge movement models. These contrasting, yet complementary, home range estimation methods were used in tandem to provide the greatest level of insight into the home range of tagged fishes. MCPs provided a maximum estimate of home range size by considering the entire area encompassed by polygons (all interior angles <180°) connecting the furthest-most receivers reporting detections for each fish (Heupel et al. 2004). While having a tendency to over-estimate home range size (Burgman & Fox

2003), this approach also allowed for direct comparisons to be drawn with previous studies that also applied this technique. In contrast, Brownian bridge movement models were used to define the home range of tagged fishes on a finer scale through consideration of the rate of movement and previous detection locations of each fish (Horne et al. 2007; see Heupel et al. 2018 for further discussion on these techniques).

All home range analyses were conducted using the function 'HRSummary' in the package 'VTrack' and accounted for the mean detection radius recorded for the receiver array employed in this study (approximately 165 m, Lea et al. 2016). No home range metrics were calculated for fish that were at liberty for fewer than 25 d. Individual home range plots were then compiled for each individual and presented in a composite figure plot for each size class (juvenile, small adult and large adult) (see Fig. 7). A *t*-test was employed to test for significant differences between all home range results from small and large adults. The rate at which individuals utilized their home range was also investigated. For each individual, the maximum occupancy area (represented here by 100% MCP) was calculated on a monthly basis; the time to maximum occupancy was only calculated for fish at liberty for over 100 d. The time taken for each individual to occupy 100% of its home range was then calculated and compared among size classes.

2.8. Home range size and fish length

A 2-step process was followed to investigate the relationship between home range size and fish length. Firstly, a linear model was used to examine how the maximum occupancy area for the first year of monitoring for each fish varied relative to initial fish length. The significance of fish length in this relationship was assessed using an *F*-test at an alpha level of 0.05. Secondly, the maximum area of occupancy, calculated annually for each fish for each year of the study, was compared with both initial (Year 1) and predicted (Years 2 and 3) fish length as calculated using the growth curve described above (Section 2.3).

A general linear mixed model (GLMM) with a Gaussian error structure and including fish ID as a random effect to account for repeated measures was used to assess the significance of this latter relationship. The significance of fish size was examined with a chi-squared test through the 'anova' function. Marginal and conditional R^2 values were subsequently calculated for the GLMM using the function 'r.squaredGLMM' in the package 'MuMIn' (Barton 2016) to quantify the proportion of variance explained by fish length alone, and by fish length and fish ID collectively, respectively. These analyses were conducted using the 'lme4' package in R (Bates et al. 2015, Wood 2017), and, for both models, values of maximum occupancy area were logged prior to analysis to ensure that the underlying assumptions of normality were met.

3. RESULTS

3.1. Tagging

The 17 tagged giant trevally (4 juveniles, 8 small adults, 5 large adults) ranged in size from 40.5 to 120.0 cm (mean ± SD = 82.32 ± 24.59 cm) and were monitored for between 2 and 1259 d (mean = 759.82 ± 491.58 d; Table 1). During this period, individual fish were recorded between 115 and 100 430 times (mean = 12 536.82 ± 23279.10) on 1 to 36 (mean = 23 ± 11) of the 89 acoustic receivers used for the study (Table 1). The residency indices for tagged fish ranged between 46.50 and 93.75% (mean = 67.82 ± 13.96%) (Table 1). Seven of the 17 tagged fish were detected for more than 3 yr over the study period

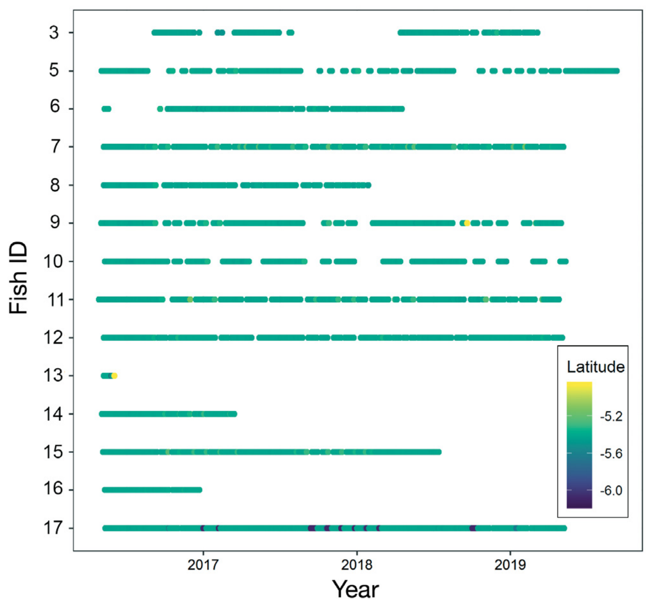

Fig. 2. Summary of 14 tagged giant trevally detections across the Amirante Bank, Seychelles, acoustic receiver array between 2016 and 2019. Colour bar indicates the latitude (° S) of receivers that recorded the detection of tagged fish

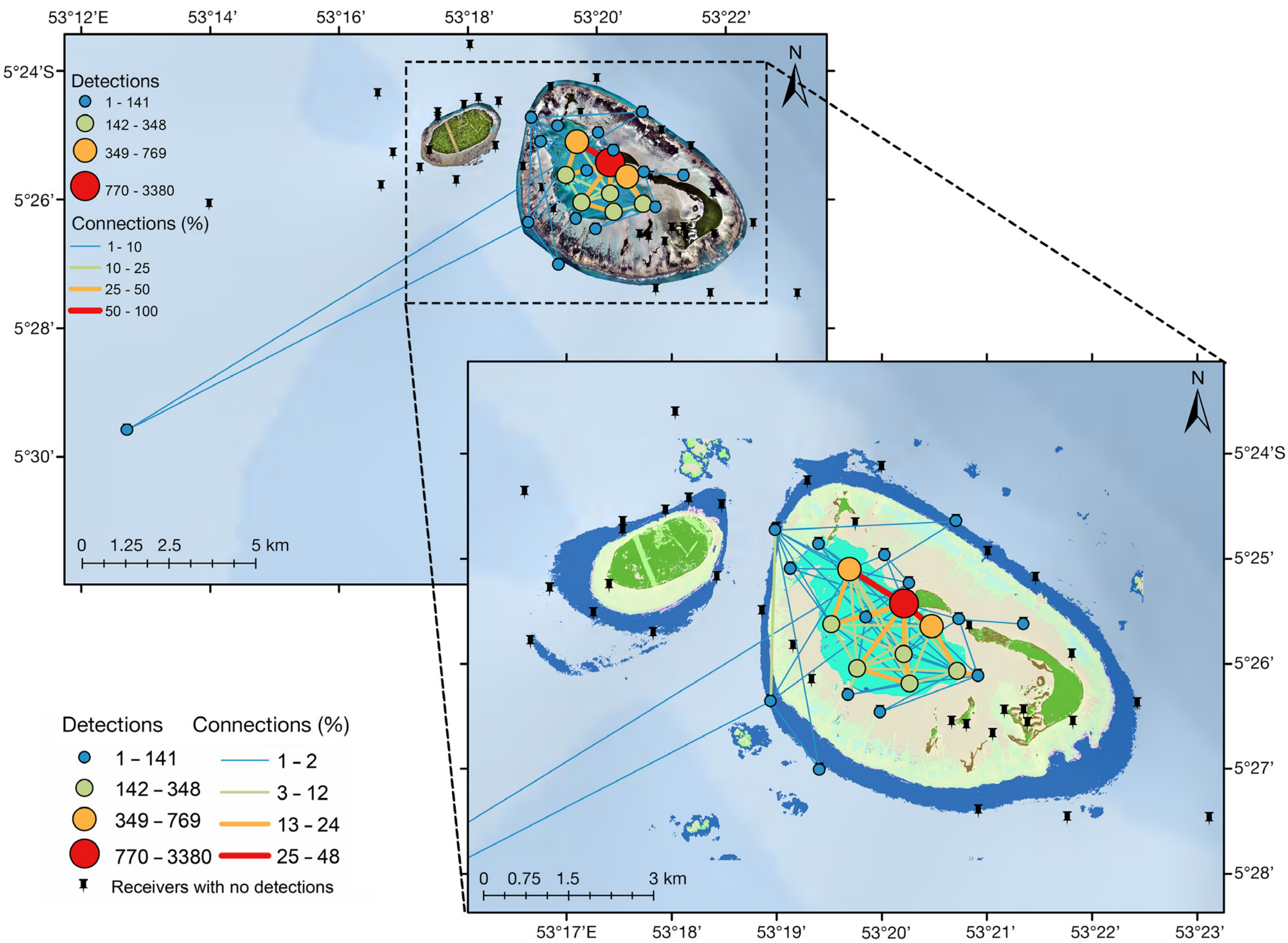

Fig. 3. Network plot of juvenile giant trevally (<60 cm fork length) showing the number of recorded detections and the connectivity (as a proportion of connections) between receivers associated with various habitat types at the study site. See Fig. 1 for habitat types

between 2016 and 2019, whilst 5 fish were recorded for between 1 and 2 yr and 4 fish (3 juveniles and 1 adult) were recorded for <1 yr (Fig. 2).

3.2. Habitat connectivity

Juvenile giant trevally (<60 cm FL) tagged at St. Joseph Atoll (n = 4) exhibited restricted movements away from tagging sites, with the majority of their detections occurring within, and on the margins of, the atoll lagoon environment (Fig. 3). However, considering the short detection period for 2 of these fish (IDs 2 and 4) and the suspected mortality of a third individual (ID 1), movements of this size class are largely representative of a single fish (ID 3). Nevertheless, substantial data (9979 detections over 425 d) were recorded for this individual, which showed limited movements within the atoll lagoon during the first year of monitoring. When detected within the bounds of St. Joseph Atoll, this fish made extensive use of the atoll lagoon and, to a lesser extent, the sand flats and sea grass habitats. This individual was recorded 150 d after tagging, on a receiver approximately 13 km to the southwest on the shallow Amirante Bank (Fig. 3), where it was detected on 17 occasions over a period of 12 d. Following this excursion from the lagoon, the fish returned to the confines of the atoll.

Small adult fish (60–100 cm FL) were detected around D'Arros Island and the northwestern boundary of St. Joseph Atoll. The highest occurrence was recorded on the eastern side of D'Arros Island in the channel opposite St. Joseph Atoll, as well as along the northern edge of the atoll (Fig. 4). These fish primarily used the shallow coral reef crest and reef drop off habitats of the island and atoll margins. They occasionally used the atoll sand flats but were never

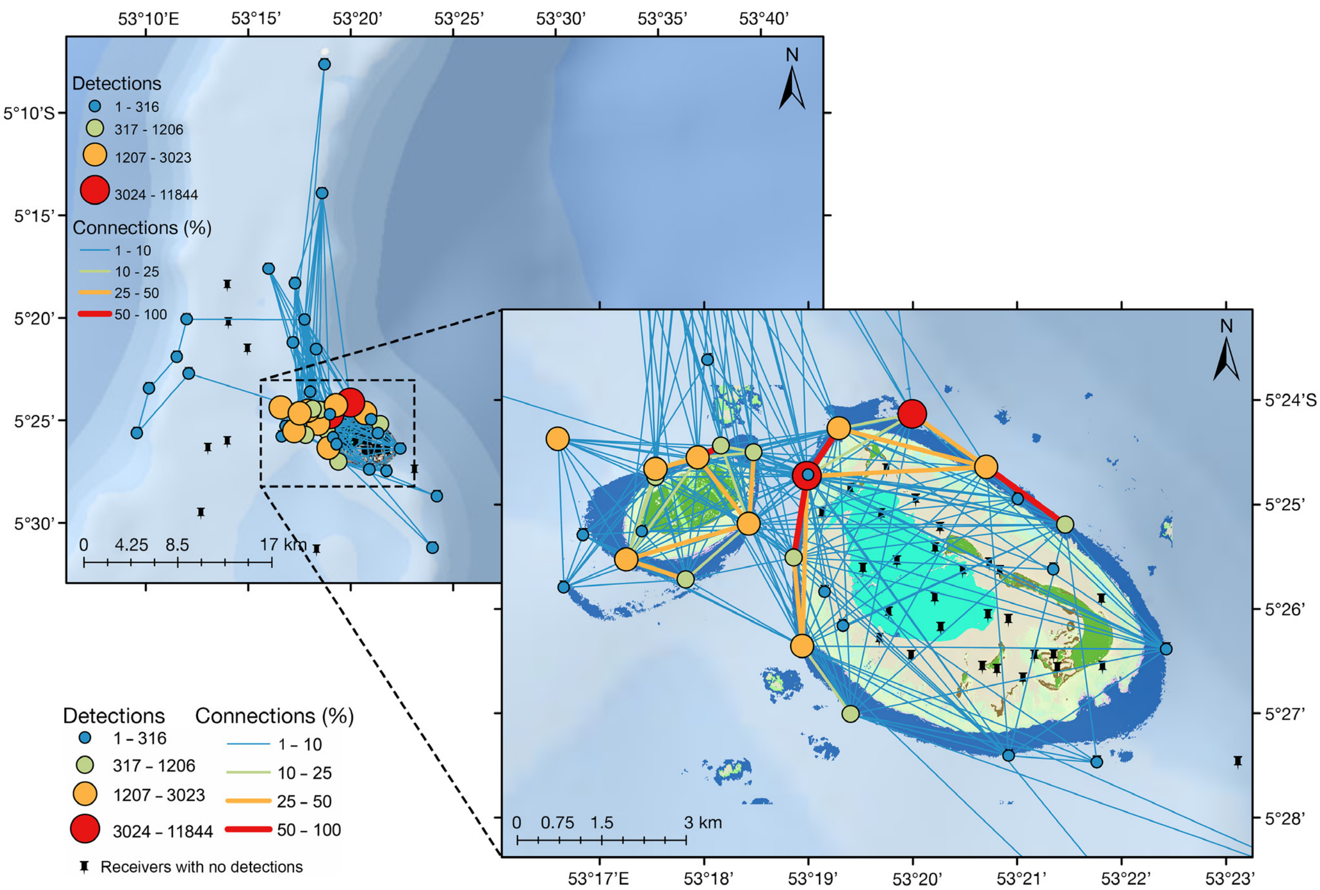

Fig. 4. Network plot of small adult giant trevally (60–100 cm fork length) showing the number of recorded detections and the connectivity (as a proportion of connections) between receivers associated with various habitat types at the study site. See Fig. 1 for habitat types

detected within the atoll lagoon (Fig. 4). Furthermore, they appeared to undertake occasional movements across the broader Amirante Bank within 31 km of D'Arros Island and St. Joseph Atoll (Fig. 4). Fish tagged at D'Arros Island were detected at St. Joseph Atoll and vice versa, highlighting the connectivity between these islands across a deep (70 m) channel spanning the 1 km gap between D'Arros Island and St. Joseph Atoll.

Similar to the small adult fish, the large adult giant trevally (>100 cm FL) were detected in habitats associated with D'Arros Island and the northwestern boundary of St. Joseph Atoll, with the highest number of detections recorded on the eastern side of D'Arros Island in the channel opposite St. Joseph Atoll (Fig. 5). Large adults were mostly recorded at the coral reef crest and reef drop off habitats on the island and atoll margins, but also used the atoll sand flats, sea grass and lagoon habitats. Furthermore, these individuals made greater use of the broader Amirante Bank than the smaller adult fish, travelling to almost all of the outer islands on the bank and covering distances of up to 88 km from the tagging location (Fig. 5). Notably, no movements were recorded at the nearby Desroches Island, approximately 40 km away, which is separated from the Amirante Bank by a oceanic trench more than 1000 m deep (Fig. 1).

3.3. Dispersal distance

The annual dispersal step distance of each fish categorized by size class ranged between 4.78 and 91.32 km (Fig. 6, Table 2). The only juvenile fish that recorded a full year of data (ID 3) exhibited a maximum step dispersal of 17.35 km during the first year of monitoring before it transitioned into the small adult size class (60–100 cm FL) in its second year. The mean ± SD small adult step dispersal distance was 13.72 ± 5.34 km, which was significantly less ($p < 0.05$) than the mean step dispersal distance of 35.29 ±

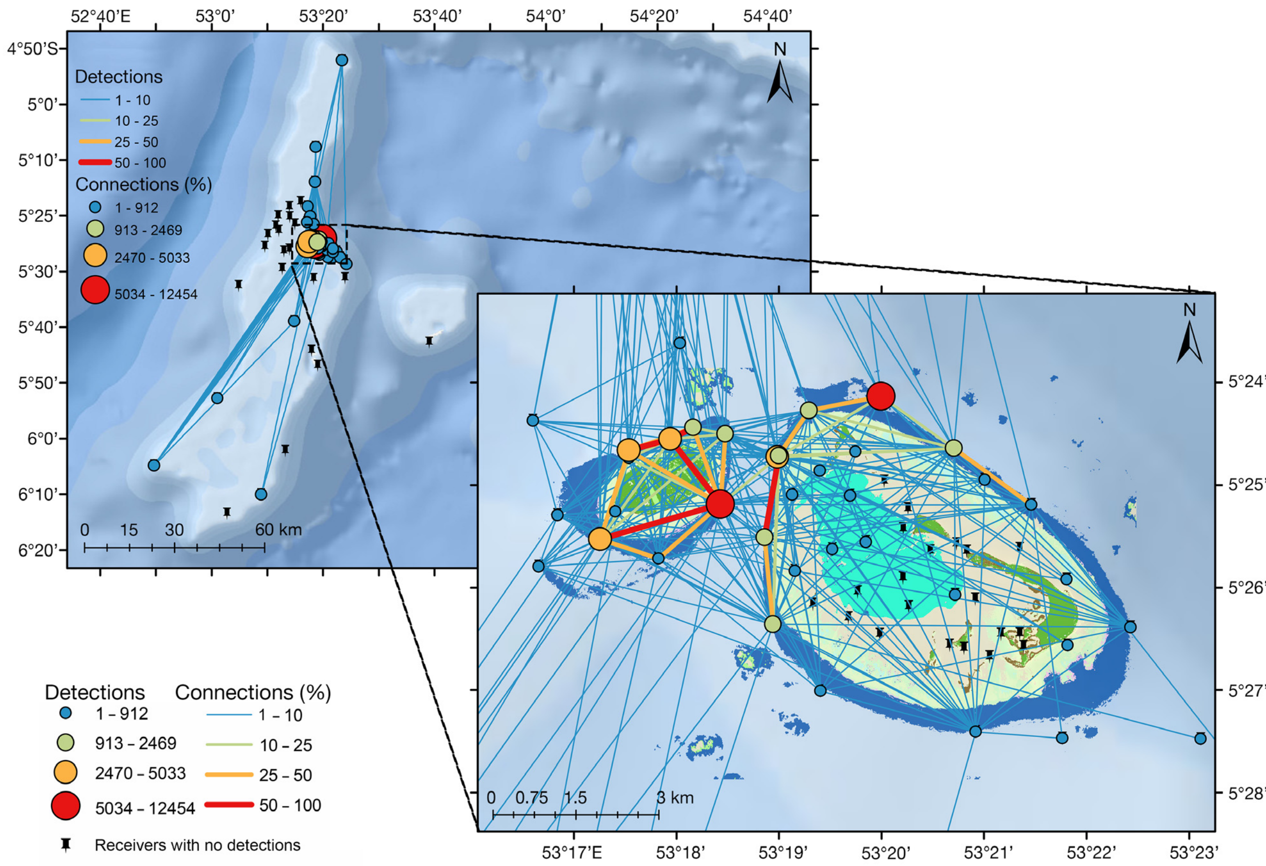

Fig. 5. Network plot of large adult giant trevally (>100 cm fork length) showing the number of recorded detections and the connectivity (as a proportion of connections) between receivers associated with various habitat types at the study site. See Fig. 1 for habitat types

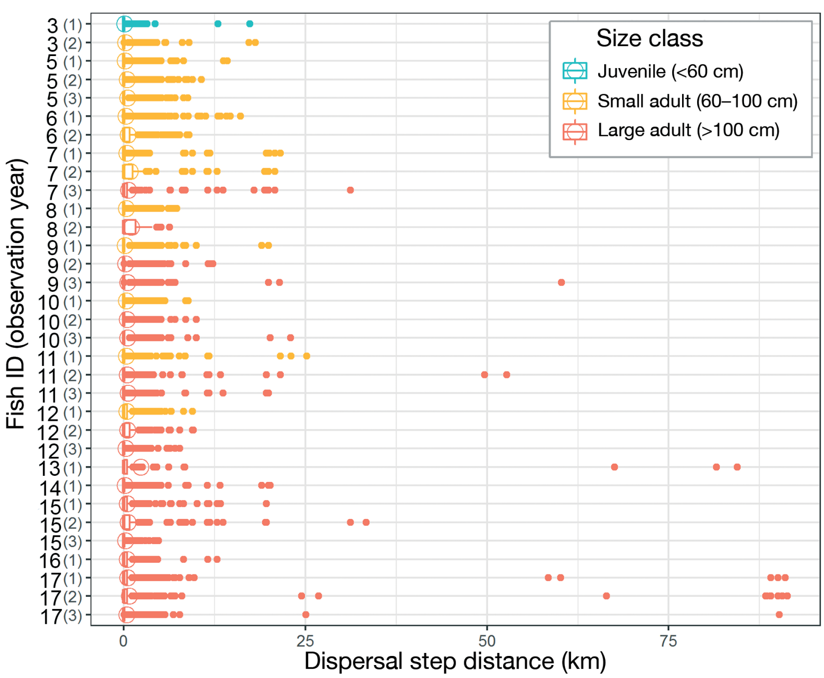

Fig. 6. Annual range, mean and maximum dispersal step distances for each acoustically tagged giant trevally within the Amirante acoustic array, Seychelles. Open circles represent mean dispersal step distance, filled dots represent outliers (>1.5× interquartile range). Colour represents initial size class for each individual at capture (ID numbers in **bold**) and the estimated size class in subsequent years after accounting for fish growth (fork length)

Table 2. Annual dispersal distance and home range metrics for tagged giant trevally. Note that a growth curve was used to assign tagged fish an annual size class (see Table A1). Core home range (50% contour) and activity spaces (95% contour) were calculated using Brownian bridge kernel utilization densities (bbKUD). Occupancy area (representative home range) was calculated using minimum convex polygons (MCPs). No home range metrics were calculated for fish that were at liberty for fewer than 25 d (see Table 1)

Fish ID	Obs. year	Fork length (cm)	Size class	Dispersal max (km)	bbKUD (km^2) core range	bbKUD (km^2) activity space	Occupancy area (MCP) (km^2)
3	1	45.00	Juvenile	17.35	2.35	49.37	38.73
3	2	61.10	Small adult	18.09	2.61	33.97	93.66
5	1	72.50	Small adult	14.22	2.37	84.74	82.61
5	2	85.71	Small adult	10.67	6.37	95.67	77.34
5	3	97.54	Small adult	8.82	3.61	73.18	70.00
6	1	77.00	Small adult	16.05	6.33	82.99	125.71
6	2	89.74	Small adult	8.95	4.61	51.41	60.78
7	1	86.00	Small adult	21.55	3.34	79.99	65.17
7	2	97.79	Small adult	20.77	5.54	138.81	55.73
7	3	108.35	Large adult	31.19	3.13	89.60	83.52
8	1	89.00	Small adult	7.30	3.80	50.32	53.69
8	2	100.48	Large adult	6.27	5.31	37.55	27.75
9	1	90.00	Small adult	19.93	3.19	74.34	106.06
9	2	101.37	Large adult	12.23	3.45	110.16	58.90
9	3	111.55	Large adult	60.24	9.00	255.89	327.08
10	1	92.00	Small adult	8.84	4.42	80.02	63.82
10	2	103.16	Large adult	10.00	8.63	171.67	53.48
10	3	113.16	Large adult	22.94	8.32	229.03	101.56
11	1	930	Large adult	25.15	1.92	71.92	162.58
11	2	1040.6	Large adult	52.71	3.77	114.36	224.70
11	3	1139.57	Large adult	19.90	6.13	94.36	112.14
12	1	93.00	Small adult	9.47	2.53	26.33	73.27
12	2	104.06	Large adult	9.55	3.01	36.40	69.78
12	3	113.96	Large adult	7.70	2.17	25.72	48.52
13	1	101.00	Large adult	84.47	2.89	210.02	654.13
14	1	103.00	Large adult	20.14	1.26	55.57	114.66
15	1	103.00	Large adult	19.64	2.76	38.86	114.16
15	2	113.09	Large adult	33.35	2.89	78.53	77.69
15	3	121.97	Large adult	4.78	0.44	3.97	26.18
16	1	105.00	Large adult	12.85	2.08	16.16	88.02
17	1	120.00	Large adult	91.08	1.13	41.25	520.53
17	2	128.22	Large adult	91.32	2.25	217.23	678.71
17	3	135.58	Large adult	90.24	1.13	26.56	650.68
			Juvenile mean	17.35	2.35	49.37	38.73
			Small adult mean (SD)	13.72 (5.34)	4.06 (1.41)	72.65 (29.94)	77.32 (21.65)
			Large adult Mean (SD)	35.29 (31.18)	3.58 (2.57)	96.24 (78.68)	209.74 (226.16)
			Minimum	4.78	0.44	1.36	26.18
			Maximum	91.32	9.00	255.89	678.71

31.18 km of the large adult size class (Table 2). Some small adult fish that transitioned into large adults during the study period exhibited an increase in the step dispersal distance with length (n = 4), although this was not always the case (n = 2, Table 2).

3.4. Home range size

The annual core home range size of tagged fish, calculated using the 50% Brownian bridge kernel utilization density, ranged between 0.44 and 9 km^2, with mean annual core home range size of 2.35 km^2 for the juvenile fish (n = 1), 4.06 km^2 for small adults and 3.58 km^2 for large adults (Fig. 7, Table 2). The annual activity space of tagged fish, calculated using the 95% Brownian bridge kernel utilization density, ranged between 1.36 and 255.89 km^2. The mean annual activity space calculated for each size class was 41.37, 72.65 and 92.24 km^2 for juvenile, small adult and large adult fish, respectively (Fig. 7, Table 2). The annual home range of tagged fish rep-

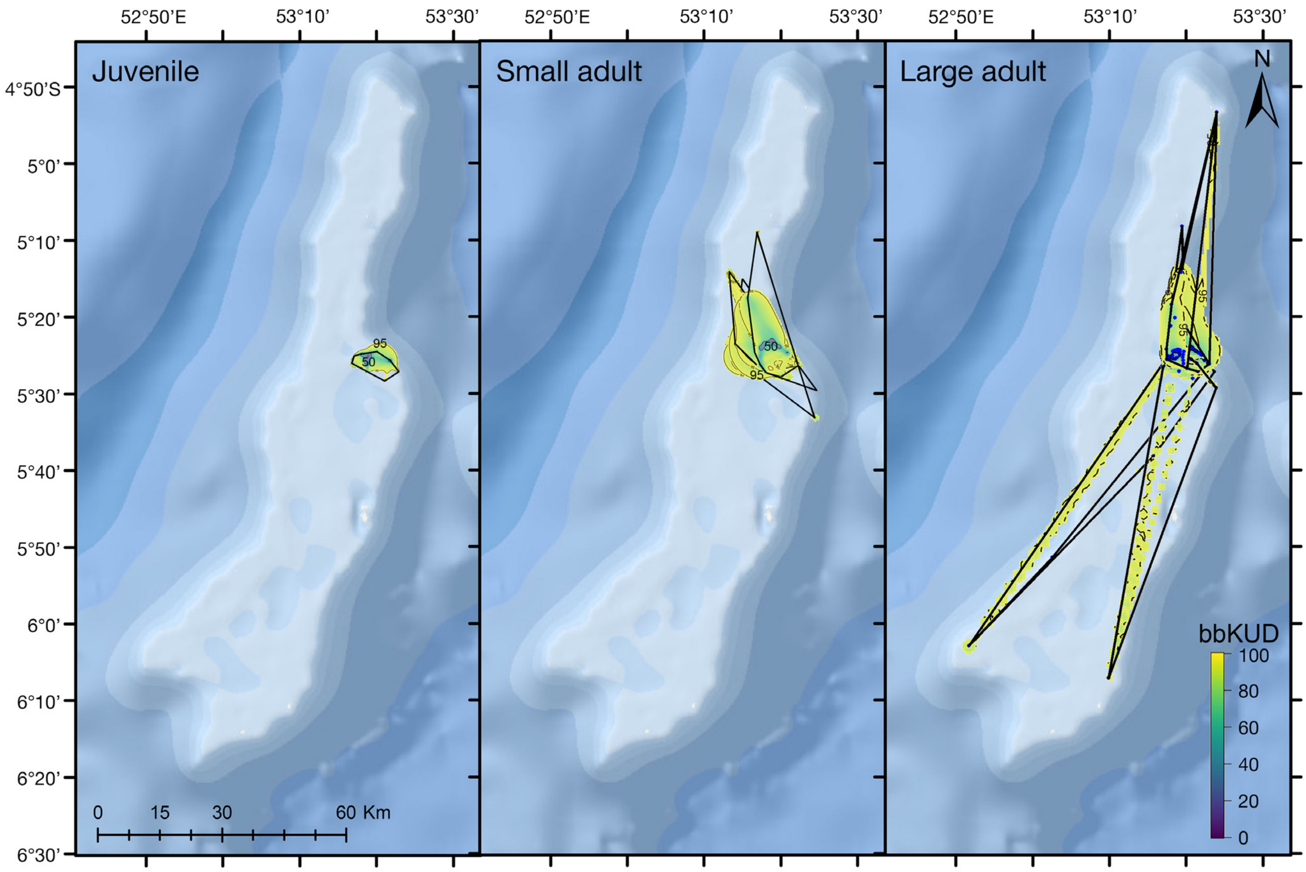

Fig. 7. Individual layered home range plots for juvenile (1 fish <60 cm fork length, FL), small adult (12 fish 60–100 cm FL) and large adult (20 fish >100 cm FL) giant trevally acoustically tagged in the Amirante Islands, Seychelles. Home ranges are represented by minimum convex polygons (solid black lines). Brownian bridge kernel utilization density (bbKUD; see legend) contours are used to define the core home range (50% contour) and activity space (95% contour) of each size class

resented by their occupancy area (MCP) ranged between 26.18 and 678.71 km^2, with a mean occupancy area of 38.73 km^2 for the juvenile fish (n = 1), 77.32 ± 21.66 km^2 for small adults and 209.74 ± 226.16 km^2 for large adults. There was no significant difference in the annual core home range or activity space between small and large adult fish ($p > 0.05$), but large adults had a significantly ($p < 0.05$) larger annual occupancy area.

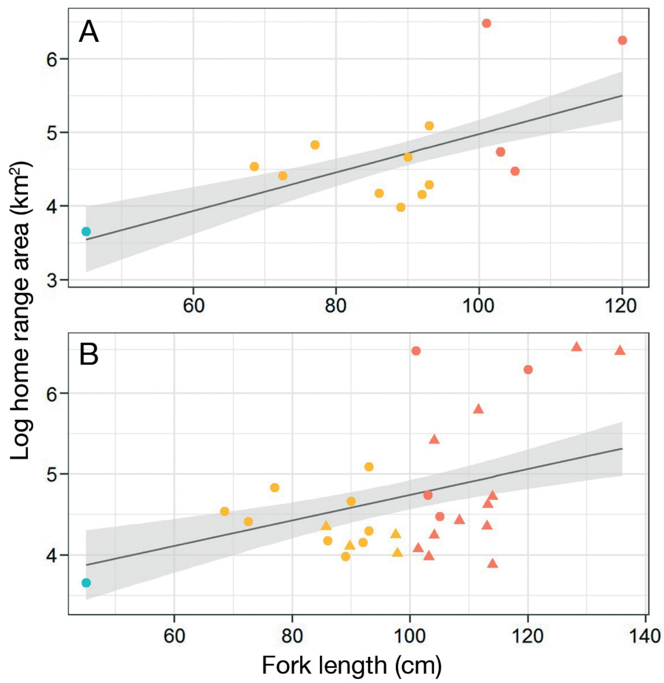

Fig. 8. Results of (A) a linear model and (B) a linear mixed model showing a significant (p = 0.02 and p = 0.04, respectively) relationship between fish length and log home range area (as represented by minimum convex polygon area) during the first year of monitoring (A) and when fish length was estimated over time (B). Circles represent initial fork length (FL) measurements of tagged fishes and triangles represent length measurements derived from a growth curve. Blue represents juveniles (<60 cm FL); yellow represents small adults (60–100 cm FL); red represents large adults (>100 cm FL)

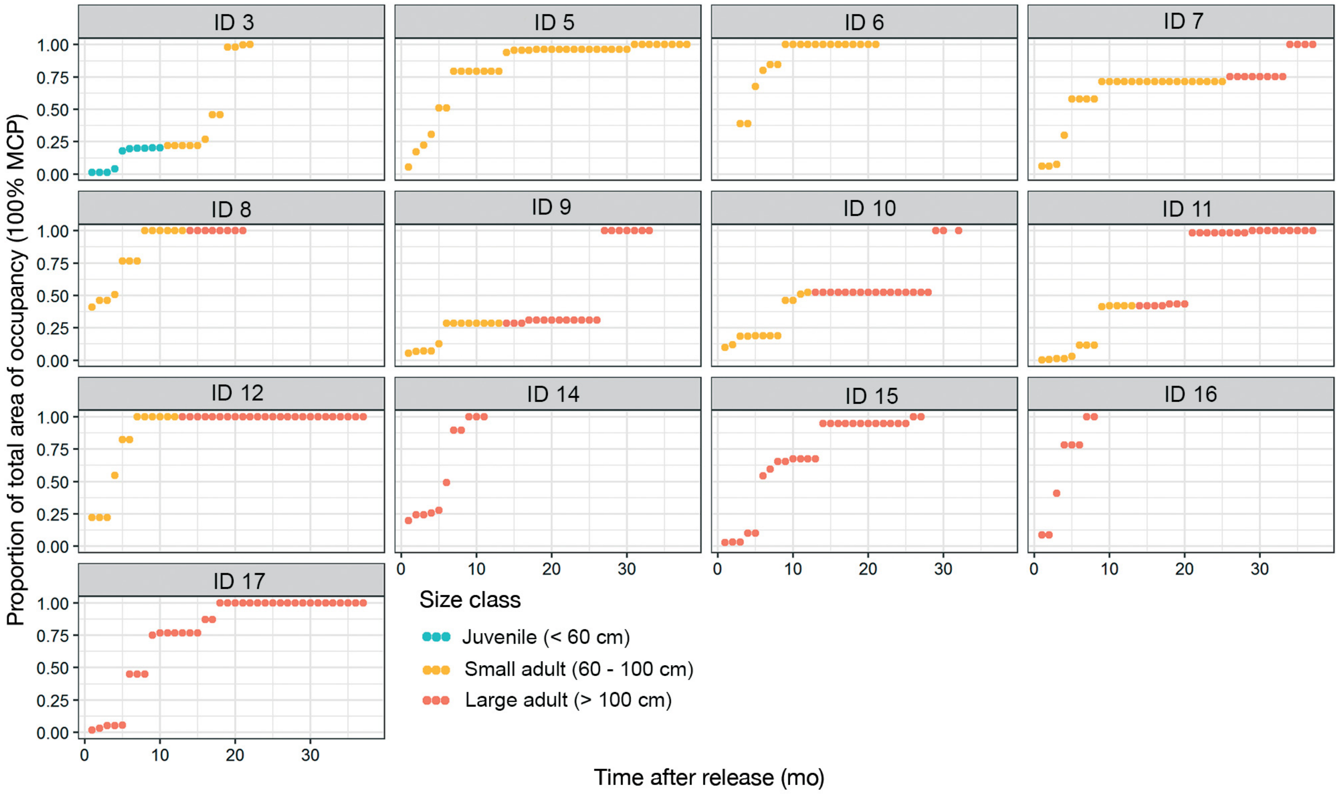

Fig. 9. Plots showing the time (post tagging) that it took for each tagged giant trevally to reach 100% of its calculated home range (represented by minimum convex polygon [MCP] plots)

3.5. Home range size and fish length

The results of the linear model indicated a significant positive relationship ($F_{1,13}$ = 7.84, p = 0.02) between the log-transformed maximum occupancy area (represented by the 100% MCP area) and fish length during the first year of monitoring (Fig. 8A), with fish length explaining 32.8% of the variation in the data. The linear mixed model revealed a similar significant relationship between fish length and logged maximum occupancy area (χ^2 = 4.25, df = 1, p = 0.04; Fig. 8B) when compared to the null model. Fish length explained 13.04% of the variation in the data (marginal R^2 = 0.13), whereas the combination of fish length and fish ID (n = 14) explained 70% (conditional R^2 = 0.70).

3.6. Time to maximum occupancy

The time it took tagged fish to reach the maximum total area of occupancy, represented by the MCP area (km^2), ranged between 7 and 34 mo (mean = 18.5 mo) (Fig. 9). This suggests that area use increases gradually as tagged fish took at least 1.5 yr to use the complete extent of their home range.

4. DISCUSSION

When investigating spatial protection for fish and their associated habitats, many studies have considered home range size and egg and larval dispersal of the species concerned (e.g. Green et al. 2015, Mann et al. 2016). However, few studies have considered the implications of changes in home range size that occur with ontogeny for large and mobile marine species. In this study, we show that for giant trevally, a top reef predator and an iconic fishery species, habitat connectivity, dispersal distance and home range size may increase significantly with fish size. Additionally, the type of habitat used by adults differs fundamentally from the more sheltered nursery habitats used by juveniles. This has important implications for spatial management of the species and the habitats that it frequents.

4.1. Detection summary

Seven out of the 17 fish tagged in this study were detected throughout the full monitoring period (3.5 yr), representing some of the longest tracked and monitored giant trevally on record (Meyer et al. 2007, Papastamatiou et al. 2015, Daly et al. 2019). Additionally, tagged fish ranged in size from 45 to 135 cm (calculated size), representing the largest range in size of tracked fish as well as some of the largest giant trevally tracked on record (Meyer et al. 2007, Lédée et al. 2015). The overall detection frequency and residency index of tagged fish within the receiver array at the study site was relatively high (mean = 67.82) and similar to previous studies (Lédée et al. 2015, Papastamatiou et al. 2015), suggesting that the receiver array at the study site provided good coverage of the movements of this species (Fig. 2, Table 1).

4.2. Habitat connectivity

Although the sample size of juveniles was limited, evidence from this study appears to support previous research, highlighting the importance of sheltered habitats for juveniles before they disperse and move between habitats over broader spatial scales when reaching approximately 50–60 cm FL (Blaber & Cyrus 1983, Wetherbee et al. 2004). Sheltered bays, lagoons and estuaries often form a critical nursery environment for juvenile fishes, as these habitats provide shelter, food and relatively low predation risk (Whitfield & Pattrick 2015). Indeed, the sheltered habitat provided by the St. Joseph Atoll lagoon may play a key role for many fish species that exhibit ontogenetic migrations between sheltered nursery habitats and more exposed coral reef-dominated ecosystems (Mumby 2006). Such nursery habitats can play a critical role in the structure, diversity and biomass of associated fish communities, and it appears that St. Joseph Atoll may be particularly important for giant trevally recruitment on the Amirante Bank, as it is one of only a few sheltered habitats within the broader region (Nagelkerken et al. 2012, Sundblad et al. 2014).

The transition from juvenile to adult habitat use in giant trevally appeared to be characterized by a substantial shift in habitat type from an atoll lagoon to a coral reef environment. Many species undertake ontogenetic migrations and transition out of one habitat to another as their requirements for shelter, food and reproduction change (Cocheret de la Morinière et al. 2003, Jetz et al. 2004, Börger et al. 2008, Kimirei et al. 2013). Indeed, the distinct change in habitat use recorded between juvenile and adult phases in this study suggests the occurrence of a shift in the functional phase of the fish. This is supported by the fact that there was a 4- to 5-fold increase in home range size (as measured by the core range, activity space and occupancy area) from the juvenile to small adult phase, which coincided with the use of new habitat types (Table 2, Fig. 4). Such a rapid increase in the area occupied by fish and associated habitat shift may be linked to attaining a size threshold where predation risk decreases substantially (Booth & Beretta 2004, Welsh et al. 2013). As giant trevally grow into adults, they would have less risk of predation from the many top predatory sharks present at the study site known to prey on small reef fish including juvenile giant trevally (Filmalter et al. 2013, Lea et al. 2016, 2020). Such a release of predation risk is probably an important factor determining the timing of the transition between juvenile and adult habitat for this species (Laegdsgaard & Johnson 2001, Booth & Beretta 2004). Additionally, the transition from juvenile habitat to adult habitat occurs close to the size at sexual maturity (60 cm), and it is likely that reproduction is also a key driver of this shift. Such an ontogenetic step change in area use and habitat type, as observed in this study, is indicative of a shift into maturity driven by reproductive demands (Welsh et al. 2013).

Large adults appeared to connect a wider diversity of habitat types from shallow reefs, atoll sand flats and lagoons to broad-ranging excursions throughout the Amirante Bank (Fig. 5). Both small and large adults appeared to share a common central area of use with similar core habitat types with a diverse and productive marginal coral reef around D'Arros and St. Joseph as well as the deep channel between these islands which has been observed to be an especially productive feature utilized by other large reef fish at the study site (Stoddart et al. 1979, Daly et al. 2018, 2020). Thus, it appears that this core area meets the trophic demands of all small adult fish, but potentially not the large adult fish that range throughout the Amirante Bank (Glass et al. 2020). However, the increased use of St. Joseph Atoll lagoon by large adults, compared to small adults, is interesting and potentially a factor of increased mobility but further investigation is needed to understand this. By the end of the monitoring period, the largest adult fish would have weighed in excess of 40 kg (maximum size fish ID 17 was calculated to measure 135.5 cm or 48 kg in Year 3) and as such, represented a large-bodied top predator with substantial dietary demands. To meet their energetic requirements, these large adult fish likely need to range further than smaller adults to locate sufficient feeding opportunities. Similar wide-ranging movements driven by foraging are observed in many other species and often occur as these animals need to increase their prey encounter rates (Börger et al. 2008, Imansyah et al. 2008).

4.3. Dispersal distance

The maximum annual step dispersal distance recorded by a juvenile giant trevally (ID 3) appeared to be representative of the single foray out of St. Joseph Atoll (Fig. 3). This excursion was likely the start of its transition to an adult environment, as the fish attained a size >60 cm FL within the first year of monitoring. Unfortunately, due to post-release mortality, the annual maximum dispersal distances of the other juvenile fish tagged in this study could not be determined, but observations confirmed that juveniles are likely confined to the atoll lagoon habitat. The observed and significantly ($p < 0.05$) greater annual mean step dispersal distances exhibited by large adults was most likely driven by foraging demands as discussed previously. Interestingly, for those small adult fish that were tracked over multiple years, some fish increased their maximum dispersal substantially as they grew (fish ID 9 and 10) while some others appeared to maintain relatively similar maximum dispersal distances over the monitoring period (fish ID 12). This may reflect some individual differences in habitat use. For fish ID 17, the recorded annual maximum step dispersal distance remained constant (Year 1 = 91.08 km, Year 2 = 91.32 km, Year 3 = 90.24 km). This highlights the mobility of this large adult, and it suggests that the extent of the receiver array may not have been large enough to capture its true maximum dispersal distances. Indeed, giant trevally have been tracked undertaking coastal return migrations to and from spawning aggregations of over 1200 km, emphasizing the remarkable dispersal capabilities of this species (Daly et al. 2019). In contrast, tagged fish in this study remained on the Amirante Bank and did not cross the deep channel (oceanic trench) separating the bank from Desroches Island, approximately 40 km away. Hence, it is possible that the maximum dispersal distance of giant trevally is restricted to the shallow waters (<70 m) of the Amirante Bank and that their dispersal is limited by deep waters (>1000 m) in the Seychelles. While future research will be required to confirm the restricted movements of large individuals in the region, it is important to acknowledge the possible connectivity between the Amirante Bank and other outer islands generated through the early life history stages (eggs and larvae) of the species. Evidence from genomic work indicates a panmictic population of giant trevally throughout the southwest Indian Ocean (J. R. Glass pers. comm.), suggesting that population connectivity in the Seychelles may be driven at the larval phase.

4.4. Home range

The overall annual core home range (0.44–9.31 km^2) and activity space (1.36–255.89 km^2) calculated in this study was orders of magnitude greater than the monthly core range (0.0001–0.016 km^2) and activity space (0.004–0.062 km^2) of giant trevally monitored at a coral reef in Australia (Lédée et al. 2015). This difference, however, may simply reflect the different time scales (annual vs. monthly) and the different spatial extent of the respective receiver arrays, given that the core home ranges (0.1–2.6 km) of actively tracked fish at an atoll in the South Pacific were more similar to this study (Filous et al. 2019). While the overall core home range size appears to exhibit variability amongst sites, giant trevally in various studies did appear to exhibit a persistent core area of habitat use representing a key habitat and a degree of site attachment. The size of the core range and activity space between small adults and large adults was not significantly different in this study ($p > 0.05$), although there was a significant ($p < 0.05$) increase in the maximum occupancy areas between small (92.74 km^2) and large (207.57 km^2) adult fish. The similar core ranges of small and large adults most likely represent an overlapping key habitat, while the increase in maximum occupancy areas between small and large adults appears to be driven by the increased dispersal distance undertaken by large adults.

In comparison to many other coral reef-associated teleosts, the home range size calculated for giant trevally in this study (represented by the total occupancy area, Table 2) was substantially larger (Weng et al. 2015; see their supplementary Table S1). In fact, the total occupancy area of large adult giant trevally was more similar to and or greater than several large-bodied shark species (*Negaprion acutidens*, *Carcharhinus melanopterus* and *C. amblyrhyncos*) monitored at the same study site (Lea et al. 2016). This highlights the ecological role played by adult giant trevally as a top predator linking ecological processes over large spatial scales. Indeed, the trophic position of giant trevally was recently found to be equivalent to many top predatory shark species, confirming its role as an apex predator within its respective marine communities (Glass et al. 2020).

4.5. Home-range scaling

As the requirements for resources increase with body size, an increase in home range size typically occurs (Börger et al. 2008). However, this relationship is complicated by predation risks and reproductive demands. For some reef fish, the social status linked to reproduction limits the home range of mature adults and breaks down the relationship between fish size and home range area (Welsh et al. 2013, Daly et al. 2020). However, giant trevally do not have such reproductively driven social and territorial constraints, other than the need to aggregate annually to spawn. Giant trevally have been recorded travelling over 1200 km between annual spawning aggregation events (Daly et al. 2019). Therefore, the observed relationship between fish length and home range area (Fig. 8) is likely driven by foraging events as the metabolic demands of larger fish increase with size and they range further in search of prey (Glass et al. 2020). However, fish size only explained 33% of the home range size variance in the linear model used here, suggesting that other factors are also important determinants of home range size for this species.

Besides the step change in home range location and size from juveniles to adults, likely driven by reduced predation risk and maturation, individual foraging strategies and learned behaviour may also play an important role determining the home range of these fish. Results from the linear mixed model also revealed a strong influence of individual ID (57% deviance explained) on reported maximum occupancy area in comparison to the effect of fish size (13% deviance explained). This is likely due to the relatively small cohort of tagged fishes available in this study, the tagging bias towards small and large adults (due largely to post-release mortality occurring in juveniles) and a reliance on original length measurements to estimate future fish growth and sizes throughout the monitoring period. In order to further refine the current understanding of spatio-temporal home range scaling in giant trevally relative to size, future studies should aim to increase the number of tagged individuals and ensure an even distribution of tags across ontogenetic stages throughout the entire monitoring period.

4.6. Time to maximum occupancy

The time it took individual fish to reach their total area of occupancy varied between 7 and 34 mo, suggesting that individual fish may expand their home range size over variable and long periods of time (Fig. 9). For example, large adult fish ID 12 rapidly (6 mo) utilized its total area of occupancy, whilst large adult fish ID 10 took 28 mo to utilize its total area of occupancy. Although both of these fish were large adults, presumably with similar metabolic requirements, it suggests that individuals may adopt new foraging strategies based on learned behaviour or changing prey availability over time (Hughes et al. 1992). Further research is required to better understand how important learned behavior and individual foraging strategies are in determining fish habitat use and home range size. Nevertheless, this study confirmed that the maximum extent of a fish's home range size may only be recorded after long periods (at least 18 to 34 mo). This highlights the need to carefully consider the duration of the monitoring period and the spatial extent of receiver arrays for acoustic telemetry studies that aim to define the full extent of space use and home ranges of mobile aquatic species.

4.7. Implications for conservation

This study highlighted the importance of sheltered habitat within the St. Joseph Atoll as a nursery area for giant trevally in the region and confirmed that the core areas of habitat of juveniles and small adults were spatially distinct. The sheltered habitat of St. Joseph Atoll likely plays a critical role in recruitment success of giant trevally, as well as many other nursery-dependent reef fish species, and should thus be prioritised for conservation (Nagelkerken et al. 2012, Sundblad et al. 2014). For example, the protection of St. Joseph Atoll lagoon, reef flats and associated coral reef crests and drop offs will also protect critical habitat for Endangered humphead wrasse *Cheilinus undulatus* and other vulnerable species that frequent this unique habitat (Filmalter et al. 2013, Lea et al. 2016, Daly et al. 2020). However, as highlighted in this study, prioritising the protection of St. Joseph Atoll should be done together with the surrounding marine environment to promote ecological processes and facilitate demographic and geographic linkages (Gaines et al. 2007, Green et al. 2015).

This study has shown that giant trevally are capable of wider-ranging movements than previously reported (Meyer et al. 2007, Lédée et al. 2015, Friedlander et al. 2016, Filous et al. 2017), and to effectively protect the core range and activity space of adults at this study site, we estimate that a protected area of at least 72.65 km^2 of suitable habitat would be required.

Additionally, to account for the dispersal distances and total area of occupancy of large adults, such a protected area would need to encompass at least 168.36 km^2, but up to 678.71 km^2, representing the maximum recorded occupancy area of a tagged large adult giant trevally. Protecting such vast areas represents significant challenges for management and enforcement; however, the information garnered in this study can be used to help prioritise effective conservation measures (Wilhelm et al. 2014). The newly proclaimed marine national parks in the Seychelles are a positive step towards large protected areas which may incorporate large portions of habitat of wide-ranging species (Fig. 1, Seychelles Official Gazette No. 5). Additionally, we recommend that St. Joseph be prioritised for conservation with a ban on consumptive fishing and that further research be conducted into identifying the potential spawning aggregation sites within the recorded activity space of tagged adult fish. In order to maximise the effectiveness of such a protected area, we suggest expanding it from St. Joseph Atoll to include the associated habitat of co-occurring endangered and vulnerable species to encompass an area of at least 72.65 km^2 around St. Joseph Atoll.

4.8. Summary

This study has confirmed that giant trevally exhibit an increase in space use area with increasing body size, supporting our primary hypothesis. An important driver of a shift in home range location, area and habitat type from the juvenile to adult phase appeared to be a release in predation risk and a shift to sexual maturity. The core activity space of small and large adult fish was largely similar, but the maximum dispersal distance and occupancy area of large adult fish was substantially greater than that of small adult fish, most likely driven by foraging excursions as the metabolic needs of such large fish increase. We also found that the home range of giant trevally at a tropical island and atoll marine ecosystem was larger than previously reported (Meyer et al. 2007) and that individually tracked fish took long periods of time (mean = 18.54 mo) to use the full extent of their activity space. These findings indicate that in order to effectively conserve this iconic and ecologically important top predatory fish, the conservation of sheltered nursery areas should be prioritised and that the extent of home ranges and dispersal distances of small and large adults need to be taken into consideration.

Acknowledgements. We acknowledge the logistical support provided by staff of the Save Our Seas Foundation - D'Arros Research Centre. This study was funded by a Save Our Seas Foundation Keystone Grant (no. 312). Additional support was provided by the National Research Foundation and the South African Institute for Aquatic Biodiversity through a grant administered by P.D.C. This study was conducted with permission from the NRF SAIAB Animal Ethics Committee.

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Appendix.

Table A1. Annual giant trevally size class (mm FL) calculated from the von Bertalanffy growth equation after Sudekum et al. (1991) ($L_t = L_\infty (1 - e^{-K(t-t0)})$: t = time, L_∞ = asymptotic length, K = growth coefficient. More details are provided in Sudekum et al. (1991)

ID	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7
1	405	490.18	570.75	646.98	719.09	787.31	851.85
2	425	509.10	588.65	663.91	735.11	802.46	866.18
3	450	532.75	611.03	685.08	755.13	821.41	884.10
4	470	551.67	628.92	702.01	771.15	836.56	898.44
5	725	792.90	857.13	917.90	975.39	1029.77	1081.21
6	770	835.47	897.41	956.00	1011.43	1063.86	1113.47
7	860	920.61	977.95	1032.19	1083.51	1132.05	1177.98
8	890	948.99	1004.80	1057.59	1107.54	1154.78	1199.48
9	900	958.45	1013.75	1066.06	1115.55	1162.36	1206.65
10	920	977.37	1031.65	1082.99	1131.56	1177.51	1220.98
11	930	986.83	1040.60	1091.46	1139.57	1185.09	1228.15
12	930	986.83	1040.60	1091.46	1139.57	1185.09	1228.15
13	1010	1062.51	1112.19	1159.19	1203.65	1245.71	1285.49
14	1030	1081.43	1130.09	1176.12	1219.66	1260.86	1299.83
15	1030	1081.43	1130.09	1176.12	1219.66	1260.86	1299.83
16	1050	1100.35	1147.99	1193.05	1235.68	1276.01	1314.16
17	1200	1242.26	1282.23	1320.05	1355.82	1389.66	1421.68

Editorial responsibility: Simon Pittman, Plymouth, Devon, UK
Reviewed by: 3 anonymous referees

Submitted: November 18, 2020
Accepted: January 28, 2021
Proofs received from author(s): March 25, 2021