Movement behaviour of the Green Jobfish (*Aprion virescens*), the Potato Bass (*Epinephelus tukula*) and the Giant Trevally (*Caranx ignobilis*), on South Africa’s coral reefs

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Plagiarism declaration

I know the meaning of plagiarism and declare that all of the work in this thesis, save for that which is properly acknowledged, is mine.

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Abstract

The movement behaviour of three important reef fish predators, namely potato bass (*Epinephelus tukula*), green jobfish (*Aprion virescens*) and giant trevally (*Caranx ignobilis*), were studied to provide information for marine spatial planning and to understand their ecological roles on South Africa's coral reefs. The three species were expected to display contrasting movement behaviour and to place different demands on spatial management strategies. The three species of coral reef meso-predators, potato bass (n=35), green jobfish (n=38) and giant trevally (n=9) were tagged with acoustic transmitters and released within a widespread receiver array (n=46) spanning approximately 306 km of coastline, which included the iSimangaliso Wetland Park (IWP), South Africa, and Ponta do Ouro Partial Marine Reserve (PPMR), Mozambique. The resulting telemetry data were used to investigate (1) the extent of their movements, (2) temporal patterns of movement, and (3) movements and connectivity between different management zones within the IWP, South Africa’s largest coastal marine protected area. An analysis of 892 552 detections over a period of six and a half years, using a novel residency index, showed that green jobfish and potato bass exhibit high site fidelity with residency index values ranging from 61.6 to 100 % (mean = 85.2 %) for green jobfish and from 87.3 to 99.9 % (mean = 95.0 %) for potato bass. Individual green jobfish and potato bass were detected at a similar number of receivers (mean 3 [± 0.4] and 3.3 [± 0.8]), respectively. In contrast, giant trevally had lower site fidelity with residency index values ranging from 49.4 to 92.3 % (mean = 66.9 %) and undertook frequent but temporally predictable long-distance migrations (mean maximum dispersal distance = 189.00 km [± 40.3]), often returning to their home range. On average individual giant trevally were detected on 13.8 (± 1.5) receivers. Previous literature showed variable temporal patterns of movement for green jobfish although the results of this study showed no evidence of cyclical patterns of movement, further investigation would be required to confirm this result. Potato bass exhibited both 12 hr and 24

hr temporal patterns with the 12 hr pattern appearing indicative of tidally influenced cyclic movement and 24 hr patterns appear to indicate diel patterns. Giant trevally were almost exclusively detected during the day when present on the reefs, but left their home reefs on predictable summer migrations to a known aggregation site in Mozambique as observed by Daly et al. 2019. Green jobfish and potato bass crossed an average of 0.6 (± 0.9 and 0.4) management zones (mean zone length 22.5 km [± 4.1]) per tagged fish compared to giant trevally, that crossed on average 2.4 (± 0.9) management zones per tagged fish in the IWP. Border crossings between South Africa and Mozambique were observed in all three species, two from green jobfish and three from potato bass, and all five detected giant trevally. Green jobfish and potato bass with significant detections (>100) appeared to undertake little to no movement beyond their home range, reef and zone. No migratory or aggregatory behaviour was identified, possibly indicating localised spawning aggregations on each reef complex/zone. Therefore, current MPA size (10 700 km^2) should provide complete protection of green jobfish and potato bass within sanctuary zones of the IWP. Giant trevally appeared to be adequately protected within sanctuary zones of the IWP but are vulnerable during summer spawning migrations north, to Mozambique. A closed season during this migratory period could help safeguard giant trevally and ensure the greatest chance of them reaching the aggregation site. This interzonal connectivity should be considered when updating management plans of each zone within the IWP, the PPMR, future marine protected areas and the management of the species themselves.

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Introduction

Fish movements

Fish movements and migrations are important processes in marine ecosystems (Dingle and Drake 2007, Liedvogel et al. 2013). Better feeding opportunities, reduced predation, life stage requirements, seasonal changes, or increased reproductive fitness are possible drivers that may influence movements (Able and Grothues 2007). Movement behaviour can impact population and community structure and dynamics and will influence genetic mixing (Turchin 1988, Jones 2005, Abecasis et al. 2009). The distance, frequency, and time of occurrence of these movements and migrations can also affect the threats and resilience of a species to both naturally and anthropogenic changes or impacts (Cowley et al. 2017). Reliable data on ecologically and economically important species can aid in determining the relative effectiveness of current or future conservation or management measures aimed at the protection or management of the fishery in question (Attwood et al. 2007, Pilling et al. 2009, Melnychuk et al. 2017). Therefore, a better understanding of movement behaviour and migrations, as well as reef fish connectivity between and among different habitats and zones of differing stages of protection, is invaluable information for understanding the ecology of a species in order to effectively manage and conserve it (Meyer et al. 2000). Fundamentally, it adds to the chances of successfully implementing a conservation and management plan of fish stocks of socio-economic and ecological value and those of concern to conservationists (Able and Grothues 2007, Leenhardt et al. 2015).

The spatial management of these extensive ecosystems requires in-depth knowledge of connectivity between reef units as certain reefs are zoned as no-take sanctuaries, while others are multiple-use zones, permitting activities such as SCUBA diving and fishing (Dames et al.

2020). No-take sanctuaries are important as they closely represent previously undisturbed ecosystems and have the potential to replenish fish stocks in areas open to fishing through spill-over. Recent studies have shown that no-take sanctuaries have significantly larger (size) and higher abundances of predatory and target species compared to multiple-use zones (Mann 2012, Floros et al. 2013). It is thus important to determine which of the reefs, if any, are acting as sources or sinks of adult fish so that management of the MPA zones can be aligned accordingly.

Coral reefs of South Africa

Coral reefs are one of the most impacted of all marine habitats (Halpern et al. 2008) and are constantly under threat by a number of anthropogenic disturbances (Pauly 1995, Jackson et al. 2001, Knowlton and Jackson 2008). Surveys suggest that 19% of all coral reef systems have been lost or significantly degraded, with a projection of a possible 35% disappearing in the next 20-40 years (Wilkinson 2008). Worldwide, coral reefs provide both large economic and ecosystem services with an estimated value around US$30 billion per annum (Nellemann et al. 2009) and incalculable ecosystem services.

South Africa’s coral reefs are dispersed over approximately 150 km along the north-eastern (Maputaland) coast of KwaZulu-Natal (KZN). These high latitude coral reefs are the only tropical coral reef systems of their kind in South African waters. They can be found within the iSimangaliso Wetland Park (IWP) (Schleyer et al. 2018) and are some of the most southern coral reefs in the world (Ramsay 1996). The IWP consists of submarine canyons, coral reefs and a steep and narrow continental shelf (Ramsay 1994). The coral reefs of the IWP are not true coral reefs and differ in that most morphological features in the substrata are missing and instead are comprised of underwater, fossilised dune beach rock (Riegl et al. 1995). This substrate forms gullies and associated small channels and ledges which have formed perpendicular to the prevailing swell direction over time (Riegl et al. 1995). This current controlled reef system has an extremely narrow continental shelf of only 3 km (Ramsay 1994). The major current is the Agulhas current which predominantly moves poleward (Schumann 2012). The coral reefs of the IWP exhibit similarities in coral and fish species with other coral reefs of the West Indian Ocean and Indo-Pacific coral reefs, yet differ in terms of current, sedimentation and light (Riegl et al. 1995, Floros et al. 2013). They are rich in diversity and can be found within two of South Africa's long-standing contiguous marine protected areas (MPA) which form part of the IWP. By studying fish movements within the IWP it will provide a broad understanding of the efficacy of the protected area with regards to protecting the key species which live within it. In order to study fish movement patterns within and among the coral reefs of the IWP and surrounds, passive acoustic telemetry is used.

Passive acoustic telemetry

In the terrestrial environment, the tracking of large animal movements is relatively easy through the use of GPS-linked collars, tags, trail cameras, or simply visual observations (Kays et al. 2015, Cowley et al. 2017, Udyawer et al. 2018). The tracking of aquatic-based animals such as fish provides a myriad of challenges, with the inability to physically observe the animal for an extended period of time as well as the lack of defined boundaries (Hussey et al. 2015). The lack of boundaries is particularly difficult in the study of marine species due to the sheer magnitude of many species' distribution. Significant advances and developments in tracking technology have greatly increased the efficacy and decreased the cost of aquatic animal tracking (Heupel and Webber 2012). Advances in acoustic telemetry have markedly improved a researcher's ability to monitor animal movement patterns over large spatial and temporal scales beyond what can be physically observed. Acoustic telemetry allows for the simultaneous tracking of a large number of individuals for extended periods by deploying animal-borne acoustic transmitters within a network of fixed receiver stations (Clements et al. 2005). Acoustic telemetry also allows for the tracking of both multiple individuals as well as multiple species within the same receiver array (Kessel et al. 2014). This method can be applied to a greater number of individuals for longer periods of time while at the same time being more cost-effective than satellite or GPS tracking devices (Hussey et al. 2015).

Acoustic tracking began in the 1970s with active acoustic telemetry where tagged animals were physically followed using a directional hydrophone (Kessel et al. 2014). This was highly labour intensive, dependent on weather and sea conditions and only practically and physically limited to short periods of time. The development and refinement of passive acoustic telemetry whereby multiple fixed, hydrophone receivers are positioned across the study site to form a tracking array was a much more efficient, less labour intensive and more cost-effective method. The refinement of passive acoustic telemetry combined with its autonomous nature of data collection allows for marine animals to be tracked continuously for 24 hours a day in all and any weather conditions (Kessel et al. 2014), although detection power may be reduced during rough weather. Previously, physical tracking was hindered by adverse weather and mainly restricted to daylight hours.

Once successfully implemented, passive acoustic telemetry allows for data about an individual’s natural movements to be collected without the influence of an observer (Cowley et al. 2017). The cost-effective nature, increased development, and successful usage of robust methods to analyse the data acquired from passive acoustic telemetry have led to greater use of passive acoustic tracking arrays worldwide. As a result, multiple international collaborations have been formed to share data gathered by these acoustic receiver arrays such as the Australian-based Integrated Marine Observing System (IMOS), the Canadian-based Ocean

Tracking Network (OTN) and the South African-based Acoustic Tracking Array Platform (ATAP) (Mann et al. 2015, Udyawer et al. 2018, Murray et al. 2022).

Categorizing patterns of fish movements is aided by the use of Dingle (1996)'s broad classification of animal movement. Dingle (1996) proposed three main movement types: station-keeping, ranging and migration. There are a multitude of reasons why a fish or group of fish would move, foraging and spawning are two common drivers. Dingle (1996) broadly classified movements into those that remain in an individual's home range (station-keeping) and those that go outside (ranging and migration). Station-keeping generally involves movements within a home range which can include foraging, diel movements and territoriality (Dingle 1996). Furthermore, station-keeping movements are generally repetitive, covering short spatial and temporal scales (Dingle 1996). Other forms of movement include ranging which can be larger exploratory movements outside of traditional home ranges or within large home ranges (Dingle 1996). Another movement style categorized by Dingle (1996) is migration. This is when animals exhibit more persistent, predictable, and directed large-scale movements to a predetermined area (Dingle 1996).

Periodicity

Acoustic telemetry has helped researchers to uncover where fish move, but equally as important is understanding when a fish moves. Once you understand the when and where, it brings researchers closer to understanding why a fish moves. Movement patterns can be identified temporally with many reef fish, sharks and large predatory fish displaying diel, tidal, lunar and/or seasonal periodicity (Lowe et al. 2006, Meyer et al. 2007a, Meyer et al. 2007b, Speed et al. 2011, Lédée et al. 2015, Papastamatiou et al. 2015, Filous et al. 2017, Daly et al. 2019, Evans 2021). These temporal movement patterns could be attributed to diel day/night foraging, feeding over certain tidal periods, seasonal and lunar migrations for spawning, or changing seasonal sea conditions. Evidence for lunar periodicity for spawning aggregations in relation to increased detection frequency during the full moon has been found in species within the Carangidae (Sley et al. 2012, Daly et al. 2019), Lutjanidae (Jackson et al. 2006, Nanami and Yamada 2009) and Serranidae (Starr et al. 2007, Mann et al. 2009, Bijoux et al. 2013) families.

Species profiles

This study aimed to investigate the ecological connectivity of coral reef-associated fish on South African coral reefs using acoustic telemetry. Three important top predatory reef fish species were chosen to investigate the likely implications of fish movement behaviour on the effectiveness of current zonation in the IWP MPA. Thus, the rationale behind choosing the species are: (1) they occur within the IWP, (2) they are species of direct economic interest, and (3) they are ecologically important as top predators of the reef systems.

Green jobfish (*Aprion virescens*) is a predatory reef fish species of the snapper family (Lutjanidae) that ranges throughout the tropical Indo-Pacific, from east Africa to Hawaii and from southern Japan to Australia (Allen 1985, Everson et al. 1989). Within southern Africa, it is distributed from its southern limits of Pondoland in the Eastern Cape, KZN, and into Mozambique, becoming more common north of St Lucia (KZN). Green jobfish inhabits areas from inshore reef systems to deeper reefs and sea mounts from the surface to over 100 m in depth (Allen 1985, Floros and Maggs 2013).

Juveniles have been recorded both on inshore shallow reef systems as well as offshore, likely dispersed with the current as eggs and larvae are pelagic (Leis and Lee 1994). These diurnal feeders’ diet consists mainly of fish, crustaceans, and cephalopods (Allen 1985, Kuiter and Tonozuka 2001). They are gonochoristic spawners with aggregations observed in Palau

(Johannes 1981). Spawning in southern African waters being observed from January through to May (van der Elst 1993) and again in November (Allen 1985). The spawning season off the coast of Hawaii peaks between the months of May and August (Everson et al. 1989). The age at 50 % maturity differs between regions but is estimated to be three to four years in the East African context (van der Elst 1993). Length at 50 % sexual maturity has been estimated between 70 and 75 cm total length (van der Elst 1993), 41 and 46.5 cm standard length in Kenyan waters (Talbot 1960), and 42.4 and 47.5 cm fork length in Hawaii (Everson et al. 1989). Maximum recorded length is 112 cm (Lablache et al. 1988). Green jobfish display sexual dimorphism, with females reaching a larger maximum size than males, yet no significant difference in maximum age was found (M. O'Malley et al. 2021).

Green jobfish has a model-estimated trophic level of 4.3 ± 0.4 se (Froese and Pauly 2022). It has a life history and ecological characteristics model-estimated vulnerability of moderate (40 out of 100) (Cheung et al. 2005) with a population doubling time estimated at a median, minimum of 1.4 to 4.4 years (Froese et al. 2017). Green jobfish were commonly targeted by recreational fishers within the IWP until fishing for it was banned in 2011 (Dames et al. 2020). It is still a common target for recreational fishermen outside of the IWP.

Potato bass (*Epinephelus tukula*) is in the grouper family (Serranidae). It is one of the largest fish species of the IWP weighing up to 80 kg and attaining over 200 cm total length and an age of 26 years (Grandcourt 2005). They are a territorial species that can be aggressive towards intruders (Murase et al. 2018). Potato bass are widely but sparsely populated throughout the indo-pacific. In South African waters they are known to occur as far south as the Protea Banks off southern KZN, stretching north into the IWP (Floros and Fennessy 2013). Adults are a reef-dwelling species found on prominent reefs and seamounts from 10 to 400 m in depth (Sink and Sink 2012), while juveniles can be found in surf zone tidal pools, rocky gullies and overhangs

(Heemstra and Randall 1993). As they get larger, juveniles will move to shallow or surf zone reef systems.

Generation time is estimated to be 8.5 years (Grandcourt 2005). Adults have a large variety in their diet, ranging from fish to crustaceans, cephalopods and rays (Floros and Fennessy 2013). Juveniles feed more regularly on small fish and crustaceans with an estimated trophic level 4.2 ± 0.68 se (Froese and Pauly 2022). Potato bass have a protogynous reproductive style and their eggs and larvae are pelagic (Yeh et al. 2003). Spawning has been recorded during summer and spring. The location of the southern African population's spawning ground believed to be northern KZN or southern Mozambique (van der Elst 1993). Another population spawns off the east coast of Kenya, Mafia Island (Nzioka 1979). Spawning aggregations are also thought to occur off the Seychelles based on fishermen's reports (Robinson et al. 2004).

Potato bass are under formal protection in South Africa and adjacent Mozambique. Potato bass are a species known to be indicators of fishing pressure and influenced by human activities such as SCUBA diving (Dames et al. 2020). Potato bass vulnerability based on life history and ecological characteristics model is estimated to be high to very high (66 out of 100) (Cheung et al. 2005). Little is known about the movement patterns of this species; however, unpublished tag recapture data from the Oceanographic Research Institute showed a high propensity for resident behaviour.

Giant trevally (*Caranx ignobilis*) is the largest of the Carangidae family and is an aggressive top predator on the reefs of the IWP. It is common among tropical and subtropical marine areas, most often in close proximity to reef systems (Maggs and Mann 2013). They are typically shallow water fish but have been recorded in depths of down to 188 m (Mundy 2005). This species is distributed widely throughout the Indian and central Pacific Oceans (Froese and Pauly 2022). It has a South African distribution from its effective southern limits of the Eastern

Cape, becoming more common further north (Heemstra and Heemstra 2004). It is a common reef predator in the IWP and Mozambique. Juveniles are found in estuaries and surf zone systems with adults preferring shallow reef systems and also frequenting estuaries (Sudekum et al. 1991 , van der Elst 1993).

Giant trevally eat mainly fish but also squid and other cephalopods, crustaceans and even sea birds (van der Elst 1993). They are gonochoristic and engage in broadcast spawning (Sudekum et al. 1991) in large spawning aggregations (Daly et al. 2019). Maturity is reached after approximately three to four years at a fork length of 60 to 65 cm (van der Elst 1993). Specimens have been recorded at over 80 kg and over a fork length of 160 cm. Maximum ages have been estimated at 25 (Andrews 2020) and 31 years (Pardee et al. 2021). Giant trevally have a trophic level of 3.5 to 5 (Glass et al. 2020) with a very high life history and ecological characteristics model estimated vulnerability (74 out of 100) (Cheung et al. 2005).

Giant trevally are both a recreational and commercial target throughout its range, yet very little valuable information is available to implement effective management of this species (Cheung et al. 2005). They are not heavily targeted in the IWP; however, they are allowed to be kept if caught outside of sanctuary zones. Little is known about the movement patterns of this species within the IWP.

Species movement patterns

Green jobfish movement patterns have been studied in Hawaii using acoustic telemetry and, in the Maldives, using conventional dart tags. Seasonal, diel, tidal, inter-atoll and long-distance dispersal movements of green jobfish were assessed. Meyer et al. (2007b) observed in Hawaii, no inter-atoll movements yet found they exhibited seasonal site fidelity to core regions of the reef system. These core regions ranged from 12 to 19 km in length. Both diel and tidal temporal movement patterns of green jobfish were identified although individual variation within the population was observed with some individuals exhibiting cyclical patterns of movement and other fish did not. Seasonal migrations of green jobfish included winter absences with summer activity within the core habitat regions. Filous et al. (2017) found that green jobfish exhibit low residency and site fidelity with a mean detection index of 21 % in Hawaii. Green jobfish were found to be significantly more active during daylight hours within the study area which could indicate diel movement patterns, or this could be as a result of reduced detection efficacy within the design of receiver array. A mark recapture pilot study by Sattar et al. (2012) in the Maldives using dart tags found 42 % of green jobfish tagged were recaptured less than one kilometer away from where they were released. Another 30 % were recaptured within five kilometers from the point of release. One individual was seen to exhibit a 22 km inter-atoll movement. These active hunters are equipped with a lunate tail, which can provide both short powerful bursts of speed and keep a fish constantly moving but is not designed for long-distance, wide-ranging movements (van der Elst 1993).

Very few studies have been conducted on the movement patterns of potato bass. During a mark recapture study using dart tags of surf-zone fish within the IWP, Mann et al. (2015) deduced from the data derived from 11 recaptures that potato bass moved an average of 182 m (± 322 m). Using the movement classification system from Dingle (1996), Mann et al. (2015) classed potato bass as resident station-keepers. No evidence of seasonal/spawning migrations was found yet this may have been due to the limiting nature of mark recapture and/or that the study was conducted in the surf zone environment which is the nursery grounds for potato bass. The majority of tagged fish were juveniles and not yet sexually mature. All fish were less than 90 cm, the length at which 50 % of potato bass mature (van der Elst 1993). Potato bass have been classified as a resident species by Floros and Fennessy (2013). Potato bass are large, robust, territorial, ambush predators using their large mouth to ambush and suction feed on prey. Their large shape and size, large pectoral and caudal fins and big mouth are indicative of their ambush hunting strategy and lack of necessity to actively hunt beyond their home reef. Their low aspect ratio, rounded tail is built for extremely short but fast lunges from a standing start but are hydrodynamically inefficient for any sustained swimming (van der Elst 1993, Helfman et al. 2009). Using both their caudal and pectoral fins, potato bass are able to maintain a fixed hovering position within their territory waiting to ambush prey.

A number of studies have already been conducted on the movements of giant trevally using acoustic telemetry to investigate site fidelity, home range and other long-range movements in Hawaii (Lowe et al. 2006, Meyer et al. 2007a, Papastamatiou et al. 2015, Filous et al. 2017, Evans 2021), Australia (Lédée et al. 2015), Seychelles (Daly et al. 2021) and South Africa and southern Mozambique (Daly et al. 2019). The studies in Hawaii, Seychelles and Australia were all conducted on giant trevally populations specifically on coral atoll habitats, a habitat type vastly different to the coral reefs of the IWP in geology, morphology, distance between reefs and ocean conditions. Previous studies showed that giant trevally express moderate to high fidelity to specific core sites with defined home ranges (Lowe et al. 2006, Meyer et al. 2007a, Lédée et al. 2015, Papastamatiou et al. 2015, Filous et al. 2017, Evans 2021), combined with infrequent longer migrations from approximately 29 to 38 km (Meyer et al. 2007a, Daly et al. 2021).

Diel patterns of movement have also been studied including tidal, lunar, seasonal, day-night and 24 hr patterns of movement. Studies found the giant trevally exhibited strong diel (Lowe et al. 2006, Meyer et al. 2007a, Lédée et al. 2015, Papastamatiou et al. 2015, Filous et al. 2017, Daly et al. 2019, Evans 2021) and lunar (Daly et al. 2019) patterns of movement. Giant trevally were detected more often during the day (Meyer et al. 2007a, Filous et al. 2017, Daly et al.

2019), contrary to Lédée et al. (2015) who found them to be more active at night. Giant trevally are believed to be more active at night (Meyer et al. 2007a); however, individuals were all caught during the day with receivers placed in areas known to hold giant trevally during the day. They may leave the receiver array at night, thus resulting in fewer detections at night in studies by Lowe et al. (2006), Meyer et al. (2007a), Lédée et al. (2015), Papastamatiou et al. (2015), Filous et al. (2017) and Daly et al. 2019. A lack of detections at night may also be as a result of poorer performance of acoustic receivers at night due to increased reef noise (Payne et al. 2010, How and de Lestang 2012, Kessel et al. 2014), highlighting the importance of range testing receivers in the field to compare differences in performance between day and night. Giant trevally are active predators that feed over vast areas of reef, surf zone and estuaries within their home range. They rely on speed and aggression to hunt. Their forked, low aspect tail is designed for sustained and efficient swimming and high speeds (van der Elst 1993, Helfman et al. 2009).

Marine Protected Areas

Marine protected areas (MPAs) are promoted by many as a holistic conservation strategy that can jointly address the current and future impacts of overfishing, habitat degradation, and unsustainable tourism on coral reefs (Kelleher and Kenchington 1992) and pottentially aiding in the resilience of coral reefs to climate change (Lubchenco et al. 2003, Mumby et al. 2006, Mumby and Harborne 2010). They act to conserve high genetic diversity; species-specific functionality (Graham and Nash 2013, Pinsky and Palumbi 2014, D'Agata et al. 2016, Friedlander et al. 2016) and rare or endemic species through the protection of connectivity at an individual, community, population, species and habitat level (Jones et al. 2007, Grober-Dunsmore et al. 2009, Haddad et al. 2015). Importantly, they also act to preserve and manage commercial and recreational fish stocks (Hockey and Branch 1997). As beneficial as MPAs may be, they certainly cannot entirely solve the threats of climate change, ocean acidification or plastic pollution; however, they are important in reducing and helping us understand the impacts of such threats (Carilli et al. 2009, Côté and Darling 2010, Micheli et al. 2012, Martin and Watson 2016, Mellin et al. 2016, Sink 2016). The recovery of depleted fish stocks within MPAs can also aid in mitigating against the mismanagement or complete lack of management of certain species or habitats.

MPAs are largely aimed at mitigating the adverse consequences of both direct and indirect anthropogenic activities or influences in specific locations (Sale et al. 2005, Mora et al. 2006). The classification or zonation of the MPA itself determines the degree to which it is protected. MPAs are generally split into two broad classifications or zonation's: areas that permit limited resource use (multiple-use zones) and fully protected no-use and no-take zones (sanctuary areas). Sanctuary zones are entirely closed off to any and all forms of resource use, thus eradicating all fishing pressure from the area. Through the removal of all fishing pressures, sanctuary zones provide an effective refuge for marine life (Sobel and Dahlgren 2004). Sanctuary areas have in many cases greatly enhanced reef fish populations within their boundaries by way of greater abundance, greater mean size, increased biomass and higher density of larvae of targeted fish species (Russ and Alcala 1996, Barrett et al. 2007, Unsworth et al. 2007, Lester et al. 2009). These factors, in turn, are expected to benefit fisheries adjacent to sanctuary zones through the net export of post-recruitment adult fish ('spillover effect') and the net export of emigrant larvae ('larval subsidy effect') (Afonso et al. 2009).

MPA size, distance from each other and both genetic and ecological connectivity all need to be considered during MPA design (Halpern and Warner 2003). Connectivity can be described as the extent to which populations or communities are linked by the exchange of eggs, larvae, juveniles, or adults (Sale et al. 2010). There are two main forms of connectivity: genetic and ecological connectivity. Genetic or evolutionary connectivity can be described as gene flow occurring between different populations of the same species over generations (Palumbi 2003). Ecological or demographic connectivity is the exchange of individuals across all or any life stages between different populations of a species at different locations (Sale et al. 2010). Ecological connectivity is a vital aspect of fisheries-management implementation of no-take sanctuary zones, as it can provide spillover from reserves into multiple-use zones and so improve fish stocks (Kritzer and Sale 2004).

Aims of this study

This study aimed to investigate the ecological connectivity of coral reef-associated fish on South African coral reefs using acoustic telemetry. This study focused on two main objectives.

The first objective of this work was to describe, quantify and categorise the spatial and temporal movement behaviour of each of the three species in the IWP. The movement behaviour was considered alongside other aspects of the life-histories of the species to provide a clearer understanding of their movement dynamics and functional roles in the local ecosystem. The second objective was to use the new information to assess the current zonation of the IWP in terms of the protection and management of the fisheries. Specifically, this study quantified the spatio-temporal movements of individual fish of each species relative to zonation, and with the use of appropriate metrics, provided an assessment of the extent to which the current zonation is likely to affect the mortality risks of fish in the IWP.

Although only three species were investigated, the fact that they are ecologically and economically important, and that they might serve to illustrate the range of behaviours that other species possess, should provide useful empirical data to serve as rational basis for zonation. It is vital to better understand the movements of some of these species between and within the multiple management zones as it will likely have important implications for the spatial management of the species and zones within this biologically, economically and historically important reserve. The findings of this study could have both ecological and management applications.

Methodology

Three species were selected to investigate residency, temporal patterns of movement and connectivity; green jobfish (*Aprion virescens*), potato bass (*Epinephelus* tukula) and the giant trevally (*Caranx ignobilis*). A field-based study was conducted in the iSimangaliso Wetland Park (IWP) along the Maputaland coast of Kwa-Zulu Natal from 2013 to 2020 to collect acoustic telemetry data from the three species.

Study site

The iSimangaliso Wetland Park (IWP) is one of South Africa’s longest standing contiguous Marine Protected Areas (MPA) with multiple zones of different levels of protection and is approximately 10 700 km^2 (Dames et al. 2020). It is a trans frontier park which is conjoined with the Ponta do Ouro Partial Marine Reserve (PPMR) of southern Mozambique sharing similar reef systems and species while having differing levels of protection and monitoring. The coral reefs of the IWP stretch for approximately 122 km covering a large area of habitable waters for all three study species. The IWP and PPMR consist of some of the most southern coral reefs in the world with an abundance of ecologically important species (Floros 2010, Schleyer et al. 2018, Dames et al. 2020).

The main study site was located among the coral reefs within the IWP which is situated on the north-east (Maputaland) coast of South Africa (refer to map (Fig 1)). The IWP is comprised of a complex of MPA’s with varied levels of protection ranging from multiple-use zones to sanctuary zones. The IWP MPA complex runs from its southern latitudinal limit of 28.5224 °S to the border with Mozambique of 26.8579° S (Fig 1). Whereas the study site is within the IWP, acoustic receivers were deployed outside the IWP to detect occurrences of long-distance dispersals. These receivers were located as far north as Santa Maria (Mozambique) and as far south as iFafa on the southern coast of KZN (Table 1, Fig 1). There are several offshore management zones within the IWP (Fig 1). These management zones include the iSimangaliso Offshore Controlled-Pelagic Linefishing Zone South (IOCPLZS), iSimangaliso Offshore Controlled-Pelagic Linefishing Zone North (IOCPLZN), which are both multiple-use zones, the iSimangaliso Offshore Wilderness Zone (IOWZ), Sodwana Diving Restricted Zone (SDRZ) and the iSimangaliso Offshore Restricted Zone North (IORZN), which are sanctuary or restricted use zones. Receivers were placed in all offshore zones with the exception of the IORZS due to it being a deep-water sanctuary zone with no shallow (<30 m) reef systems. The PPMR of southern Mozambique was also equipped with several receivers to detect cross-border movements. The PPMR recently became a part of the Maputo National Park; however, the marine reserve will be referred to as the PPMR throughout this study. The placement of the sanctuary zones is such that it protects the three major reef complexes within the IWP. These include the southern reef complex within the IOWZ, the central reef complex within the SDRZ and the northern reef complex within the IORZN.

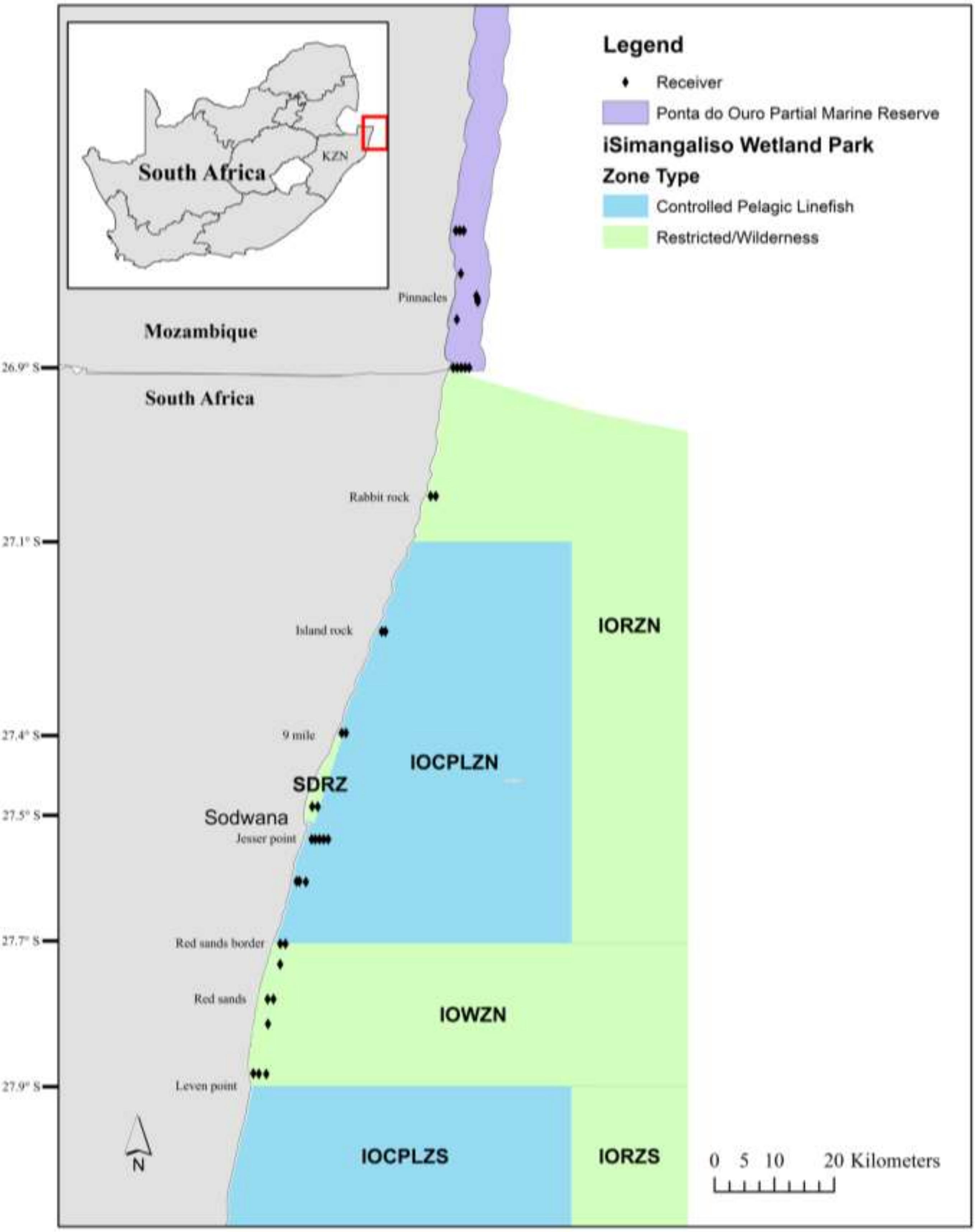


Figure 18: Site map of the study area showing sanctuary and multiple-use zones within the iSimangaliso Wetland Park (IWP) and Ponta do Ouro Partial Marine Reserve (PPMR). These zones include: iSimangaliso Offshore Controlled-Pelagic Linefishing Zone South (IOCPLZS), iSimangaliso Offshore Restricted Zone South (IORZS), iSimangaliso Offshore Wilderness Zone (IOWZ), iSimangaliso Offshore Controlled-Pelagic Linefishing Zone North (IOCPLZN), Sodwana Diving Restricted Zone (SDRZ), iSimangaliso Offshore Restricted Zone North (IORZN).

Receiver array

Acoustic receivers (InnovaSea VR2W) were placed at strategic locations between important reef complexes in the different MPA zones. These consist of self-contained, single-channel (69 KHz) underwater receivers that listen continually for the presence of coded pulse acoustic transmitters. Three sanctuary and two multiple-use reefs were included as study sites and three receivers placed on sand between reefs at two different depths: 18 m and 30 m (see study site map (Fig 1)). Receivers were fixed to a mooring rope 2.5 m off the bottom substrate and anchored using a 50 kg section of railway line tethered to a float as illustrated by Cowley et al. (2017). In key areas such as zonal and international borders, three to five receivers were placed in a horizontal line. They were approximately 800 m apart as the effective receiver range is 400 m (refer to *Range testing* (page 32)), which allows the receivers to retain an overlap in receiver range. Deployment and placement of the receivers were done using SCUBA. In addition to these receivers, data were also obtained from a larger network of receivers maintained by the Acoustic Tracking Array Platform, hosted by the South African Institute of Aquatic Biodiversity (Murray et al. 2022). During the study period, 40 receivers detected tagged fish in this study, 24 of them within the IWP, 13 in the adjacent PPMR and 3 positioned outside of the study array, south of the IWP (Fig 1 and Table 1).

Table 5: Details of all receivers at which fish tagged in this study were detected, including the location, date of deployment and position.

Receiver name	Receiver location	Deployment date	Receiver latitude	Receiver longitude
2MR1	2 Mile reef	2013/09/20	-27.512	32.687
2MR2	2 Mile reef	2013/09/20	-27.512	32.695
9MR1	9 Mile reef	2013/09/21	-27.402	32.732
9MR2	9 Mile reef	2013/09/21	-27.402	32.738
Canyon001	Sodwana canyon	2018/05/28	-27.625	32.678
Canyon002	Sodwana canyon	2018/05/28	-27.838	32.621
Canyon003	Sodwana canyon	2018/05/28	-27.913	32.618
ISR1	Island rock	2016/12/05	-27.250	32.792
ISR2	Island rock	2016/12/05	-27.250	32.797
JP001	Jesser point	2013/12/03	-27.561	32.686
JP002	Jesser point	2013/12/03	-27.561	32.692
JP003	Jesser point	2013/12/03	-27.561	32.698
JP004	Jesser point	2013/12/03	-27.561	32.705
JP005	Jesser point	2013/12/03	-27.561	32.711
Leven	Leven point	2014/08/12	-27.912	32.599
Malongane	Ponta malongane	2015/11/25	-26.782	32.905
Mamoli 1	Ponta mamoli	2015/11/28	-26.713	32.911
MOZ001	Mozambique border	2012/11/30	-26.855	32.899
MOZ002	Mozambique border	2012/11/30	-26.855	32.905
MOZ003	Mozambique border	2012/11/30	-26.855	32.911
MOZ004	Mozambique border	2012/11/30	-26.854	32.917
MOZ005	Mozambique border	2012/11/30	-26.854	32.923
Pinnacle Temporary 1	Ponta malongane	2015/11/25	-26.754	32.936
Pinnacle Temporary 2	Ponta malongane	2015/11/25	-26.752	32.936
Pinnacle Temporary 3	Ponta malongane	2015/11/25	-26.749	32.935
Pinnacles 1	Ponta malongane	2011/11/18	-26.756	32.936
Pinnacles 2	Ponta malongane	2013/11/12	-26.747	32.934
Pinnacles 3	Ponta malongane	2013/11/12	-26.750	32.936
Red Sands SAEON	Red sands reef	2018/09/13	-27.749	32.639
RR1	Rabbit rock	2015/11/17	-27.047	32.865
RR2	Rabbit rock	2015/11/17	-27.047	32.873
RS1	Red sands reef	2013/09/22	-27.801	32.620
RS2	Red sands reef	2013/09/22	-27.801	32.629
RSB1	Red sands border	2018/01/17	-27.718	32.639
RSB2	Red sands border	2018/01/17	-27.718	32.647
Santa Maria Mid	Santa Maria	2019/03/13	-26.094	33.007
Santa Maria North	Santa Maria	2019/03/12	-26.094	33.011
Santa Maria South	Santa Maria	2019/03/13	-26.098	33.007
Santa Maria Inshore	Santa Maria	2020/03/13	-26.089	32.973
Sod1 20m	Sodwana	2018/05/22	-27.624	32.664
Sod1 30m	Sodwana	2018/05/22	-27.624	32.668
Sod3 30m	Sodwana	2018/05/22	-27.913	32.607
Techobanine 1	Ponta techobanine	2015/11/28	-26.649	32.903
Techobanine 2	Ponta techobanine	2015/11/28	-26.649	32.909
Techobanine 3	Ponta techobanine	2015/11/28	-26.649	32.915
Black Rock	Black rock	2015/06/19	-30.170	30.830
Ifafa	iFafa	2015/03/20	-30.466	30.659
MAP001	Maphelane	2018/07/25	-28.406	32.443
Park Rynie	Park rynie	2015/02/19	-30.339	30.740

Acoustic tagging and monitoring

A total of 82 fish: 38 green jobfish, 35 potato bass and 9 giant trevally were fitted with acoustic tags for this study (Fig 3). All fish were captured, tagged and released within the IWP with tagging spread across multiple reef complexes and zones within the IWP (Fig 3) . The capture of the selected species was done from a semi-ridged vessel using baited barbless hooks. Green jobfish and giant trevally were caught using a fishing rod, while the larger potato bass were caught using a baited buoy system (Daly et al. 2014). Using rods, reels and specific lures, giant trevally and green jobfish can be relatively selectively targeted as opposed to the unselective method of baiting. The large baits and hooks used for targeting potato bass generally exclude all smaller species of fish. Only mature fish were used in the study. Practically, maturity was indicated by size: green jobfish > 40 cm, giant trevally > 60 cm and potato bass > 80 cm (van der Elst 1993) (Table 2). The sex of all fish was not determined and could not be inferred and was therefore not included in the study.

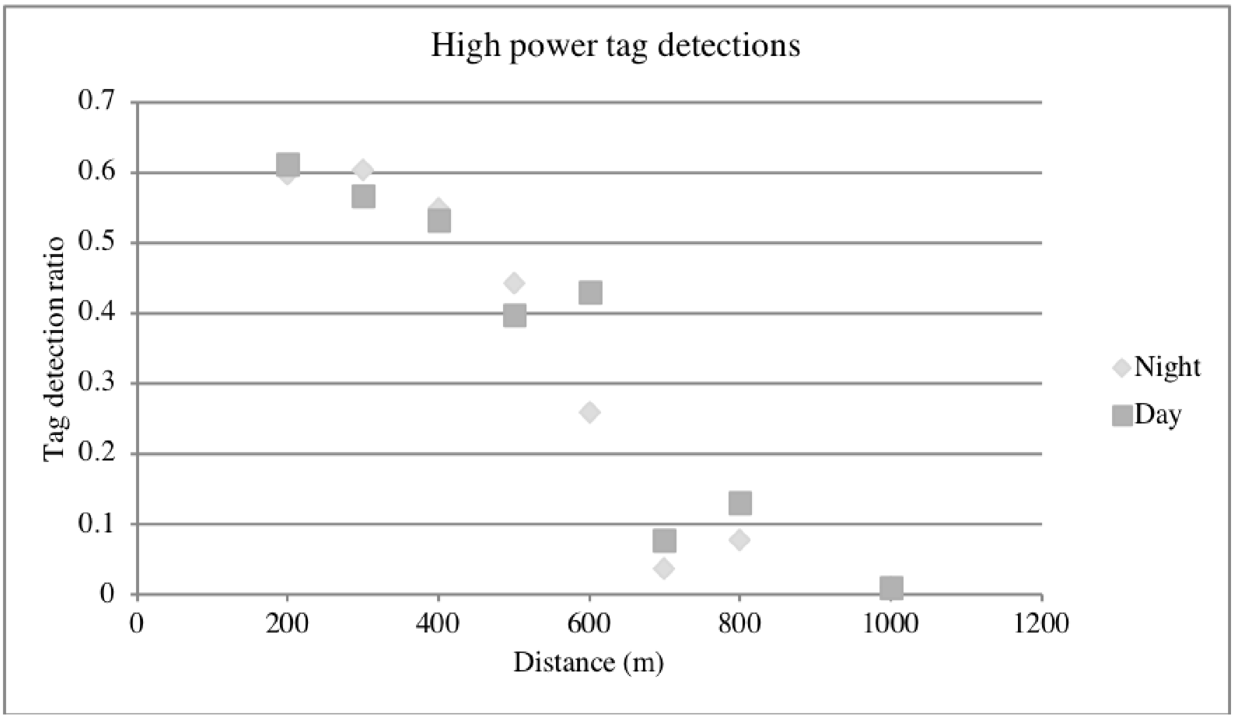
Once caught, the fish were landed on a plastic stretcher and transferred to a large trough on the vessel. A constant supply of oxygen was provided by way of buckets of fresh sea water added continuously to the trough. Captured fish were placed in the trough, ventral side up, such that the ventral surface was above the water line, but the gills remained submerged. Acoustic transmitters (V16, nominal delay 45 s or 60 s, high and low power, expected battery life 1095 – 3650 d) (Table 2), were sanitized using surgical sterilant (F10) and inserted into the peritoneal cavity through a 2 cm incision slightly off the ventral midline. A mixture of both high and low power tags were used. Tags that have an expected life of 3650 days are low power tags and tags with an expected life of less than 3650 days are high power tags (Table 2). The incision was then closed with two independent sutures using synthetic absorbable surgical sutures (CliniSut). The incision was then coated with an anti-septic powder forming an adhesive gel covering (unknown veterinarian).

The entire capture and tagging operation lasted 10 − 15 min. All individuals were measured and tagged with an external dart tag to alert the tagger in the event of a recapture of a tagged fish. Fish were then placed in a second holding trough containing fresh seawater to enable full recovery before they were released. Tagged fish were released within the vicinity (< 1 km) of the capture location and all swam away strongly (Fig 3). The receivers recorded continuous tracking of fish movements throughout the study period (7 years). Data were retrieved from the receivers every four months.

Range testing

Range tests were performed to estimate acoustic detection range for determining receiver spacing and analyzing acoustic data (Fig 2). High and low power tags were used to test the range in this study. Tags of both types were placed at 100 m intervals, starting from 200 m and ending at 1000 m from the receiver to estimate the decay in detection probability with distance. Tags were left for a 24 hr period to compare the number of detections between day and night and to estimate diel variation. There are several sources of detection variability in marine environments which include: sea conditions (Payne et al. 2010), current (How and de Lestang 2012), turbidity (Sakabe and Lyle 2010), salinity (How and de Lestang 2012), water temperature/thermoclines (How and de Lestang 2012), upwellings (Singh et al. 2009), receiver location/depth (Andrews et al. 2007), transmitter location in the fish, biofouling (Heupel et al. 2006) and interference/background noise (Payne et al. 2010) which can be both natural and anthropogenic.

There are many ways in which detection range can be calculated as there is no universally standardized definition for calculating detection range. The calculation of detection range as put forward by Kessel et al. (2014), “the relationship between detection probability and the distance between the receiver and tag” was used in this study. The detection probability was plotted against distance (Fig 2). Detection probability is a ratio of the number of detections received vs the number of expected detections emitted. Detection range of receivers was adopted at a tag detection ratio of 50 % which equates to a detection range of approximately 400 m according to range test data. A total of 46 receivers in the main study site of the IWP and PPMR, each with a detection range of 400 m (0.5 km ^{2}) equates to an approximate detection area of 23.12 km^2 in receiver coverage. The approximate area of waters shallower than 100 m (taken to be the maximum offshore range of coral reef fish) within the IWP and PPMR is 1500 km^2. The effective receiver coverage is thus 1.54 % of the suitable habitat for the three study species.



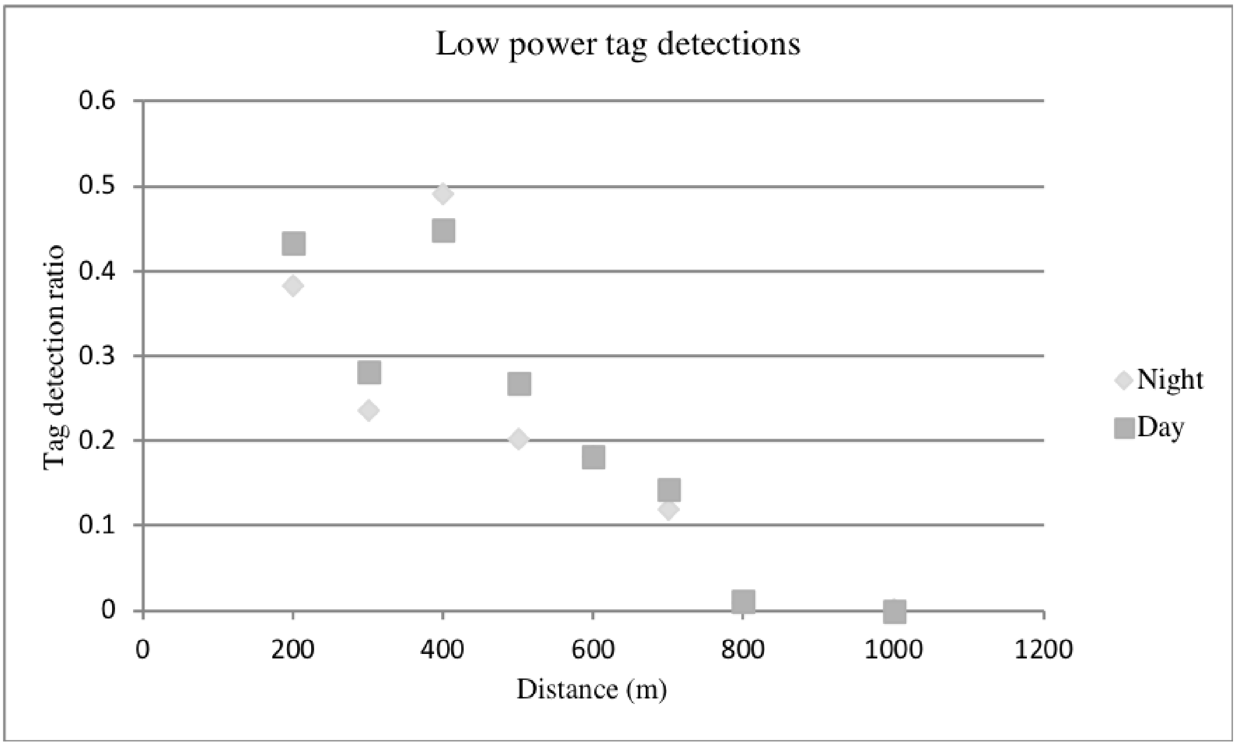


Figure 19: Range test metrics for acoustic receiver data for both high and low power tags comparing tag detection ratio against distance (m) across day and night.

Table 6: Tagging details of green jobfish (*Aprion virescens*), giant trevally (*Caranx* ignobilis) and potato bass (*Epinephelus tukula*) fitted with acoustic tags for this study, showing, species, fork length (cm), catch area, release date (yyyy/mm/dd) and tag expected life (days)(low power(3650), high power (<3650)) in order of release date.

Fish ID	**Species**	**Release date (yyyy/mm/dd)**	**Catch area**	**Fork length**	**Tag expected life (Days)**
JB1	Green jobfish	2013/12/07	Leadsman	68	1229
JB2	Green jobfish	2014/03/26	9-mile reef	48	1135
JB3	Green jobfish	2014/03/27	Leadsman	56	1135
JB4	Green jobfish	2014/03/28	9-mile reef	45	1135
JB5	Green jobfish	2014/03/30	Leadsman S	48	1135
JB6	Green jobfish	2014/03/30	Leadsman S	45	1135
JB7	Green jobfish	2014/04/30	Red Sands	48	1135
JB8	Green jobfish	2014/04/01	7-mile reef pinnacles	45	1135
JB9	Green jobfish	2014/04/02	7-mile reef	42	1135
JB10	Green jobfish	2014/08/16	Red sands receiver	80	1229
JB11	Green jobfish	2014/08/16	Red sands middle	62	1229
JB12	Green jobfish	2013/12/10	Leadsman	59	1229
JB13	Green jobfish	2014/08/16	Red sands boundary	67	1229
JB14	Green jobfish	2015/11/19	Island Rock	60	1316
JB15	Green jobfish	2015/11/19	Rabbit Rock	80	3650
JB16	Green jobfish	2015/11/23	Rabbit Rock	59.5	1316
JB17	Green jobfish	2015/11/23	Rabbit Rock	74	3650
JB18	Green jobfish	2015/11/23	Rabbit Rock	69	3650
JB19	Green jobfish	2016/12/06	Kosi	79	1910
JB20	Green jobfish	2016/12/06	Kosi	65	1910
JB21	Green jobfish	2016/12/06	Kosi	70	1910
JB22	Green jobfish	2016/12/07	Kosi	77	1910
JB23	Green jobfish	2013/12/12	Red sands boundary	65	1229
JB24	Green jobfish	2016/12/07	Kosi	60	1910
JB25	Green jobfish	2017/12/04	Mbibi	55	1317
JB26	Green jobfish	2017/12/04	Mbibi	69	1910
JB27	Green jobfish	2017/12/04	9-mile reef	52	1317
JB28	Green jobfish	2017/12/04	7-mile reef	79	1910
JB29	Green jobfish	2017/12/05	Red sands	51	1317
JB30	Green jobfish	2017/12/05	Red sands	58	1317
JB31	Green jobfish	2017/12/06	Red sands	66	1910
JB32	Green jobfish	2016/05/03	Bhanga	89	1135
JB33	Green jobfish	2014/03/28	9-mile reef	60	1228
JB34	Green jobfish	2014/03/30	Leadsman S	71	1228
JB35	Green jobfish	2014/03/30	Leadsman S	79	1228
JB36	Green jobfish	2014/04/03	Red Sands	85	1228
JB37	Green jobfish	2014/03/25	5-mile reef	53	1135
JB38	Green jobfish	2014/03/25	2-mile reef	50	1135
GT1	Giant trevally	2016/02/25	St Lucia MPA Sanctuary	86.5	2712
GT2	Giant trevally	2016/05/03	9 North (Bhanga Nek)	69	2712
GT3	Giant trevally	2015/02/19	St Lucia MPA Sanctuary	61.5	2347
GT4	Giant trevally	2015/11/11	Leven Point	98	2347
GT5	Giant trevally	2017/02/07	St Lucia MPA Sanctuary	84	3197
GT6	Giant trevally	2018/01/31	6km south of Sodwana	101	3197
GT7	Giant trevally	2016/11/30	Near Leven Point	103	3197
GT8	Giant trevally	2016/12/02	Near Leven Point	69	3197
GT9	Giant trevally	2016/12/02	Near Leven Point	105	3197
PB1	Potato bass	2013/12/04	Leadsman	118	3102
PB2	Potato bass	2013/12/09	9-mile reef	146	3102
PB3	Potato bass	2013/12/11	2-mile reef	125	3102
PB4	Potato bass	2014/03/26	Mbibi	141	3650
PB5	Potato bass	2014/03/27	Leadsman	135	3650
PB6	Potato bass	2014/03/29	Mbibi	135	3650
PB7	Potato bass	2014/03/31	Leadsman N	128	3650
PB8	Potato bass	2014/03/31	Leadsman N	117	3650
PB9	Potato bass	2014/03/31	Red sands 2 receiver	130	3650
PB10	Potato bass	2014/04/01	Anton’s	95	3650
PB11	Potato bass	2014/04/02	7-mile reef	132	3650
PB12	Potato bass	2013/12/04	Red sands	126	3102
PB13	Potato bass	2014/04/02	7-mile reef	115	3650
PB14	Potato bass	2015/11/17	Roman rock	126	3650
PB15	Potato bass	2015/11/19	Roman rock	133	3650
PB16	Potato bass	2015/11/24	Elusive	123	3650
PB17	Potato bass	2015/11/24	Elusive	151	3650
PB18	Potato bass	2015/11/24	Roman rock	105	3650
PB19	Potato bass	2016/07/12	2MR Anton’s	90	3650
PB20	Potato bass	2013/12/04	Red sands	122	3102
PB21	Potato bass	2016/12/06	Kosi	121	3650
PB22	Potato bass	2016/12/06	Kosi	130	3650
PB23	Potato bass	2016/12/06	Kosi	130	3650
PB24	Potato bass	2016/12/07	Kosi	146	3650
PB25	Potato bass	2016/12/07	Kosi	136	3650
PB26	Potato bass	2017/12/05	Red sands	116	1910
PB27	Potato bass	2017/12/05	Red sands	129	1910
PB28	Potato bass	2017/12/06	Stringer	145	1910
PB29	Potato bass	2017/12/06	Stringer	123	1910
PB30	Potato bass	2013/12/04	Red sands	109	3102
PB31	Potato bass	2013/12/06	Mbibi	140	3102
PB32	Potato bass	2013/12/07	Leadsman	119	3102
PB33	Potato bass	2013/12/07	Red sands	90	3102
PB34	Potato bass	2013/12/08	9-mile reef	135	3102
PB35	Potato bass	2013/12/08	9-mile reef	125	3102

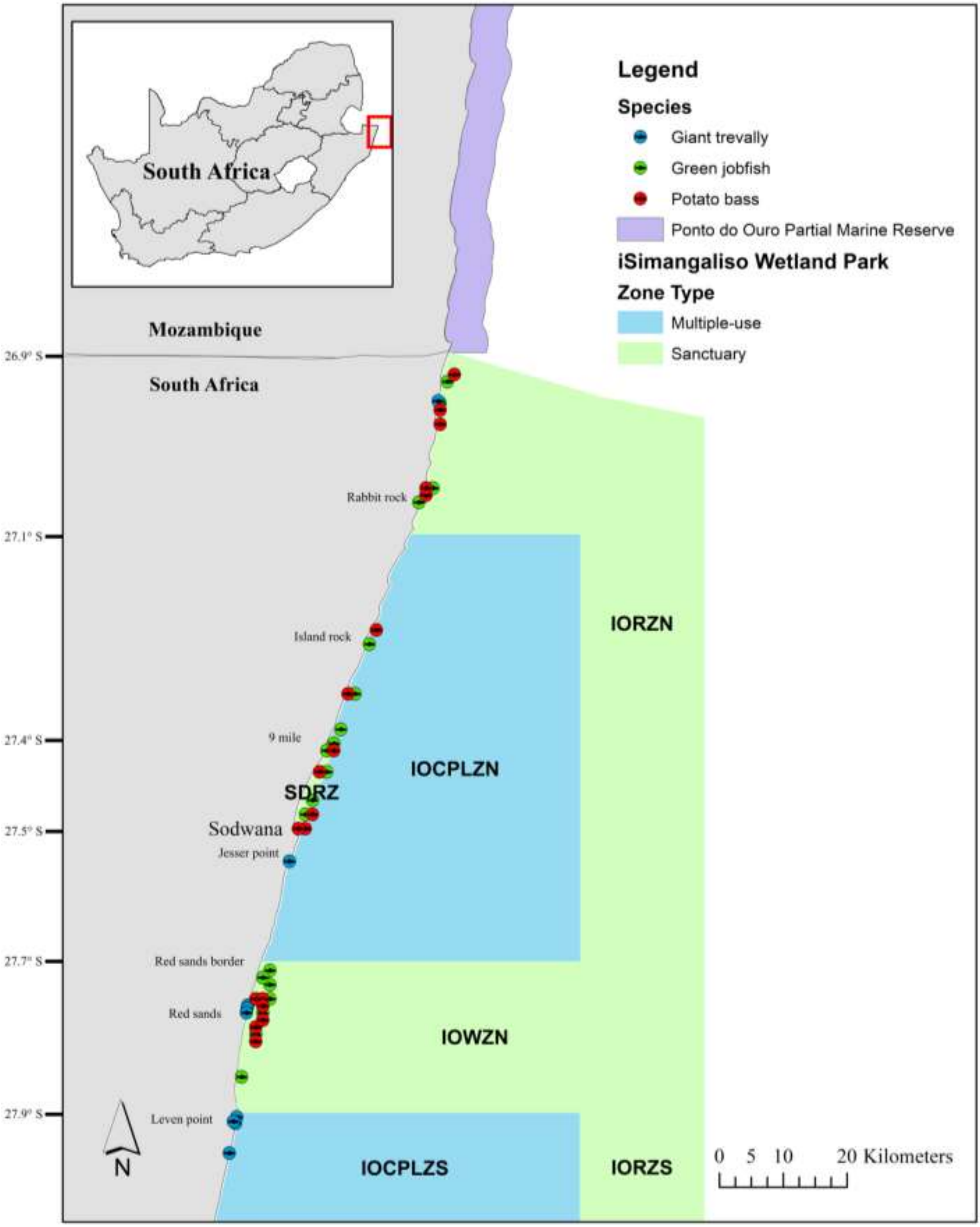


Figure 20: Approximate fish release locations of acoustically tagged green jobfish (*Aprion virescens*), giant trevally (*Caranx ignobilis*) and potato bass (*Epinephelus tukula*) in this study, accurate to 500 m from symbol.

Data analyses

Following the methodology used by Udyawer et al. (2018), a quality control and false detection check was performed on these data. These included checks for abnormally fast movements between receivers whereby the speeds of all fish movements were calculated using the time and distance between detections at non-neighbouring receivers. Movement speeds greater than 15 km per hour were counted as false detections and the second detection was removed. If this occurs between neighbouring receivers closer than 1 km to each other, it was ignored. R Studio and the Animal Tracking Toolbox (ATT) in the *Vtrack* package was used to transform individual detection data with metadata including: time and date, transmitter serial number, geographic position and receiver serial number, into a multitude of standardized detection metrics for each transmitter. These detection metrics include, number of detections, number of days at liberty, number of days detected, number of receivers which detected the transmitter, detection index and residency index for each individual. Of the 82 fish that were tagged, only 50 individuals were detected during the study period and included in the analyses.

Detection and residency indices

A detection index (DI) was calculated for each fish using the number of days a tagged fish was detected by the receiver array, divided by the total number of days the tag was active using the tag expected life. This value was multiplied by 100 to give a percentage, which indicates the extent of presence within the entire receiving range of the array.

A residency index (RI) specific to this study was created that considered detection frequency at each receiver *r,* for each fish *i,* and using the Shannon-Weiner diversity index to reflect the diversity and evenness of receivers that detected fish. A low index reflects an even spread among a high number of receivers, whereas a high index reflects a concentration of detections at one or a few receivers. The index is calculated as follows:

$$\mathrm{SW}max = -\sum[(\mathrm{P}r) \times \ln(\mathrm{P}r)]$$

Where SW*max* is the maximum possible Shannon-Weiner index that a fish can score if it triggers all receivers with equal frequency, calculated by the probability of detection at each receiver P*r* calculated as $\frac{1}{total\ number\ of\ receivers}$, multiplied by the log of P*r* for each receiver.

For each fish *i,* at every receiver *r*:

$$\mathrm{SW}d_i = -\sum[(Pd_{ri}) \times \ln(Pd_{ri})]$$

Where SWd_i for each fish *i,* is the sum of the Shannon-Weiner of detections, calculated by the proportion of detections P*d* at each receiver *r*, calculated by $\frac{number\ of\ i\ detections\ at\ receiver\ r}{total\ number\ of\ i\ detections}$, multiplied by the log of P*d* .

The RI for each fish *i,* is then calculated by 1 minus the Shannon-Weiner index of detections (SWd_i) divided by the Shannon-Weiner index of receivers (SW*max*), multiplied by 100 to give a percentage.

$$\mathrm{RI}i = [1 - (\frac{\mathrm{SW}d_i}{\mathrm{SW}max})] \times 100$$

The higher the RI percentage for each fish, the more resident that fish is to a specific receiver or set of receivers. The lower the RI value, the greater the spread of detections across the receivers and thus the less resident the fish is to a specific area. The RI is averaged across all fish with more than 1000 detections for each species to get an RI for each species.

Dispersal statistics

Measures of dispersal distance were used to investigate the spatial patterns of movement of all tagged fish. These metrics were calculated for each tagged fish using functions and tools provided by the 'Vtrack' package and its extension, the 'Animal Tracking Toolbox' within the R statistical environment (Version 1.3.1073) (Campbell et al. 2012) as illustrated by Udyawer et al. (2018). The dispersal step distance is the minimum distance travelled between subsequent detections in the receiver array. Dispersal step distances were calculated using the Animal Tracking toolbox function, 'dispersalSummary'.

Periodicity

This study covered numerous temporal periods including diel, tidal, lunar, seasonal, and annual cycles during the sevens years of continuous data collection. A study of this length, spanning multiple cycles provides the data needed to identify cyclical patterns of movement. The exact date and time stamp (yyyy/mm/dd hh:mm:ss) was recorded with each detection during the study period. A time series was created from detection data that were expressed as the frequency of detection for every hour. Rose plots (Oriana (version 4) and fast Fourier transform (FFT) analyses (R statistical environment (Version 1.3.1073)) were generated to identify the dominant activity peaks and frequencies in the detection data. Rose plots, are pie charts using time data, converted to frequency data in 2 hr bins used to identify patterns in time usage throughout 24 hr. Rao's spacing test (U) and Raleigh test (z) for significance were conducted for each plot. The Rao spacing U test, tests for uniformity in the circular data in order to determine if there is significant directionality. The Raleigh z test, tests for the presence of periodicity/non-uniformity in sporadically sampled circular data. The mean vector time (µ) was also calculated which is the mean time found across the time data. Rose plots, Rao's spacing test and Raleigh tests were created and conducted using Oriana (Version 4).

Spikes in the FFT plot indicated the dominant movement frequencies. The sampling frequency was once per hour, limiting the analysis to frequencies less than 0.5 per hour. The intention was to detect diel (24 hr) and tidal (6/12 hr) cycles.

Subsets of the detection data were used. Not all tagged fish yielded data that met the criteria to accurately run these analyses due to a shortage of continuous detections at a single receiver. Individuals of each species with the most detection data were selected as representatives of the species. Green jobfish (Tag ID JB15) detection data from January to March of 2017 at the Rabbit Rock 1 receiver was selected as it had the highest number of detections at a single receiver over a three-month period. Potato bass (Tag ID PB 17) detections from January to March of 2017 at the Island Rock 1 receiver was selected for the same reasons. Giant trevally (Tag ID GT4) detection data from April 2016 to March of 2017 at the Leven point receiver was selected as it had the highest number of detections at a single receiver over a period of a 12 months. Rose plots and FFT analyses were generated using the same data subsets to allow comparisons of results.

Movements beyond release locations

Using the zonal position of each receiver on which a fish was detected, a record was taken of the number of zones in which the fish was detected outside of the zone in which it was released. All instances of tagged fish that entered a new zone outside of the zone in which they were released were tabulated. If a fish was detected on numerous consecutive occasions in the same zone it was counted as a single visit to that zone. The average number of zones crossed per fish of each species was calculated by dividing the total number of zones crossed by the number of fish of each species, green jobfish (n=30), potato bass (n=15) and giant trevally (n=5).

The management zones included in the table are as follows: iSimangaliso Offshore Controlled-Pelagic Linefishing Zone South (IOCPLZS), iSimangaliso Offshore Controlled-Pelagic

Linefishing Zone North (IOCPLZN), which are both multiple-use zones, iSimangaliso Offshore Wilderness Zone (IOWZ), Sodwana Diving Restricted Zone (SDRZ), iSimangaliso Offshore Restricted Zone North (IORZN), which are all sanctuary or restricted use zones. Also included is the Ponta do Ouro Partial Marine Reserve (PPMR) which can be found across the South African border in southern Mozambique.

Latitudinal movement patterns

Latitudinal detection plots across the study period were created to allow for the visualisation of any north-south migrations. Patterns of repetitive or cyclic movements between reef complexes within the IWP and PPMR were identified by plotting fish detections against the latitudinal position of each detection. Due to the north-south orientation of the reef complexes and narrow continental shelf within the IWP and PPMR, large westerly movements are impossible and large easterly movements are unlikely. By plotting detections against latitude, patterns of migration for each species could be identified. Plots for all five giant trevally and four potato bass and four green jobfish were constructed. Only potato bass and green jobfish with adequate continuous detections were used.

Connectivity

Using , detection data for each species at all receivers were used to create a connectivity matrix for each species. These metrics were calculated for each tagged fish using functions and tools provided by the 'Vtrack' package and its extension, the 'Animal Tracking Toolbox' within the R statistical environment (Version 1.3.1073) (Campbell et al. 2012). The connectivity matrices had elements which corresponded to the frequency of detection of the individual fish at a particular receiver in a particular time period. By using the connectivity matrices within ArcMap, network connectivity plots were created that represented the joins between receivers with subsequent detections. This provides a visual representation of the distribution of activity space use among the management zones of the IWP and PPMR. Connectivity plots were created for each species, giant trevally (n = 5), green jobfish (n = 30) and potato bass (n = 15). Network plots were created using the programme ArcMAP 10.6 (ESRI). Node size and colour represent the total number of detections at each receiver. Lines represent the movement of a tagged individual between receivers. Thickness and colour of lines represent the frequency of movement between receivers.

Results

Detection and dispersal summary

Between November 2013 and July 2020, 30 (79 %) of the tagged green jobfish, 5 (56 %) of the tagged giant trevally and 15 (43 %) of the tagged potato bass were detected by 40 of the South African and southern Mozambican acoustic receivers. Individual fish were detected on multiple receivers in the iSimangaliso Wetland Park (IWP) and outside the park (Table 1). The total number of detections recorded were 892 552. The number of detections of each species and individual varied considerably. For giant trevally, the average number of detections was 1914, ranging from 561 to 3082 over a period of 1214 to 1668 days (Fig 4). Giant trevally exhibited greater dispersal distances than both green jobfish and potato bass (Fig 5).

Green jobfish *(Aprion virescens)*

A total of 122 803 (mean = 4093) ranging from 2 to 52 664 detections were recorded from detected green jobfish (n = 30) over a period of 912 to 1660 days (Fig 4). Green jobfish were detected by a range of 1 to 8 receiver (mean = 3.03) of a possible 46. The number of detection days per for fish ranged from 1 to 700 (mean = 101) (Fig 4). The detection index (DI) ranged from 0.08 to 56.91 % (mean = 7.82 %). Among individuals with greater than 1000 detections, the mean DI was 16.57 %. The maximum dispersal step distance for tagged fish ranged from 0.78 to 54.48 km (mean = 16.49 km) (Fig 6) with an overall mean of 0.52 km. No apparent difference in dispersal step distance per size class was noted. The residency index (RI) for green jobfish with more than 1000 detections ranged from 61.6 % to 100 % with a mean RI of 85.2 % (Table 3).

Giant trevally (*Caranx ignobilis*)

A total of 9570 (mean = 1914) detections were recorded from giant trevally (n = 5) over a period of 1214 to 1668 days (Fig 4).. The tagged fish were detected at a range of 9 to 17 receivers (mean = 13.8) per individual of a possible 46. Two separate individuals were detected by 17 receivers (Table 3). The number of detection days ranged from 44 to 260 (mean = 115) (Fig 4). The DI ranged from 3.62 to 20.27 % (mean = 8.34 %). Among individuals with greater than 1000 detections, the mean DI was 9.37 %. The maximum dispersal step distance ranged from 133.01 to 340.15 km (mean = 189.00 km) (Fig 7) with an overall mean of 1.08 km. No apparent difference in dispersal step distance per size class was noted. The RI for giant trevally with more than 1000 detections ranged from 49.4 % to 92.3 % with a mean RI of 66.9 % (Table 3).

Potato bass (*Epinephelus tukula*)

A total of 750 179 (mean = 50 679) ranging from 5 to 236 177 detections were recorded from detected fish (n = 15) over a period of 912 to 2375 days (Fig 4). The highest number of individual detections was recorded by a fish (Tag ID PB16) across three receivers, detected for a total of 1068 days. Potato bass were detected at a range of 1 to 13 receivers (mean = 3.33) per individual of a possible 46. The number of detection days ranged from 1 to 2195 (mean = 429) (Fig 4 & Table 3). The DI ranged from 0.04 to 92.69 % (mean = 20.94 %). Among individuals with greater than 1000 detections the mean DI increased to 51.91 %. The maximum dispersal step distance for a fish ranged from 0.78 to 62.71 km (mean = 16.94 km) (Fig 8) with an overall mean of 1.73 km. Dispersal step distances appear greater for large adults (>110cm) compared with that of small adults (90-110cm) The RI for potato bass with more than 1000 detections ranged from 87.3 % to 99.9 % with a mean RI of 95.0 % (Table 3).

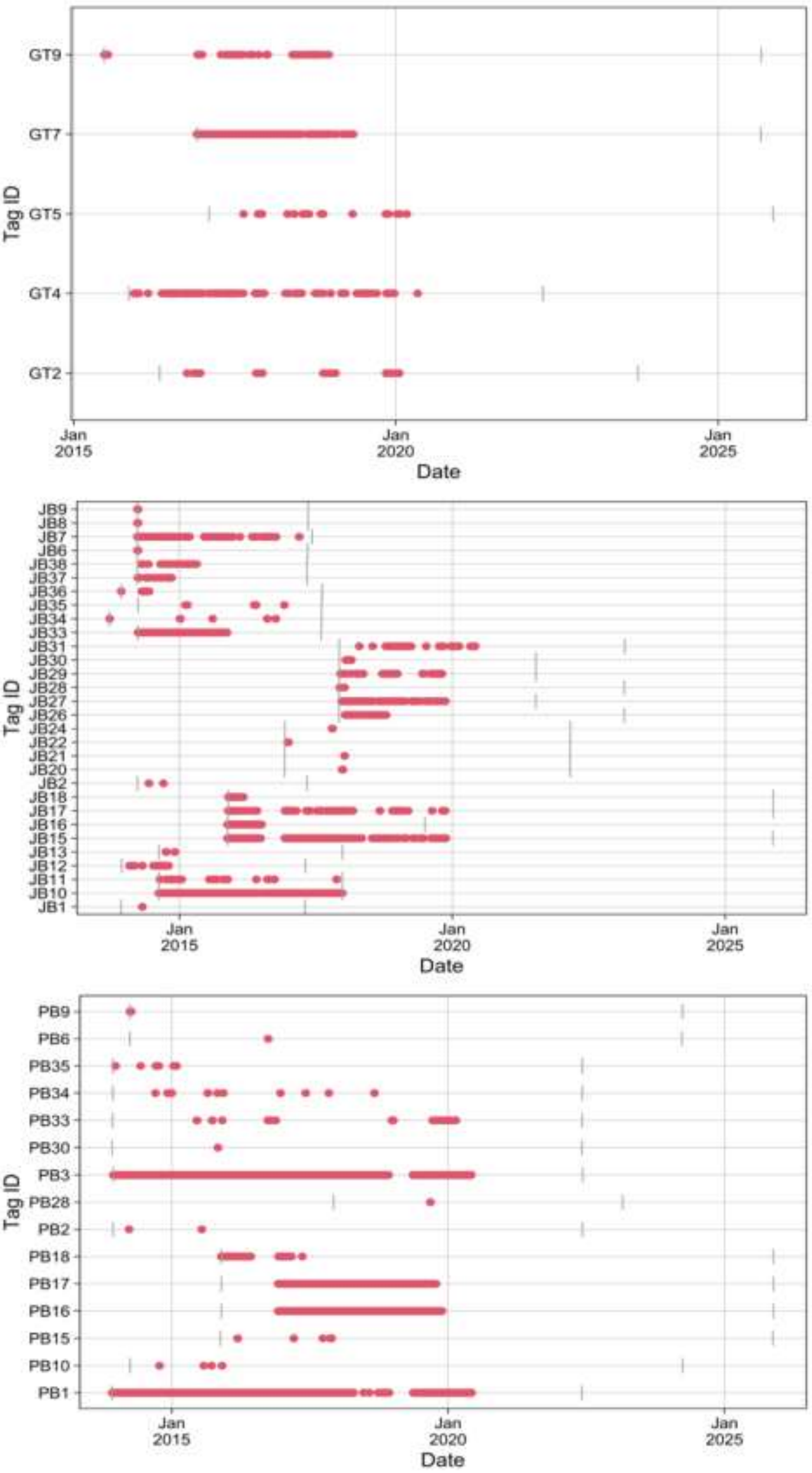


Figure 21: Summary of detection days for each of the study species: giant trevally (*Caranx ignobilis*) (GT), green jobfish (*Aprion virescens*) (JB) and potato bass (*Epinephelus tukula*) (PB) throughout the study period. Vertical grey lines indicate the start and end of the tag expected life.

Table 7: Fish detection summary of green jobfish (*Aprion virescens*) (n = 30), giant trevally (*Caranx ignobilis*) (n=5) and potato bass (*Epinephelus tukula*) (n=15) fitted. Fish were monitored for between 912 and 2375 d.

Tag ID	Species	Fork length (cm)	Days at Liberty	No. of Detections	No. Receivers	Days Detected	Detection Index (%)	Residency Index (%)
JB2	Green jobfish	48	1135	2	1	2	0.18	100.00
JB21	Green jobfish	70	1277	6	3	1	0.08	70.39
JB1	Green jobfish	68	1229	9	1	1	0.08	100.00
JB28	Green jobfish	79	914	11	3	3	0.33	70.62
JB20	Green jobfish	65	1277	42	5	5	0.39	74.13
JB35	Green jobfish	79	1228	66	3	6	0.49	90.23
JB24	Green jobfish	60	1276	80	4	3	0.24	86.67
JB37	Green jobfish	53	914	81	2	19	2.08	92.07
JB9	Green jobfish	42	1143	96	1	5	0.44	100.00
JB38	Green jobfish	50	1135	134	2	44	3.88	87.96
JB34	Green jobfish	71	1419	157	5	6	0.42	87.82
JB6	Green jobfish	45	1140	171	1	5	0.44	100.00
JB22	Green jobfish	77	1276	181	4	8	0.63	65.25
JB13	Green jobfish	67	1229	192	1	4	0.33	100.00
JB30	Green jobfish	58	913	202	2	8	0.88	81.66
JB29	Green jobfish	51	913	487	4	56	6.13	80.45
JB11	Green jobfish	62	1229	855	2	28	2.28	90.21
JB12	Green jobfish	59	1229	1089	2	33	2.69	95.60
JB26	Green jobfish	69	914	1187	7	123	13.46	81.93
JB8	Green jobfish	45	1142	1210	1	5	0.44	100.00
JB18	Green jobfish	69	1656	1880	2	59	3.56	92.09
JB7	Green jobfish	48	1171	2088	3	161	13.75	84.61
JB31	Green jobfish	66	912	2246	7	84	9.21	61.58
JB16	Green jobfish	59.5	1320	2906	2	196	14.85	87.86
JB27	Green jobfish	52	1317	3042	8	156	11.85	61.58
JB36	Green jobfish	85	1345	5436	3	41	3.05	83.91
JB17	Green jobfish	74	1656	8328	2	243	14.67	87.82
JB33	Green jobfish	60	1228	8813	6	425	34.61	90.23
JB10	Green jobfish	80	1230	29142	2	700	56.91	97.19
JB15	Green jobfish	80	1660	52664	2	604	36.39	98.35
GT9	Giant trevally	105	1281	561	17	54	4.22	44.67
GT7	Giant trevally	103	1283	1267	9	260	20.27	92.30
GT5	Giant trevally	84	1214	1615	13	44	3.62	60.15
GT4	Giant trevally	98	1668	3045	17	142	8.51	65.77
GT2	Giant trevally	69	1494	3082	13	76	5.09	49.35
PB28	Potato bass	145	912	5	1	1	0.11	100.00
PB6	Potato bass	135	2260	5	2	2	0.09	81.86
PB2	Potato bass	146	2370	9	2	2	0.08	90.60
PB34	Potato bass	135	2371	14	1	13	0.55	100.00
PB10	Potato bass	95	2257	22	2	4	0.18	91.79
PB9	Potato bass	130	2258	23	4	8	0.35	74.58
PB15	Potato bass	133	1660	42	8	10	0.60	49.10
PB30	Potato bass	109	2375	68	2	1	0.04	87.44
PB35	Potato bass	125	2371	113	13	17	0.72	42.52
PB33	Potato bass	90	2372	1273	2	35	1.48	96.68
PB18	Potato bass	105	1655	22694	2	257	15.53	99.94
PB1	Potato bass	118	2375	53625	2	1799	75.75	99.00
PB17	Potato bass	151	1655	212571	3	1018	61.51	88.59
PB3	Potato bass	125	2368	233538	2	2195	92.69	98.27
PB16	Potato bass	123	1655	236177	3	1068	64.53	87.32
Mean		85.50	1395	118089.50	2.00	535.00	11.81	83.69
SD		53.03	367.70	167000.94	1.41	753.78	21.65	16.17

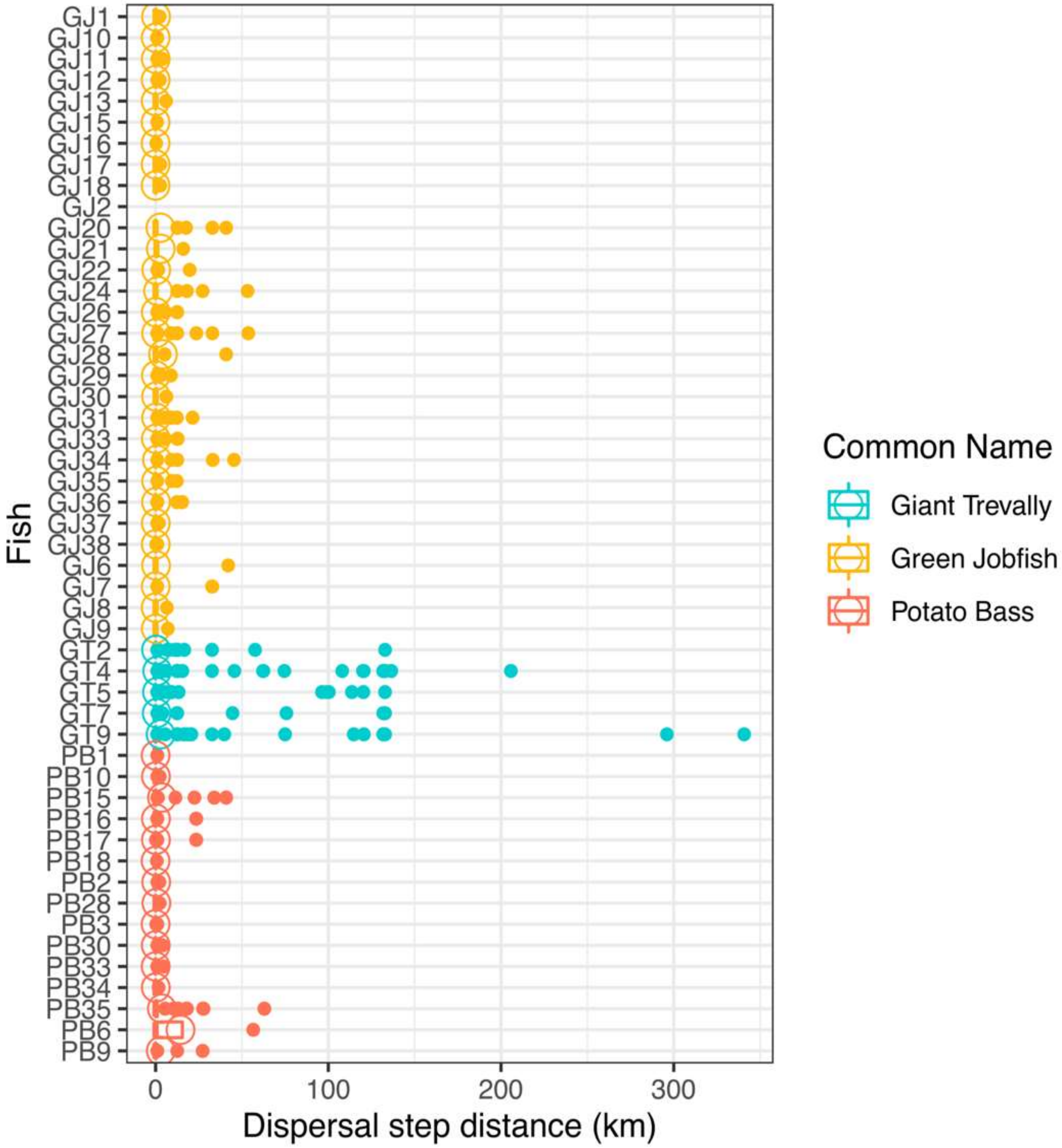


Figure 22: Dispersal step distances (km), range, mean and maximum, for each detected, acoustically tagged, fish, green jobfish (*Aprion virescens*) (GJ), giant trevally (*Caranx ignobilis*) (GT) and potato bass (*Epinephelus tukula*) (PB) estimated from raw detections. Open circles represent mean dispersal step distance, filled dots represent outliers (>1.5× interquartile range). Colour represents initial size class for each individual at capture.

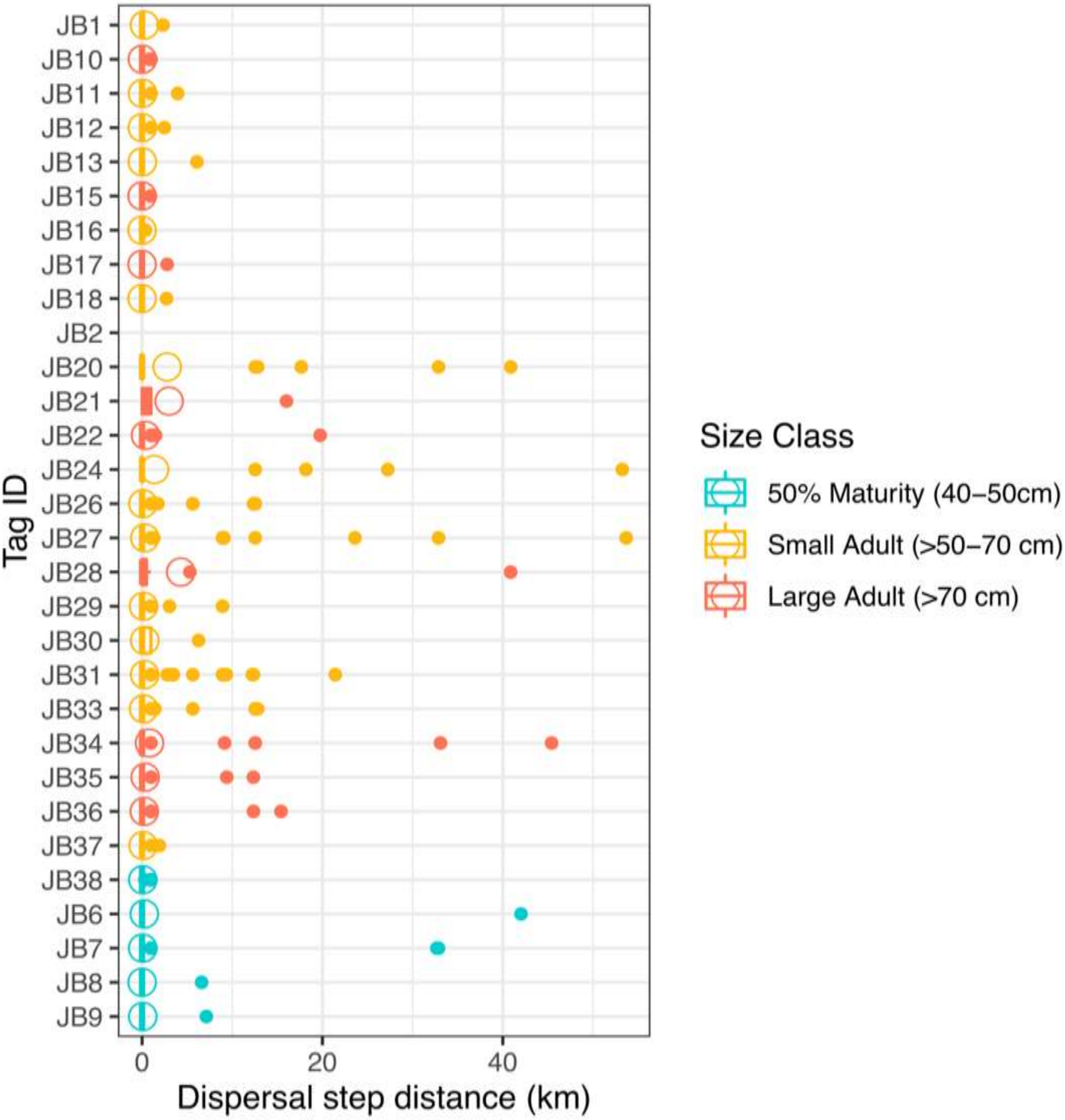


Figure 23: Dispersal step distance of acoustically tagged green jobfish (*Aprion virescens*) (JB) in three size classes namely "50% Maturity (40-50 cm)", "Small Adult (>50-70cm) "and "Large Adult (>70cm)". Open circles represent mean dispersal step distance, filled dots represent outliers (>1.5× interquartile range). Colour represents initial size class for each individual at capture.

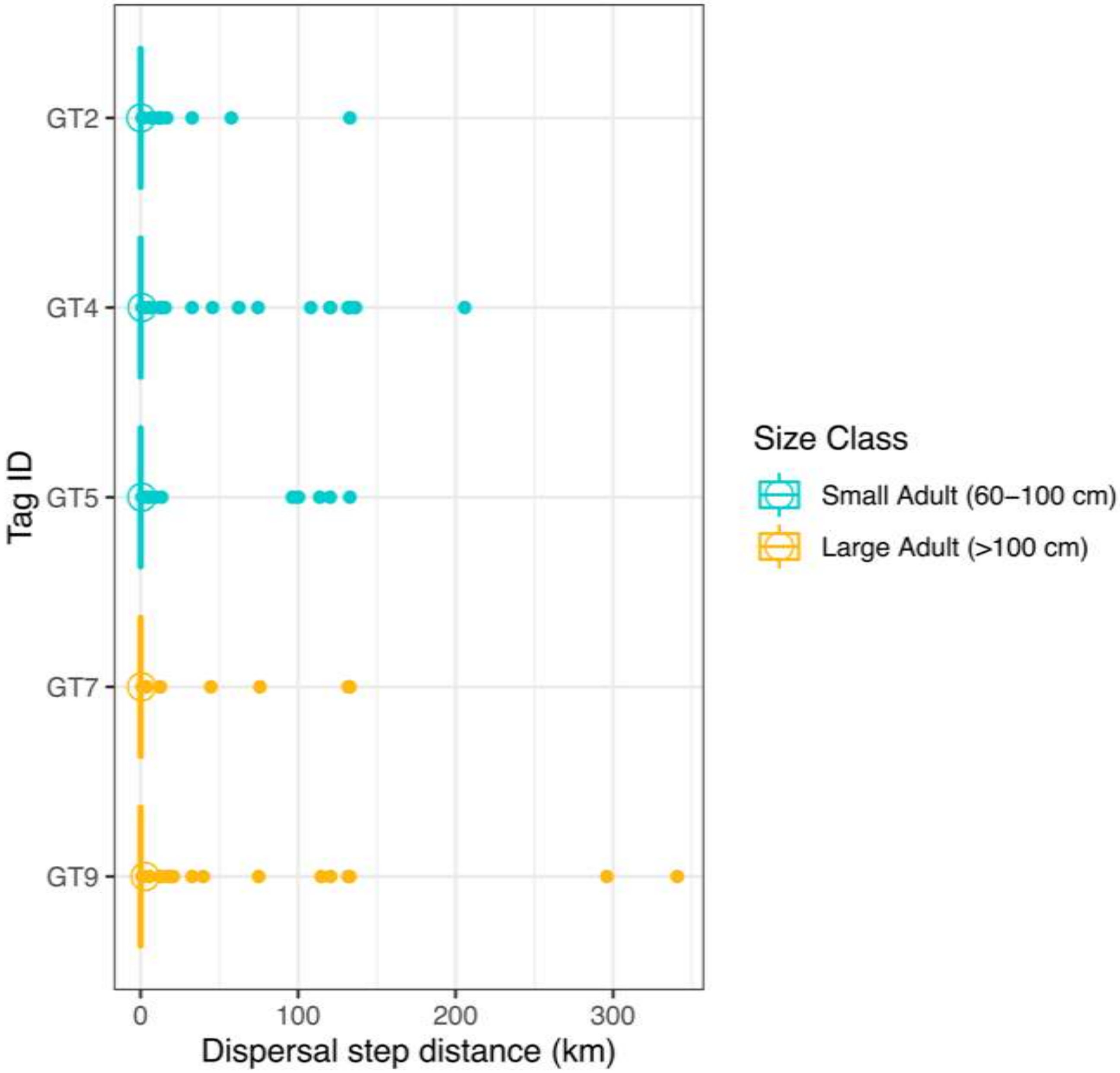


Figure 24: Dispersal step distance of acoustically tagged giant trevally (*Caranx ignobilis*) (GT) in two size classes namely "Small Adult (60-100 cm)" and "Large Adult (>100 cm)". Open circles represent mean dispersal step distance, filled dots represent outliers (>1.5× interquartile range). Colour represents initial size class for each individual at capture.

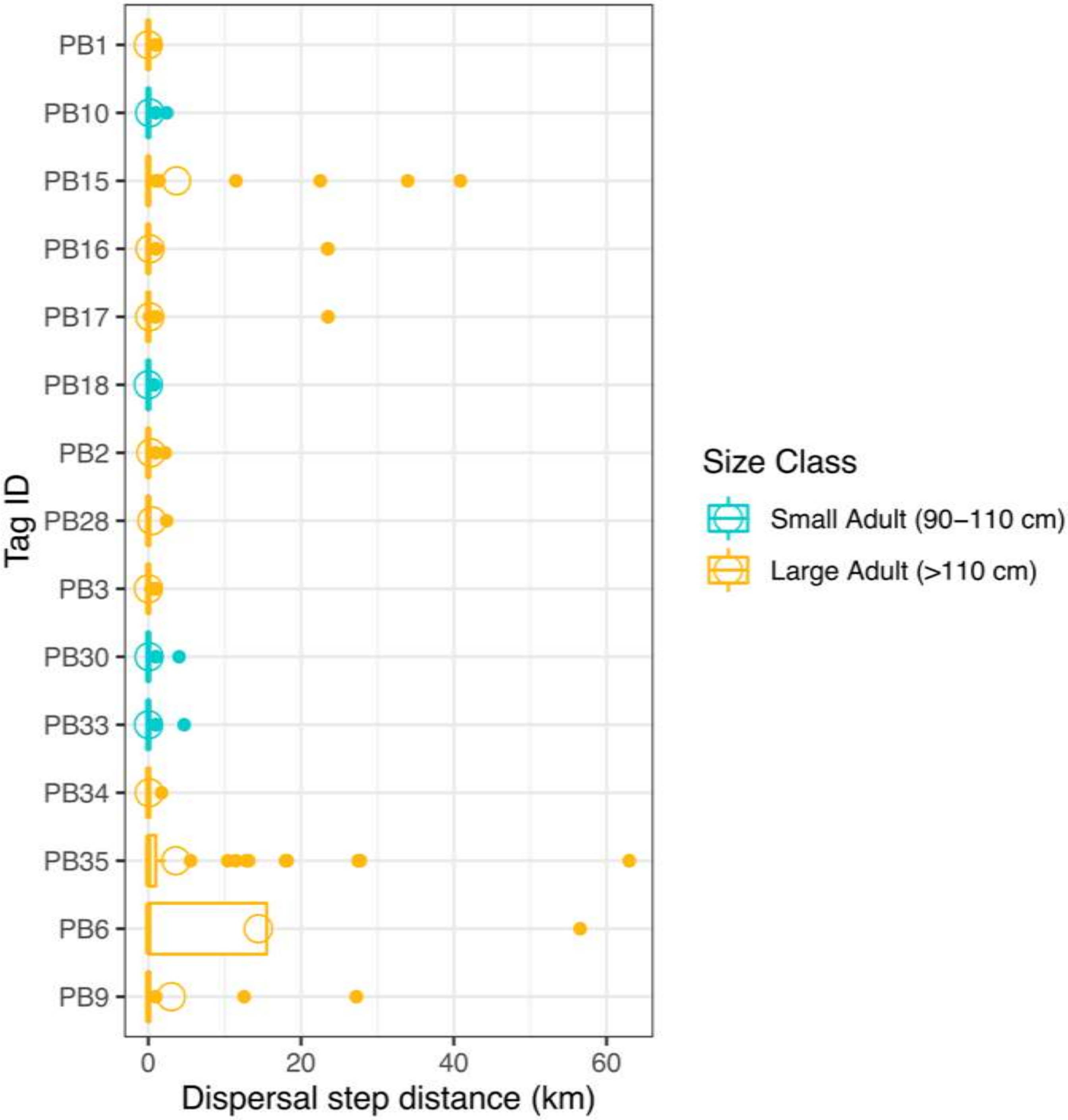


Figure 25: Dispersal step distance of tagged potato bass (*Epinephelus tukula*) (PB) in two size classes namely “Small Adult (90-110 cm)” and “Large Adult (>110 cm)”. Open circles represent mean dispersal step distance, filled dots represent outliers (>1.5× interquartile range). Colour represents initial size class for each individual at capture.

Periodicity

Fast Fourier Transformation (FFT) analyses for green jobfish (Tag ID JB15) at the Rabbit rock 1 receiver showed little evidence to support periodicity, both diel (12 hr) or tidal (6 hr) (Fig 9). The rose plot results were significant ($p < 0.01$) for both the Rao’s spacing test ($U = 316.07$) and the Raleigh test ($z = 58.64$) with a mean vector time (μ) of 11:54 AM.

Rose plots for potato bass (Tag ID PB17) at the Island rock 1 receiver showed some evidence of directionality (Fig 10a), yet FFT analyses showed a strong peak in spectral density at 24 hr and a minor peak at 12 hr (Fig 10b). The rose plot results were significant ($p < 0.01$) for both the Rao’s spacing test ($U = 337.46$) and the Raleigh test ($z = 329.29$) with a mean vector (μ) of 14:09 PM.

Rose plots for giant trevally (Tag ID GT4) at the Leven point receiver showed evidence to support directionality. The majority of detections with a 12 hr period between 3:00 AM and 15:00 PM (Fig 11a). The rose plot results were significant ($p < 0.01$) for both the Rao’s spacing test ($U = 1687.38$) and the Raleigh test ($z = 429.27$) with a mean vector time (μ) of 09:27 AM. The FFT analysis did not identify any patterns, possibly due to the lack of detections (Fig 11b). Only 1236 detections were recorded at the Leven point receiver over a period of 1 year which is not enough for any obvious patterns to be found in the FFT analysis.

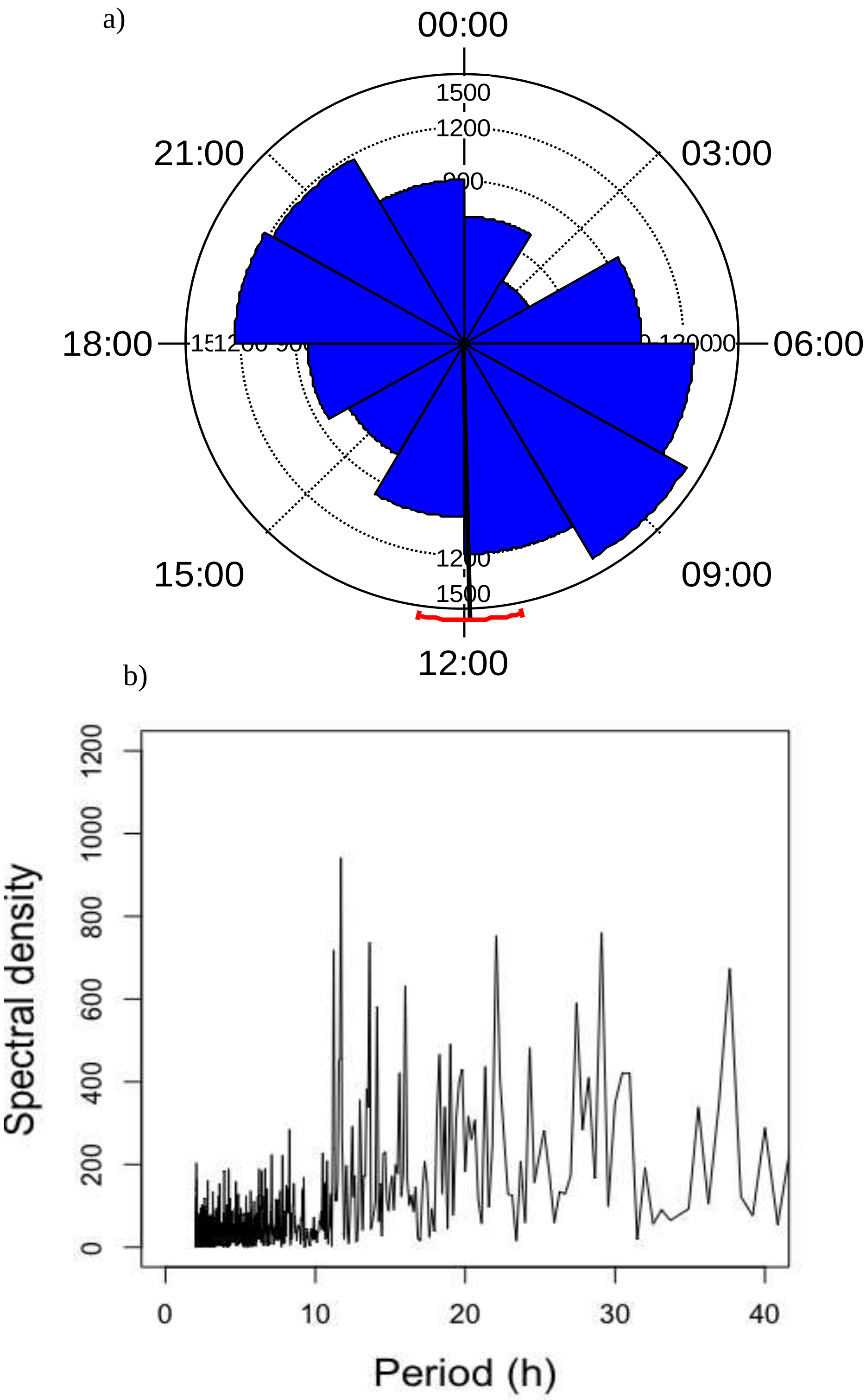


Figure 26: a) Rose plot of the number of detections per 2 hr bin for a 3 month time period of green jobfish (*Aprion virescens*) (Tag ID JB15) from January to March of 2017 at the Rabbit Rock 1 receiver. The black line indicates mean vector time (μ) with red error bars. b) Fast Fourier Transform analysis for the same fish over the same time period at the same receiver showing spectral density over a 40 hr period. Peaks indicate frequencies of dominant cycles in behaviour patterns.

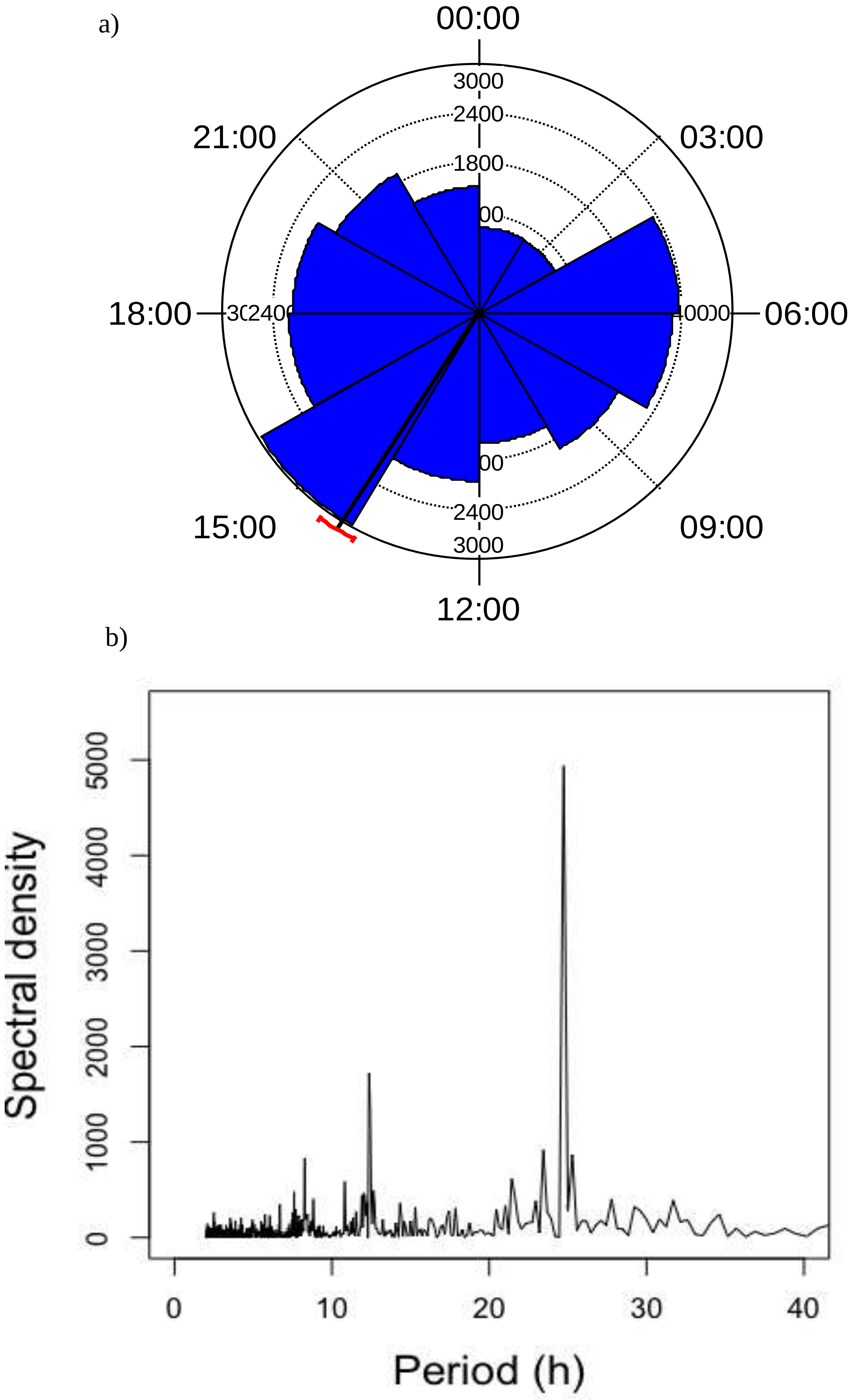


Figure 27: a) Rose plot of the number of detections per 2 hr bin for a 3 month time period of potato bass (*Epinephelus tukula*) (Tag ID PB 17) from January to March of 2017 at the Island Rock 1 receiver. The black line indicates mean vector time (µ) with red error bars. b) Fast Fourier Transform analysis for the same fish over the same time period at the same receiver showing spectral density over a 40 hr period. Peaks indicate frequencies of dominant cycles in behaviour patterns.

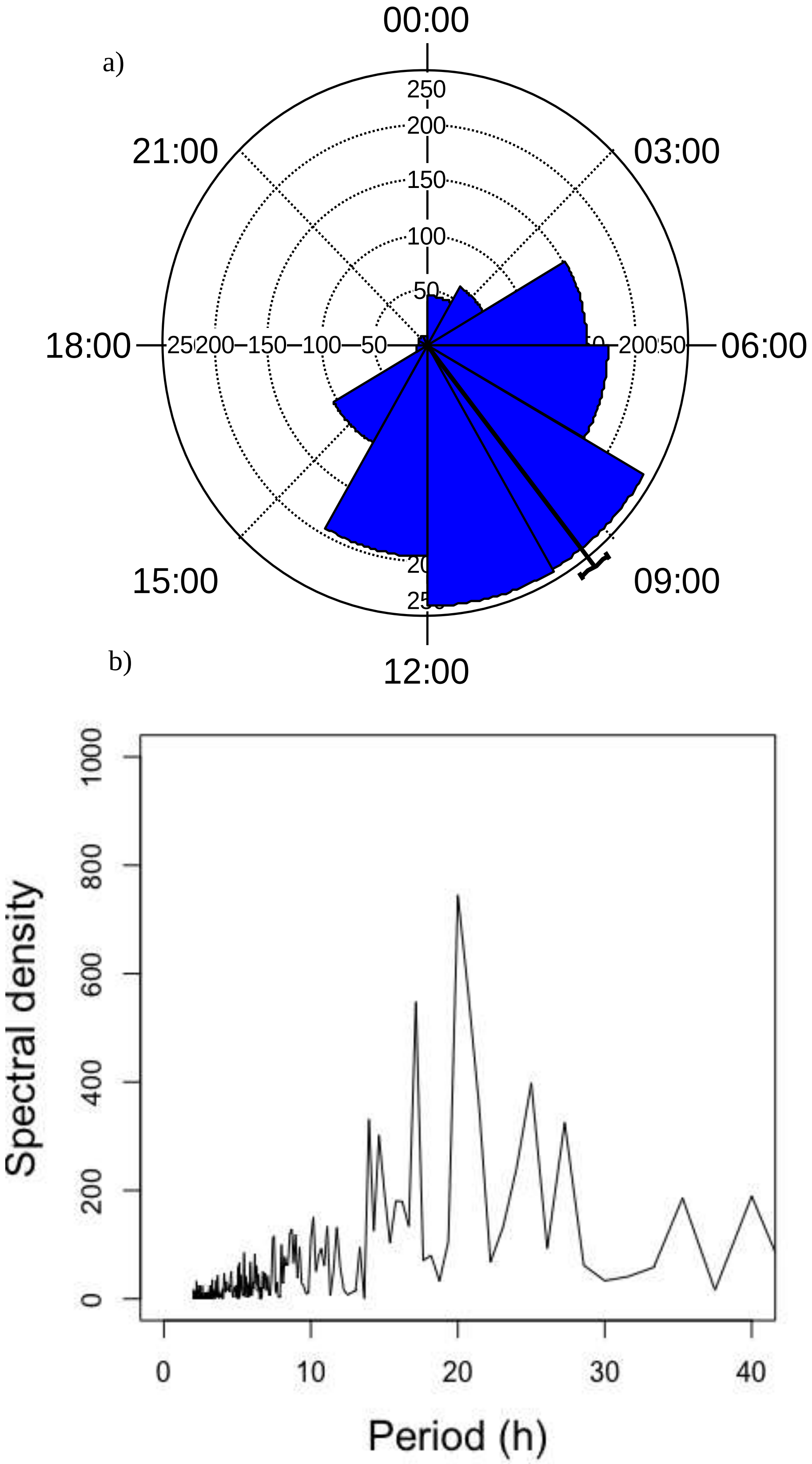


Figure 28: a) Rose plot of the number of detections per 2 hr bin for a 1 year time period of giant trevally (*Caranx ignobilis*) (Tag ID GT4) from April 2016 to March of 2017 at the Leven point receiver. The black line indicates mean vector time (μ) with red error bars. b) Fast Fourier Transform analysis for the same fish over the same time period at the same receiver showing spectral density over a 40 hr period. Peaks indicate frequencies of dominant cycles in behaviour patterns.

Movements beyond release locations

Fish of all species were detected in all protected zones within the iSimangaliso Wetland Park (IWP) and Ponta do Ouro Partial Marine Reserve (PPMR) (Table 4). Among the 30 green jobfish, 14 sanctuary zones and 4 multiple-use zones were visited. The average number of new zones crossed into per detected fish was calculated (Table 4). On average, each green jobfish crosses 0.6 new zones. Four of the 30 green jobfish conducted cross border movements from the IWP to the PPMR.

Among the 15 potato bass, 7 sanctuary zones and 2 multiple-use zones were visited. On average, each potato bass crosses 0.6 new zones. Two of the 15 potato bass conducted cross border movements from the IWP to the PPMR.

Among the five giant trevally, 11 sanctuary zones and 1 multiple-use zones was visited. On average, each giant trevally crosses 2.4 new zones. All five of the detected giant trevally conducted cross border movements from the IWP to the PPMR (Table 4).

Table 8: Summary of individual tagged fish per species who entered into new zones other than that in which they were released after tagging. Three sanctuary zones, border crossings into the PPMR, all multiple-use zones and a weighting of the number of new zones fish were detected in by the number of detected fish for each species (n).

Species	IOWZN	SDRZ	IORZN	PPMR	IOCPLZN & IOCPLZS	Zone crossings per fish
Green jobfish (n=30)	3	7	2	2	4	0.6
Potato bass (n=15)	1	1	2	3	2	0.6
Giant trevally (n=5)	4	2	0	5	1	2.4

Latitudinal movement patterns

The latitudinal movement patterns for all five detected giant trevally (Fig 12) clearly show them undergoing austral summer (October-February), north-south migrations to the southern Mozambique aggregation site. Detection data for some of the individuals: GT4, GT7 and GT9, shows them returning to the same latitudinal zone after each migration indicated by the large amount of detections at the same latitude (Fig 12 (GT 4,7 &9)). The home range of GT4 and GT7 can be identified as being in close proximity to the leven point receiver at the southern end of the IOWZN. The migration distance is estimated as 130 km each way from the leven point receiver to the aggregation site for these two fish.

This is in contrast to latitudinal movement plots for green jobfish and potato bass. No clear latitudinal movement patterns were identified for green jobfish (Fig 13) or potato bass (Fig 14). Tag ID JB31 differed from other green jobfish in that it appears to have made two, mid-summer, southern movements to the same latitudinal area (-27.912 (Leven point receiver)), both times returning to latitudinal area from which it left. Detections for each individual are almost entirely at the same latitudinal zone with almost zero north-south movements detected.

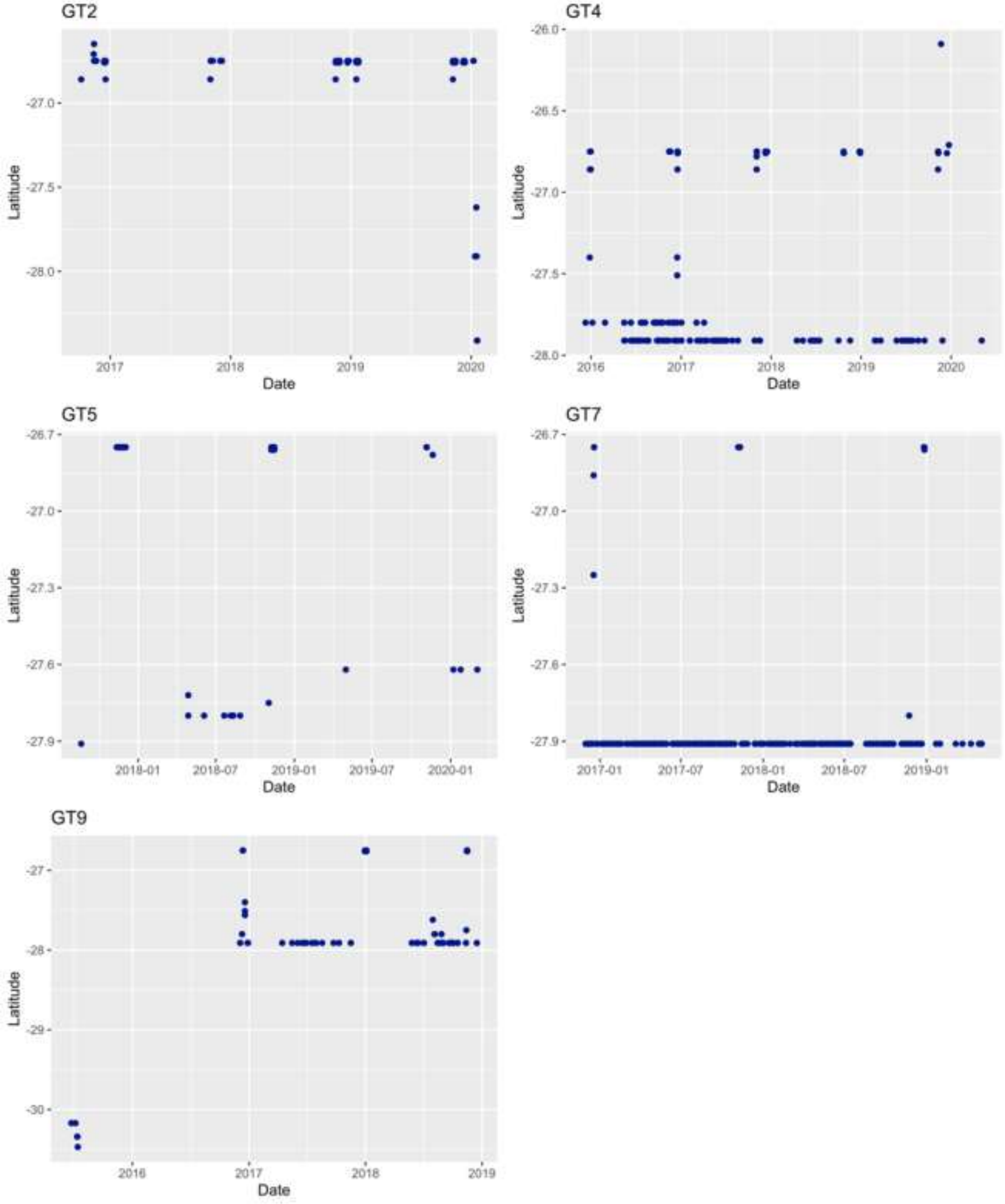


Figure 29: Latitudinal detection plot across the study period for all detected giant trevally (*Caranx ignobilis*) (GT).

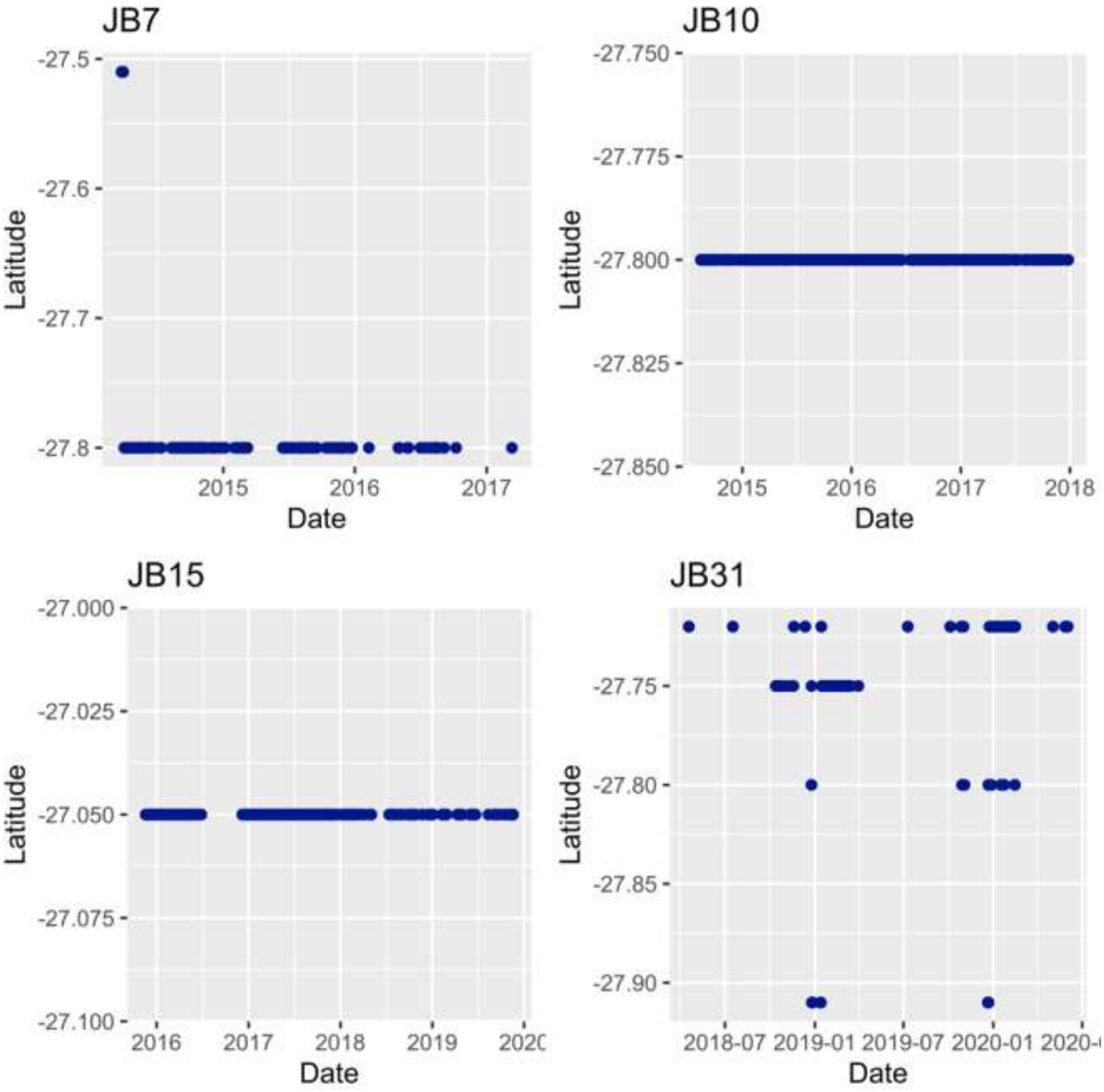


Figure 30: Latitudinal detection plot across the study period for four highly detected green jobfish (*Aprion virescens*) (JB).

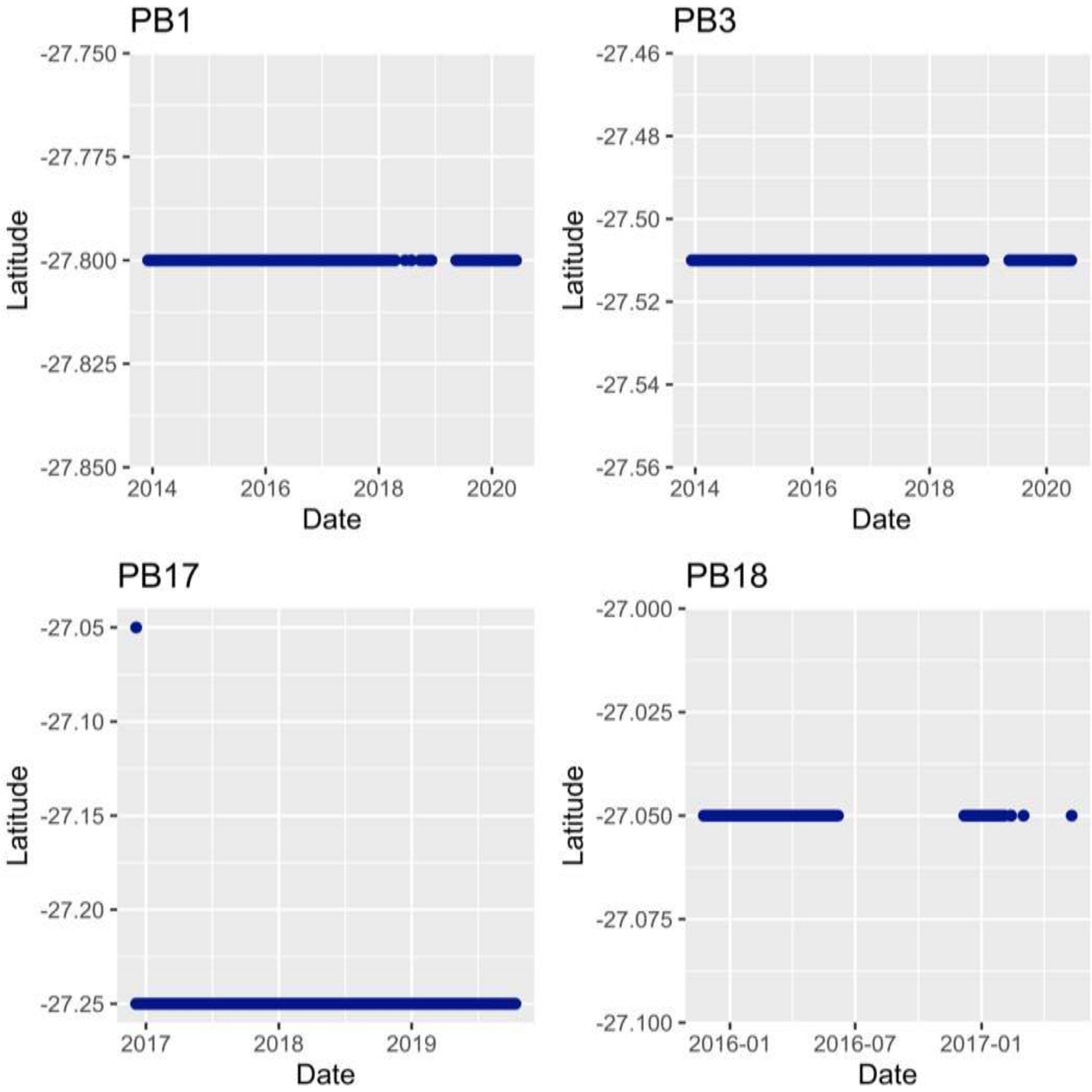


Figure 31: Latitudinal detection plot across the study period for four highly detected potato bass (*Epinephelus tukula*) (PB).

Connectivity

Connections between all management zones of the IWP and border crossings into the PPMR can be seen for all three species (Fig 15, 16 & 17). Giant trevally (Fig 15) moved the longest distance between receivers on the southern coast of KZN and receivers within the IWP. However, they also yielded the lowest number of connections of the three species between any two receivers. The maximum number of connections for giant trevally was five. Green jobfish (Fig 16) and potato bass (Fig 17) had a maximum of 1263 and 47 921 connections between any two receivers, respectively.

Giant trevally had the lowest number of detections per receiver, followed by green jobfish and potato bass which had the highest. The connectivity plots provide a visual representation of the distribution of activity space use among the management zones of the IWP and PPMR. These are clearly visible for all three species at differing levels. A greater number of long-distance connections between receivers can be clearly seen for giant trevally (Fig 15) compared to green jobfish (Fig 16) and potato bass (Fig 17).

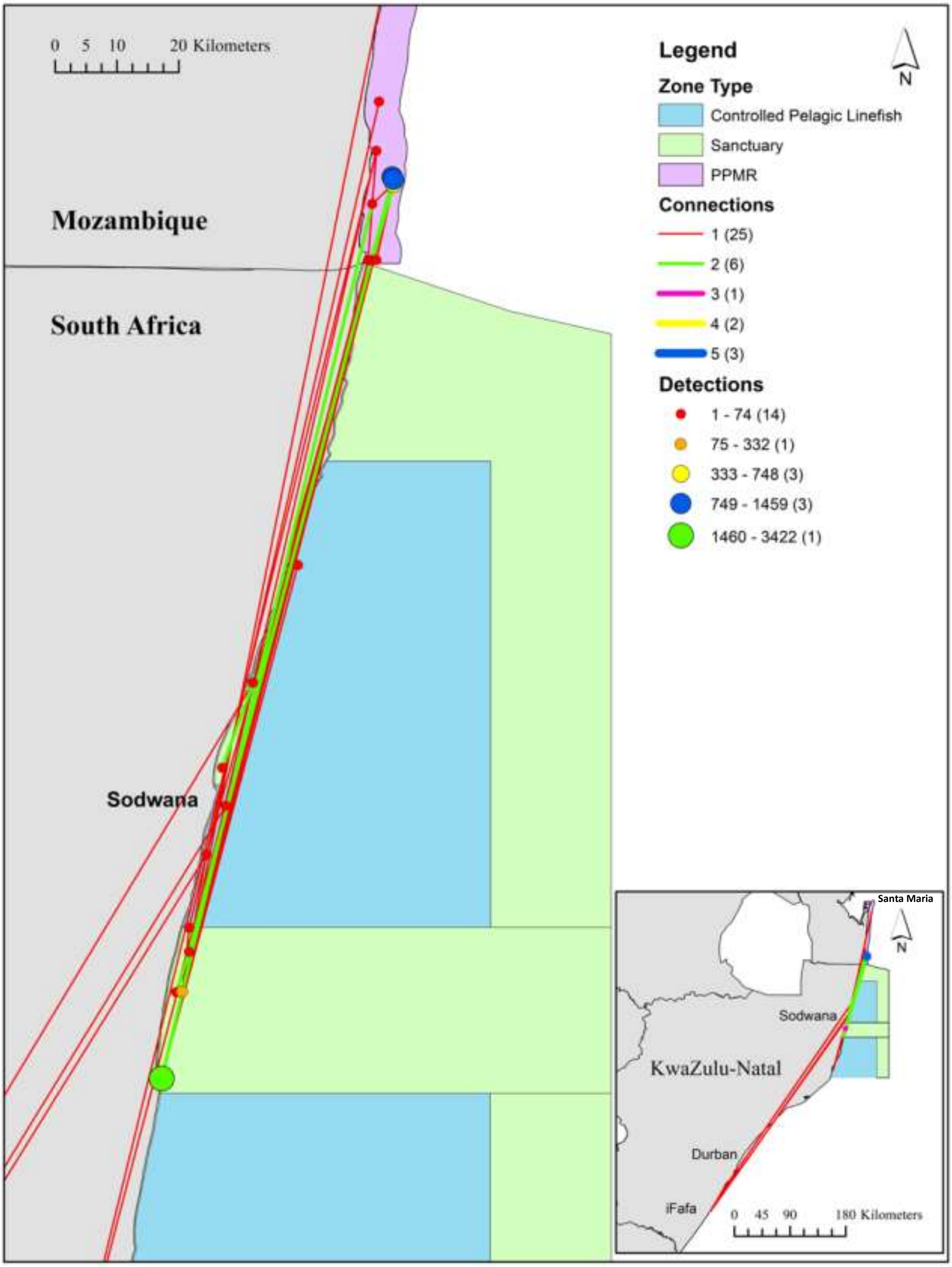


Figure 32: Connectivity plot for giant trevally (*Caranx ignobilis*) (n = 5) within the IWP and PPMR, showing the number of detections at each receiver (coloured circles), the connection strength between receivers (coloured lines) and count of each feature in brackets.

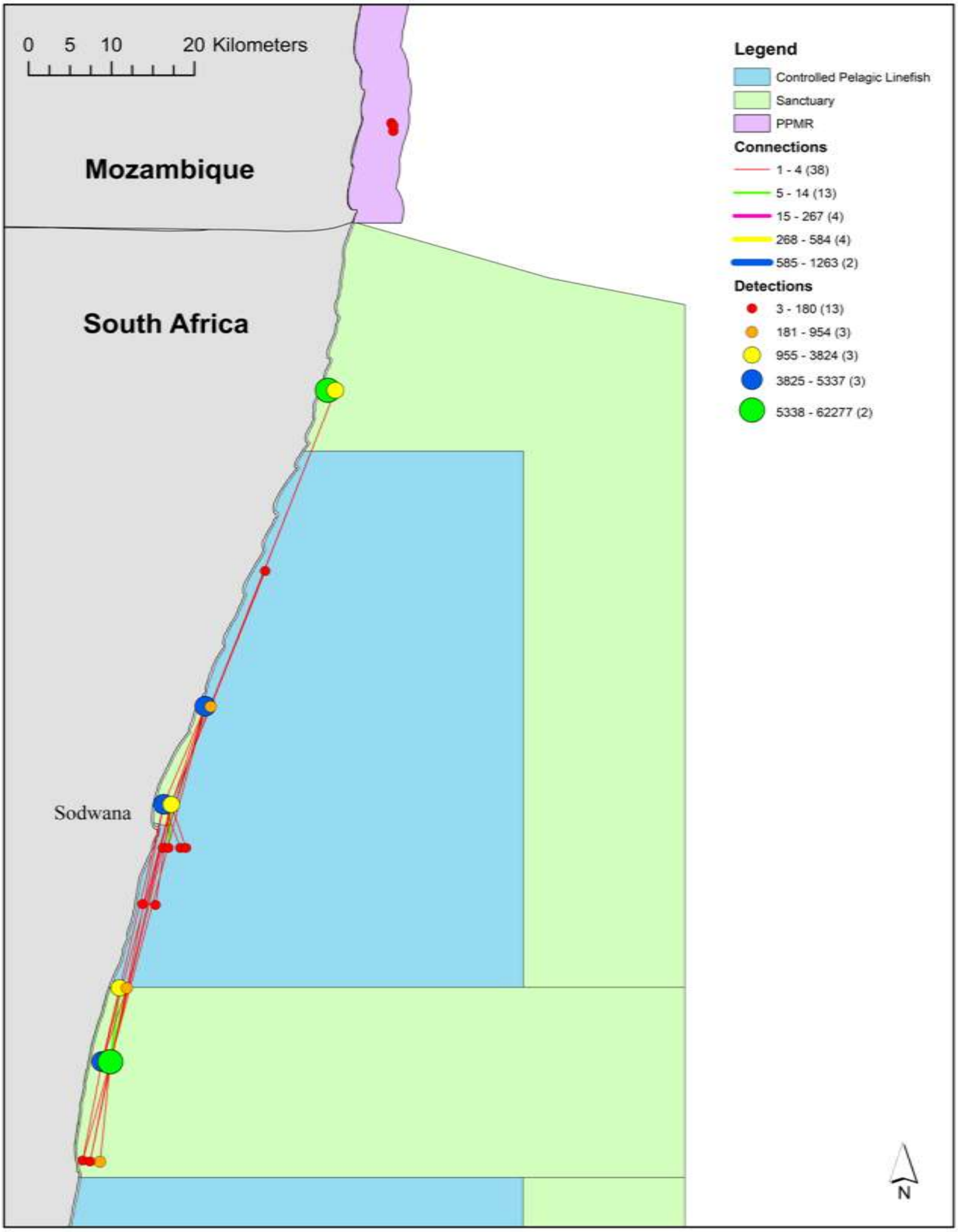


Figure 33: Connectivity plot for green jobfish (*Aprion virescens*) (n = 30) within the IWP and PPMR, showing the number of detections at each receiver (coloured circles), the connection strength between receivers (coloured lines) and count of each feature in brackets.

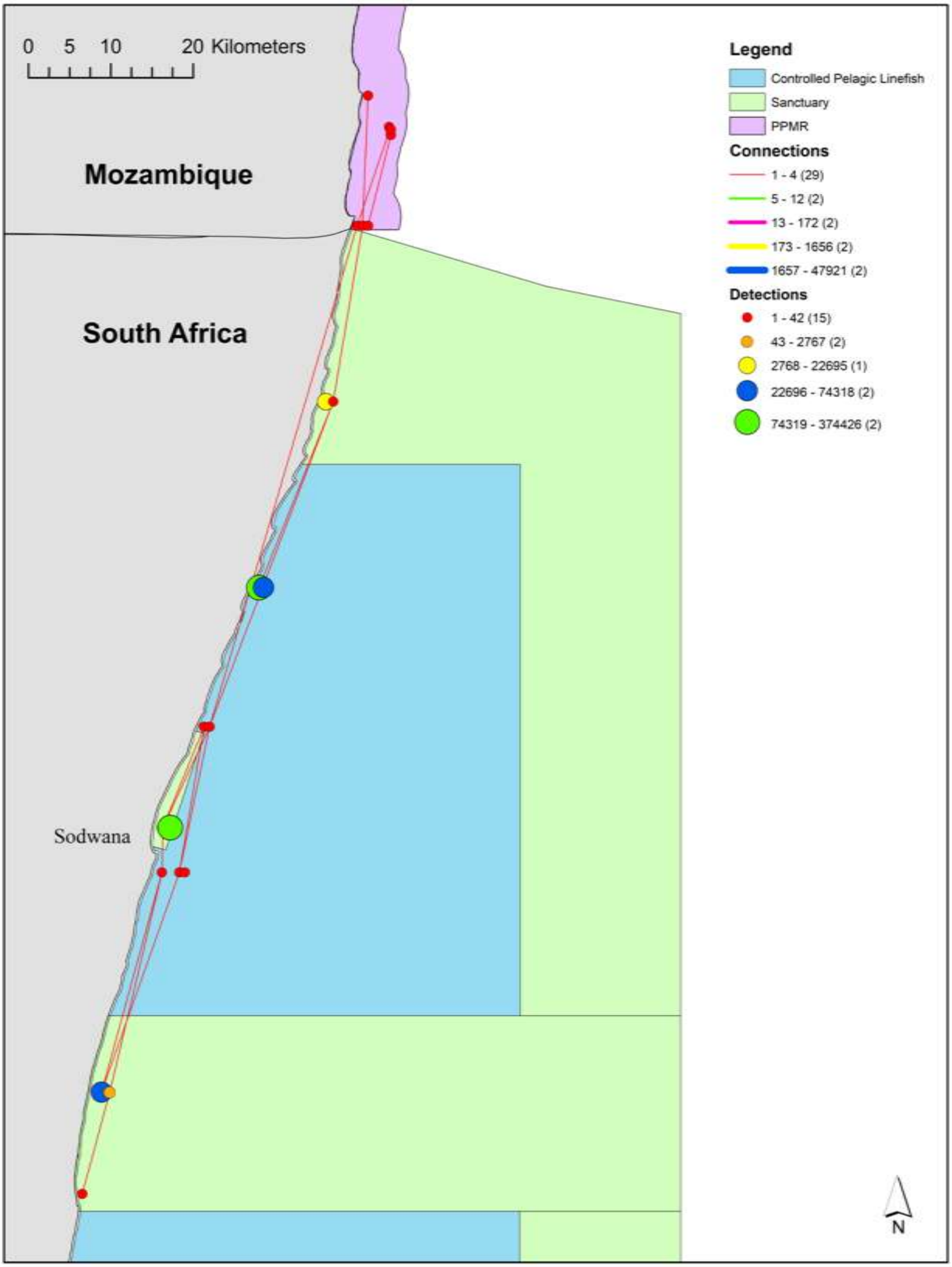


Figure 34: Connectivity plot for potato bass (*Epinephelus tukula*) (n = 15) within the IWP and PPMR, showing the number of detections at each receiver (coloured circles), the connection strength between receivers (coloured lines) and count of each feature in brackets.

Discussion

This study represents one of the longest studies (seven years of data) on tropical reef fish using passive acoustic telemetry in southern Africa. The study tracked 82 fish fitted with acoustic tags and monitored them for seven years. Additionally, it was the first to study the movement patterns of potato bass using acoustic telemetry, as all previous studies used mark-recapture methods (Mann et al. 2015). The results from the study of three top predatory reef species highlighted the difficulties in designing zonation schemes that will aid in a holistic management plan that encompasses the protection of all species. The transboundary movements and movements between management zones of some of the fish (primarily giant trevally) highlight the challenges of using spatial protection for species moving between different management zones. The first objective to quantify and categorise the spatial and temporal movement behaviour of each of the three species in the iSimangaliso Wetland Park (IWP) resulted in the calculation of detection, residency and periodicity indices. The results are considered alongside aspects of life-history and morphology of each species to provide a clearer understanding of their population dynamics and functional roles in the local ecosystem.

Detection and residency summary

The post release detection frequency of tagged fish in this study was relatively low for potato bass (15 out of 35), green jobfish (30 out of 38) and giant trevally (5 out of 9), when compared to other studies using similar methods on reef fish (Filous et al. 2017, Daly et al. 2019, Daly et al. 2021) .It was assumed that the poor detection rates of released fish were because the fish were released too far from receivers or possibly suffered from post-release mortality.

Potato bass made up 30 % of all detected fish in this study yet had 85.2 % of all detections which considerably was more than the 13.7 % by green jobfish and 1.1 % by giant trevally.

The high percentage of tagged potato bass that were not detected is likely because they are reef associated and the receivers were placed on sand between reef complexes. Furthermore, the assumption must be made that tagged individuals will behave in the same manner as before being handled and surgically implanted with a tag (Brown et al. 2011). More likely, the low percentage of tagged potato bass detected is due to their high site fidelity to small home ranges which may not overlap with the detection range of any receiver. This idea is reinforced by the results which highlight that certain potato bass that were released within close proximity to a receiver, were detected consistently by that same receiver across multiple years, thus explaining the high number of detections relative to the other species. The biggest limitation to this study is that the original study was designed to detect connectivity between zones and not to study home range metrics or temporal patterns of movement. It is for this reason that receivers were placed on sand at the edge of the major reef complexes as well as between major reef complexes. The lack of receivers on the reef complexes themselves meant that there was a significant lack of detections from potato bass and green jobfish that live primarily on the reef complex itself. Potato bass and green jobfish were detected by an average of three receivers compared with the average of 14 for giant trevally. Despite tagged giant trevally having been detected the least at only 1.1 % of detections, they were still detected by 11 more receivers on average than both potato bass and green jobfish, indicating larger patterns of movement.

The detection index (DI) of all three species in this study were low compared to that of similar studies (Meyer et al. 2007a, Meyer et al. 2007b, Sattar et al. 2012, Filous et al. 2017, Daly et al. 2021, Evans 2021) and could be a result of a lack of comprehensive receiver coverage (1.54 %) over the large study site (approx. 1500 km^2). Receivers were spread throughout the large IWP, across its different zones and major reef systems. A DI reflects how long each tagged fish is detected within the array during the given study period. It gives no indication of residency or affiliation to a certain set of receivers or area. A DI works well in areas such as coral atolls where receiver coverage can sometimes be 100 % of the study area but this is not feasible within the IWP. The geography and findings of this study are unlike similar studies on the atolls of Hawaii (Lowe et al. 2006, Meyer et al. 2007a, Papastamatiou et al. 2015, Filous et al. 2017, Evans 2021) and the Seychelles (Daly et al. 2021) which found that giant trevally and green jobfish were confined to small atolls with no evidence of inter atoll movements of giant trevally and green jobfish. Accurate home range size metrics were unable to be calculated due to the lack of continuous detection data as a result of low effective receiver coverage within the IWP and the placement of receivers on sand between reefs. More fine scale studies on specific reef systems within the IWP would need to be conducted to accurately determine home range size and other activity space use metrics such as fixed kernel utilisation distribution and brownian bridge kernel distribution models (Udyawer et al. 2018). The design of the acoustic receiver array will ultimately determine the resolution of the detection data (Heupel et al. 2006).

To more accurately assess the residency of each species in a wide-ranging receiver array, a novel residency index (RI) was created for this study. It used a Shannon-Weiner diversity index to represent the spread of detections across the receivers. The high average RI for potato bass (95 % [± 5.6]) and green jobfish (85.2 % [± 13.7]) show that they are both highly resident species to their home reefs. Examples of this can be shown by individuals such as Tag ID (PB1, PB3, PB17, JB7, JB10, JB15) which had significant, almost continuous, daily detections over multiple years by receivers in the same area. This provides evidence that both potato bass and green jobfish have circumscribed spatio-temporally distinct territories (Koenig et al. 2017). Potato bass were found to have a higher RI than green jobfish, likely due to their different foraging methods with potato bass being ambush predators and green jobfish patrolling their home reef, actively hunting prey. Giant trevally were found to have the lowest RI (66.9 % [± 18.3]), possibly due to their annual coastal migrations related to spawning activity and highly active hunting style. The low standard deviation in RI values for potato bass indicates little variability in residency between individuals. Green jobfish and giant trevally have a larger standard deviation in values respectively indicating greater variability in residency between individuals likely due to their active hunting style, often following schooling baitfish.

Periodicity

No discernible cycles in activity were found for green jobfish (JB 15) at the Rabbit rock 1 receiver; however, rose plots indicated a 12 hr pattern with the highest proportion of detections between the hours of 6am-12pm and 6pm-12am (Fig 9). Meyer et al. 2007b showed individual variation in diel cyclical patterns of jobfish in Hawaiian atolls where there were dominant 24hr peaks in detections of 13 of the 16 jobfish assessed and significant differences in night and day detections for 18 of the 28 highlighting individual variability within this species. Filous et al. (2017) found summer presence and winter absences for green jobfish indicating migration. Neither of these were found in this study. Tidal cycles are likely to play a larger role in fish movement patterns on coral atolls than they would in open ocean reefs such as the IWP (Lédée et al. 2015, Lea et al. 2020), whereas thermoclines and ocean currents are likely to a greater influence on fish movement in the IWP (Maree et al. 2000). Seasonal spawning of green jobfish in southern African waters has been observed from January through to May (van der Elst 1993) and again in November (Allen 1985). No patterns of aggregations were identified during these months, indicating that the spawning that is occurring is likely localised and in smaller groups.

Strong diel movement patterns were identified for potato bass at the Island rock 1 receiver, with the results of the Fast Fourier Transformation (FFT) analyses (Fig 10) showing that potato bass exhibited strong diel movement patterns (reflected in a 24h spike) and tidal patterns (reflected in a 12h spike). Tidal patterns of movement are likely linked to feeding, whereas diel cycles could be as a result of daily patrols of an individual's territory. Strong diel patterns have been found in other grouper species (Koeck et al. 2014), it is possible that the strong diel spike found in this study could be associated with the potato bass being active during the day and resting in caves during the night, as was found with the dusky grouper (*Epinephelus marginatus*) in France (Koeck et al. 2014). The strong tidal peak observed in the potato bass data could have been associated with feeding. However, range tests of receivers were not conducted in Koeck et al. (2014). Therefore differences in day and night time detections could be due to external factors such as water temperature and thermoclines (How and de Lestang 2012), and differences in day and night time background reef noise (Payne et al. 2010) .

The FFT analysis conducted on detection data from GTs (see Fig 11) suggested that there were no diel or tidal movement patterns. However, it is likely that individual fish did not produce enough continuous detections at any receivers because they were mobile and only recorded sporadic detections and hence diel or tidal patterns were not apparent in the data. Similar to the results of Meyer et al. (2007a) and Filous et al. (2017), giant trevally detections were concentrated during the day time. Lédée et al. (2015) found the opposite with the majority of detections occurring at night. It is clear that giant trevally occupy different areas between day and night. A bias towards mainly daytime detections could be that the receiver array is situated either in areas that giant trevally utilise during the day or the array is situated where they are present at night. Giant trevally are believed to be more active at night (Meyer et al. 2007a) so it is most likely that tagged giant trevally in this study moved beyond the receiver array during the night, potentially feeding in deeper waters (Evans 2021) or in the shallow surf zone at night. Reductions in receiver performance at night can occur; however, sentinel tag and receiver range tests conducted for this study did not indicate any significant difference in performance between day and night, indicating that these detection data are accurate (How and de Lestang 2012, Kessel et al. 2014). Furthermore, loss of range would also not account for the complete absence of any detections during the night time period for the individual giant trevally. Due to a lack of significant continuous detection data for most tagged fish, specific individuals with good detection records were used to analyse temporal patterns of movement.

Green jobfish, potato bass and giant trevally have contrasting movement patterns that correspond with their morphology and life history. Green jobfish are mid-water predators that show strong site fidelity in this study. In the IWP, spawning potentially occurs in smaller, more frequent localised aggregations within their home range or reef complex as larger aggregations would have likely been shown by the data. Their lunate tail corresponds with their movement style identified in this study. Their morphological characteristics are aligned with their foraging style and movement patterns. They are station-keepers that patrol their home range to forage. The lack of temporal patterns of movement identified for green jobfish indicate that movement may be reactive to unpredictable factors such as thermoclines, current and water temperature.

The high level of residency found for potato bass could be a result of their morphological characteristics and reproductive strategy (Helfman et al. 2009). Other grouper within the Serranidae family have been observed feeding cooperatively with moray eels (Bshary et al. 2006). This indicates a high level of intimate knowledge and relationships of a home reef that more mobile species would likely not achieve. The high residency found for potato bass corresponds with their territoriality (Murase et al. 2018) and protogynous reproductive strategy (Yeh et al. 2003). The few cases of larger ranging movements identified in this study may be a result of either searching for better habitats and spawning opportunities or they themselves are pushed out of their home reef by a larger competitor. The presence of small testes in potato bass is indicative of a small level of sperm competition, typical of a protogynous reproductive style and the absence of aggregatory mating (Mackie 2007, Erisman et al. 2013). Diel patterns identified for potato bass are likely a result of foraging and territoriality.

Giant trevally are wide-ranging predators that feed over vast areas of reef, surf zone and estuaries within their home range. They rely on speed and aggression to hunt. Their forked, low aspect tail is indicative of the ranging movement style and ability to migrate the long distances identified in this study (van der Elst 1993, Helfman et al. 2009). Their gonochoristic, broadcast spawning strategy is what drives the summer migrations every full moon to an aggregation site in southern Mozambique, returning each time to their home range.

It must be stated that perioditic analyses were only conducted using a single fish of each species due to insufficient continuous detections which we recognise is not representative of the population especially given the individual variability in cyclical patterns in other species. However, despite this, a strong diel and tidal pattern was observed in the data and cannot be ignored.

Interzonal and latitudinal movement

The second objective of this study was to assess the current zonation of the IWP in terms of the protection and management of the fisheries. In order to do this, long distance and interzonal movement patterns of each species relative to zonation were quantified to provide evidence that any or all of the study species move between management zones with varying levels of protection. Further research could establish how effective the iSimangaliso MPA might be for providing protection from fishing related mortality.

The IWP reef systems occur in a north-south orientation on a narrow continental shelf. The species in this study generally occur on reef systems less than 100 m deep. Therefore, they are restricted to primarily north-south movements by the orientation of the South African coastline and the continental shelf. It is for this reason that large movements can be expressed as shifts in latitude. The horizontal strings of receivers at zonal and international borders provide the best chance at detecting large north-south movements within the IWP and PPMR.

Movements between all zones within the IWP and PPMR was found for all three species. Potato bass and green jobfish showed similar movements between management zones with both species having a ratio of crossing into 0.6 new zones per detected fish. Whereas, giant trevally on average, crossed into 2.4 new management zones per detected fish. This higher value is likely as a result of the summer, lunar migration of giant trevally to southern Mozambique (Daly et al. 2019), in which they cross multiple zones to and from the spawning location. From connectivity plots we can see that even resident species such as potato bass do undertake interzonal movements and even cross border movements. Tagged fish of all three species moved into every management zone within the study site, with the exception of giant trevally, which were not detected in the iSimangaliso offshore restricted zone (IORZN). However, all five detected giant trevally crossed the border into the PPMR, thus it can be assumed that all five fish crossed the IORZN during their aggregatory migration. One giant trevally undertook a long-distance movement from the IWP to southern KwaZulu-Natal (KZN), indicating that the receiver array used in this study was capable of detecting instances of long-distance movement of tagged fish if they occurred.

Annual northerly migrations during the summer months were recorded for giant trevally. These fish return to the same latitudinal range after every migration, indicating that these fish have a circumscribed feeding area that they return to after each migration (Fig 12). Contrary to giant trevally, no clear migratory or aggregatory patterns were identified for green jobfish and potato bass. Van der Elst (1993) suggested that the spawning grounds of potato bass was in northern KZN or southern Mozambique. Green jobfish and potato bass were both found to be resident to a circumscribed area, year-round for several years. The lack of evidence of migratory or aggregatory behaviour could be an indication that green jobfish and potato bass spawn locally within their home range.

Using the results found in this study and following the fish movement classification system put forward by Dingle (1996), both potato bass and green jobfish can be classified as station-keeping species, with infrequent occurrences of ranging. This behaviour is similar to that found by Maggs et al. (2013) in other serranids, *Epinephelus andersoni* and *Epinephelus marginatus*, in the Pondoland MPA of South Africa. Giant trevally exhibit ranging behaviour within a large area and display multiple summer migrations coinciding with the full moon, consistent with those documented by Daly et al. (2019), returning to a core home range after aggregating.

Implications for management

Acoustic telemetry has yielded more robust information than was available in the past for marine spatial planning in so far as it effects fisheries management (Halpern et al. 2010, Crossin et al. 2017). This analysis of acoustic telemetry can become a crucial tool in improving Marine Protected Areas (MPA) design, efficacy and management strategies in the IWP. It has provided valuable information about the residency of three ecologically important reef fish, their movements among management zones and identified temporal spawning migrations and locations.

MPAs are generally effective at protecting site attached species with small home ranges, yet can be less effective for highly mobile, less site specific species, with larger home ranges (McCook et al. 2010, Currey et al. 2014, McLaren et al. 2015, Crossin et al. 2017). Acoustic telemetry can aid in identifying whether current MPA boundaries are adequate in terms of size and location for these three species. The extent to which the current zonation of MPAs protects each species needs to be understood so that it can be better scaled to encompass the movement patterns of each species.

The design of the IWP sanctuary zones is such that it protects a majority of the three major reef complexes within the IWP. By doing this, sanctuary zones protect a majority of the suitable area for all three reef associated study species. The placement of the IWP sanctuary zones is close enough to allow for movement between zones for even highly resident fish species such as mature potato bass and green jobfish. These highly resident species are protected throughout the IWP, with potato bass also being protected nationally; however, sanctuary zones provide pristine, undisturbed reef habitats and ecosystems that help support large populations of these important species. The abundance of potato bass within the IWP was observed to be notably greater inside sanctuary zones (Floros 2010, Mann 2012). Potato bass are a key indicator of reef health in the IWP and reefs of South Africa and are uncommon outside of the IWP due to their high susceptibility to fishing pressures (Floros 2010). Within the IWP (10 700 km^2), approximately 4700 km^2 fall within sanctuary zones. Based on the residency of green jobfish and potato bass, the size and placement of the current sanctuary zones appears sufficient to protect the large populations of these species. Furthermore, it functions effectively as a sanctuary, while still allowing for the safe movement of individuals between zones and reef systems. This provides the assurance that current MPA design is adequate in protecting the fish that are already resident within the protected zones.

Green jobfish, a formerly unprotected species within the IWP, received formal protection inside the borders of the entire IWP as of July 2011 (Dames et al. 2020). The small home range of green jobfish relative to the large size of the IWP, and the likelihood of local spawning, suggests that green jobfish populations within the IWP are well protected. Formal protection within the IWP allows for the safe movement of adult green jobfish within and between all zones of the IWP if any movements beyond their home range occur. It remains an unprotected species outside of the IWP, both in South African and Mozambique waters. As a result of the high residency found for this species, additional forms of protection outside of the IWP should be considered.

Giant trevally are not formally protected inside or outside of the IWP and are allowed to be kept if caught within the IWP, with the exception of sanctuary zones (Fig 1). As a result of their high mobility, ranging behaviour and frequent migrations, giant trevally are more vulnerable to capture as they move beyond sanctuary zones to where they are not protected. The sanctuary zones within the IWP act as safe havens for migrating giant trevally as they make their way from their home range to the aggregation site in southern Mozambique. From the results of this study, it appears that giant trevally have latitudinal home ranges to which they return, after each migration. Giant trevally that have home ranges in sanctuary zones will therefore be protected unless their home range extends beyond the borders of the sanctuary zone. The pristine reef habitats within the sanctuary zone provide the conditions to support a large population of giant trevally. Unfortunately, the aggregation occurs outside of South Africa and the IWPs borders. However, a potential strategy for ensuring the protection of giant trevally could be to implement a closed season during the peak of their summer spawning migration to ensure the greatest number of individuals reach the aggregation site.

If green jobfish and potato bass are conducting localised spawning, the IWP provides valuable protection of green jobfish and potato bass populations, potentially acting as sources of emigrating individuals that may colonise and possibly repopulate reef systems outside of sanctuary zones and the IWP itself (Afonso et al. 2009). The IWP represents the southern stronghold for all three of these wide-ranging Indian Ocean species and may be important in protecting genetic diversity unique to this region. Individuals of all three species exhibited cross border movements into the PPMR, highlighting the need for long-term and transboundary collaboration between management and policy makers of the IWP and PPMR. Additionally, formal protection of the giant trevally aggregation sight in the PPMR could be a vital step to protecting giant trevally populations in South Africa and southern Mozambique.

Conclusion

Green jobfish and potato bass exhibited high levels of residency within the iSimangaliso Wetland Park (IWP). No migratory or aggregatory behaviour was observed, suggesting that these species may be undergoing localised spawning on their home reef complexes. The combined reproductive strategy, feeding behaviour and morphology all contribute to the high residency of these two species (van der Elst 1993, Dingle and Drake 2007, Helfman et al. 2009). The results of this study show that green jobfish and potato bass exhibit limited movements within the boundaries of the IWP and therefore current management strategies within the IWP appear to be adequate for the protection of these two species. Giant trevally exhibited moderate residency with greater ranging movements, most likely associated with their active feeding style. They exhibited predictable, seasonal and lunar controlled migrations to southern Mozambique to an aggregation site, subsequently returning to their home range. Although giant trevally are not a threatened species, they have no formal protection outside of sanctuary zones in the IWP and Mozambique. Giant trevally with home ranges within sanctuary zones are well protected, when not migrating. Their aggregation site in Mozambique is vulnerable to exploitation and could be made an exclusion zone for fishing during the summer months. Management of the fisheries in South Africa and the IWP could provide further protection of the migration itself and impose a closed season during the summer spawning months. It is clear that the southern coral reefs found within the IWP are well protected and provide a pristine refuge for these two highly resident, and one moderately resident, reef-associated fish at the southern end of their geographic ranges. Future studies should consider a fine scale approach, with a large percentage of receiver coverage of an individual reef complex for greater resolution in order to determine spatio-temporal patterns of movement more accurately.

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