Movement ecology of a West African sciaenid fish, *Argyrosomus coronus*, in southern Angola

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Ethics statement

All research activities were conducted under the Rhodes University Animal Ethics and Standards Council Approval Number DIFS 2 2015.

Abstract

Argyrosomus coronus is a large sciaenid species with a primary distribution between Cape Frio, in Namibia, and Luanda, in Angola, where it exists as a panmictic stock. Early juveniles (< 300 mm TL) occur on muddy offshore substrata (50–80 m deep) and at one year of age they recruit into the inshore zone. Adults are thought to predominantly occur inshore. Spawning occurs in the species during late spring. The species is heavily targeted by the recreational, subsistence, artisanal and commercial fisheries as juveniles through to adults and there are signs of population decline with declines in catch per unit effort (CPUE) and maximum size.

A basic understanding of their movement ecology has emerged from previous studies, based on conventional tagging (mark-recapture) and CPUE monitoring from a shore-based recreational fishery. Juveniles were thought to be resident, with larger fish undertaking long distance migration southward in the austral summer and returning during the austral winter. In addition to the fishery-related threats faced by the species, the southern Angolan region has been identified to be an ocean warming hotspot, and this has been linked to a southward distribution shift and the recent hybridisation of *A. coronus* with its congener *A. inodorus*, in Namibia. This study aims to expand the knowledge of the movement ecology of *A. coronus* and to interrogate our current understanding of the movement patterns of the species using passive acoustic telemetry.

Passive acoustic receivers were deployed at three study sites, Flamingo, where all tagging occurred, which lies ~ 200 km north of the Angolan border with Namibia, is a relatively exposed stretch of coastline; Tombua Bay, which lies 30 km south of Flamingo, is a small, sheltered natural embayment; and Baia dos Tigres, which lies 100 km south of Tombua Bay, is a sheltered lagoon in the lee of an island ~ 10 km from the mainland. Tagging occurred in two batches, one year apart. In the first batch, sub-adults (n = 3) and adults (n = 17) were tagged and monitored for two years. In the second batch, juveniles (n = 7) and sub-adults (n = 3) were tagged and monitored for one year.

The first objective of this thesis (Chapter 3) was to examine the spatio-temporal dynamics of *A. coronus* at a regional-level (across study sites, to investigate the prevalence of the longshore migration), and at a local-level (within a study site), and to categorise the movement behaviour of juveniles, sub-adults and adults. Traditional seasons were not used in this thesis, as the study region alternates between 'warm' periods (up to ~ 26 °C mean daily water temperature), when Angola Current water covers the area, and 'cold' periods (down to ~ 15 °C mean daily water temperature), when Benguela Current water covers the area. A high degree of residency of tagged fish to the Flamingo study site, where tagging was conducted, was found, with juveniles and sub-adults never being detected outside of the Flamingo study site. Five adults (29 %) were detected haphazardly for between one and 36 days at Tombua Bay, following which they were typically detected again at the Flamingo study site. No fish were ever detected at the southernmost site, Baia dos Tigres, suggesting that none migrated to Namibia.

Within the Flamingo study site, adults were found to group at the inshore mid-region of the study site during 'cold' periods, dispersing again during 'warm' periods, when there was a concomitant offshore shift in their area use. This explained the absence of the species from catches in the shore-based recreational fishery during 'warm' periods. These results challenge previous migration hypotheses for the species. Therefore, longshore return migrations which were evident from previously conducted conventional tagging, are probably not the norm for the species, but likely occur at a low frequency.

The species exhibited a high degree of residency to their tagging site, despite the drastic seasonal changes in water temperatures and station-keeping was the dominant behaviour across all life stages. The constrained area-use noted in this study, relative to the known distribution of the species, suggests that *A. coronus* exists as a metapopulation, consisting of a network of subpopulations interconnected by gene flow that is most likely facilitated during their pelagic egg and larval phase.

The second objective of this thesis was to examine the group formation observed at the Flamingo study site during 'cold' periods (Chapter 4). While this grouping of individuals was found to be correlated with water temperature, it was unlikely to be a causal relationship, as the water temperature was not dissimilar to adjacent areas. The area where individuals were concentrated is known to frequently attract large shoals of their dominant prey, *Sardinella aurita.* While the timing of this group formation aligns with a pre-spawning period, no studies

have assessed the existence of local spawning. *A. coronus* were, however, likely utilising an abundant prey source, during the important pre-spawning period, in order to build up energy reserves. Group formation is a common feature of sciaenids, but literature on the subject is restricted to spawning congregations. Fish are not only more vulnerable to capture during these periods but may also be disturbed during these potentially important social periods.

The third objective of this thesis was to investigate the presence of sociality in the species (Chapter 5). Evidence for sociality during and outside the seasonal group formation was explored using network analyses. There was evidence for sociality, with several groups, characterized by co-locations among individuals, identified. While these groups were fluid through time, there was evidence of persistent sociality, with two individuals in particular being consistently co-located over the entire study period. Due to the persistent nature of sociality, group foraging is suggested as an explanation for this, with anecdotal evidence of coordinated hunting supporting this.

Acoustic telemetry vastly improved the knowledge of the movement ecology of *A. coronus*. Despite their panmictic population genetic structure, they were found to be largely resident, likely occurring as a metapopulation across their distribution, with egg and larval dispersal likely the primary mechanism for maintaining panmixia. Evidence for sociality was also found, which was previously unexplored in the species. The persistent nature of social groupings throughout the year, suggests that it may be linked with group foraging and is supported by anecdotal evidence of coordinated hunting by the species. While this study highlights the value of acoustic telemetry in studying movement ecology, it also shows the importance of drawing on multiple methods to fully understand a species' spatial ecology, including mark-recapture, population genetics, and fishery catch and effort data.

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Chapter 1: General Introduction

1.1 Coastal environment

The coastal environment includes the region where terrestrial, marine and atmospheric environments interact (Ray 1991), the clear delimitation of which is usually impossible to define (Carter 1999). The marine component of this region is the most biodiverse zone in the global oceans (Ray 1991). It is a zone of high primary productivity, hosting both benthic and pelagic primary producers (Longhurst et al. 1995; Gattuso et al. 2006) with upwelling events providing important nutrients which fuel high productivity (Hutchings et al. 1995). Globally, the near-coastal terrestrial zone (within 100 km of the ocean) is home to a significant proportion of the human population, estimated at 23 % in 1990 (Small and Nicholls 2003). The proportion is highest in developing countries due to their reliance on the marine natural resources (Magadza 2000) including subsistence activities due to its high productivity. The intertidal zone provides resources such as molluscs and crustaceans (Cockcroft et al. 2002) while the shallow sub-tidal zone provides resources to shore-based fisheries utilising linefishing gear and gill or seine nets. Nearshore zone resources may be harvested through the use of small powered or unpowered vessels and hook-and-line fishing gear or gill nets (Cockcroft et al. 2002; Ravikumar et al. 2016).

1.2 Fisheries management

Due to a high and increasing reliance of humans on resources provided by the coastal ecosystems (Belhabib et al. 2015), their effective management should be a priority. The management of marine living resources, which are targeted for harvesting, requires consideration of all components of the complex socio-ecological system (Voss et al. 2014). One fundamental component is the biology and ecology of the system and this requires knowledge of the life history traits, reproductive biology, resource and environmental requirements and their spatial ecology of the primary target species (Attwood and Farquhar 1999; Parrish 2005). Without knowledge of these key components, management and conservation efforts are unlikely to succeed as they cannot be suitably tailored to address the needs of the species of concern.

Various approaches to managing the effects of fisheries on their target species are available to management authorities (King 2007). Fish that are captured with hook and line are typically managed using technical measures such as size limits and catch restriction measures such as bag limits. These measures are possible in hook and line fisheries as fishing gear targets individuals, and thus each captured individual can be inspected and, provided the fishing is not done at great depths, released successfully, if they are not of legal size or beyond the bag limit of the fisher. To be effective, fisheries regulations typically require active enforcement to maintain compliance and ensure that the resources benefit the rightful stakeholders (King 2007). Technical and catch measures require enforcement while on the water and fishing is underway, or at landing points before the fish are processed or sold at the market. Artisanal, subsistence and recreational fishing is typically done by small groups of individuals who may be widely distributed across the fishing areas, and catches may be landed at many small points along the coastline (McClanahan and Castilla 2007; McCluskey and Lewison 2008). These characteristics make monitoring and enforcement a challenge requiring extensive manpower and coordination to be effective (King 2007). In developing countries, the resources to effectively monitor and enforce regulations are unlikely to be available.

In settings where fishing effort is dispersed and monitoring and enforcement capacity is constrained, spatial management approaches may be more effective (King 2007). This is because enforcement activities do not have to target individual fishers or vessels, but can be designed to protect a specific management area. However, practices allowed in a managed area may not always be homogeneous and may allow extractive and non-extractive uses based on the management objectives and the socio-economic considerations (Guarderas et al. 2008).

1.3 Spatial ecology

Spatial ecological knowledge is fundamental to inform the management approach for a species and will have increased importance in ecosystem-based approaches to management (Lowerre-Barbieri et al. 2019). At the simplest level, this knowledge can provide insight into the size of the area that individuals in a population occupy (Crossin et al. 2017). The intraspecific dynamics within the distribution of a species can then provide insight into the level of interaction across the species range. When these data are combined with population genetics information, decisions on whether to view a species as a single mixed population across the distribution, or as smaller units that require individual consideration can be made (Lédée et al.

2021). Understanding the spatial ecology of a species is also critical if a spatial management approach is adopted. Key to this would be to estimate the typical core use area size of a species (Abecasis et al. 2014; Lee et al. 2015), identify any predictable spawning related movements and congregation areas (Gurshin et al. 2013), and identify any ontogenetic shifts in habitat use (Galaiduk et al. 2017). An effective spatial plan should adequately account for each of these critical spatial components, otherwise populations may remain vulnerable due to the risks faced outside of managed areas.

The area use of animals is influenced by various factors. At a broad geographic scale, species' distributions are determined by abiotic factors through their influence on physiology (Rijnsdorp et al. 2009; Potts et al. 2014a). Physical barriers to movement may further restrict a species' distribution and gene flow between adjacent habitats separated by the barrier (Guillot et al. 2009; Hirschfeld et al. 2021). In the marine environment, oceanographic features including currents and upwelling tend to be the leading driving force of species' distributions through effects on water temperature (Henriques et al. 2012, 2016). Currents may also physically influence species' distributions by providing a passive means of dispersal and colonisation of new regions, typically during early life stages including eggs and larvae (see section 2.1.1 for insight into the oceanography of the study region) (Beckley 1995; Pattrick et al. 2013). At a finer scale within distribution ranges, the resource requirements of fishes and interactions with other animals including predators, typically determine their space use. Resource abundance and predation risk tend to be balanced through habitat selectivity (Griffiths 1997a; Dahlgren and Eggleston 2014).

One focus of debate in movement ecology theory centres on animal migration. While a large proportion of the authors contributing to this body of work were entomologists and ornithologists, their goal was generally to develop definitions that would be applicable across all animal taxa (e.g. Kennedy 1985; Dingle and Drake 2007; Dingle 2014a). While they fulfilled their ambition, these terms and definitions have, however, been used inaccurately and ambiguously, making the building of a reference framework and common understanding of animal movement behaviour challenging (Dingle and Drake 2007). This is particularly true for the term "migration". Any study on animal movement behaviour should, therefore, clearly define how commonly used terms are interpreted in the context of the study. The respective definitions of common terms in the context of this study are discussed below.

An early definition offered for migration that is still widely regarded as relevant was produced by Kennedy (1985 pg 8) as "Migratory behaviour is persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence." This is the definition adopted in this thesis. While it still leaves room for interpretation, it infers that migration is a unique form of movement, occurring for a longer period and distance than more frequent movements observed in a species. Even though it allows for passive displacement, it suggests that there is a voluntary aspect in embarking on a movement. It also advocates that during the migration, a migrant is not distracted by stimuli and resources that it would otherwise show interest in; however, migrants may switch between migrating and foraging during the journey (Kennedy 1985; Dingle and Drake 2007; Dingle 2014a).

The literature on fish migration is dominated by studies on salmonids, anguillids, sharks, and major fishery species, predominantly from the northern hemisphere (Harden Jones 1968; McKeown 1984; Morais and Daverat 2016). There are few studies investigating migration patterns of coastal fishery species, particularly along the African coastline. An exception to this within the same region as this study, is Winkler (2018) who investigated the spatio-temporal dynamics of *Lichia amia*. The paucity of knowledge on the topic in the region may be ascribed to low research effort focussing on movement studies, but also because of the lack of well-known, notable migrations within the region. Fishes in the area that do undertake large migrations may be cryptic during their passage along migration pathways, going largely undetected by man. An example of such is seen in *Anguilla* spp., the adults of which travel from freshwater environments through estuaries into the ocean and then traverse several hundreds of kilometres to their spawning grounds (Réveillac et al. 2009). Arguably, the most notable ichthyofaunal concentration and large-scale movement in southern Africa is the "sardine run". This event sees a concentration of *Sardinops sagax* along the north-east coast of South Africa, coupled with a longshore north-easterly movement up the coast, pursued by a myriad of predators (O'Donoghue et al. 2010). The motivation for this migration is still uncertain (Fréon et al. 2010; van der Lingen et al. 2010), and whether it fits the definition of a true migration is questionable as their fate is unknown; their movement may not necessarily be terminated upon discovery of suitable resources. The paucity of research on fish movement, particularly in the African context, may be a contributing factor hampering researchers' ability

to develop a theoretical framework around the evolutionary development of fish movement patterns, to the extent that entomologists and ornithologists have.

A conceptual framework for movement studies has been proposed by Nathan et al. (2008) and conceptualises movements in the context of various internal and external factors. Three internal factors include the internal state of an organism, their mechanisms and ability for movement, and their mechanisms and ability to navigate their environment. External factors are environmental and influence all three internal factors, by affecting the internal state of the organism, their ability to move, and their ability to navigate within the environment. The framework emphasises the importance of understanding the proximate and ultimate causes of movement behaviours in movement ecology studies. Cooke et al. (2022) discussed this framework in relation to fish ecology and showed it to be a useful tenet, particularly for informing species conservation and management efforts through the linking of the movement of individuals and their environment.

One of the defining characteristics used to classify movement behaviours is the relative distance covered during such behaviour and, while sharing the same terms for behaviours across taxa is important, the actual distances are highly taxa specific (Harden Jones 1968; McKeown 1984; Dingle 2014a; Couto et al. 2016). Broadly, movements are classified as either those that occur within a determinable home range, which is an area that possesses suitable resources and within which an organism spends a large proportion of its time, or those that take the animal considerably beyond this home range, either temporarily or permanently (Dingle 2014a). Movements by an organism that occur within a home range are categorised as 'station-keeping' (Kennedy 1985). These movements tend to be concerned with acquiring/utilising resources (which may include food, shelter, mates and others) during periods when their availability within the home range is sufficient for the organism to remain there (Dingle and Drake 2007; Dingle 2014a). The terms 'foraging' and 'commuting' describe locomotory behaviours concerned with resource acquisition, and are considered 'station-keeping' behaviours, which occur within a home range (Dingle and Drake 2007; Dingle 2014a). Foraging movements are repeated on relatively small spatiotemporal scales and are temporarily halted when a suitable resource is found and utilised (Kennedy 1985; Dingle and Drake 2007; Dingle 2014a). Commuting, on the other hand, involves consistent, longer, return journeys between geographically separate resources that occur on a relatively short time scale (Dingle and Drake 2007; Dingle 2014a).

Movements that take an organism far beyond this home range also relate to resource acquisition, and ideally precede the eventuality that the resource(s) become limiting (Dingle 2014a). The terms 'ranging' and 'migration' generally infer a movement of an organism beyond its home range area. Ranging is an exploratory behaviour which ends when suitable resources are encountered (Dingle and Drake 2007). This behaviour is similar to foraging, except that it traverses the home range boundary. Migration is unique in that the migrant's arresting response to otherwise suitable resources is inhibited for some period (Kennedy 1985; Dingle and Drake 2007; Dingle 2014a). This inhibition eventually ceases and the migrant is again receptive to stimuli from suitable resources, and other movement behaviours may resume (Kennedy 1985; Dingle and Drake 2007). Animals that undertake migrations possess a suite of specialised characteristics, including morphological, behavioural and physiological adaptations, which make up what is termed their 'migration syndrome', that influence how an organism expresses migration behaviour, including responses to stimuli, during the migration (McKeown 1984). Similar migration syndromes may be observed across a range of taxa but there is no evidence of a common ancestry for this (McDowall 1997; Piersma et al. 2005).

These long distance movements may fulfil several important roles for species that undertake them. Migration may be an important component in the life history of certain abundant fish species (Harden Jones 1968). This may be due to it allowing migrants to exploit abundant resources in the area that the animals relocate to, but also by having all or part of a population moving between regions allows for an increased total carrying capacity, compared with the scenario of a non-migratory population in any single region (Harden Jones 1968).

Shifts between areas may have an ontogenetic component (Dahlgren and Eggleston 2014). In many fishes, migration may occur at a fixed stage in their life history. This pattern varies both between and within species (McKeown 1984). Different areas may be suited to different life history stages, with ontogenetic shifts between these areas increasing survival and the acquisition of suitable resources (Harden Jones 1968). Nevertheless, the most noteworthy migrations of fish are undertaken by adults, to facilitate spawning or feeding (Harden Jones 1968). The timing of fish migrations tends to be predictable, with migrations to spawning areas suitably cued to coincide with gonad development (McKeown 1984). The timing of migrations to feeding areas ensures that food availability at the destination is favourable relative to the departure area (McKeown 1984). The proximate factors informing such migrations tend to be abiotic and include changing temperature, photoperiod, salinity, precipitation, lunar cycles or

currents (Harden Jones 1968; McKeown 1984; Dingle 2014a). In the ocean, currents play a significant role in guiding migrants and facilitating their return to a common area (Harden Jones 1968; McKeown 1984). In terms of their pattern, fish migrations tend to be to-and-fro in nature with the extent of return to a specific location or general area, variable (McKeown 1984). Migrants may return on the same route that they previously took, due to orientation mechanisms that guided their journeys or because of constraints of passage imposed by the environment (McKeown 1984). In populations that undertake a migration, this behaviour may be obligate or facultative, and may only include a portion of the population – a phenomenon termed partial migration (Jonsson and Jonsson 1993). This intra-population variability in migration strategies may increase resilience to population-level adverse effects (Kerr and Secor 2012). Further intra-population variability includes conspecific interactions such as group formations and sociality. Knowledge of these phenomena provides important insight into the spatial ecology of fishes (Cooke et al. 2022).

1.4 Group forming behaviours

During the life history of fishes, interactions with conspecifics are inevitable to some degree, with group formation being a common phenomenon. Fish may form conspecific groups due to various internal or external factors; these are discussed and defined by Dingle (2014b). As external forces, abiotic factors, including water temperature or habitat availability, may force fish into a restricted area, with the presence of other conspecifics at the same location having no attractive effect on newly joining individuals. This process is referred to as ‘physical concentration’. Alternatively, conspecifics may be attracted to an area and form a group, due to the presence of a resource patch or due to the presence of other conspecifics. If the group formation occurs due to the presence of conspecifics, some authors refer to this phenomenon as ‘congregation’. Group spawning may be an example of such a behaviour, whereby individuals are attracted by the presence of conspecifics. If the group formation occurs due to a factor such as resource availability, and the presence of conspecifics do not exert any attraction to others joining the group, some authors refer to this phenomenon as ‘aggregation’. Certain feeding events may develop into an aggregation as foraging individuals locate a favourable resource. These are the definitions adopted in this thesis.

1.5 Sociality

Interactions among conspecifics which occur together may vary in complexity. Sociality describes interactive behaviours among individuals or groups of individuals, typically conspecifics, beyond a simple group formation. Social behaviour in fishes may confer several advantages upon participants. These may be involved with avoiding predation (Kasumyan and Pavlov 2018), including improved predator detection (Ward et al. 2011), predation risk dilution (Lehtonen and Jaatinen 2016) and predator confusion (Kunz et al. 2006). Social behaviour may also increase foraging efficiency and improve locomotory efficiency (Peichel 2004). Social behaviours may be short-lived, such as over a spawning period in pair-spawning species, or more long-lasting, for example in harem breeding species (Rao and Devi 2004). In addition to external effects and group level advantages of sociality, it may also drive physiological processes, such as the maintenance of sex structure in harem forming fishes such as the anemonefish (Madhu and Madhu 2006).

1.6 The genus *Argyrosomus*

The *Argyrosomus* genus comprises nine species globally (according to Fishbase, accessed 01 September 2023). The genus is represented by four species along the south and west coast of southern Africa from Mozambique to Angola. This includes *A. coronus* Griffiths and Heemstra 1995, which occurs primarily between Cape Frio in Namibia (although tagged fish have been recaptured south of this) and Luanda (Henriques et al. 2018), *A. japonicus* (Temminck and Schlegel 1843), which occurs between Cape Point in South Africa and southern Mozambique, *A. inodorus* Griffiths and Heemstra 1995, which occurs between northern Namibia and the Kei River in South Africa (Figure 1.1) (Griffiths and Heemstra 1995) and *A. thorpei* (Smith 1977) which occurs between Algoa Bay, South Africa and Xai-Xai, Mozambique. *Argyrosomus coronus* has the most northerly distribution of these four species, with its southern distribution range overlapping with *A. inodorus* in northern Namibia (Holtzhausen et al. 2001). In the southern end of this region, along the south coast of South Africa, there is an overlap in the distribution between *A. inodorus* and *A. japonicus*. The mid-range of the distribution of *A. inodorus* is separate from both other species (van der Bank and Kirchner 1997). The distribution of *A. thorpei* overlaps with that of *A. japonicus* south of Maputo, as well as with *A. inodorus* between the Kei River and Algoa Bay, where there is an overlap of three species (Figure 1.1). The genus comprises some of the most important fishery species along the

southern African coastline (Griffiths 1996; Holtzhausen et al. 2001; Potts et al. 2009, 2010b). Species in the genus are generally considered to have a coastal orientation but also occur in estuaries (Griffiths 1996; Childs 2013), or in deeper waters offshore and they are commonly demersal, preferring muddy or sandy substrata and turbid waters (Lal Mohan 1984; Griffiths and Heemstra 1995; Griffiths 1996).

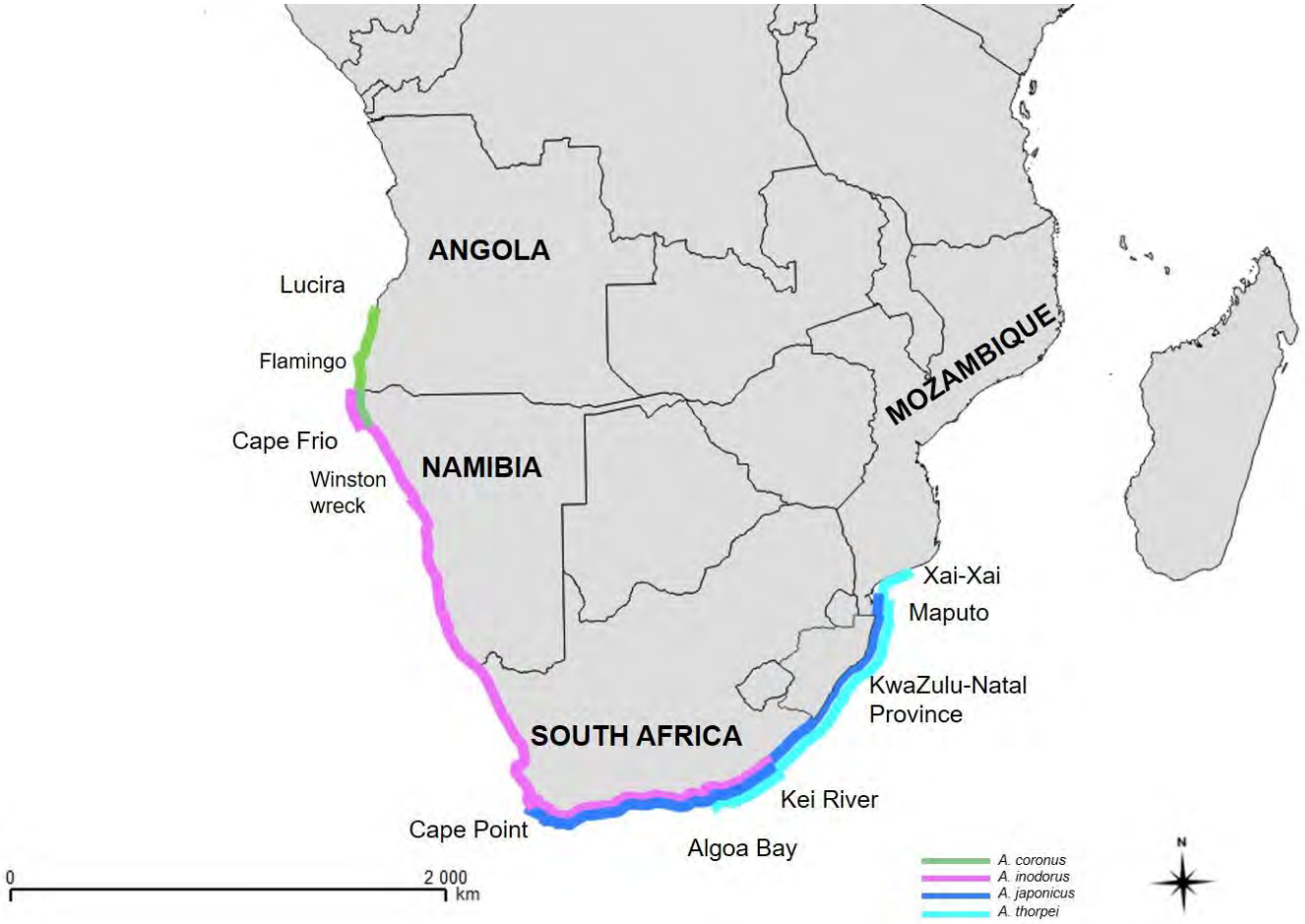
While there are similarities among *Argyrosomus* spp., there are differences in their distributions, habitat use and life history traits. In South Africa, *A. japonicus* makes use of estuaries as a nursery area, with early juveniles <15 cm total length considered estuary-dependent (Griffiths 1996). An ontogenetic shift sees later-stage juveniles and adults utilising the marine environment to a greater extent (Griffiths and Heemstra 1995; Childs 2013). Estuaries and the surf-zone provide juveniles with refuge from nearshore predators (Ebert 1991a; Smale and Badenhorst 1991; Griffiths 1996, 1997a) and provide suitable food resources (Griffiths 1997a). South African *A. japonicus* have been suggested to undergo a spawning migration to KwaZulu-Natal Province (Figure 1.1) during spring, although spawning was also thought to occur in Eastern Cape and Western Cape provinces (Griffiths and Heemstra 1995). These localised spawning events suggested by the latter authors lends support to the metapopulation dynamics advocated for the species by Childs (2013), who found that adults monitored using acoustic telemetry exhibited high levels of residency to the ~65 km wide Algoa Bay, where tagging occurred in their study.

Argyrosomus inodorus juveniles in South Africa occur close inshore, moving offshore as they grow. Adults and sub-adults were found to occupy deeper offshore waters during the austral winter and they were restricted to shallower inshore water during austral summer, in the southern Cape region (Griffiths 1997b). This seasonal pattern was attributed to the contraction of the range of suitable water temperatures during summer (Griffiths 1997b). In the Namibian population the surf zone is an important habitat, and they are only typically found in water depths of between one and 20 m (Griffiths and Heemstra 1995). Spawning in the species occurs throughout the South African distribution during spring, in water shallower than 50 m (Griffiths 1997b). Namibian *A. inodorus* spawning behaviour is described by Holtzhausen et al. (2001). Spawning occurs in summer at the southern end of their distribution, in the Namib Naukluft Park, following a southerly migration. Adults return to their habitats in the north after spawning. Larvae are thought to drift in the northerly flowing current, into the West Coast Recreational Area where they mature to juvenile stage. Juveniles of age ~2 years continue a

northward movement into the Skeleton Coast Park where they eventually recruit into the mature adult population. Population genetics have indicated isolation of the Namibian and South African *A. inodorus* populations by the Lüderitz upwelling cell (Henriques et al. 2015).

Argyrosomus thorpei is an under-studied species. What is known is that it inhabits coastal waters where it is predominantly observed in line-fish catches outside of the surf zone, to depths of 80 m, although occasional shore-based catches do occur (Griffiths and Heemstra 1995). It is thought to be a largely resident species (van der Elst 1993). Juveniles occur on sand or mud substrata while adults favour reef (Griffiths and Heemstra 1995; Fennessy and Mann 2013). Spawning is known to occur between June and September (austral winter) in the Thukela Banks region of KwaZulu-Natal (Fennessy and Winker 2020), where juveniles utilise an abundant penaeid prawn food resource (Fennessy 1994).

A)



B)

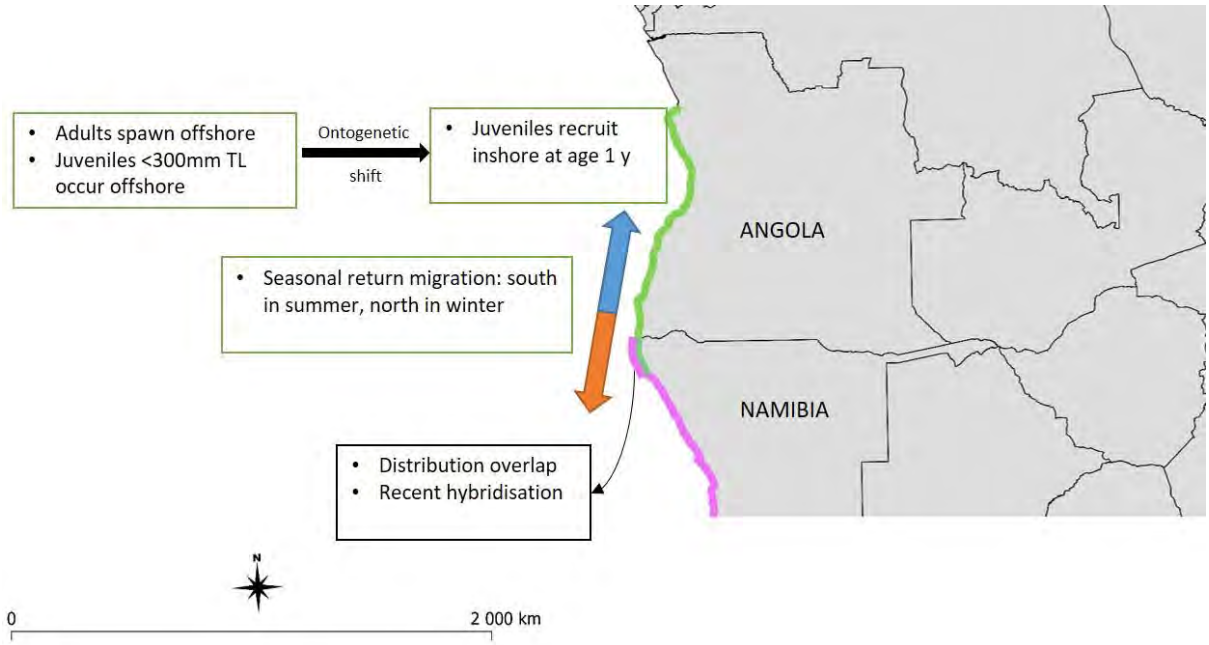


Figure 1.1: A) Distribution of four *Argyrosomus* spp. in southern Africa between Angola on the west coast and Mozambique on the east coast. Other locations referred to in text illustrated for reference. B) Annotated distribution of *A. coronus* and *A. inodorus* in Angola and Namibia illustrating relevant aspects of their spatial ecology.

Early juvenile *A. coronus* (< 300 mm TL) occur on muddy substrata in depths of 50-80 m (Potts et al. 2010b). Following this phase, at one year of age, they recruit into the inshore zone (Potts et al. 2010b). Adults are thought to occur predominantly inshore, undertaking some offshore excursions where spawning was suggested to occur during late spring, in November (Potts et al. 2010b).

A basic understanding of the movement ecology of *A. coronus* has emerged from previous studies. These were based primarily on data collected from shore-based anglers, including conventional tagging and catch per unit effort (CPUE) monitoring along the Flamingo coast (Figure 1.1) (Potts et al. 2010b, 2018). Conventional tagging of 966 individuals occurred between 2005 and 2013 (Potts et al. 2018). A relatively good recapture rate of 7.6 % was achieved in this study. An ontogenetic difference in area use was noted, with juveniles remaining resident to their tagging sites, while larger fish underwent longer distance movements. The longest movements reported in this study were from the Flamingo coast 755 km southwards into Namibia, where fish were recaptured near to the Winston wreck. These

recaptures were of adult fish and occurred during summer (Potts unpublished data). Adult fish were recaptured along the Flamingo coast during winter in years subsequent to tagging. Catch per unit effort data indicated high catch rates for *A. coronus* during winter along the Flamingo coast, with a near absence of the species during summer months (Potts et al. 2010b, 2018). Combined, the conventional tagging and CPUE data indicated a longshore southerly movement of the species during summer, with an absence of the species from shore-based catches during this period. This led to the hypothesis that *A. coronus* underwent a longshore southerly migration during summer, returning to southern Angola and the Flamingo coast during winter (Potts et al. 2010b).

Several fishery sectors capture *A. coronus*, as outlined by Potts et al. (2010b). The species is predominantly targeted by recreational anglers in southern Angola. This fishery captures fish from juveniles larger than 300 mm TL up to large adults of over 1 600 mm TL. Shore-based subsistence and boat-based artisanal fishers operating throughout the region, primarily targeting reef fishes, capture *A. coronus* from juvenile stages of 300 mm TL to adults >870 mm TL. Commercial purse-seine vessels occasionally capture groups of large adult *A. coronus* >1 000 mm TL but these are deemed incidental. Economically the recreational fishery is a highly lucrative sector, contributing high value to the local economy in an area with little employment opportunity (Potts et al. 2009). Due to this economic value, and the reliance of local subsistence and artisanal fishers on shared fishery resources for their livelihoods, consideration should be given to mitigating the deleterious effects of the recreational fishery on the very resource upon which it relies.

The *A. coronus* population in southern Angola has exhibited signs of high exploitation levels. Despite a large average size and high CPUE in the recreational fishery in 2010, the lack of large fish of up to 50 kg, which used to be captured regularly (Griffiths and Heemstra 1995), and indications of declining catches at that stage led to the suggestion that the population may be under threat (Potts et al. 2010b). A subsequent study that estimated the changes in eggs per recruit (EPR, which indicates the likelihood of a population's persistence through a measure of reproductive output rate), based on annual length-frequency data, found a definite decline in EPR over the period 2005 to 2013 to below 10 % of the unexploited estimate, indicating a stark population decline (Beckensteiner et al. 2016). These authors do caution this interpretation, offering the alternative that a climate-change mediated distributional shift (Potts et al. 2014b) may, at least partly, account for the reduced EPR at the monitoring site in southern Angola.

Investigating the movement ecology of the species was suggested by the authors to elucidate whether the estimated reduction in EPR could be attributed to emigration from the study region, perhaps as a consequence of climate change, or whether it could be ascribed to fishing mortality.

An additional threat faced by *A. coronus* in the region was recently identified during a population genetics study. This study found evidence of hybridisation with the sympatric *A. inodorus* (Potts et al. 2014b). While their distributions were known to overlap, *A. coronus* typically favoured warmer water further north of *A. inodorus*. Climate change driven southerly intrusion of warmer water further into Namibia is thought to have resulted in reproductive area overlap between the two species resulting in the production of hybrids (Potts et al. 2014b). This region has been designated a climate change hotspot as it is experiencing a rapid rate of water temperature change, which is likely to continue into the future (Hobday and Pecl 2014).

Fundamental knowledge on the spatial ecology of *A. coronus* has been generated. Their core distribution is known, and their existence as a panmictic population has been shown, as well as their potential for long distance movements. Seasonality in their area use has been identified with a longshore return migration hypothesis offered to explain this. Threats to the population have been identified and are principally in the form of over-exploitation and hybridisation. However, there remains uncertainty in the high resolution movement ecology of the species and the migration hypothesis remains untested. This study aims to expand our knowledge of the movement ecology of the species, to better understand patterns and processes identified using complementary techniques including population genetics, CPUE data and mark-recapture techniques.

1.7 Biotelemetry

Movement studies rely on observing the location of unique individuals over time (Pine et al. 2012). In fishes in the marine environment this is typically achieved through mark-recapture or telemetry techniques (McFarlane et al. 1990; Heupel et al. 2006). Mark-recapture involves capturing a specimen, marking it with a unique identifier internally or externally, releasing it back into its natural environment and recapturing it at a later stage (Pine et al. 2012). This technique provides low resolution spatial information, generally with only a release location and a recapture location (Lucas and Baras 2000). It relies on good reporting rates of recaptures

of tagged animals by fishers, and a representative spread of fishing effort across the distribution of the species to obtain the best movement information (Lucas and Baras 2000; Pollock et al. 2001). Telemetry techniques involve a two-part technology: a unique transmitter which is attached to a study specimen and a receiver which senses and logs the presence of transmitters (Heupel et al. 2006). In the marine environment, acoustic telemetry is a commonly used technology, due to density constraints on other technologies such as radio telemetry (Drenner et al. 2012). Receivers used in acoustic telemetry studies occurring over large distances (tens of km) are typically fixed in place via anchors on the seafloor and deployed as an array over the study site (Heupel et al. 2006). These receivers passively log any transmitters carried by fish that move within detection range of the receivers. This technology allows for the concurrent monitoring of many animals, each with a unique identification number, over multiple years, dependent on the battery life of the transmitters. Through different receiver array designs various research questions can be addressed including fine-scale area or habitat use, and passage and direction of animals undertaking long distance movements (Heupel et al. 2006).

Acoustic telemetry has provided valuable insight into marine animals' movement ecology that other techniques have been unable to (Matley et al. 2022). The technique is, however, an imperfect one. Acoustic telemetry studies are typically limited in their rigour due to the high cost of the technology and limited research budgets which leads to relatively low sample sizes of study animals being achieved (Crossin et al. 2017). The probability of detecting tagged animals is also constrained by the size and extent of the acoustic receiver array. The nature of the technology, using sound transmission, also makes it sensitive to environmental perturbations (Payne et al. 2010). This can result in study animals being missed by the acoustic receivers, particularly in difficult to monitor environments such as surf zones where mooring of instruments is challenging and usually avoided, and their efficacy hampered due to environmental noise. Acoustic telemetry is still, however, a worthwhile tool for studying movement ecology.

1.8 Objectives

This study aims to expand our knowledge of the movement ecology of *A. coronus* in southern Angola through the use of acoustic telemetry. In particular, the objectives of the study were to:

1. Investigate the seasonal area use patterns of juvenile, sub-adult and adult *A. coronus* in southern Angola and test the hypothesis of a seasonal longshore migration from southern Angola into northern Namibia in summer, with a return to southern Angola in winter,
2. Interrogate a group formation phenomenon at the Flamingo study site, and
3. Examine the level of interaction among individuals through a network analysis approach.

This thesis consists of six chapters. The general introduction (Chapter 1) and general materials and methods (Chapter 2) contextualise the study in terms of its relevance to the species, and describe the research approach undertaken. General temporal and ontogenetic patterns in area use by *A. coronus* and the migration hypothesis are addressed in Chapter 3. A group formation phenomenon that was observed during the study is interrogated in Chapter 4 to determine the demographics of the participants, drivers of, and possible reasons for the phenomenon. The extent of sociality in the species is examined in Chapter 5. Finally, the general discussion (Chapter 6) makes a contribution to our understanding of the ecology and conservation of *A. coronus*, and provides recommendations for future research to further our understanding of fish behavioural ecology.

Chapter 2: General Materials and Methods

2.1 Study site

The study was undertaken in the Namibe Province in southern Angola (Figure 2.1). Angola is situated on the west coast of Africa. It neighbours Namibia in the south, Democratic Republic of Congo in the north and Zambia in the east. Angola's coastline is ~1 400 km long, on the eastern Atlantic Ocean. The coastline occurs between the latitudes of 6.07 and 17.25 °S, excluding the exclave of Cabinda. Details presented here on the demographics, climate, agriculture and fisheries were sourced from Encyclopaedia Britannica (Clarence-Smith and Thornton 2022). Angola had an estimated population of just over 33 million people in 2022, with 34.5 % living in rural areas as of 2018. Angola gained independence from Portugal in 1975 after a 14-year struggle, following which it experienced a 27 year-long civil war. The effects of this tumultuous history are still evident in the country today.

The Angolan climate is tropical, with a clear dry season. The climate is influenced by the intertropical convergence zone, ocean currents and elevation. Climatic variation across the country is caused by differing patterns in rainfall, which decreases in a southerly direction and nearer to the coast. As evidence of this, coastal annual rainfall in the north, at the capital of Luanda, is ~330 mm compared to the southernmost areas, which receive ~50 mm. The arid climate, particularly in the south of Angola, makes land-based livelihoods challenging for the people inhabiting the region, leading to a reliance on marine resources.

Arable land in Angola is limited, while even this is said to be under-utilised. The country's history as well as the presence of land mines have hindered current agricultural practices. In terms of subsistence, cassava is an important food crop, while coffee and sugar are major commercial cash crops.

The Angolan fisheries, prior to independence, were highly productive. The fishing fleet consisted of ~700 vessels, providing work to 13 000 people. Shoaling pelagic species were the primary target, including sardines and mackerel. These were processed in Angolan factories and largely exported to western markets. Local markets and neighbouring countries were

supplied dried or cured fish. Post-independence, the fisheries were over-exploited by foreign vessels and the processing infrastructure was shut down or destroyed.

As in other developing countries, Angolan coastal communities rely extensively on the coastal ecosystem for their livelihood (du Preez 2009). With a tumultuous history of colonisation and a protracted civil war, a large proportion of the population is impoverished. Coastal resources have drawn a great number of people to the coast for sustenance and small-scale trading of fishery products. In southern Angola, where the present study was based, several fishery sectors including subsistence, artisanal, semi-commercial and recreational sectors operate in the coastal waters (Potts et al. 2009, 2010b). Fishes in the family Sciaenidae make up important components of the subsistence, artisanal and recreational fisheries in the region (Potts et al. 2009, 2010a).

Early marine research conducted in southern Angola focussed on oceanography (Hirst and Hastenrath 1983; Shannon et al. 1987; Meeuwis and Lutjeharms 1990), with little effort on the nearshore region and on the biology of the ocean inhabitants, except for biodiversity assessments from trawl surveys (Bianchi 1992); the long civil war was likely a major reason for this. After the civil war, marine resource exploitation became a priority in national policy (Potts et al. 2009). Fisheries included subsistence, artisanal, recreational (largely catering for foreign visitors), and commercial purse-seine fleet sectors (Potts et al. 2009, 2010b). Gear used in the subsistence and artisanal fisheries included hand lines, gill nets (Potts et al. 2010b) and fish traps (personal observation), generally operated from a vessel launched from fishing villages. Shore-based fishing dominated the recreational sector in the south of Angola, with the occasional boat-based fishing expedition conducted.

Ichthyological and fisheries studies began in southern Angola in 2006 through a partnership with a local recreational fishing lodge (Potts et al. 2009). This partnership has contributed significant knowledge on the value of fisheries to the region and the biology of several species captured in the fisheries, with emphasis on the primary target species of the recreational fishery, namely *Argyrosomus coronus*, *Lichia amia* and *Pomatomus saltatrix* (e.g. Potts et al. 2008, 2009, 2016; Henriques et al. 2012, 2018). The current study benefitted from this continued partnership, in terms of logistics of conducting this work, and through previously collected biological and movement ecology data on *A. coronus*.

Three sites were chosen for this study: the Flamingo coastline, Tombua Bay and Baia dos Tigres (Figure 2.1). The three study sites each represent different environments. The Flamingo study site is a relatively exposed coastline with sandy beaches and occasional rocky outcrops, with submerged low-profile scattered reefs in between a predominantly sandy substratum. This stretch of coastline is utilised for recreational fishing activities by Flamingo Lodge. Fishing by the lodge is focussed along ~30 km of coastline. Tombua Bay lies ~30 km south of the Flamingo study site. This small (2 km × 5 km) natural embayment provides a sheltered habitat from oceanic swell. It is utilised as a low-traffic port, largely by fishing vessels. The benthos consists of sand/mud sediment and is highly impacted through pollution from nearby developments. Baia dos Tigres lies ~80 km south of Tombua Bay. This relatively large (23 km × 10 km) sheltered lagoon is protected from oceanic swell by an island, Isla dos Tigres. The benthos at this site consists of sand/mud sediment. This site is a very remote location that was accessed with the assistance of an Angolan Ministry of Fisheries patrol ship, due to the narrow beach on the mainland flanked by steep dunes which makes boat towing extremely dangerous and reliant on suitable weather, tide and sea conditions to be accessible. Baia dos Tigres lies ~60 km north of the Cunene River (Figure 2.2), which forms the border between Namibia and Angola, and is the only perennial estuary in the region (Boyer et al. 2000).

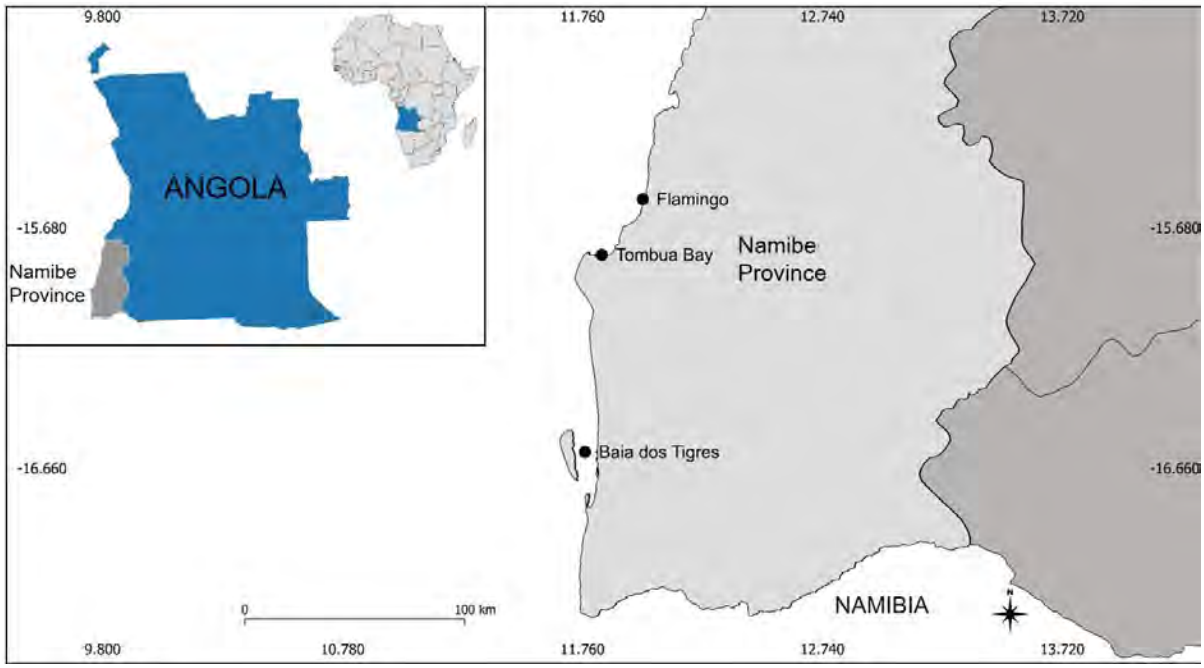


Figure 2.1: Location of Namibe Province in southern Angola (inset) and the three study sites: Flamingo, Tombua Bay and Baia dos Tigres. Namibia is shown to the south. Latitude and longitude indicated along the margins.

2.1.1 Oceanography

The southern Angolan region is oceanographically dynamic. It is situated at the confluence of the warm, nutrient-poor, southerly flowing Angola Current, and the cool, upwelled, nutrient-rich northerly-flowing Benguela Current, known as the Angola Benguela Frontal Zone (ABFZ) (Figure 2.2) (Meeuwis and Lutjeharms 1990; Veitch et al. 2006; González-Dávila et al. 2009). The front occurs between 14 and 16 °S and exhibits cyclical shifts, migrating south in austral summer when the Angola Current dominates, and north in austral winter when the Benguela Current dominates (Meeuwis and Lutjeharms 1990). The shifting of the ABFZ results in vast water temperature differences between austral summer and winter periods in the study region (Meeuwis and Lutjeharms 1990), with minima of ~15 °C and maxima of ~27 C° being recorded at the Flamingo study site during austral winter and summer, respectively (Potts et al. 2010b).

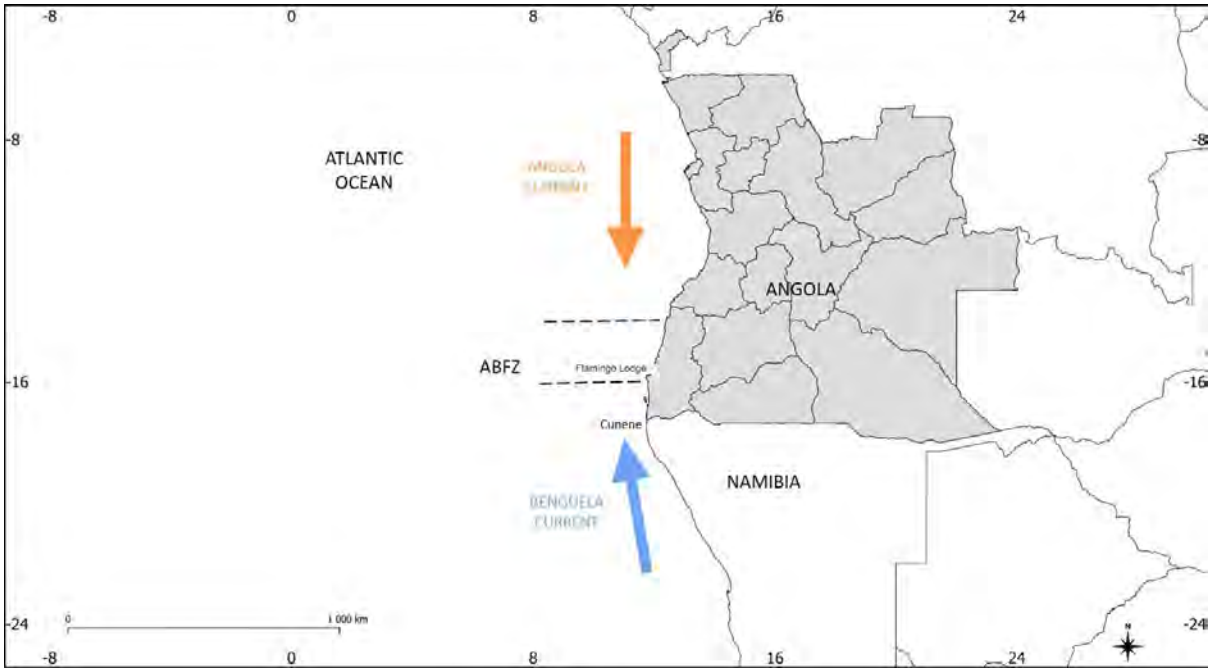


Figure 2.2: Orientation of major oceanographic features including the location of the Angola Benguela Frontal Zone (ABFZ) and key landmarks pertinent to the study region, including the Cunene River, and the neighbouring country, Namibia.

Climate change effects are already apparent in the region, which occurs within a climate change hotspot (Hobday and Pecl 2014). In addition to physiological constraints on species in the region (Potts et al. 2014a), the effect of ocean warming has been forecast to increase hypoxia at the ABFZ, likely to lead to reductions in fishery biomass (Monteiro et al. 2008). This is

partly due to increased poleward movement of the ABFZ, which leads to greater warming of the coastal waters of southern Angola as the Angola Current intrudes further south. Already, over a 17-year period between 1982 and 1999, an increase of 0.6 °C was noted in sea surface temperature of the ABFZ (Monteiro et al. 2008).

In order to simplify analyses and cater for the thermal dynamics particular to the study region, traditional seasons (i.e. summer, autumn, winter, spring) were not used in analyses in this thesis. Instead, due to the marine environment in the region being dominated by the seasonally shifting ABFZ, two distinct periods were categorised, referred to as 'cold' – when the ABFZ shifts northwards and Benguela Current waters intrude into the study region – and 'warm' – when the ABFZ shifts southwards and Angola Current waters intrude into the study region. These periods were not delineated in time, which would be arbitrary to the ecology of the area, but based on when the oceanographic shift was observed, based on *in situ* water temperature measurements. The entire study included two 'cold' (classified as periods C1 & C2) and two 'warm' (classified as periods W1 & W2) periods.

Underwater temperature recorders (UTR; HOBO U22-001 and Star-Oddi Starmon Mini units) were deployed alongside acoustic receivers at nine stations in the Flamingo study site array (see section *2.2.1 Acoustic telemetry array* below). All loggers at the Flamingo study site, except the southernmost logger, were deployed in pairs, perpendicular to the shore – one on the inshore station and one on the offshore station. The loggers on the inshore stations were deployed at depths of between 8 and 11 m, while those deployed on offshore stations were at depths of between 23 and 29 m. Temperature sampling, at one-hour intervals, was continuous for all except two loggers due to equipment malfunction mid-way through the study period. Water temperature monitoring occurred simultaneously at Tombua Bay and Baia dos Tigres study sites.

'Cold' and 'warm' periods were classified based on monthly counts of days that the mean daily temperatures at the mid-region of the Flamingo study site array (station F7) were above a threshold of 20 °C (Figure 2.3). Months where <3 days had mean daily temperature >20 °C were classified as 'cold', and those with >3 days with mean daily temperature >20 °C were classified as 'warm'. This resulted in C1 spanning the period from the study start in September 2013 up to and including December 2013, W1 spanning from January 2014 up to and including

May 2014, C2 spanning from June 2014 up to and including October 2014 and W2 spanning from November 2014 up to and including May 2015.

To further describe the thermal regime at the Flamingo study site, which was the primary study site and where fish were tagged and predominantly detected, average daily temperatures were calculated for each temperature logger across the monitoring period. These were then summarised per period as means of the average daily temperature, aggregated according to whether the loggers were placed inshore (~10 m deep) or offshore (~26 m deep). To investigate variability, the means of the minimum (mean T_{min}) and maximum (mean T_{max}) average daily temperatures per period per logger were calculated. These temperature data were plotted to illustrate the temperature trends at the Flamingo study site.

Mean daily average temperatures were consistently cooler offshore than inshore (Figure 2.4). Mean inshore temperatures ranged from 18.07 °C (T_{min}: 16.09 °C; T_{max}: 20.52 °C) and 17.01 °C (T_{min}: 15.26 °C; T_{max}: 21.76 °C) during C1 and C2 respectively, to 20.78 °C (T_{min}: 17.85 °C; T_{max}: 24.50 °C) and 21.08 °C (T_{min}: 17.78 °C; T_{max}: 25.94 °C) during W1 and W2 respectively. Mean offshore temperatures ranged from 17.14 °C (T_{min}: 15.65 °C; T_{max}: 18.95 °C) and 16.27 °C (T_{min}: 14.68 °C; T_{max}: 21.00 °C) during C1 and C2 respectively, to 19.28 °C (T_{min}: 16.74 °C; T_{max}: 22.67 °C) and 19.32 °C (T_{min}: 16.53 °C; T_{max}: 23.62 °C) during W1 and W2 respectively.

2.2 Research approach

The knowledge gaps on the movement ecology of *A. coronus* in southern Angola were addressed using passive acoustic telemetry techniques (see aims in Chapter 1). This was done using strategic receiver placement at three divergent study sites, informed by prior range testing, to monitor fish tagged with acoustic transmitters at the Flamingo study site.

2.2.1 Acoustic telemetry array

2.2.1.1 Range testing

Range testing was conducted prior to the initial deployment of the receiver array in order to

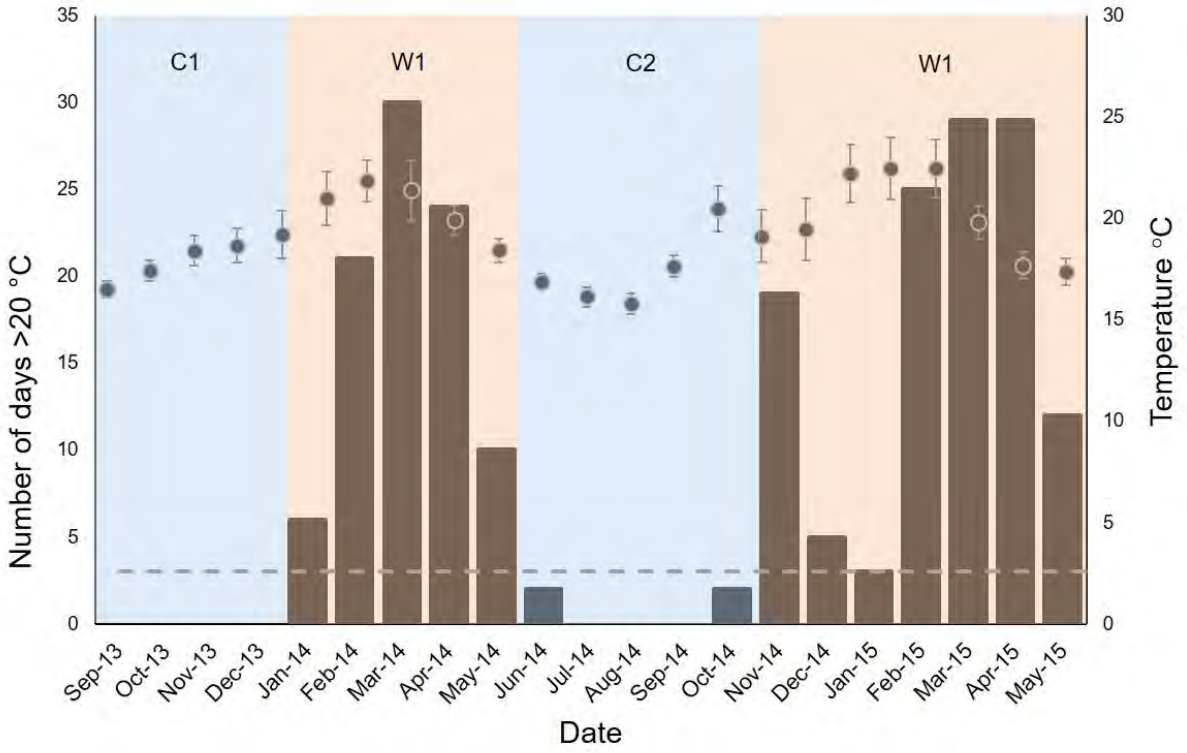


Figure 2.3: Water temperature trends at mid-region (station F7) of the Flamingo study site used to delineate 'warm' and 'cold' periods. Bars indicate number of days per month mean daily temperature > 20 °C. Dashed line indicates threshold number (three days) for period delineation as 'cold' (<3 days; blue shading) or 'warm' (>3 days; orange shading). Monthly mean water temperatures plotted as points, error bars indicate mean daily minima and maxima observed each month.

inform the placement and spacing of receivers. The test was run over eight consecutive days, during winter when the sea is at its roughest in the area, therefore the results were indicative of reception during poor acoustic conditions and represent a conservative reception range. Due to logistical constraints, range testing prior to instrument deployment was limited to only one of the three sites – the Flamingo study site. As this site is far less sheltered than the highly protected Tombua Bay and Baia dos Tigres, detection distance estimates based on range testing here would provide the most conservative estimates of the three study sites.

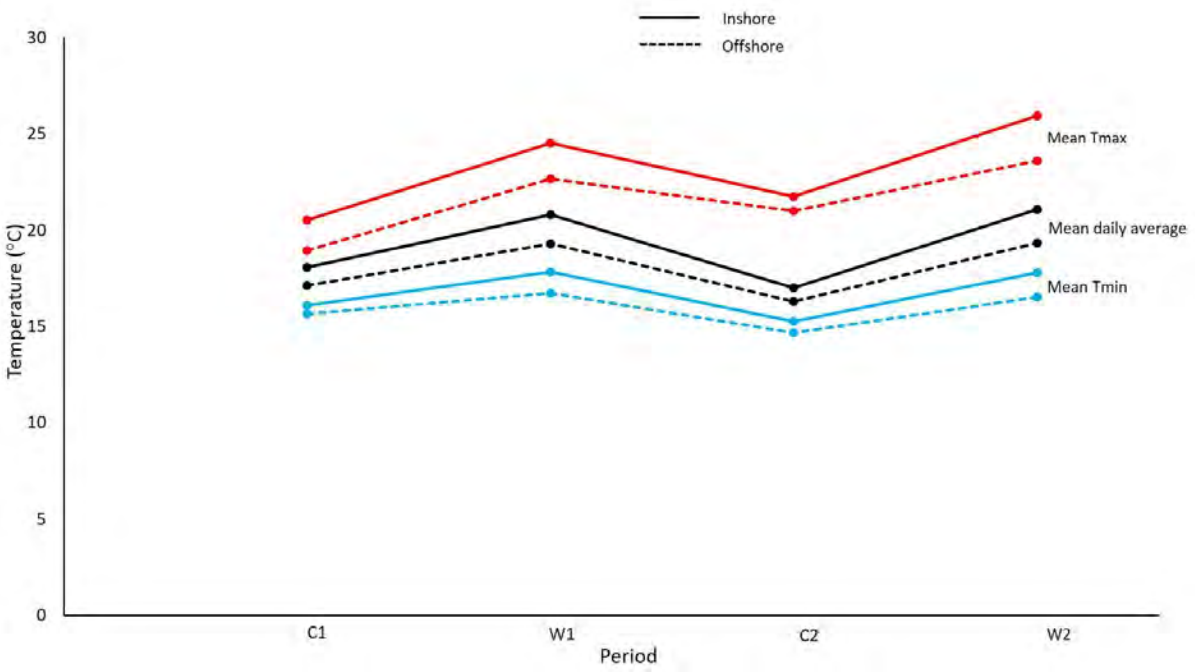


Figure 2.4: Average daily temperature trends on inshore and offshore stations during each monitoring period at the Flamingo study site. Mean daily average across all stations per period, mean minimum average daily temperature across all stations per period, and mean maximum average daily temperature across all stations per period presented.

Range testing utilised a dedicated array consisting of two receivers and four tags (Figure 2.5). The tags used in the range test were the same tags that were later inserted into larger fish (adults and sub-adults) during the first phase of tagging in 2013 (VEMCO V16 4H-158dB output, 45-65 s (average 55 s) delay). The array was deployed perpendicular to the shore with one receiver close inshore and the other receiver further offshore. The inshore receiver was placed 400 m offshore of the coastline and the offshore receiver was placed 1 000 m offshore of the first receiver (Figure 2.5). A tag was placed on each of the two receiver moorings, another tag mooring was deployed 250 m offshore of the inshore receiver, and the final tag mooring was deployed 400 m offshore of the inshore receiver mooring. The array design enabled the reception at six distances to be tested simultaneously: 0 m, 250 m, 400 m, 600 m, 750 m and 1 000 m.

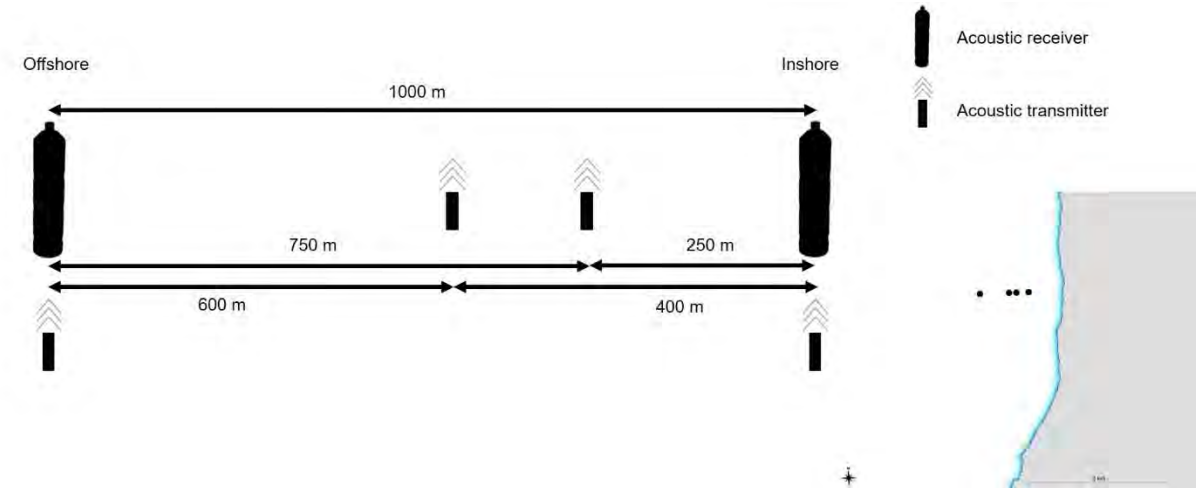


Figure 2.5: Range testing array design. Distances between receivers (VEMCO VR2W) and tags (VEMCO V16-4H) indicated by arrows. Array deployed perpendicular to shore starting 400 m from the shore as per inset map. Blue shading distinguishes ocean from land

2.2.1.1.1. Range testing data analysis

The daily proportion of tag transmissions that were detected by the receivers, after screening for false detections (see approach to false detections below in section 2.4) P_{det} was calculated by dividing the number of valid detections D by the daily number of transmissions Tr

$$P_{det} = \frac{D}{Tr}$$

The number of daily transmissions of range test tags was calculated using the following equation:

$$Tr = \frac{t}{T_{tag}}$$

where t is the time available in a given day of range testing (units: seconds) and T_{tag} is the average delay of the tag, as per manufacturer's specifications (55 s).

The average (± SD) daily proportion of transmissions detected for each distance was calculated and plotted (Figure 2.6). As there were two values for the '0 m' and '1 000 m' distances, the average of the two values was used in each case.

Logistic regression was used to determine distances at which detection efficiency declined. The approach modelled the proportion of detections (response variable) by the distance between receiver and transmitter (predictor variable):

$$Proportion \sim Distance + \varepsilon$$

A logistic model was used due to the response variable being proportional data. The analysis was done using the *glm* function in the **stats** package in *R* v 4.0.3 (R Core Team 2020).

2.2.1.1.2. Range test results

The mean proportion of detections of the range test tags varied from 0.29 ± 0.13 at 1 000 m to 0.72 ± 0.02 which was the proportion of detections at both 0 m and 400 m (Figure 2.6). The logistic regression model indicated that the proportion of detections at distances between 0 m and 750 m were not significantly different from each other, however, the proportion of detections at 1 000 m were significantly lower than the others ($p < 0.05$). A conservative detection distance of 600 m was thus used to guide receiver array design.

2.2.1.2 Acoustic receiver array design and deployment

Three sites were selected at which to place acoustic receivers (Figure 2.1). The entire array consisted of 39 receivers. The array comprised three receiver 'curtains', two at the Flamingo site (Figure 2.7a) and one at Baia dos Tigres (Figure 2.7c), to monitor long-distance longshore movements of tagged fish. Receivers configured in a 'curtain' array are intended to capture all movements by tagged animals past an area (Heupel et al. 2006), which in this study were points along the coastline. The remaining receivers were deployed to investigate area use within the study regions.

The Flamingo study site array consisted of 19 receivers deployed along ~ 23 km of coastline. Two curtains were used at this study site, with 1.2 km spacing between adjacent receivers in the curtains based on range testing results. One curtain of three receivers, was deployed in the southern region and one curtain of four receivers, was deployed in the northern region of this study site, to monitor movements into and out of the recreational fishing area. The curtains extended into deeper waters (40 m in the south and 54 m in the north) than the other receivers (~ 30 m maximum depth) deployed at this site and were intended to detect any longshore

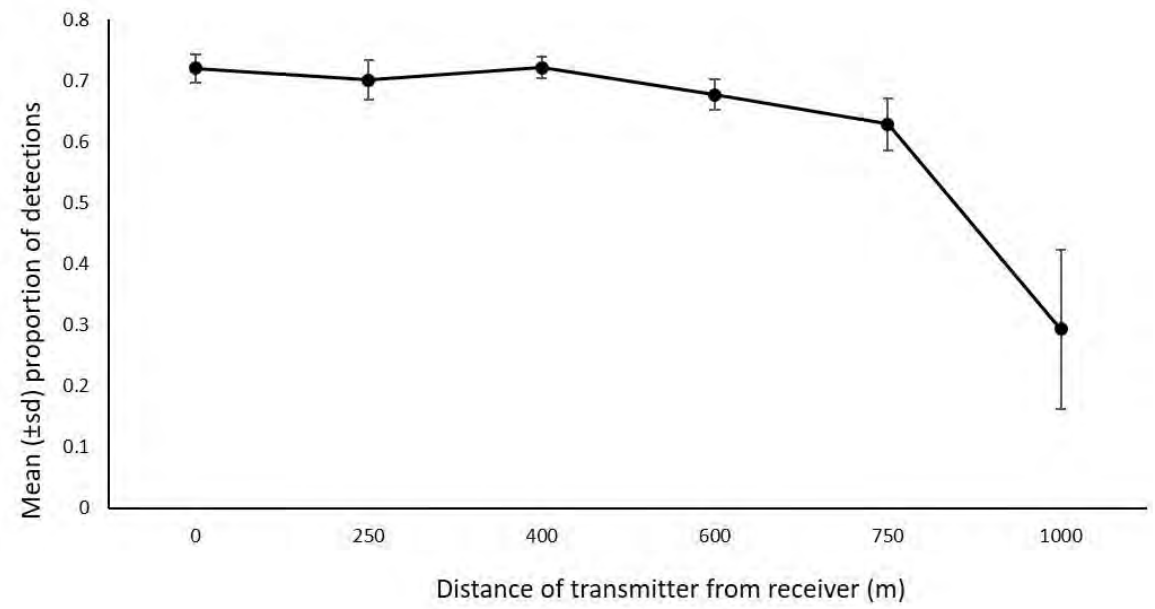


Figure 2.6: Daily mean proportion of transmissions of range test tags detected at six distances by two receivers over an eight-day deployment period. Range testing was conducted at the relatively exposed Flamingo study site with one receiver deployed ~ 400 m offshore and the second receiver a further 1 000 m offshore. Four transmitters (V16-4H) were used: one deployed with each receiver, one 250 m offshore of the inshore receiver and 750 m from the offshore receiver, and one 400 m offshore of the inshore receiver and 600 m from the offshore receiver.

movement that occurred further offshore. The remaining receivers were deployed in pairs, perpendicular to the shore 1.2 km apart, with 3-4 km between adjacent pairs of receivers. The paired receivers allowed for investigation of area use by tagged fish, as well as monitoring inshore-offshore movements.

The Tombua Bay array consisted of four receivers deployed as a double curtain (Figure 2.7b). This allowed for directional movements into and out of the bay to be monitored. Broad regions of high use within the bay could also be identified by this array design due to the small size of the bay.

The Baia dos Tigres array comprised 16 receivers. The third curtain utilised in the study was deployed toward the northern tip of the island and consisted of 10 receivers, eight inside the

lagoon, and two on the seaward side of the island, with the deepest deployed on the 55 m contour. The remaining six receivers were deployed to facilitate the investigation of area use by tagged fish within the lagoon.

Receiver moorings were standardised throughout the array. These consisted of a ~2 m long mooring rope, anchored to the seabed using ~50 kg railway track, suspended above the bottom using two in-line 200 mm diameter trawl floats. Receivers (VEMCO VR2W) were attached to the moorings, in an upward orientation, using cable ties. The moorings and receivers were coated in marine antifouling paint, to reduce the impact of biofouling on receiver efficiency. Two moorings at the Flamingo study site (FN4 & FS3) and two moorings at the Baia dos Tigres study site (BT9 & BT10) were equipped with Sub Sea Sonics acoustic releases. All other moorings were serviced by SCUBA divers.

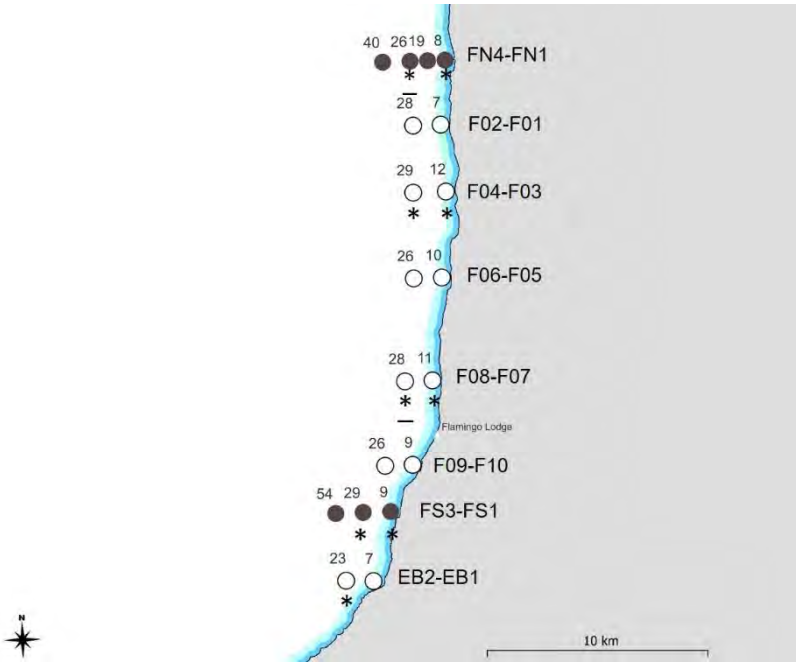
The first deployment of acoustic receivers and temperature loggers was completed on 2 October 2013. Subsequently, receivers and moorings were serviced, telemetry and temperature data were downloaded, and instruments redeployed on two occasions: during June 2014 and July 2015. Due to logistical constraints in importing acoustic receivers, fish were tagged prior to receiver deployment.

2.2.1.3 Sentinel tags

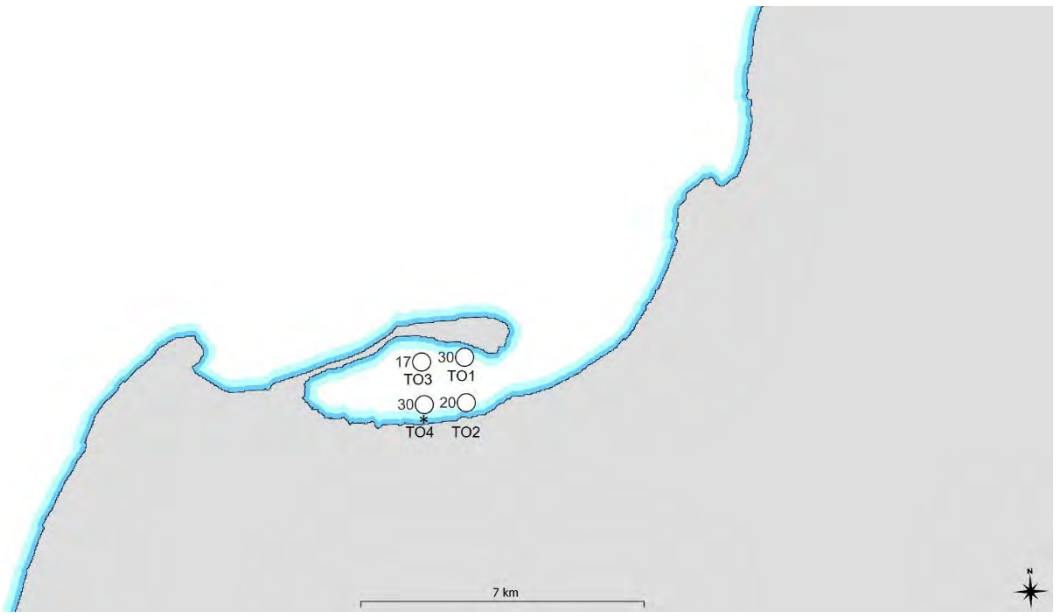
Testing the efficiency of equipment within an acoustic telemetry array is paramount in understanding and interpreting results with confidence (Heupel et al. 2008). Insight into how environmental conditions may influence the efficacy of acoustic telemetry technology, and whether any environmental conditions generate artificial rhythmic patterns in acoustic telemetry data, is important when interpreting these data (Heupel et al. 2008; Payne et al. 2010). The use of 'sentinel tags', which are tags that are moored within an acoustic telemetry array within detection range of one or more receivers, in an acoustic telemetry study facilitates the detection of such rhythmic patterns, and allows for them to be accounted for, where present (Payne et al. 2010). In a study of how biofouling affected acoustic receiver performance, receivers like those used in the present study and similarly coated with anti-fouling paint, exhibited minor declines in efficacy over the two-month study period (Heupel et al. 2008). Due to the remote nature of the southern Angolan study area, which was serviced once annually,

longer-term data from the sentinel tag deployments could not be reliably used due to the presence of biofouling on both the acoustic receivers and the sentinel tags utilised in the study, with the contribution from each in any trends observed being unknown. Biofouling on transmitters is not reflective of a natural phenomenon, therefore introduces a confounding factor that cannot be accounted for. The use of sentinel tags in the present study was aimed at identifying short-term (daily) rhythmic patterns in detection efficacy, rather than absolute detection efficacy over the long term. A two-month sentinel tag dataset was therefore used, due to the potential reduced performance of the system during the full deployment period.

a)



b)



c)

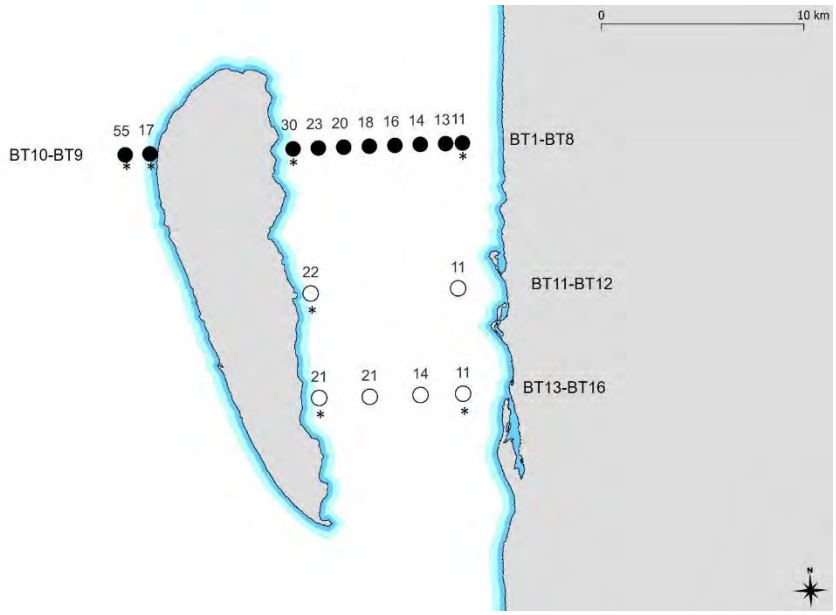


Figure 2.7: Receiver array design at a) Flamingo, b) Tombua Bay and c) Baia dos Tigres. Black filled points indicate receivers in a 'curtain' layout, intended to detect any longshore movements by tagged fish. Numbers indicate bottom depth (m) at receiver mooring. Station labels indicated in text on maps. Asterisks indicate stations where a temperature logger was deployed together with an acoustic receiver. Two temperature loggers at the Flamingo study site malfunctioned mid-way through monitoring – indicated by underlined asterisks. Blue shading distinguishes ocean from land.

Two sentinel tags (VEMCO V13-1H, 400-440 s nominal delay, 153 dB power output; similar to the lowest power output tags deployed in smaller fish) were deployed from 8 August 2014 to 5 July 2015 in the Flamingo receiver array. One tag was deployed 200 m inshore of receiver F5 (tag deployed 200 m from the shore) and the other tag was deployed midway between receivers F5 and F6 (Figure 2.8). Data used in analyses covered the period 8 August to 6 October 2014.

Mean (± SD) hourly detection rate (DR) was calculated across the monitoring period for each possible tag and receiver combination (receiver F5-T1, F5-T2, F6-T2; T1 was beyond detection range for F6 so this combination was not considered). To calculate mean DR, monthly means of the total number of sentinel tag detections per hour were calculated. Detection rates were then calculated by dividing the number of hourly sentinel tag detections by the total number of

tag transmissions per hour, based on the mean tag transmission delay period (420 s). Hourly means (± SD) were then averaged across all months and are depicted in Figure 2.9. To test for

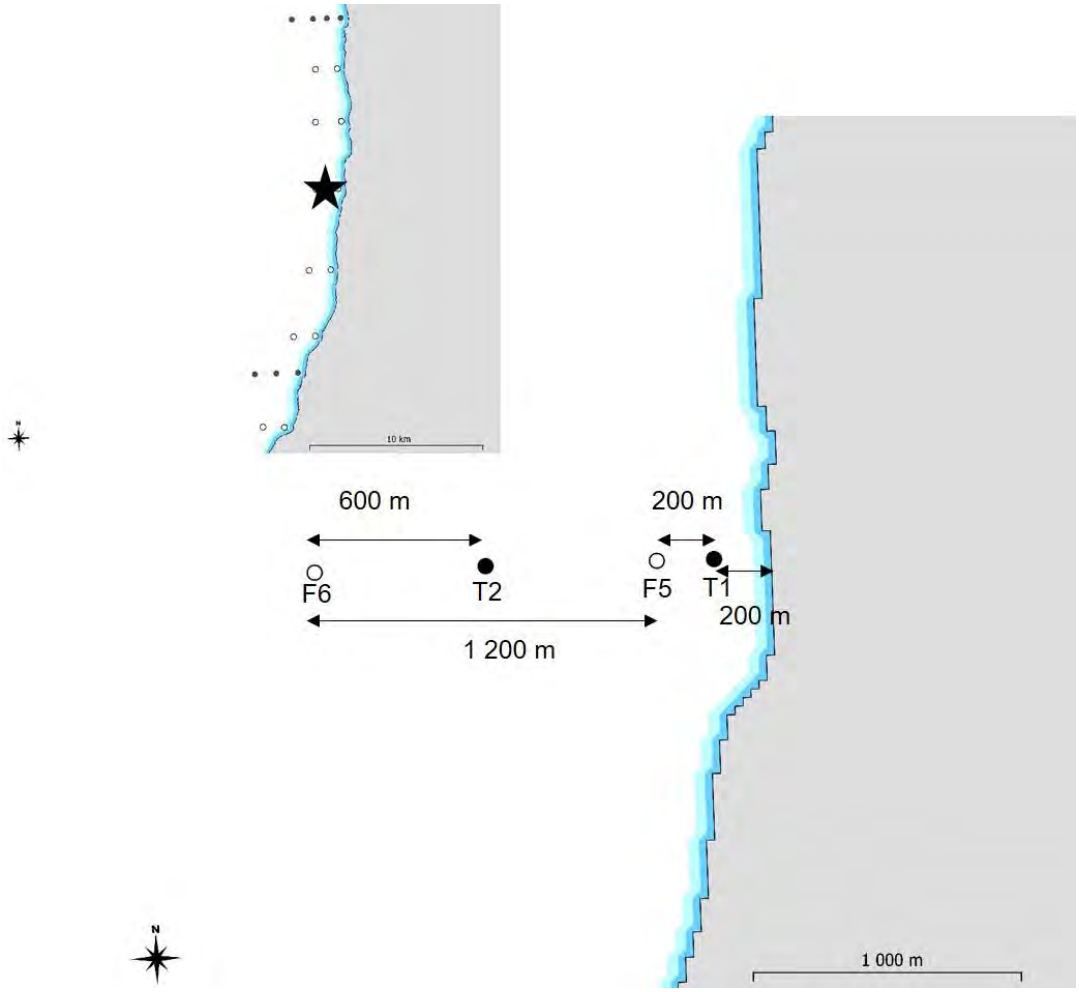


Figure 2.8: Position of sentinel tags (black points; T) relative to nearest receivers (F6 and F5). Black star in inset indicating position within the Flamingo array of receivers. Tag 1 was 200 m offshore and from receiver F5 and tag 2 was equidistant (600 m) from each receiver. Blue shading distinguishes ocean from land.

statistical trends in the mean hourly DR, a logistic regression model was fitted to the proportional data. Detection rate was the dependent variable and hour of the day was the predictor variable.

Detection rate showed no relationship with time of day (no coefficients [hours of the day] were significantly different to the intercept or one another; $p > 0.05$), indicating that there was a lack of daily rhythmic cycles in the data. This removed concern that patterns in environmental

conditions (at least over hourly time scales) may confound any patterns observed in the data collected by the receivers on study animals.

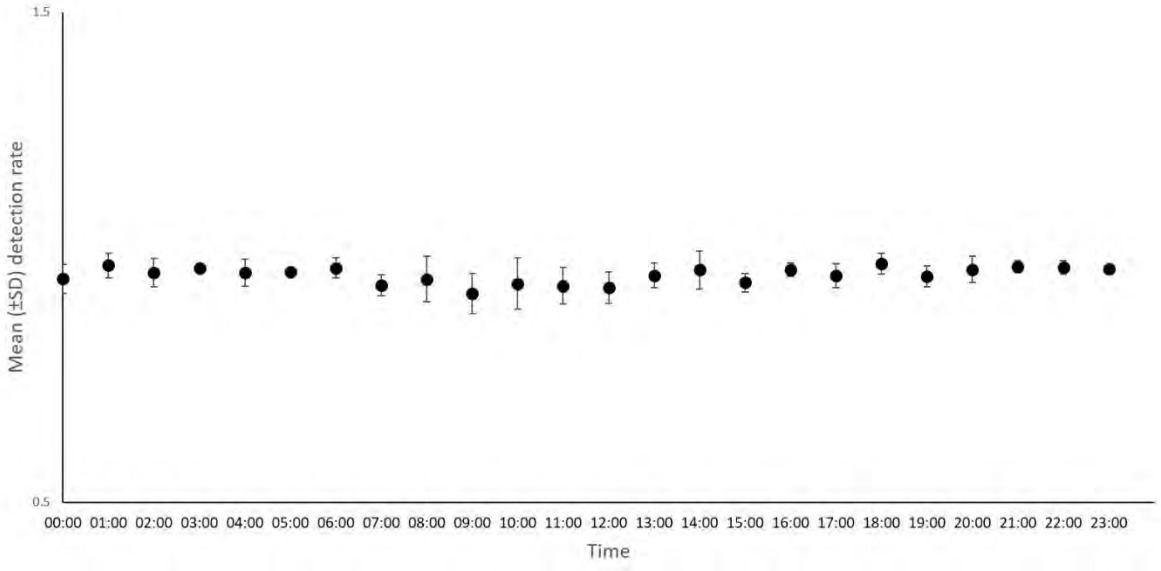


Figure 2.9: Hourly mean detection rate of sentinel tags recorded by acoustic receivers during a two-month long monitoring period between August and October 2014 at the Flamingo study site. Detection rate indicates number of detections logged by receivers as a proportion of the total number of sentinel tag transmissions based on the mean transmission delay.

2.3 Fish tagging

Fish tagging occurred in two phases (Figure 2.10). During Phase I (August 2013), 20 large fish (range: 780-1155 mm total length (TL), mean ± SD: 966.5 ± 111 mm) were tagged with VEMCO V16 tags (4H model with 158 dB power output, 45-65 s (average 55 s) delay, minimum battery life ~ 780 days). Based on the length-at-50% maturity (870 mm TL), these fish were classified as sub-adults and adults. During Phase II (June 2014), 10 smaller individuals (range: 460-765 mm TL, mean: 559 ± 99.3 mm) were tagged using VEMCO V13 tags (1H model with 153 dB power output, 45-65 s (average 55 s) delay, minimum battery life ~367 days). Fish in Phase II were classified as juveniles and sub-adults. Tagging effort occurred throughout the Flamingo study site, covering ~23 km of coastline (Figure 2.10). Tags that were retrieved from fishers who had captured tagged fish were reused where possible.

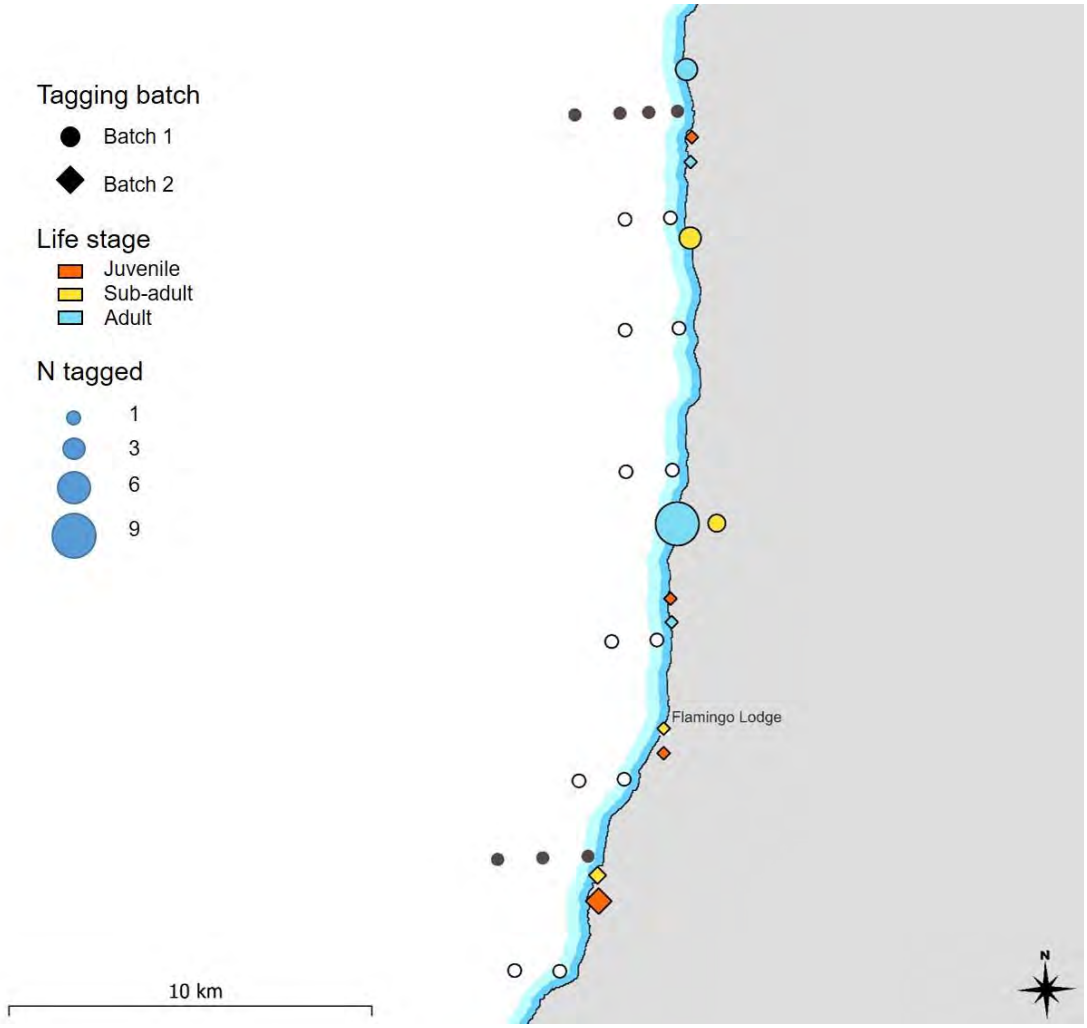


Figure 2.10: Tagging locations for *A. coronus* tagged in two batches (August 2013 and June 2014) along the coastline at the Flamingo study site. Symbol shape and colour depicting different tagging batches and life stages respectively. Size of symbols indicating number of fish tagged at a location. Acoustic receivers indicated by closed and open black points. Blue shading distinguishes ocean from land.

Fish were captured from the shore, using rod and line, with either baited hooks or artificial lures. Hooked fish were landed using a wet soft cloth sling, and carried up the beach to a 60 l anaesthetic bath, made up of a solution of 2-phenoxyethanol and seawater at a concentration of 0.5 ml/l seawater. This anaesthetic was found to have no effect on plasma osmolality, which is used as a proxy to measure physiological stress, in a congener *A. japonicus* (Bernatzeder et al. 2008) and therefore deemed to be suitable in the present study. The fish were left in the anaesthetic bath until they were unable to maintain equilibrium and were unresponsive to external physical stimuli. The average (± SD) exposure time to the anaesthetic was 02:12 ±

00:19 (mm:ss). Once anaesthetised, fish were transferred to a vinyl surgery-sling, and placed ventral side up, to allow for an incision to be made on the ventral surface of the abdomen. An incision was made 1-2 cm lateral to the mid-ventral line, ~5 cm behind the tip of the pectoral fin. An acoustic tag was then inserted into the body cavity through the incision. Incisions were sutured closed with three sutures (Clinisilk® 3/0 [for smaller sub-adults and juveniles] or 2/0 [for larger sub-adults and adults], non-dissolving sutures). During surgery, the fish's gills were kept moist by covering the head and gills with a damp cloth and continually pouring seawater over the gill region. The surgery process took on average 06:23 ± 00:55 mm:ss (Table 2.1). Once sutured, the incision was coated with an antiseptic powder-gel to facilitate healthy healing of the incision. Fish were then moved to a recovery bath containing ~ 80 l of aerated seawater. The fish were observed until they were able to maintain equilibrium unassisted and were responsive to external physical stimuli at which point they were deemed to have recovered (average recovery time was 04:11 ± 01:09 mm:ss). The recovery bath containing the fish was then carried into the sea and the fish was released (release process took 01:06 ± 00:26 mm:ss). Throughout the surgery procedure, the fish's eyes were shielded from direct sunlight to prevent any potential UV damage, and to minimise stress. The entire surgery process, from immersion in anaesthetic bath until release, took on average 13:52 ± 01:57 mm:ss (Table 2.1).

Tagging effects and tag retention by tagged specimens are important considerations when conducting acoustic telemetry studies. These effects were not directly tested in *A. coronus* in this study; however, a comprehensive study was conducted on the congener *A. japonicus* by Childs et al. (2011). These authors found no deleterious physiological effects, with good survival and tag retention indicating that acoustic telemetry was a suitable technique to employ on the species. It was assumed in the present study that similar effects would be observed in *A. coronus*. The acoustic telemetry data collected for *A. coronus* during this study did not indicate any need for concern regarding tag retention or survival, with the majority of specimens actively moving about the receiver array for the duration of the monitoring period.

2.4 Data processing

Data was downloaded from the receivers using the *VUE* software and from the temperature loggers using the software supplied by the manufacturers (SEASTAR and HOBOWARE) twice during the study period: in June 2014 and July 2015. Prior to analyses, detection data were screened for false detections, according to the procedure outlined by (Pincock 2012). The

acoustic technology employed works on a single frequency (69 kHz), thus unique transmitter coding is achieved by varying the timing between individual pings making up the pulse train, of each transmission by a transmitter. This makes it possible for transmitters to periodically overlap in transmission, which are sometimes decoded and logged as a valid detection by a receiver as they mimic a valid transmitter's pulse train. These are easily identified and removed from a dataset if the tag IDs are not known from the study area. False detections are also usually infrequent due to the random delay programmed into the tags between transmissions, so a false ID will not be logged multiple times in a short time period. Where a transmitter ID is recognised as potentially emanating from a specimen within the study, false detections can be identified by their unlikely location between successive detections, with the distance between receivers being greater than the animal is able to swim in the given time period. They can also be identified by their low rate of detection at a particular receiver, without being detected at a nearby receiver in a reasonable time period. The *FDA Analyzer* in the *VUE* software package was used to identify potentially spurious detections, which were then examined and removed if deemed appropriate. Flagged detections which could be corroborated with nearby receivers within the same hour were regarded as legitimate and were retained in the dataset. If they could not be corroborated, they were removed from the dataset.

Table 2.1: Details of fish tagged with acoustic transmitters at the Flamingo study site during 2013 and 2014. Single asterisks indicate fish that were harvested by fishers and reported during the study period. Double asterisk indicates a fish that was captured by fishers prior to first receiver deployment.

Fish ID	Date tagged	Length (mm TL)	Tag model	Surgery duration (mm:ss)	Procedure duration (mm:ss)	Life stage	Age estimate (yr)	Mass estimate (kg)
01	2013-08-14	780	V16-4H	05:06	11:00	Sub-adult	3.0	4.8
02	2013-08-22	950	V16-4H	04:46	10:47	Adult	4.5	9.0
03	2013-08-22	950	V16-4H	06:52	12:55	Adult	4.5	9.0
04	2013-08-15	1 084	V16-4H	06:45	18:01	Adult	6.0	13.6
05	2013-08-15	960	V16-4H	05:20	12:59	Adult	4.6	9.3
06	2013-08-15	1 150	V16-4H	06:44	16:20	Adult	6.7	16.3
07	2013-08-15	980	V16-4H	05:36	14:02	Adult	4.8	9.9
08	2013-08-17	940	V16-4H	05:26	12:38	Adult	4.4	8.7
09	2013-08-17	960	V16-4H	07:26	12:44	Adult	4.6	9.3
10	2013-08-16	960	V16-4H	07:48	14:51	Adult	4.6	9.3
11*	2013-08-21	950	V16-4H	07:56	16:10	Adult	4.5	9.0
12	2013-08-20	930	V16-4H	05:56	11:02	Adult	4.3	8.4
13	2013-08-21	900	V16-4H	06:12	12:50	Adult	4.0	7.6
14	2013-08-22	1 000	V16-4H	09:25	15:25	Adult	5.0	10.5
15	2013-08-22	1 120	V16-4H	06:28	14:00	Adult	6.3	15.0
16	2013-08-22	1 155	V16-4H	06:43	16:20	Adult	6.7	16.5

17	2013-08-22	1 050	V16-4H	05:50	11:30	Adult	5.5	12.3
18*	2013-08-22	815	V16-4H	07:27	14:45	Sub-adult	3.3	5.5
19	2013-10-03	845	V16-4H	05:20	12:55	Sub-adult	3.6	6.2
20*	2013-08-22	850	V16-4H	07:16	13:25	Sub-adult	3.6	6.3
21	2014-07-08	1 000	V16-4H	07:39	14:39	Adult	5.0	10.5
22	2014-06-27	1 100	V16-4H	06:22	15:36	Adult	6.1	14.2
23	2014-06-07	464	V13-1H	07:03	15:03	Juvenile	0.8	0.9
24	2014-06-18	648	V13-1H	04:30	18:25	Sub-adult	2.0	2.7
25	2014-06-18	490	V13-1H	06:05	11:15	Juvenile	1.0	1.1
26	2014-06-23	460	V13-1H	05:15	11:13	Juvenile	0.8	0.9
27	2014-06-24	616	V13-1H	05:33	11:22	Sub-adult	1.8	2.3
28	2014-06-24	466	V13-1H	04:33	10:10	Juvenile	0.9	1.0
29	2014-06-30	566	V13-1H	04:50	10:35	Juvenile	1.5	1.8
30	2014-07-06	595	V13-1H	06:14	14:40	Juvenile	1.7	2.1
31	2014-07-07	765	V13-1H	06:14	17:10	Sub-adult	2.9	4.5
32	2014-07-11	520	V13-1H	05:20	10:48	Juvenile	1.2	1.3
33**	2013-08-22	760	V16-4H	05:56	12:35	Sub-adult	2.9	4.4

Chapter 3: Coastal Zone Area Use Dynamics of *Argyrosomus coronus* in Southern Angola

3.1 Introduction

Assessing how animals utilise space is fundamental for understanding their ecology. Knowledge of abiotic and biotic drivers and any constraints on the space use of a species can aid in the interpretation of its current distribution (Morin et al. 1992; Buisson et al. 2007; Brownscombe et al. 2019), infer historical distribution (Pont et al. 2015), and predict future distributions based on environmental change (Pont et al. 2015; Young and Carr 2015).

The population structure of fish species may vary. A species may occur in a single, mixed population throughout its distribution with gene flow occurring unhindered within the population (Roberts and Ayre 2010), or a species may occur as several subpopulations, with low levels of gene flow maintaining connectivity among them, jointly forming a metapopulation (Kritzer and Sale 2004; Metcalfe 2006). If subpopulations cease to be genetically connected, the independent populations that they form may be subjected to different selection pressures and this will, in turn, drive divergent evolution (Henriques et al. 2016).

Studying how animals utilise space requires insight into an animal's movement at various spatial and temporal scales. This is complex and the theory has seen much debate over several decades (Myers 1949; Southwood 1962; Kennedy 1985; Dingle and Drake 2007) (see Chapter 1 for more in-depth discussion). Research tools and techniques that provide important information about a fish species' spatial ecology include population genetic studies (White et al. 2009; Roberts and Ayre 2010; Bennett et al. 2017) and movement studies such as mark-recapture, acoustic telemetry (Heupel et al. 2006; Thorstad et al. 2013) and otolith microchemistry (Walther and Limburg 2012; Smith and Kwak 2014; Starrs et al. 2016). Together, these techniques contribute to our understanding of a species' population structure.

Understanding the spatial ecology of a species is important from a fishery management and conservation perspective (Nanami et al. 2013; Lowerre-Barbieri et al. 2019). Knowledge of stock delineation is critical in determining the approach to a management strategy, particularly in terms of whether a population can be managed as a single unit, or whether any significant

structuring needs to be considered in the approach (Bennett et al. 2017; Voss et al. 2018). When considering conservation strategies, such as marine protected area (MPA) design, insight into area use and movement pathways are paramount (Meyer et al. 2007; Costello et al. 2010).

The southern Angolan study region has been identified as a climate change hotspot (Hobday and Pecl 2014) with sea surface temperature warming at a rate of nearly 10 times the global average recently (Potts et al. 2014b). This phenomenon has already been linked with a distribution shift by *A. coronus*, which has led to the species hybridising with *A. inodorus* in Namibia (Potts et al. 2014b). Understanding the species' movement ecology, particularly in relation to water temperature changes, may aid in understanding how climate change will affect the species.

Previous studies on *A. coronus* in southern Angola provide some insight into their broad-scale spatial use patterns. Catch data from local fishers showed that early-stage juveniles smaller than 300 mm TL occurred offshore over muddy substrata in depths of 50–80 m (Potts et al. 2010b). A recent study used a multi-method approach to look into the movement ecology of *A. coronus* using fishery-dependent data (conventional tagging and standardised catch rate) and acoustic telemetry data (Potts et al. 2018). This study covered an eight-year period, between 2005 and 2013. The conventional tagging component of the study, which reported a 7.6 % recapture rate (75 fish), found that only 6.6 % (five fish) of recaptures occurred outside of the Flamingo study site tagging area. Two fish were recaptured <30 km north of the Flamingo study site in autumn and three fish were recaptured south of the Flamingo study site, one at the Cunene mouth in spring and two further south, in northern Namibia during summer ('warm' period). The standardised catch rates for the area exhibited a peak in August ('cold' period) decreasing to zero between November and April ('warm' period). Similar lines of evidence have been used to suggest that *A. coronus* undertake a seasonal longshore migration aligned with the shifting ABFZ, moving southwards into northern Namibia during summer ('warm' period) and northwards into southern Angola during winter ('cold' period) (Potts et al. 2010b). A study on the biology of *A. coronus* in southern Angola suggested that spawning occurred in spring (around November), based on gonad development states (Potts et al. 2010b). The spawning habitat of the population is unknown, but it is suggested to be offshore due to the paucity of ripe gonads in fish caught by shore-based fishers (Potts et al. 2010b).

The aim of this chapter is to examine the spatio-temporal dynamics of *A. coronus* at a broad-scale (at the regional level, among all study sites) and at a local-scale (at the study site level). This information was used to categorise the movement behaviour of different life history stages of *A. coronus* by examining the seasonal movements of juvenile, sub-adult and adult individuals within each of three different study sites (described in Chapter 2): Flamingo (a relatively exposed stretch of coastline), Tombua Bay (a small, natural embayment) and Baia dos Tigres (a coastal lagoon formed between an island and mainland Angola). To achieve this, all acoustic telemetry data from the two-year monitoring period for all individuals was used. The main hypothesis was that adult *A. coronus* in southern Angola undertake an annual large scale to-and-fro longshore migration synchronised with the seasonally shifting ABFZ, and that the juveniles and sub-adults remain resident to the study site where they were initially captured and tagged, based on evidence from previous catch data and conventional tagging data (Potts et al. 2010b, 2018). While the acoustic telemetry component of the study of Potts et al. (2018) sheds some doubt on the seasonal longshore migration hypothesis for *A. coronus*, this chapter further interrogates this, and provides a comprehensive analysis of the broad and fine-scale spatio-temporal patterns at different life history stages of the species.

3.2 Materials and methods

For details on the study sites, acoustic tagging approach and receiver array design, see Chapter 2.

3.2.1 Broad-scale area use

Data regarding the general trends in detections at a broad-scale were summarised by grouping data within each of the three study sites (Flamingo, Tombua Bay, Baia dos Tigres). This included the numbers of juvenile, sub-adult and adult fish that were tagged and recaptured, the number of tagged fish that were detected, the number of days that fish were detected, the number of receivers on which fish were detected and the longshore displacement of tagged individuals from the Flamingo study site.

To provide a broad depiction of the spatio-temporal dynamics of tagged fish over time, the location of each individual relative to each of the study sites was plotted over time. The detections for each fish at the Flamingo site were summarised in terms of the number of days

they were detected relative to days monitored overall and during each monitoring period (C1, W1, C2 & W2), the number of receivers detected at and the proportions of detections on inshore vs offshore receivers. The detections for each fish at the Tombua Bay site were summarised in terms of when they occurred, relative to detections at the Flamingo site, and their duration.

3.2.2 Local-scale area use at the Flamingo study site

Local-scale analyses were conducted to better understand area use within one study site, specifically in terms of the longshore distribution of tagged fish, and their utilisation of inshore and offshore zones along a depth gradient. The Flamingo study site was the sole focus of these analyses due to the higher resolution of receivers at this site and the paucity/absence of detections at the other two sites. This study site was also the sole site where tagging was conducted for this study. Detection data from all of the Flamingo study site receivers, for all fish detected at this site during the study duration, were used in analyses. Local area use was considered in terms of both longshore area use and inshore/offshore area use along the depth gradient.

3.2.2.1 Longshore area use

To investigate the longshore dynamics of tagged fish in the Flamingo study site array, receivers were classified according to the line (perpendicular to the shore) in which they occurred. Receivers at the northernmost line were assigned a value of 1, with incremental values assigned for each line south of here, up to 8 for the southernmost line. Detections were summarised as daily counts of tagged fish detected on each receiver line (1 – 8) and plotted against time.

A Generalised Linear Model (GLM) was used to determine the effect of period, and region within the array, on the daily number of tagged adult fish that were detected. Adults were the focus of this analysis due to an interesting observation of these fish seeming to concentrate in the mid-region of the array at certain periods of the year. Other life stages exhibited much greater restrictions in their movements, not lending themselves to this analysis. To simplify model interpretation, only detections from the two northernmost and southernmost lines and receiver F07 from the ‘Mid’ region of the array were considered in the analysis (see Figure 2.7a). The ‘North’ region consisted of receivers FN1–FN4, F01 and F02, the ‘South’ region

consisted of receivers EB1, EB2 and FS1–FS3, and only detections from receiver F07 were used from the 'Mid' region of the array as by far the greatest number of detections in the Mid region (98 %) were observed at this receiver. The daily number of fish detected within each of the regions, 'North (N)', 'South (S)' and 'Mid' was calculated. A quasi-Poisson distribution was used for the GLM as the response variable was discrete counts, and the data violated the assumption for the Poisson distribution that its mean equals its variance. The GLM was described as:

$$Frequency \sim Period + Region + \varepsilon$$

$$\varepsilon \sim \text{quasi-Poisson}\ (\mu)$$

where *Frequency* is the number of tagged fish detected daily (response) with predictors '*Period'* (with levels 'cold' or 'warm') and '*Region'* (with levels 'N', 'S', 'Mid').

3.2.2.2 Depth use

To assess how tagged fish utilised different depth zones, it was assumed that the depth of the receiver where a detection was made could be used as a proxy for the depth of the fish (previously done, for example, by Pendleton et al. (2019)). This was because the study species is largely demersal and the topography of the ocean floor was fairly uniform within the Flamingo study site array. A depth value for each fish on each day was calculated as:

$$D_{ij} = \sum_{r=1}^{n} P_{rij} \times D_{rij}$$

$$P_r = \frac{D_r}{TD}$$

where D_{ij} is the depth (m) for the *i*th fish on the *j*th day of the study period, P_r is the daily proportion of detections of a fish at the *r*th receiver and *TD* is the total number of daily detections for a fish in the study area (Flamingo). These daily depth values were plotted as a time series.

Following depth assignment, detections were grouped into 10 m bins (except for the first bin, which spanned 8 m, because the shallowest receiver was at a depth of 7 m) (7–15 m; 16–25 m; …; 46–55 m; 5 bins in total) and the daily number of tagged fish that were detected in each bin was calculated. To examine how different life history stages were distributed across depth zones, during different times of the year, the daily number of fish that were detected in each

depth bin was modelled, using a GLM (with a quasi-Poisson distribution due to the response variable being discrete counts, and the data violating the assumption that its mean equals its variance), against predictors using the following model:

$$Frequency \sim Period + Depth + Life\ history\ stage + \varepsilon$$

$$\varepsilon \sim \text{quasi-Poisson}\ (\mu)$$

where *Frequency* is the number of tagged fish detected daily (response) with predictors *Period* (levels 'cold', 'warm'), *Depth* (bins 1–5), *Life history stage* (levels – 'adult', 'sub-adult', 'juvenile'). All statistical analyses were conducted in *R* v 4.0.3 (R Core Team 2020).

3.3 Results

3.3.1 Overview

Tagged fish were detected for varying periods post-release, ranging from three to 457 days (median = 91.5 days) (Appendix Table A1). Sub-adult (n = 3) and adult (n = 17) fish tagged in 2013 (batch 1) were detected on 40-102 days (median = 49 days) and on 28-457 days (median = 313.5 days), respectively, throughout the 616-day monitoring period. Juvenile and sub-adult fish tagged in 2014 (batch 2), were detected on 3-97 days (median = 20.5 days) and 25-75 days (median = 68 days) respectively, during the remainder of the monitoring period.

During the study period four fish were confirmed recaptured and their transmitters returned to the author (see Chapter 2 Table 2.1). One was a sub-adult that was captured without ever being detected, and hence was excluded from all analyses. Two were sub-adults captured within four months of their release, and one was an adult captured seven months after release. No transmitters were returned from fish that were tagged in batch 2; however, one of these fish was never detected. On two occasions contact was made with the author regarding fish that were captured but neither attempts to obtain the tags or their identification number were successful.

Detections of *A. coronus* occurred largely on inshore receivers across all life stages. While all life stages were typically detected more during 'cold' periods, juveniles and sub-adults showed a general trend of decreasing detections over time. Juveniles were detected predominantly on inshore receivers throughout the monitoring period (median proportion of detections on inshore receivers = 0.69, range: 0.54-1.00) (Table 3.1). Detections of juvenile fish were concentrated

Table 3.1: Detection summary of all tagged *A. coronus* at Flamingo study site. Life stages are indicated for each individual, and include juvenile (J), sub-adult (S) and adult (A) stages. RC indicates a fish that was harvested and the tag returned to the author. NA indicates that a fish had not yet been tagged in a given period.

Fish ID	**Date tagged**	**Life stage**	**Length (mm total length)**	**Number of days monitored**	**Number of days detected**	**Number of receivers detected at**	**Proportion of detections at Flamingo inshore receivers (the remainder are detections at offshore receivers)**	**Proportion of days fish were detected during cold (C1 & C2) and warm (W1 & W2) periods**			
								C1 (100 day period)	W1 (151 day period)	C2 (153 day period)	W2 (212 day period)
01	2013-08-14	S	780	650	39	6	0.98	0.39	0.00	0.00	0.00
02	2013-08-22	A	950	650	261	11	0.47	0.31	0.19	0.41	0.60
03	2013-08-22	A	950	650	389	10	0.94	0.87	0.88	0.86	0.18
04	2013-08-15	A	1084	650	373	13	0.98	0.94	0.76	0.93	0.09
05	2013-08-15	A	960	650	337	16	0.74	0.57	0.32	0.52	0.73
06	2013-08-15	A	1150	650	29	19	0.55	0.23	0.01	0.03	0.00
07	2013-08-15	A	980	650	100	10	0.77	0.55	0.30	0.00	0.00
08	2013-08-17	A	940	650	375	13	0.83	0.40	0.62	0.68	0.66
09	2013-08-17	A	960	650	215	17	0.91	0.28	0.17	0.54	0.37
10	2013-08-16	A	960	650	456	19	0.91	0.97	0.79	1.00	0.42
11	2013-08-21	A	950	206	52	9	0.97	0.30	0.30	RC	RC
12	2013-08-20	A	930	650	379	19	0.37	0.72	0.48	0.42	0.80

13	2013-08-21	A	900	650	57	17	0.44	0.06	0.03	0.16	0.10
14	2013-08-22	A	1000	650	425	22	0.84	0.89	0.94	0.46	0.58
15	2013-08-22	A	1120	650	326	20	0.30	0.61	0.76	0.03	0.68
16	2013-08-22	A	1155	650	397	21	0.82	0.56	0.49	0.86	0.43
17	2013-08-22	A	1050	650	252	22	0.63	0.76	0.27	0.38	0.35
18	2013-08-22	S	815	59	0	NA	NA	RC	RC	RC	RC
19	2013-10-03	S	845	639	102	15	0.09	0.43	0.39	0.00	0.00
20	2013-08-22	S	850	112	49	8	0.91	0.49	RC	RC	RC
21	2014-07-08	A	1000	361	86	5	0.07	NA	NA	0.01	0.40
22	2014-06-27	A	1100	372	302	16	0.98	NA	NA	0.79	0.75
23	2014-06-07	J	464	392	3	4	1.00	NA	NA	0.02	0.00
24	2014-06-18	J	595	363	12	2	1.00	NA	NA	0.08	0.00
25	2014-06-18	S	648	381	25	2	0.49	NA	NA	0.16	0.00
26	2014-06-23	J	466	375	97	8	0.68	NA	NA	0.63	0.00
27	2014-06-24	J	460	376	0	NA	NA	NA	NA	0.00	0.00
28	2014-06-24	S	616	375	73	3	0.97	NA	NA	0.38	0.07
29	2014-06-30	J	520	358	29	4	0.69	NA	NA	0.16	0.02
30	2014-07-06	S	765	362	69	5	0.11	NA	NA	0.27	0.14
31	2014-07-07	J	566	369	4	2	0.67	NA	NA	0.02	0.00
32	2014-07-11	J	490	381	71	3	0.54	NA	NA	0.33	0.09

in period C2, the first period post juvenile tagging (median proportion of monitoring days fish detected = 0.13, range: 0.02-0.63), for fish that were detected at some point, compared to period W2 (median proportion of monitoring days fish detected = 0, range: 0-0.09) for the same fish. Sub-adults were detected primarily on inshore receivers during the monitoring period (median proportion of detections on inshore receivers = 0.7, range: 0.09-0.98). Sub-adult detections were concentrated in period C1 (median proportion of monitoring days fish detected = 0.43, 0.39-0.49 days), decreasing for the remaining periods to a median proportion of 0 (range: 0-0.14 days) during the final period, W2. Adults were primarily detected on inshore receivers (median proportion of detections on inshore receivers = 0.80, range: 0.07-0.98). Detections of adults were higher in periods C1 (median proportion of monitoring days fish detected = 0.57, range: 0.06-0.97) and C2 (median proportion of monitoring days fish detected = 0.46, range: 0-1) than during W1 (median proportion = 0.4 days, range: 0.01-0.94 days) and W2 (median proportion = 0.42 days, range: 0-0.8 days).

3.3.2 Broad-scale area use

No fish were ever detected in the Baia dos Tigres array, while only adults were detected in Tombua Bay (Figure 3.1). Juveniles and sub-adults appeared to be less mobile than adults, with no detections occurring outside of the Flamingo study site array.

The five fish that were detected in Tombua Bay were all relatively large adults (960 – 1 155 mm TL, Table 3.2). Visits to Tombua Bay were of short duration, lasting between one and 36 days. All fish, except one (Fish 14, 1 050 mm TL), were detected in the Flamingo array subsequent to their detection in Tombua Bay (Table 3.2). The timing of visits to Tombua Bay showed no clear pattern, with fish being detected during both ‘warm’ and ‘cold’ periods (Table 3.2).

3.3.3 Local-scale area use at the Flamingo study site

3.3.3.1 Longshore area use

Inter-annual trends in the longshore distribution of tagged fish were similar to each other during the two ‘cold’ periods (C1 & C2) and during the two ‘warm’ periods (W1 &W2). Adult fish

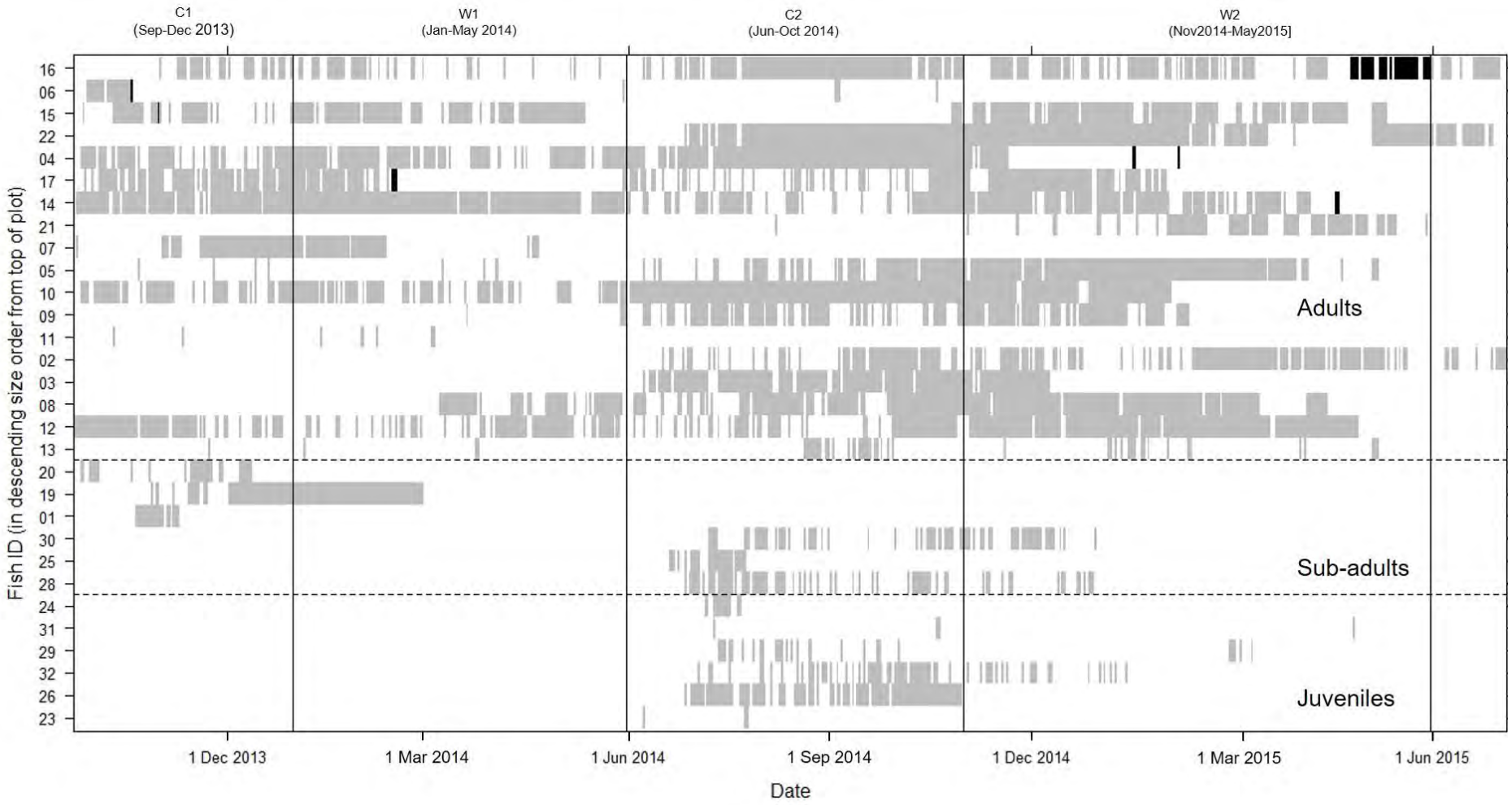


Figure 3.1: Presence of all tagged fish in the Flamingo (grey) and Tombua (black) arrays. Periods delineated by vertical lines. Horizontal dashed line separates juveniles (bottom pane), sub-adults (middle pane) and adults (top pane).

Table 3.2: Tagging and detection summary information of fish undertaking movements from the Flamingo study site (FL) to Tombua Bay (TO).

Fish ID	Length when tagged (mm TL)	Tagging location (nearest receiver)	Tagging date	Life stage	Date last detected at FL before TO	Dates detected at TO (designated period)	Dates returned to FL (designated period)	No of days between departure from, and return to FL	No of days undetected between departure from, and return to FL
06	960	F7	15 Aug 2013	Adult	18 Oct 2013	19 Oct 2013 (C1)	30 May 2014 (warm)	224	223
15	1 000	F1	22 Aug 2013	Adult	30 Oct 2013	31 Oct 2013 (C1)	1 Nov 2013 (cold)	2	1
17	1 155	F1	22 Aug 2013	Adult	12 Feb 2014	14 Feb 2014-16 Feb 2014 (W1)	30 May 2014 (warm)	107	103
14	1 050	F1	22 Aug 2013	Adult	06 Apr 2015	18 Apr 2015-19 Apr 2015 (W2)	-	-	-
16	1 120	F1	22 Aug 2013	Adult	13 Apr 2015	28 May 2015-31 May 2015 (W2)	1 Jun 2015 (cold)	49	45

were grouped at the mid-reaches of the array during the 'cold' periods, with the highest number of individuals detected at receiver F07 (Figure 3.2). This trend was accompanied by a concomitant decrease in the presence of fish at the northern- and southernmost regions of the array. The GLM indicated that there were significant changes in area use by fish during 'cold' vs 'warm' periods. While a greater proportion of fish were detected in the northern region compared to the southern region across periods, both regions exhibited a decline in the daily proportion of fish detected during the 'cold' periods ('North' (N): 10 %, 'South' (S): 5 %) compared to the warm periods (N: 16 %, S: 9 %) (Table 3.3).

Overall, the GLM predicted that the daily proportion of adult fish that were detected during the 'cold' periods was significantly higher in the 'mid' region (24 % of tagged adults) compared to the edges of the Flamingo study site array (N: 10 %, S: 5 %; Table 3.3). During the 'warm' periods the GLM predicted that the proportion of fish detected at the 'mid' region would decline (to 3 %) while it would increase in the 'north' (to 16 %) and 'south' (to 9 %) (Table 3.3).

Table 3.3: Outputs from the GLM predicting the daily proportion of adult fish detected in the three regions at the Flamingo study site (North (N), South (S), Mid) during the different 'warm' and 'cold' periods. Estimates of coefficients are relative to the intercept proportion, in a multiplicative relationship.

Coefficients [(Factor)level]	**Proportion of total number of fish detected relative to intercept**	**Std Error**	**t**	**p-value**
Intercept (N:Cold)	0.10	0.04	-53.19	< 0.05
(Region) Mid	2.42	0.05	16.87	< 0.05
(Region) S	0.46	0.08	-9.89	< 0.05
(Period) Warm	1.56	0.05	8.34	< 0.05
(Region) Mid:(Period) Warm	0.29	0.07	-17.63	< 0.05
(Region) South:(Period) Warm	0.93	0.09	0.76	0.45

Null deviance: 2492 (degrees of freedom = 1841)

Residual deviance: 1701.6 (degrees of freedom = 1836)

Pseudo-r^2 = 0.32

Fitted model had significantly lower deviance compared to null model (χ^2, $p < 0.05$)

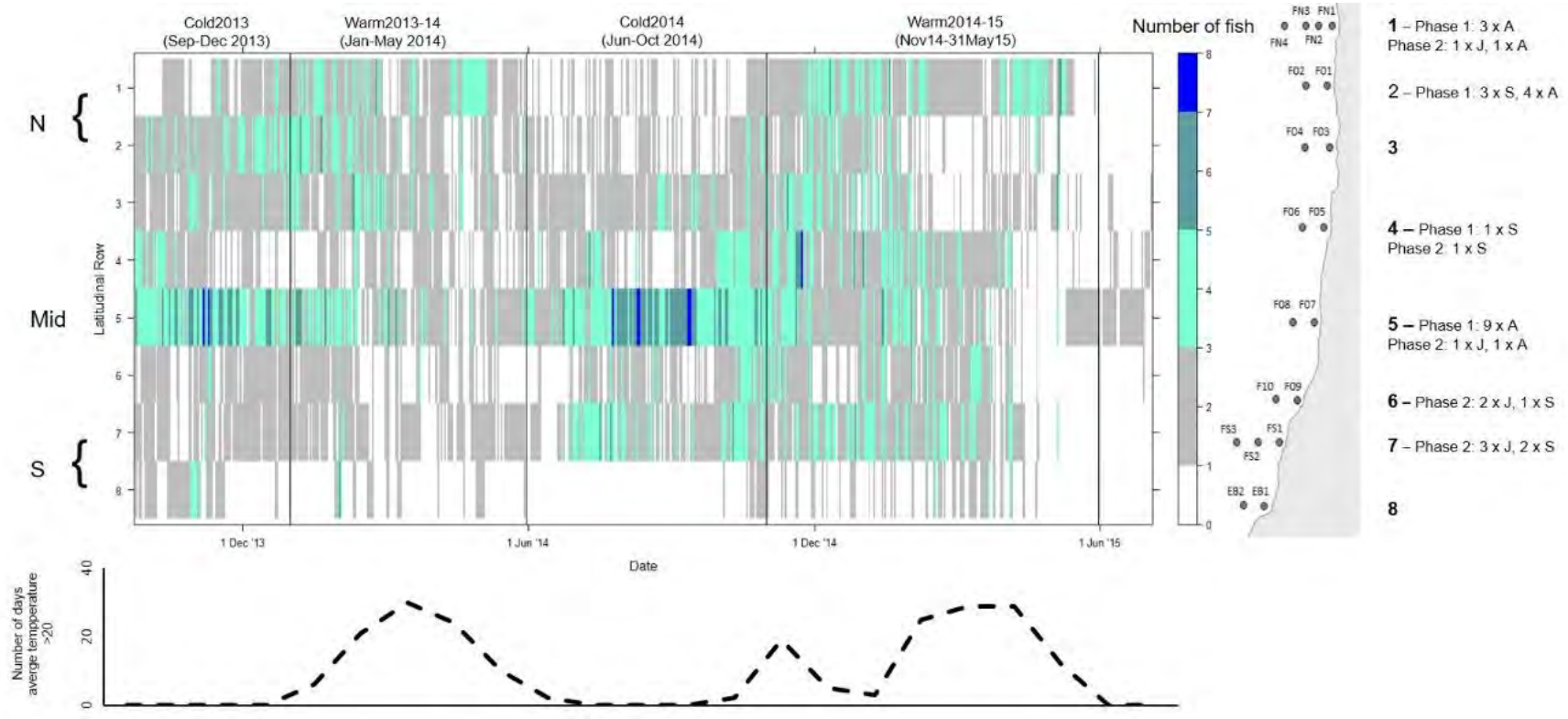


Figure 3.2: Daily number of fish of all life history stages detected at each receiver row (top) and trend in water temperature (bottom) during the two-year study period. Position of receivers and respective row (1 – 8) referred to in the plot indicated on map (right). Number of fish (J: juveniles, S: sub-adults, A: adults) tagged at each row indicated by text next to map during phase one (2013) and phase two (2014) of tagging. Colour scale inclusive of lowest number of fish.

3.3.3.2 Depth use

Depth use by *A. coronus* was found to vary ontogenetically and during different periods (Figure 3.3). The GLM found significant effects of both of these variables on the depth distribution of tagged fish (Table 3.4).

The GLM predicted a higher presence of adults in the shallowest, inshore depth bin (7 – 15 m) during 'cold' periods (25 % of tagged fish) compared to 'warm' periods (17 % of tagged fish) (Figure 3.3). Sub-adult fish were also predicted to exhibit a stronger inshore presence during 'cold' periods (52 % of tagged fish) than during the 'warm' periods (36 % of tagged fish). Juveniles were not predicted to exhibit any seasonal differences in their depth usage, with detections primarily occurring between 7 and 35 m, and fewer detections occurring on deeper receivers. Although there was seasonality in the depth distribution of adults and sub-adults, the shallowest regions were predicted to be utilised more extensively overall than deeper areas, with a greater proportion of fish predicted to be detected between 7 and 15 m than any other depth category for all three life history stages during both 'cold' and 'warm' periods.

Table 3.4: GLM output predicting the daily number of tagged fish detected in the different depth bins during the different cold and warm periods and at each life history stage. Estimates of coefficients are relative to the intercept proportion, in a multiplicative relationship.

Coefficients [(Factor) Level]	Proportion of total number of fish detected relative to intercept (multiplicative relationship of coefficients relative to intercept)	Std Error	t	p-value
(Intercept) Cold: DepthBin1: Juvenile	0.25	0.05	-26.76	< 0.05
(Period) Warm	1.07	0.15	0.43	0.70
(DepthBin) 2	0.56	0.03	-21.22	< 0.05
(DepthBin) 3	0.53	0.05	-14.05	< 0.05
(DepthBin) 4	0.33	0.15	-7.30	< 0.05
(DepthBin) 5	0.37	0.24	-4.19	< 0.05
(Life hist) Adult	0.98	0.05	-0.45	0.65
(Life hist) Sub-adult	2.08	0.07	10.71	< 0.05
(Period) Warm: (Life hist) Adult	0.69	0.15	-2.49	0.01
(Period) Warm: (Life hist) Sub-adult	1.44	0.17	2.12	0.03
Null deviance: 1951.6 (degrees of freedom = 2240)				
Residual deviance: 1094.9 (degrees of freedom = 2231)				
Pseudo-r^2 = 0.44				
Fitted model had significantly lower deviance compared to null model (χ^2, $p < 0.05$)				

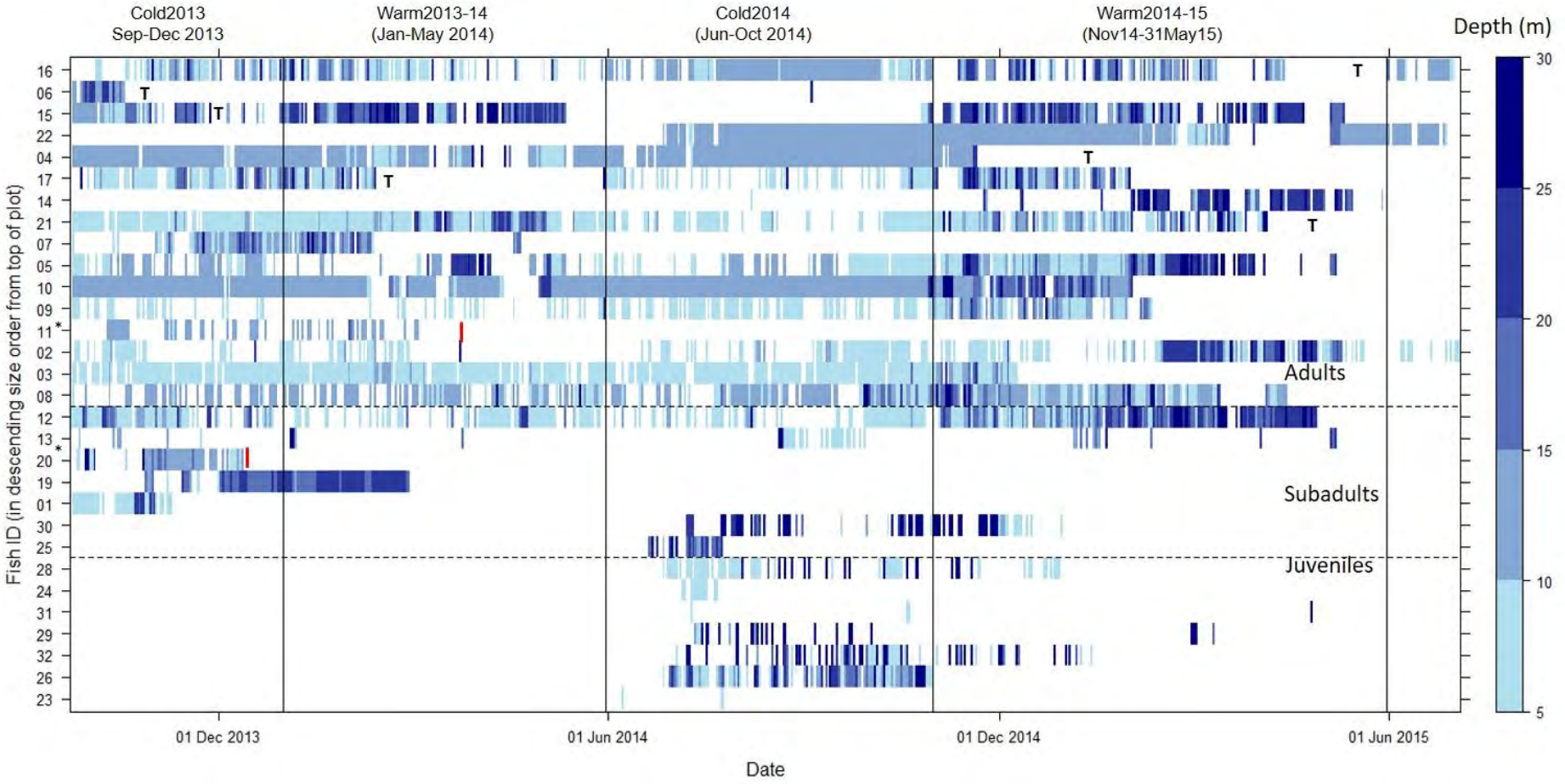


Figure 3.3: Daily average weighted depth position of each tagged *A. coronus* in the Flamingo array, based on bottom depth at receivers where fish were detected.

*: Recaptured; red bar denotes recapture date

T: Visit to Tombua Bay

3.4 Discussion

No evidence in support of the return longshore migration hypothesis was found in this study. Seasonal behavioural patterns were, however, noticed, which aid in explaining the patterns that were initially observed by Potts et al. (2010b) in the shore-based fishery, which led to the formulation of the migration hypothesis. In particular, during the times of the year defined in this study as 'cold' periods, adult fish were located in shallower waters closer inshore, while during the 'warm' periods they were located in deeper waters further offshore. The consequences of this observed residency at the population level are discussed.

The findings of this study provide context for understanding the conventional tagging and CPUE data from the shore-based fishery operating at the Flamingo study site. The shore-based fishery-dependent data suggested an absence of *A. coronus* from the area during warm months of the year (from November until March). This led to the hypothesis that this species undergoes an annual longshore return migration, following the ABFZ, which moves south into northern Namibia during the 'warm' period, and north back into Angola during the 'cold' period months (Potts et al. 2010b). Combining these earlier findings with insights from acoustic telemetry, however, provides a more holistic understanding of the spatial ecology of *A. coronus*. Acoustic telemetry highlighted the predominantly resident nature of individuals to a given area, suggesting that only a small proportion of the population undertakes long distance movements as was evident from the conventional tagging data – a facet that would have been missed by a stand-alone acoustic telemetry study. The absence of the species in the shore-based fishery during the warmer months can be explained by the offshore shift, into deeper waters, that was observed in this study (Figure 3.3). A concurrent acoustic telemetry study to the present one in the same study sites, conducted on another large predatory teleost that occurs in the region *Lichia amia*, found that some monitored individuals did in fact undergo a southerly longshore return migration during austral summer ('warm' period); however, there was a contingent that remained at the Flamingo study site year-round (Winkler 2018). These two acoustic telemetry studies emphasise the advantage of adopting a multi-method approach, particularly using methods that complement one another to provide a broader understanding of the spatial ecology of the study species.

The high degree of residency and seasonal patterns in depth use uncovered by this study are novel findings for *A. coronus* in southern Angola. These patterns indicate that the species is

able to withstand the dynamic eurythermal conditions that the area experiences, with the shifting of the ABFZ which resulted in inshore temperatures ranging from 15.3 °C (minimum daily average during C2) to 25.9 °C (maximum daily average temperature during W2). The offshore movement in warmer months may be a result of their food resources and therefore their foraging area shifting offshore, outside of the surf zone. Indeed, small pelagic fishes, which are their dominant dietary item (Potts et al. 2010b) are commonly observed in the nearshore zone in the cold periods, but tend to have a more offshore orientation during the warm period (Potts WM pers. comm.).

Station-keeping was the dominant movement behaviour observed by all life stages at the Flamingo study site. Less than one third of tagged adult fish (28%), and typically the larger individuals, made brief visits to Tombua Bay (~30 km south of the Flamingo study site) where they spent between 1 and 31 days. Following these visits, the tagged fish returned to the Flamingo study site. These movements are likely best classified as 'foraging' due to the relatively small distance travelled (~30 km), and because they are comparable in distance to movements within the Flamingo study site (which covered ~24 km of coast line), whereby an animal moves around in search of suitable resources (Dingle and Drake 2007; Dingle 2014a), rather than ranging, which involves movement beyond the core use area (Dingle and Drake 2007), and one would expect to cover relatively greater distances than observed here.

The prolonged absence of detections of several of the fish that visited Tombua Bay (Table 3.2), however, does provide ambiguity as these fish may have travelled further to the south, but not as far as Baia dos Tigres. This may be indicative of a longer-distance ranging movement (Dingle 2014c), but unfortunately it is unknown where they went due to the absence of detections of these animals over these periods. These movements were unlikely to have been longshore migrations into Namibia, primarily because they were not detected on either their initial southward or northward return migration past Baia dos Tigres.

There are parallels between the movement patterns observed in this study and those of their conspecifics around the world. An acoustic telemetry study on *A. japonicus* in South Africa also found a high degree of residency of monitored fish to the ~1 660 km^2 bay (~60 km straight-line distance between the bay boundaries) in which the fish were tagged, even though variability in their movement behaviour by different contingents was noted, and similar to *A. coronus*, seasonal shifts in area use were observed (Childs 2013). Similarly, a study on *A.*

japonicus in Australia found that one portion of the population remained resident to the tagging area for the duration of the experiment. However, a second component of the population undertook largescale migrations of up to 594 km to overwintering grounds after spawning at the tagging and aggregation site (Barnes 2015). While the possibility of the existence of a resident contingent and a migrating contingent cannot be ruled out for *A. coronus*, based on current knowledge of the species, it seems to be unlikely. The recapture of two adults in Namibia, over 700 km south of the tagging site at Flamingo, out of 966 fish that were tagged with conventional tags across all life stages captured in the fishery between 2013 and 2015 (Potts et al. 2018) may suggest that there are only low levels of long-distance movements by adult fish. This strategy has been observed in another coastal species, *Lithognathus lithognathus* in South Africa and may be a strategy that maintains genetic connectivity among the metapopulation (Bennet 2012).

There is a possibility that the sampling design of this study may have excluded a migratory contingent. For example, tagging efforts for *A. coronus* focussed on the 'cold' periods and this was also the case for the conventional tagging research. The migratory contingent was possibly not present or present in low numbers during these cold periods and therefore, increased tagging efforts in the study region further offshore, beyond the reach of the shore-based fishery, would enable further testing of the hypothesis that there is no large migratory contingent of *A. coronus* in the area that spends the warmer months in deeper waters further offshore in the region. Nevertheless, the findings from this study support other studies on the *Argyrosomus* genus that suggest that they exhibit plasticity in their movement behaviours; however, resident behaviour appears to be commonplace.

The lack of any significant longshore movements of animals in this study has implications for our understanding of the population structure of *A. coronus*. Metapopulation ecology views a species' distribution as a network of discrete populations that are interconnected by gene flow, with each local population primarily driven by internal processes (Hanski 1998; Kritzer and Sale 2004). Several lines of evidence indicate that *A. coronus* exists as a metapopulation that comprises several subpopulations with some genetic connectivity evident. Comparing the size of the monitored Flamingo study site (~24 km) where tagged fish were largely resident, to the known distribution of the species (~1 500 km; from northern Namibia to northern Angola), supports the fact that the fish in this study were part of a subpopulation, with several subpopulations likely to occur throughout the distribution. The panmixia observed by

Henriques et al. (2018) in a population genetics study, indicates that mixing occurs throughout its range.

Panmixia of *A. coronus* is likely to either be facilitated by dispersal of eggs and larvae, or by a small proportion of adults ranging or migrating. Let us assume that *A. coronus* has a four-week pelagic phase, including egg and larval stages, prior to early juvenile recruitment, as occurs in *A. japonicus* prior to them recruiting into estuaries (Griffiths 1996). Considering a mean longshore drift velocity of 0.3 $m.s^{-1}$ (well within the range reported for surface current velocities by (Mohrholz et al. 2001) throughout the region), a substantial dispersal distance of up to 726 km may be achieved. This is greater than half the length of the entire Angolan coastline of ~1 200 km (straight-line distance). A four-week pelagic phase may in fact be a conservative estimate for the genus, as larval duration in *A. regius* lasts ~51 days post-hatching (Solovyev et al. 2016), so even greater dispersal than was estimated is a possibility. This is admittedly a very crude approach to estimating passive drift potential, but illustrates it as a possible mechanism contributing to panmixia. With greater knowledge of the oceanography of the region, more complex current and particle dispersal modelling could refine this estimate. In relation to the second possible mechanism contributing to the population mixing, conventional tagging has indicated low levels of considerable longshore movements by adult *A. coronus*, from the Flamingo study site into Namibia over 700 km to the south. Low levels of dispersal have been shown to maintain genetic mixing among subpopulations (Mills and Allendorf 1996; Vucetich and Waite 2000), so these longshore movements may contribute to genetic mixing if the individuals are spawning when undertaking these migrations. Both recaptures of tagged fish in Namibia occurred between November and December, which falls within the period that sexually mature gonads were observed in *A. coronus* in southern Angola (Potts et al. 2010b), which means that the fish that travelled into Namibia may have spawned.

The discovery of hybrid *A. coronus* x *A. inodorus* (*A. inodorus* typically occur further south than *A. coronus*) in Namibia (Potts et al. 2014b) indicates that *A. coronus* are in Namibian waters during spawning periods. It is highly likely that both dispersal of early life stages and adults spawning with other subpopulations maintain panmixia of *A. coronus* throughout its distribution. A similar dynamic was noted in *A. japonicus* in South Africa. Childs (Childs 2013) proposed that the latter existed as a large metapopulation, with localised subpopulations experiencing genetic connectivity among them. A population genetics study on *A. japonicus* in South Africa found that the population was indeed panmictic (Mirimin et al. 2016). While it is

known that a small proportion of *A. coronus* adults do undertake long distance movements along the coastline (Potts et al. 2018), it is likely that the primary contribution to gene flow occurs in the early life stages, during the pelagic egg and larval stages.

Factors affecting metapopulation dynamics may operate at the discrete subpopulation level, or at a regional level across several/all subpopulations (Kritzer and Sale 2004). In fishery species that exist as a metapopulation, fishing pressure may significantly influence population dynamics at a local-scale. The local population of *A. coronus* in southern Angola is subject to high levels of fishing pressure, with evidence of the deleterious impacts of this noted as early as 2005 (Potts et al. 2010b). Fishing pressure is, however, variable along the coast, particularly towards the southern extent of their Angolan distribution. At the Cunene Estuary mouth, which is the border between Angola and Namibia, exploitation is extremely high, with a large proportion of juveniles captured and retained by shore-based anglers (Potts et al. 2010b). This localised exploitation may affect the southern subpopulation due to the high mortality of individuals belonging to this vulnerable (juvenile) life history stage. However, the Iona National Park in southern Angola would likely afford certain parts of the southern range of *A. coronus* protection from angling, due to the difficulty in accessing the coast and the low human population density in the region. The Skeleton Coast National Park (SCNP) immediately south of this region increases this area of refuge. The SCNP covers a stretch of ~380 km of Namibian coast where fishing is mostly prohibited (Potts et al. 2010b). These areas provide some portion of the metapopulation with protection from the high fishing pressure that the species experiences throughout the remainder of its distribution. Despite these restrictions to access for anglers, the Cunene Estuary mouth has been deemed an area of high risk for the species, with Potts et al. (2010b) calling for fishing to be stopped in this region to avoid growth overfishing, as has occurred with *A. japonicus* juveniles in South Africa (Griffiths 1997c).

In addition to local-scale factors acting on subpopulations, regional-scale factors may affect the entire metapopulation. The ABFZ is a regional-scale factor that is likely to have significant influence on the *A. coronus* metapopulation. The seasonal shifting of the ABFZ leads to drastic differences in water temperature of up to 10 °C (seasonal variation from 15.8 – 25.8 °C observed at a single receiver station in this study), between austral winter ('cold' period) when the front is pushed north by the cool Benguela Current and austral summer ('warm' period) when the front is pushed south by the warm Angola Current. Any major changes in the functioning of this system would have far-reaching effects across the distributional range of

the species. A shifting thermal regime is likely to have various effects on physiology, fitness and growth (Holt and Jørgensen 2015; Pauly and Cheung 2018) and increased thermal stress may have unforeseen consequences through strengthening interactions between it and other stressors such as parasites (Bruneaux et al. 2017). There is evidence that *A. coronus* shift their area use in relation to seasonally changing water temperatures (examined more in Chapter 4), shifting offshore during 'warm' periods and more likely to make excursions further south to Tombua Bay during these periods, while shifting their area use closer inshore during 'cold' periods. Changing environmental thermal regimes would also have indirect effects on *A. coronus* through effects on their food resources.

While external drivers of metapopulation dynamics are important to consider, knowledge of internal factors such as the biology and life history of a species and their effect at a metapopulation level are also important. Considering the pattern in area use by different life history stages, acoustic telemetry data suggest an ontogenetic shift in area use occurs in the species. Juveniles and small sub-adult fish used a limited area throughout the year, with a narrow longshore range, while larger sub-adults and adult fish had a relatively greater area use and longshore ranges, although this was still largely restricted to the study site. The small area use of all life history stages, but particularly the juveniles and early sub-adults, makes the species vulnerable at a subpopulation level. Any localised event leading to high mortality of the early life history stages could reduce the subpopulation size. This is particularly relevant as the findings from this study suggest that immigration into the subpopulation from another subpopulation at later life history stages in any significant number is improbable. This effect is likely to be short-lived, if the threat to early life stages is temporary, as future cohorts should recruit into the affected area through dispersal and recruitment of early-stage fish. Hamilton et al. (2021), who studied the effects of larval dispersal dynamics on recruitment into an exploited sub-population of bumphead parrotfish *Bolbometopon muricatum* in the Solomon Islands, suggested that recruitment into the fishery through larval dispersal could sustain the fishery, even if heavily exploited. Given the lack of longshore movement in the present study, this theory has merit and suggests that dispersal of larvae of *A. coronus* may be the primary mechanism responsible for the sub- and meta-population structure.

Ontogenetic differences in spatial dynamics were noted in this study, whereby larger individuals utilised a greater area, both longshore and across the depth gradient. Adults and sub-adults exhibited a seasonal shift favouring shallower inshore waters during 'cold' periods

and deeper waters offshore during 'warm' periods. The depth utilisation metric calculated in this study would be sensitive to variations in detection efficiencies of receivers particularly if there were differences in efficiencies across depth ranges. This is likely to have been the case in this study, with shallower receivers likely to have lower detection efficiencies than deeper receivers due to wave-generated noise. This is particularly true during 'cold' periods, when the surf zone has much larger surf and is a far noisier environment, compared to calmer 'warm' periods. Therefore, use of the inshore region would likely be underestimated particularly during 'cold' periods. However, the results produced through this metric indicated a higher use of the inshore regions by juveniles and sub-adults generally, and by adults during 'cold' periods. If inshore use was underestimated, especially during 'cold' periods, then these patterns were likely to be even more pronounced in the absence of sampling bias. Juveniles utilised a far smaller area, and did not show any seasonal distributional shift. The ontogenetic shift in spatial dynamics observed in this study may suggest that *A. coronus* exhibits ontogenetic niche separation. This is frequently observed in fishes, including sciaenids such as *A. japonicus* in South Africa, which shift from being estuary dependent as early juveniles (between 20 mm and 150 mm total length) to utilising the marine environment to varying degrees depending on whether they are members of the estuarine or marine contingent (Griffiths 1996; Childs et al. 2015). Another sciaenid, *Sciaenops ocellatus* in the USA, exhibited ontogenetic segregation in habitat use with early life stages utilising estuaries and adults utilising marine environments (Rooker et al. 2010). Ontogenetic niche separation is thought to be governed primarily by differences in habitat suitability for different life stages, followed by food availability relative to their requirements, and then temporal characteristics (Schoener 1974). Ontogenetic niche separation that occurs to curtail competition for resources is thought to optimise growth rates throughout the different life history stages, and mitigate vulnerability to predation, with larger individuals being less vulnerable to predation and generally stronger competitors (Werner and Gilliam 1984). Further to reducing competition between life history stages, niche separation would lower the risk of cannibalism, which has been observed in the closely related *A. japonicus* (Griffiths 1997a), which may be a risk factor for small *A. coronus*. Indeed, niche separation observed in the present study, with larger fish utilising inshore waters and juveniles utilising deeper waters during the cold period in 2014 could be a strategy employed by juveniles to minimise the risk of predation.

In addition to the pattern in ontogenetic area use noted above, a seasonal shift in area use by adult and sub-adult fish was observed. These fish exhibited a seasonal depth-use shift,

occupying shallower water closer inshore, during the 'cold' periods and deeper water further offshore during 'warm' periods. These fish also contracted their longshore area use during 'cold' periods. The driver of this seasonal shift in area use may be related to internal (physiological) or external (environmental) factors. Physiologically, the metabolic rates of individuals would increase during warmer periods and this would likely require an increased energy intake (Collett et al. 2008). This may drive an increase in their hunting area, assuming that prey density is on average, similar throughout the year. Prey abundance and distribution can be an important environmental driver of area use (Harden Jones 1968; Kennedy 1985; Dingle and Drake 2007; Dingle 2014a). Seasonal fluctuations in prey abundance and distribution may drive predators to modify their foraging strategy to adapt to the available resources. Based on available data, however, it is difficult to determine whether physiological or environmental factors are driving the seasonal shift in space use for adults in the Flamingo site. Anecdotal evidence, however, suggests that *Sardinella aurita*, an important prey of *A. coronus* (Potts et al. 2010b), frequently accumulate in dense bait balls in the nearshore zone during 'cold' periods (Potts, personal observation). This abundant food resource would undoubtedly attract *A. coronus* to the location.

Despite the tendency of adult *A. coronus* to have larger longshore ranges than younger fish, a striking pattern that was observed during both 'cold' periods over the two-year monitoring period, was the concentration of adult fish in the nearshore region within detection range of a single receiver. A grouping of conspecific organisms can be classified according to the causal factors of the phenomenon (Dingle 2014a). Social interactions among conspecifics may drive a 'congregation'. Organisms may be forced into a particular area by winds, currents or geographic barriers causing a 'physical concentration'. If suitable locations or resources are limited, 'habitat choice' may force an aggregation. There is no evidence that the grouping of adult fish during 'cold' periods was caused by 'physical concentration' particularly because the grouping was largely limited to adults. Separating out whether the grouping was a 'congregation' perhaps linked with some aspect of reproductive behaviour as they were all reproductively mature fish that exhibited this behaviour, or 'habitat choice' if the definition is extended to include food resources which may drive an aggregation of these predators, is challenging. However, this is attempted in Chapter 4.

To conclude, from the acoustic telemetry results the hypothesis that *A. coronus* in southern Angola undertake a mass to-and-fro longshore migration that tracks the ABFZ can be rejected.

Instead, a seasonal offshore movement during 'warm' periods and an inshore movement during 'cold' periods, was noted, likely following food resources, although a physiological component to this behaviour cannot be excluded. As there was no complete absence of mature adults from the study site during the two-year monitoring period, localised offshore spawning appears to be the most likely scenario, as a previous study on the life history of the species in the region found limited numbers of mature individuals in the shore-based fishery (i.e. close inshore). The species appears to exist as a metapopulation, with the monitored animals in the subpopulation where tagging occurred showing no major longshore movements. The panmictic nature of the species throughout its distribution is likely maintained through egg, larval and possibly early juvenile dispersal as there was no evidence for large-scale emigration of monitored animals (late juveniles and older) out of the study site. Earlier conventional tagging data does, however, indicate that there is a low-level of long-distance longshore movement undertaken by mature adults, which could also contribute to genetic mixing. Conventional tagging also indicated that juveniles were restricted in their movement, in agreement with what this study suggested. To better assess the metapopulation hypothesis, further acoustic telemetry studies could be conducted with animals tagged in batches throughout the distribution of the species and with a more extensive network of receiver arrays deployed, with a similar design to that used in this study at the Flamingo site. The use of underwater sound recorders could also be used to identify spawning periods and locations of fish that utilise acoustic communication, as is common in sciaenids (Luczkovich et al. 2008). This could be a useful avenue to explore and aid in locating the spawning location of *A. coronus* in southern Angola.

Chapter 4: Assessing the Drivers of Seasonal Group Formation in a Coastal Sciaenid, *Argyrosomus coronus*

4.1 Introduction

Animal behaviours are generally interpreted through their influence on survival, growth and reproduction, with life stage strongly shaping their relative importance. In certain species, animal behaviours may result in the formation of conspecific groups. Mobile species may become concentrated in space for various reasons. Dingle (2014) identified three different mechanisms leading to a concentration of animals. Firstly, habitat choice and resource requirements may lead to conspecifics concurrently occupying the same space. Secondly, a physical concentration of conspecifics may result from oceanographic features, including temperature regimes or currents, and bathymetry. Lastly, organisms may congregate, whereby they are attracted to an area by the presence of conspecifics. The first two mechanisms are independent of the presence of conspecifics; however, the third mechanism is not. While Dingle (2014) placed these three mechanisms under the umbrella of 'aggregation', other authors only consider processes that occur independently from other individuals (e.g. being attracted to a resource independently of others) to be an aggregation (i.e. the first two mechanisms described here) (Heupel and Simpfendorfer 2005; Allaby 2010).

In this chapter (and thesis), 'aggregation' refers to a concentration of organisms in an area due to factors other than conspecifics, while 'congregation' refers to a group formation occurring due to the presence of conspecifics in an area. 'Group formation' refers to any concentration of organisms, and encompasses both aggregations and congregations. Group formation may follow various modalities. A group may begin forming through chance encounters and increase through density-dependent factors (Parrish and Edelstein-Keshet 1999), forming a congregation. The formation of a group may occur through self-organisation (as is the case in fish schooling behaviour) or in response to external stimuli including structures such as floating objects or due to local physico-chemical parameters (Flierl et al. 1999; Parrish and Edelstein-Keshet 1999; Castro et al. 2002). The size and shape of a group can vary according to resource availability, physiology, behaviour patterns and through sensory constraints on individuals in the group (Parrish and Edelstein-Keshet 1999).

From an evolutionary perspective, group formation may confer greater survival, perhaps through predator avoidance (Heupel and Simpfendorfer 2005), reduced individual predation risk (Hoare et al. 2004; Sandin and Pacala 2005), or increased reproductive output of group members (Parrish and Edelstein-Keshet 1999; Morrell and James 2008). From an energetic perspective, costs of locomotion may be reduced by school formation through reductions in drag (Weihs 1973), and foraging efficiency can be improved when foraging as a group (Clark and Mangel 1986; Ebert 1991b; Heupel and Simpfendorfer 2005). Behaviours such as mating may drive conspecific group formation for short periods (Parrish and Edelstein-Keshet 1999).

While group formation may confer several advantages to group members, there may be associated disadvantages. Groups present attractive resource patches for predators (Sancho et al. 2000; Webster 2003). Group formation may have density-dependent competitive influences, impacting the survival and access to resources of group members (Hoare et al. 2004; Webster 2004). The transmission rate of infectious diseases would also be higher when host density is increased, such as when fish form groups (Reno 1998). Nonetheless, the advantages must outweigh the disadvantages for the continued existence of this behaviour in many taxa.

Where group formation is transient, various stimuli may cue individuals to form groups. Congregations formed for spawning tend to be triggered by certain predictable rhythmic environmental variables. Lunar phase, for example, may be a cue in spawning fishes (Takemura et al. 2010). In such cases, spawning may be timed around a single lunar phase, or it may follow a semi-lunar cycle, such as during the full and new moon phases (Takemura et al. 2010). Pheremones released from mature individuals may be an important mechanism facilitating congregation prior to spawning (Chung-Davidson et al. 2010). In species exhibiting protracted spawning behaviour, congregations may track daily tides (Takemura et al. 2010), or the diel cycle (Adams et al. 2019). In schooling fish, visual cues tend to be the major mechanism through which individuals concentrate, while stimuli serving to attract individuals to an area rich in food include chemical and sound cues (Pavlov and Kasumyan 2000). Congregations of pelagic fishes may be facilitated by sound-stimuli at fish aggregation devices, outside of visual contact, on the scale of 10s to 100s of metres (Dempster and Kingsford 2003).

Group formation and space use in fishes may be influenced by environmental or biological variables. Such factors include those that are related to physico-chemistry/physiology (Childs et al. 2008; Freitas et al. 2016), ontogeny or organism size (Dulčić et al. 2002; Welsh et al.

2013; Heupel and Simpfendorfer 2014), predator avoidance (Dulčić et al. 2002), foraging (Topping et al. 2006; Taylor et al. 2013b), habitat availability (Topping et al. 2005; Lindholm et al. 2007; Taylor et al. 2013a; Furey et al. 2013), sex (Heupel and Simpfendorfer 2014) and reproduction (Kirchner and Holtzhausen 2001; Topping et al. 2006; Espinoza et al. 2016). Temperature, however, has been found to be one of the most important drivers of distribution and space use in fishes (Hubbs 1948).

Temperature has been found to be an important environmental variable for fishes at the individual level, affecting them through various mechanisms. Some of the factors influenced include growth rate (Collett et al. 2008; O'Gorman et al. 2016), reproductive output through influencing the timing and success of spawning events (Hutchings and Myers 1994; Pankhurst and Munday 2011), metabolic rate (Fonds et al. 1992; Clarke and Johnston 1999) and the timing of migration (Kuczynski et al. 2017). Area use may vary seasonally in relation to temperature through physiological constraints (Brownscombe et al. 2019). Although there is limited information on the thermal physiology of *A. coronus*, laboratory-based physiological rate measurements have been conducted on late-stage juveniles under water temperatures between 12 and 24 °C (Pringle et al. in review). This experiment found increases in the three metrics used (standard metabolic rate, maximum metabolic rate and aerobic scope), across the experimental temperature range. This experiment also measured the physiological response in *A. inodorus* from Namibia exposed to the same water temperatures, and found that *A. coronus* was better adapted to warmer waters compared to *A. inodorus*, whose aerobic scope began to decrease above 21 °C while that of *A. coronus* continued increasing. This aligns with their distribution, with *A. inodorus* typically occupying cooler waters to the south, and *A. coronus* occupying warmer waters to the north.

Group formations are common in the Sciaenidae family, with examples from many different species recorded in the literature from around the globe. However, this literature is restricted to observations of spawning congregations. While not an exhaustive list, examples of these observations include *A. japonicus* spawning in the Great Australian Bight Marine Park in Australia (Barnes et al. 2019), and examples from the USA include *Cynoscion regalis* spawning in Pamlico Sound, North Carolina (Luczkovich et al. 1999), *Sciaenops ocellatus* spawning in Mosquito Lagoon, East-Central Florida (Johnson and Funicelli 1991), *C. nebulosus* spawning in Tampa Bay, Florida (Lowerre-Barbieri et al. 2013) and *C. othonopterus* spawning in the Gulf of California (Erisman et al. 2012). In Argentina *Pogonias cromis* form

groups when spawning in Río de la Plata Estuary (Macchi et al. 2002), as do *A. inodorus* spawning in Sandwich Bay in Namibia (Kirchner and Holtzhausen 2001) and *A. regius* spawning in Gironde Estuary in France (Lagardère and Mariani 2006). While these group formations are strongly seasonally driven, in certain instances a correlation between spawning intensity and lunar phase has been found, whereby spawning is intensified either in the days preceding new and full moons (Erisman et al. 2012), or during the full moon phase (Johnson and Funicelli 1991; Lowerre-Barbieri et al. 2013).

Substrate characteristics do not seem to influence sciaenid spawning site selection. This may be because sciaenids produce buoyant, pelagic eggs (Holt et al. 1985; Johnson and Funicelli 1991; Saucier and Baltz 1993; Luczkovich et al. 1999). Rather, depth, current velocities, water temperature and dissolved oxygen tend to be more influential on spawning site selection as these characteristics have direct influence on egg survival and development (Saucier and Baltz 1993; Luczkovich et al. 2008; Lowerre-Barbieri et al. 2013).

In Chapter 3 a seasonal high-use area for *A. coronus* was observed around the inshore region in the middle of the Flamingo study site. The aim of this chapter was to investigate the dynamics of this phenomenon and explore its potential drivers. To do this, the influence of environmental variables on the group formation that occurred at the mid-region of the Flamingo study site during 'cold' periods was explored. Variables included water temperature, time of day, tide and moon phase. The correlations between group formation and these variables were then discussed in the context of the biological significance of the phenomenon, particularly in relation to reproduction and feeding behaviours.

4.2 Material and methods

4.2.1 Thermal environment

Temperature data were collected at nine acoustic receiver stations at the Flamingo study site (see Chapter 2 for details). To assess temperature dynamics across the study site, daily temperatures were summarised as means, maxima and minima, and each of these were averaged across the monitoring periods (C1, W1, C2, W2; see Chapter 2 for description of periods) and plotted for each station.

To compare the temperature regime across the Flamingo study site, the difference between temperatures for all UTR stations and F07 was calculated. Differences were calculated for daily means, maxima and minima and plotted for all four periods.

4.2.2 Demographics of group formation

The demographics of the fish that were detected at station F07 were categorised by life history stage ('juvenile', 'sub-adult' or 'adult') and whether they were fitted with an acoustic transmitter 'near' (less than 5 km) or 'distant' (more than 5 km) to station F07, in order to test whether philopatry may influence area utilisation.

Residency indices (RIs) (Abecasis and Erzini 2008) are a useful measure of how long animals utilise a specific area and allows for comparisons to be made among individual animals or groups of individuals. These indices indicate the proportion of time an animal spends at a specific location. In this study RIs were calculated for each fish by finding the proportion of days that a fish was detected at F07 during each monitoring period. Days where fish were not detected were assigned either as present at F07, if they were detected at F07 on the next day (i.e. it was assumed to have remained in the surrounding area), or absent from F07, if not detected at F07 or if they were detected at another station (i.e. it was assumed to have left F07 the day after it was last detected at F07). Residency indices were averaged per fish over both 'cold' and both 'warm' periods.

4.2.3 Fish distribution relative to thermal environment

Fish presence at the northern and southern regions of the array were compared with that at the mid-region (station F07) during the study period, and how this distribution related to temperature. This was done by plotting the daily number of fish detected in each region along with the daily mean temperature in each of these regions.

To give an overview of the temperatures at which fish were detected, the mean, minimum and maximum temperatures were calculated for each individual. As UTRs logged samples hourly, this was done using the temperature nearest in time to the detection time, from the UTR at the station where a fish was detected. These were plotted for each period (C1, W1, C2 & W2)

along with the minimum and maximum water temperatures observed and the minimum and maximum water temperatures where fish were detected.

To examine the effect of water temperature on the presence of tagged fish at station F07 a binomial Generalised Linear Model (GLM) was used. A binomial distribution was used due to the response variable being proportion data. The response variable was the daily proportion of tagged fish detected at station F07 and water temperature was the predictor variable. The model was of the form:

$$Proportion \sim Temperature + \varepsilon$$
$$\varepsilon \sim \text{binomial } (\mu)$$

The GLM was conducted using the *glm* function in the **stats** package in *R* v 4.0.3 (R Core Team 2020).

4.2.4 Cyclical drivers

Circular statistical analyses were used to investigate the relationship between fish presence at station F07 and periodic variables. The number of fish detected per hour at station F07 were calculated. These were then compared with the following circular variables: 'time of day', 'tide' and 'lunar phase'. The 'time of day' variable, with 24 x hourly categories, consisted of the hours 00:00-23:00. 'Tide' consisted of 12 x hourly incremental categories: high tide and the proceeding five hours (H, H1, H2, H3, H4, H5) and low tide and the proceeding five hours (L, L1, L2, L3, L4, L5). 'Lunar phase' was categorised according to the eight commonly recognised stages of the lunar cycle (New, Waxing Crescent, First Quarter, Waxing Gibbous, Full, Waning Gibbous, Last Quarter, Waning Crescent).

Relationships between the number of fish detected and the circular variables were analysed separately for each of the periods (C1, W1, C2, W2). Data was plotted on circular axes for each of the periods and each of the circular variables. Rose diagrams were created for each plot to illustrate the proportion of fish detected in each bin of the circular variable, with the surface area of the bins indicating the proportion of fish detections occurring in that bin relative to the other bins in the rose diagram. The mean resultant length (R) was included in the plots, as an indication of the dispersion of the detection data around the unit circle. Values of R [0, 1] ~ 1

indicate a high concentration of data at/around a specific point on the unit circle. Values of R ~ 0 may indicate a high degree of dispersion of observations around the unit circle, or values of a cyclical nature (Pewsey et al. 2013). The Rayleigh Test of Uniformity was used to test the null hypothesis of uniformly distributed observations around the circle, for each plot. Circular statistics and outputs were generated using the **circular** package (Agostinelli and Lund 2017) in *R* v 4.0.3 (R Core Team 2020).

4.2.5 Spawning periods

As period C1 overlapped with the spawning period which is said to occur between November and December (Potts et al. 2010b), this period was interrogated to determine whether the group formation could be attributed to spawning behaviour. Period C2 ended in November 2014 but this second potential spawning period was included in the analysis nonetheless. Tagged adult fish were detected within the Flamingo study site throughout both of the spawning periods occurring during this study. Detections during the spawning periods that fish were monitored, were visually inspected for diel patterns and analysed using circular techniques at the same three temporal scales as previously used: diel, tidal and lunar. Circular analyses were conducted as previously described, by analysing the number of fish detected during each bin of the respective temporal scale, and the hypothesis of uniform distribution around the circle was tested.

4.3 Results

4.3.1 Thermal environment

There were clear patterns in the water temperature regime at the Flamingo study site (Figure 4.1). The temperature in the inshore, shallow water (~10 m depth) was more variable at the station level, than in deeper water (~30 m depth). The mean daily inshore temperature was warmer in the northern (FN1 T_{ave}: C1 = 18.5 °C, W1 = 21.2 °C, C2 = 17.3 °C, W2 = 21.6 °C) than in the southern region (FS1 T_{ave}: C1 = 17.8 °C, W1 = 20.5 °C, C2 = 16.8 °C, W2 = 20.7 °C) over the whole study period. However, this north-south gradient was less distinct offshore (FN3 T_{ave} = C1 = 17.1 °C, W1 = 19.1 °C, C2 = 16.2 °C, W2 = 19.1 °C; FS2 T_{ave} = C1 = 17.1 °C, W1 = 19.2 °C, logger failed during C2 & W2). Water temperatures at station F07 were

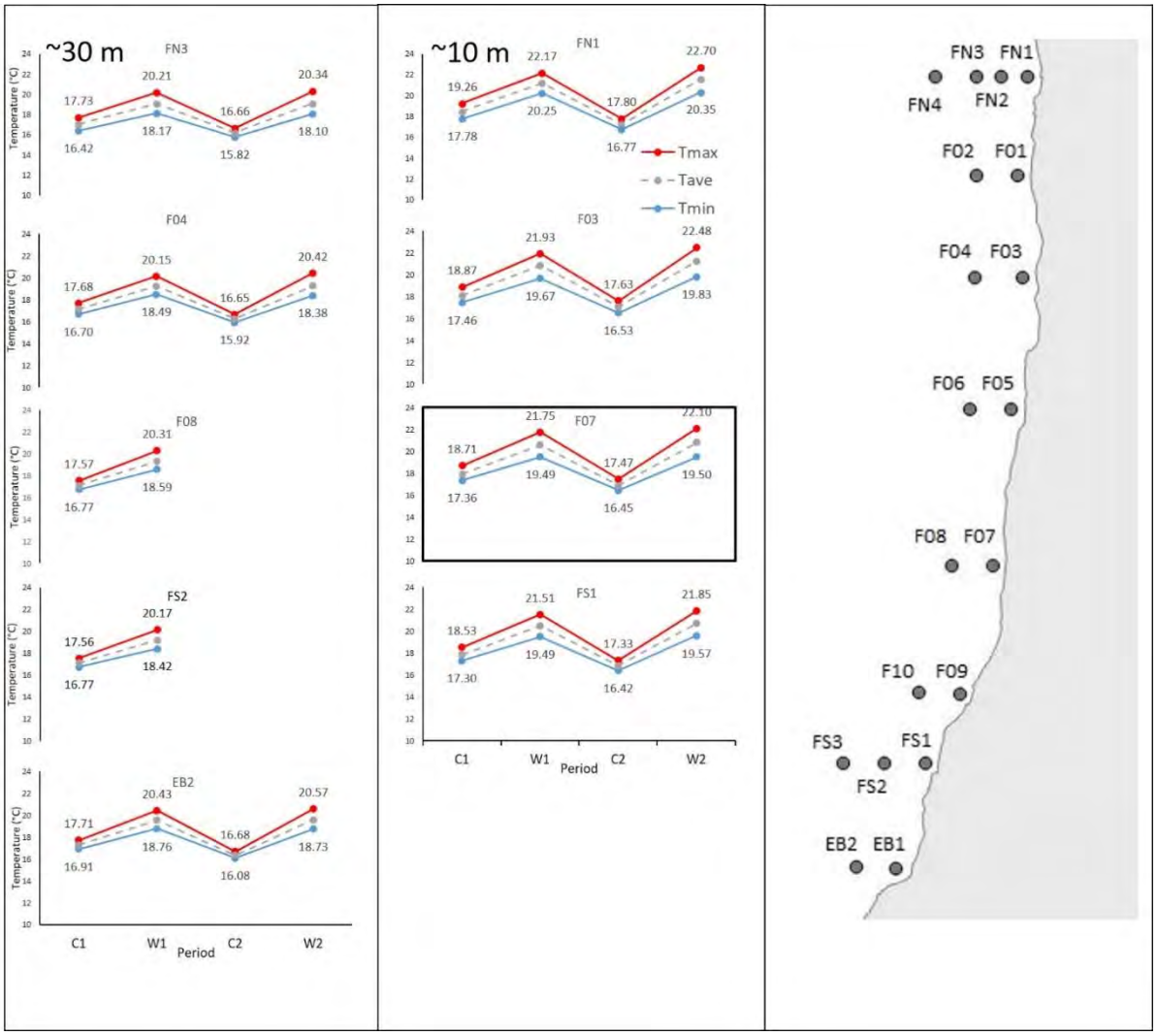


Figure 4.1: Mean daily maximum, daily minimum and daily average temperatures at Flamingo stations during each 'cold' (C1 & C2) and 'warm' (W1 &W2) period. Left panel includes data from offshore stations ~30 m deep and middle panel from inshore stations ~10m deep. Right panel indicates station distribution at the Flamingo study site. Station names indicated at the top of each plot.

similar to the entire array in all periods, particularly other inshore stations, where means differed by less than one degree Celsius (Figure 4.2).

4.3.2 Fish detections

The daily number of fish detected at F07 was higher during the 'cold' periods (C1: 3.45 ± 1.21 (mean ± sd); C2: 4.02 ± 1.43) than the 'warm' periods (W1: 1.84 ± 1.32; W2: 1.38 ± 1.17) (Figure 4.3).

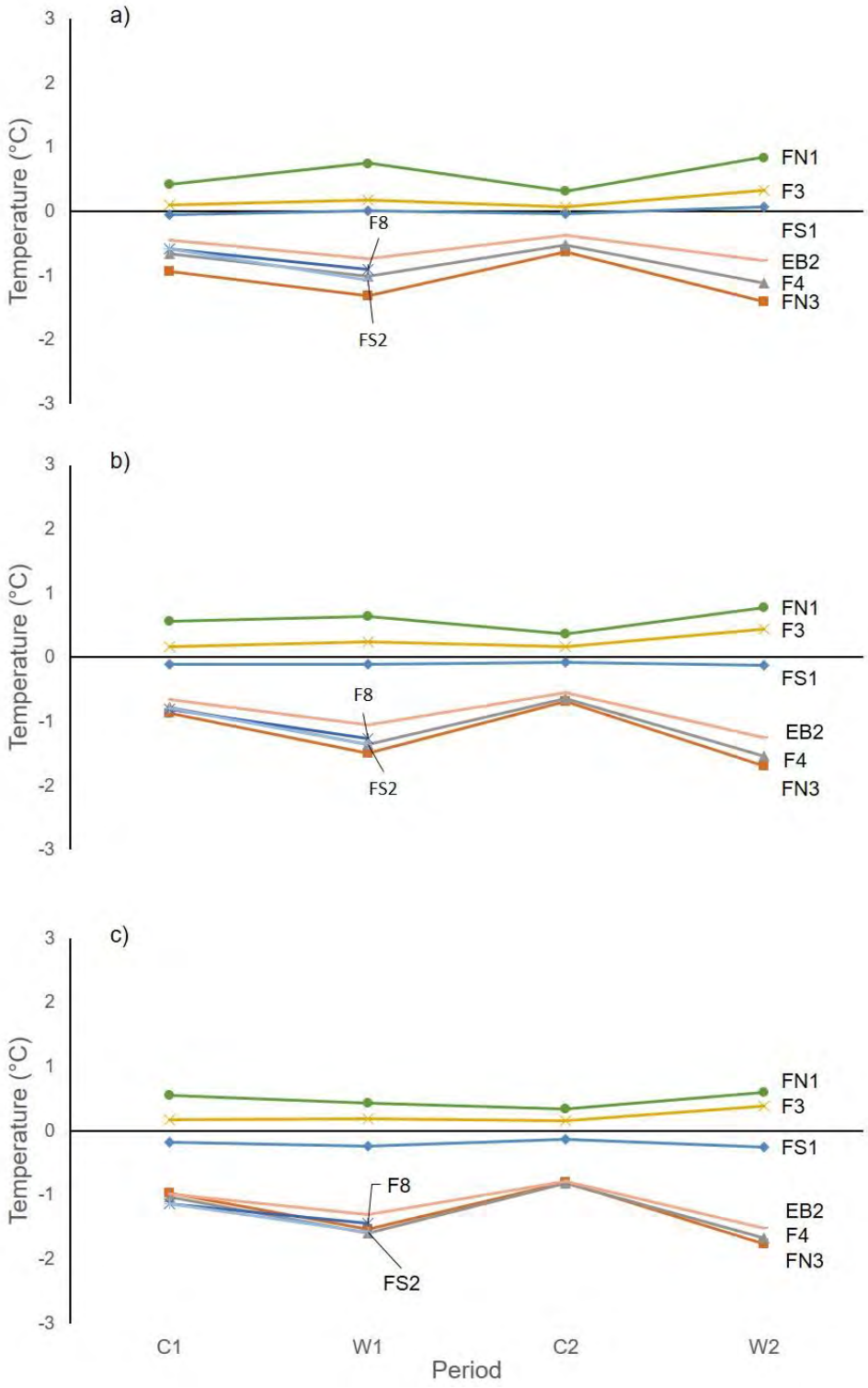


Figure 4.2: Differences between temperature metrics at all stations with temperature loggers at the Flamingo study site and station F07. Metrics include mean daily minima (a), mean daily averages (b) and mean daily maxima (c), during the four monitoring periods. Positive values indicate warmer temperatures relative to F07 and negative values indicate cooler temperatures relative to F07.

Conversely, the mean daily number of fish detected in the northern (FN1-4 & F01-02) and southern regions (FS1-3 & EB1-2) of the array was higher during the 'warm' periods (northern – W1: 1.37 ± 1.09; W2: 1.91 ± 1.23, southern – W1: 0.90 ± 0.76; W2: 1.24 ± 1.17) than the 'cold' periods (northern – C1: 0.54 ± 0.72; C2: 0.39 ± 0.55, southern - C1: 1.22 ± 0.58; C2: 0.39 ± 0.56) (Figure 4.3).

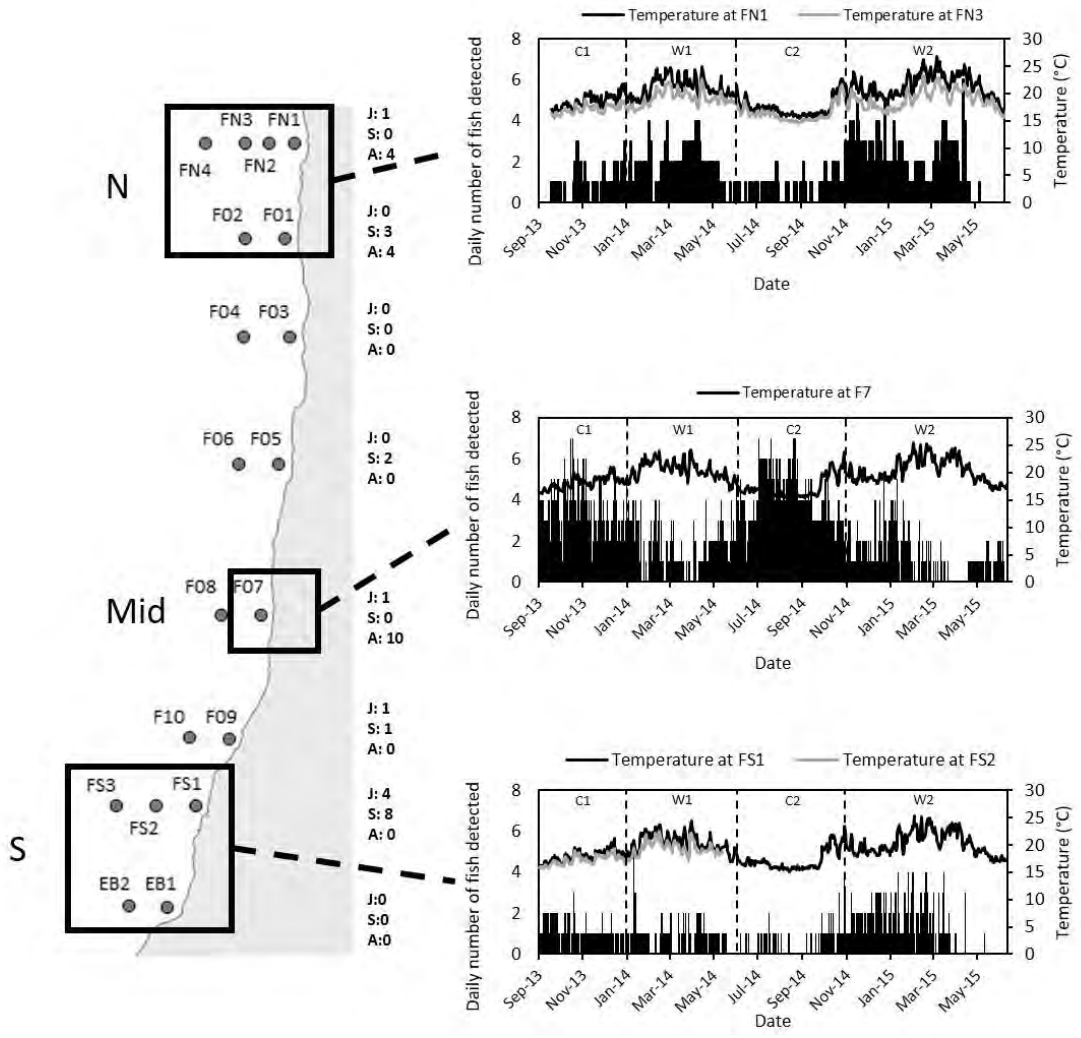


Figure 4.3: Bar plots indicating daily number of fish detected (black bars) and mean daily temperature (solid lines) at northern (N), mid (Mid) and southern (S) regions of the Flamingo study site. Number of juveniles (J), sub-adults (S) and adults (A) tagged indicated on map, relative to nearest receiver row. Numbers include one juvenile and two sub-adults that were never detected, and hence exluded from analyses.

4.3.3 Demographics of group formation

Two of the seven tagged juveniles (29 %), two of the six tagged sub-adults (33 %) and all 17 of the tagged adults (Figure 4.4) were detected at F07. One juvenile (fish 26) and one sub-adult (fish 21) were tagged < 5 km from F07 ('near'), while the other juvenile (fish 23) and sub-adult (fish 20) were tagged > 5 km ('distant') from F07. Ten adults (fish 04 – 11, fish 13 and fish 22) were tagged < 5 km from F07, while the remaining seven (fish 02, fish 03, fish 12, fish 14 – 17) were tagged > 5 km from F07.

Juveniles showed no strong association with station F07. Juveniles were not present here for longer than two consecutive days, with RI of 0.01 ± 0.009 (mean ± SD) during 'cold' periods, and 0 during 'warm' periods (Figure 4.4). The RI for the 'distant' juvenile was 0.02 and for the 'near' juvenile was 0.01.

As with the juveniles, sub-adults did not show a strong association with station F07. The sub-adults were not present for longer than two consecutive days during any period except for C1. The mean RI for sub-adults during 'cold' periods was 0.15 ± 0.17 and 0 during 'warm' periods. The RI for sub-adults was 0.27 for the 'near' fish, and 0.03 for the 'distant' fish.

Adults showed a stronger association with station F07 than the younger life stages. Seven adults that were detected here during C1 (64 % of tagged adults), were present for longer than two consecutive days. Adults' mean RI was 0.36 ± 0.37 during 'cold' periods, and 0.22 ± 0.22 during 'warm' periods and there was a general increase in RI with increasing fish size (Figure 4.4). Although there was large variability in RI, larger values were consistently observed during the 'cold' periods. The largest mean RI observed in adults during 'cold' periods was 0.99 (fish 10) compared to 0.66 (fish 22) during 'warm' periods.

4.3.4 Fish distribution relative to thermal environment

The average temperature at which fish were detected during the entire study period was 18.64 °C (range: 14.65 – 27.48 °C). The average temperature at which fish were detected inshore in the north was 20.06 °C (range: 15.44 – 26.74 °C) which was similar to the average in the south where it was 20.03 °C (range: 14.94 – 25.72 °C). At station F07 fish were detected at an average water temperature of 18.06 °C (range: 14.96 – 27.48 °C) across the study period.

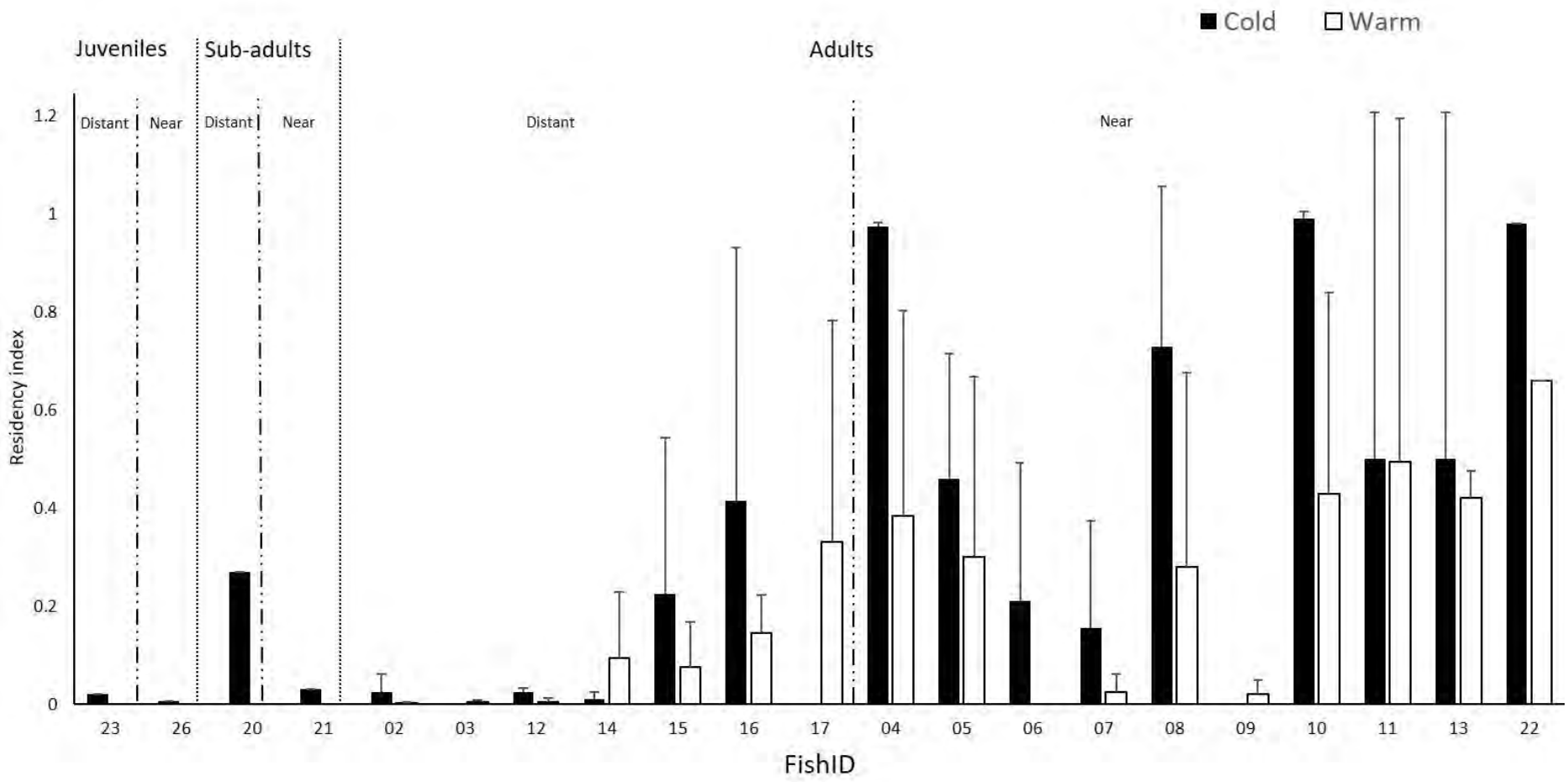


Figure 4.4: Average (±SD) daily residency indices of fish that were captured and tagged near (< 5km) or distant (> 5km) to station F07, that were detected at this station. Fish in increasing size order from left to right within each category.

During period C1, the average water temperature at which fish were detected inshore in the north was 18.75 °C (range: 16.87 – 21.89 °C) and in the south it was 17.84 °C (range: 15.92 – 21.15 °C) (Figure 4.5). At station F07 fish were detected at an average water temperature of 17.96 °C (range: 15.87 – 21.58 °C).

During period W1, the average water temperature at which fish were detected inshore in the north was 20.28 °C (range: 17.11 – 25.82 °C) and in the south it was 21.11 °C (range: 16.51 – 24.80 °C) (Figure 4.5). At station F07 fish were detected at an average water temperature of 20.12 °C (range: 16.99 – 24.82 °C).

During period C2, the average water temperature at which fish were detected inshore in the north was 19.13 °C (range: 15.44 – 21.39 °C) and in the south it was 16.69 °C (range: 14.94 – 21.94 °C) (Figure 4.5). At station F07 fish were detected at an average water temperature of 16.74 °C (range: 14.96 – 22.59 °C).

During period W2, the average water temperature at which fish were detected inshore in the north was 20.32 °C (range: 16.49 – 26.74 °C) and in the south it was 20.24 °C (range: 16.82 – 25.72 °C) (Figure 4.5). At station F07 fish were detected at an average water temperature of 19.68 °C (range: 16.82 – 27.48 °C).

The GLM examining the relationship between temperature and fish presence at station F07, found that mean daily temperature was a significant predictor of the proportion of fish present at this location (Figure 4.6; Table 4.1). The model predicted that more fish would be detected at F07 when the water temperatures were cooler.

4.3.5 Cyclical drivers

4.3.5.1 Time of day

There was no consistent diel pattern in the proportion of fish detected at station F07 over the entire study (Figure 4.7 A). During the cold periods the mean times of the highest proportion of fish detected occurred late at night into the early morning (C1: μ = 03:39; C2: μ = 00:33). Departure from uniformity in the proportion of fish detected throughout the day during ‘cold’

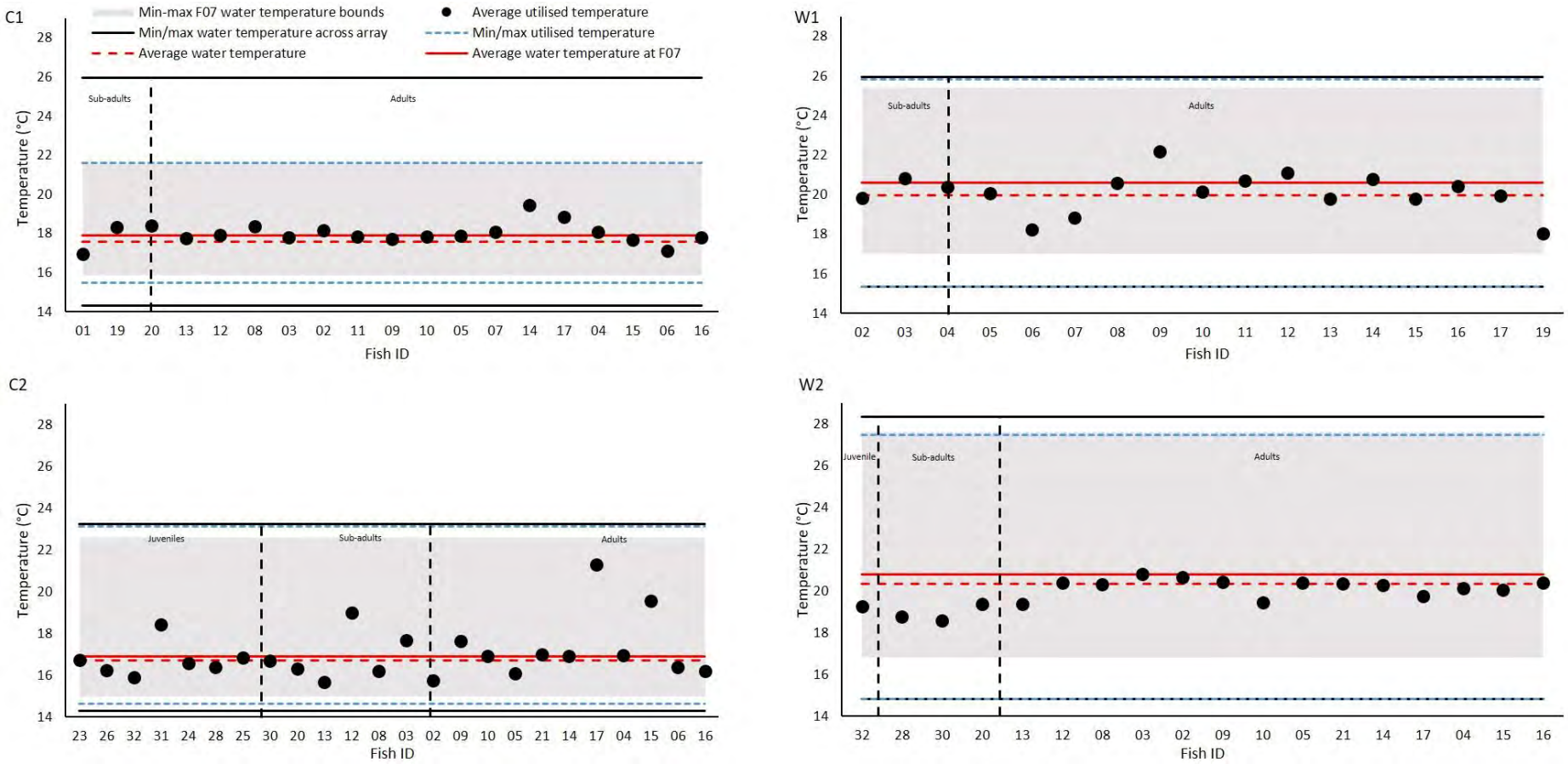


Figure 4.5: Summary of water temperatures at which fish were detected across all receivers at the Flamingo study site relative to mean, minimum and maximum observed values and average water temperature during 'cold' (C1 & C2) and 'warm' (W1 & W2) periods. Water temperatures at F07 (mean, minimum, maximum) indicated separately. Fish ID in order of increasing size from left to right of plots.

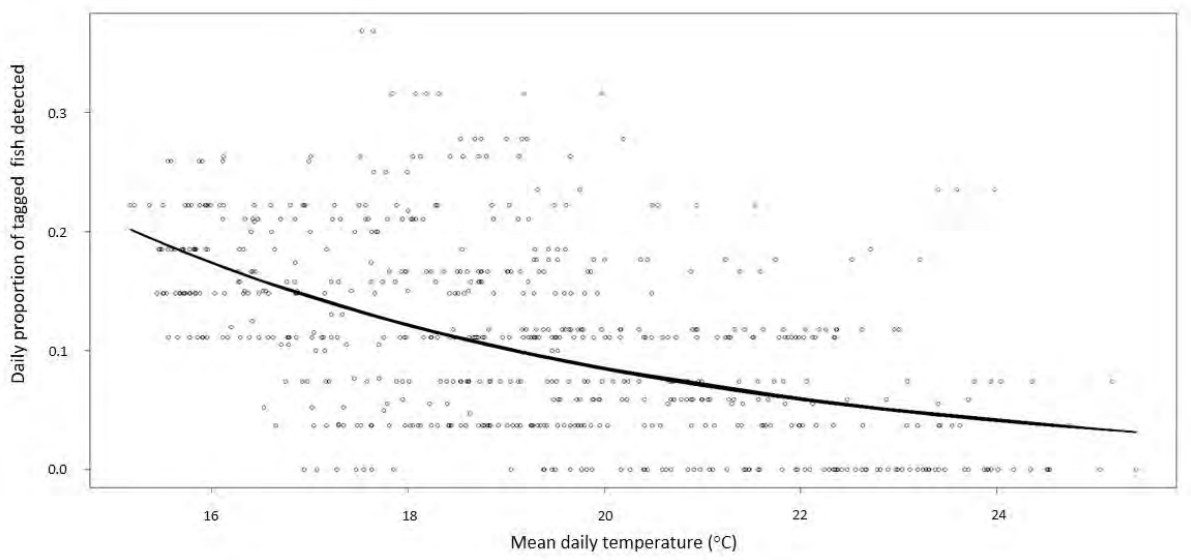


Figure 4.6: Generalised linear model fitted to the observed data of daily proportion of tagged *Argyrosomus coronus* detected at different mean daily temperatures at station F07 at the Flamingo study site during the full study period.

Table 4.1: Output of a binomial Generalised Linear Model predicting the proportion of tagged *Argyrosomus coronus* detected daily at station F07 at the Flamingo study site at different mean daily water temperatures. The coefficient relates to the intercept in a multiplicative manner.

Coefficients	Estimate	Std Error	Z	p-value
Intercept	3.11	0.22	5.23	<0.05
Mean daily temperature	0.84	0.01	-15.28	<0.05

Null deviance: 987.42 (degrees of freedom = 647)
Residual deviance: 734.12 (degrees of freedom = 646)
Fitted model had significantly lower deviance compared to null model (χ^2, $p < 0.05$)

periods was detected by the Rayleigh Test of Uniformity ($p < 0.05$); however, the low R values (C1: R = 0.09; C2: R = 0.13) indicated a very low concentration of observations. During 'warm' periods the mean time of the highest proportion of fish detected occurred close to midnight (W1: 00:18; W2: 00:09). Despite the reduced number of fish detected daily during the warm periods, departure from uniformity was evident ($p < 0.05$) and there appeared to be a stronger

diel pattern (W1: R = 0.27; W2: R = 0.40), with more fish being detected at night than during the day.

4.3.5.2 Tide

The proportion of fish detected at station F07 exhibited no evidence of tidal periodicity (Figure 4.7 B). The extremely small R-values (C1: 0.05, W1: 0.06, C2: 0.04, W2: 0.07) indicated that there was a broad spread of detections throughout the tidal cycle, although there was evidence of departure from uniformity ($p < 0.05$ in all cases). Although no strong relationship was evident, the mean tide when the number of fish peaked coincided with high tide (H), or 1 h before high tide (L5), for all periods.

4.3.5.3 Lunar phase

The proportion of fish detected at station F07 was predominantly unrelated to lunar phase with no consistent patterns between periods (Figure 4.7 C). Only during W1 was there any concentration of fish detections, whereby more fish were detected during the moon phases between last quarter and first quarter, with an average midway between new and waxing crescent, and R = 0.25. The 'cold' periods had very low concentration of fish being detected relative to the tide (C1: R = 0.09, μ = waning gibbous; C2: R = 0.04, μ = first quarter-waxing gibbous), but departure from uniformity was detected during both periods ($p < 0.05$). The pattern during W1 was not consistent with W2, which did not show departure from uniformity ($p = 0.09$), with low concentration of observations (R = 0.04).

4.3.6 Spawning periods

There were no distinct detection patterns evident in the tagged adult fish during either of the spawning periods (November – December) that were monitored (Figure 4.8). Presence of tagged fish was haphazard throughout the spawning periods, with little consistency among individuals. Circular plots at the circadian, tidal, and moon phase scale also indicated an absence of consistent trends across both spawning periods that were monitored (Figure 4.8). However, detections did show a clear relationship between the presence of adults and time of day during the second spawning period (Figure 4.8 A). During this period, the mean detection

time was 00:12, with a strong non-uniformity in the detection time ($R = 0.5$, $p < 0.05$). During the first spawning period, the mean detection time was 03:49, with non-uniformity being detected ($p < 0.05$); however, the concentration of observations was very low ($R = 0.1$).

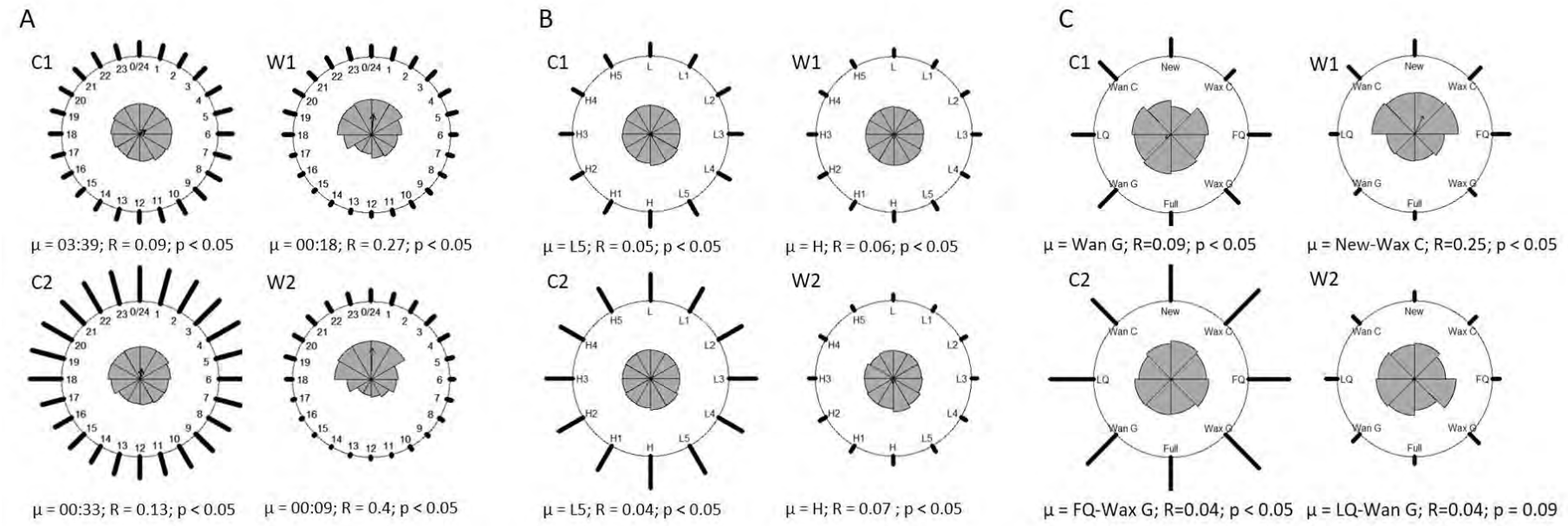


Figure 4.7: Hourly number of tagged fish detected at station F07 during the 24h period (A), the tidal cycle (B) and the lunar phases (C) during the four monitoring periods (C1, W1, C2 & W2). The surface area of the rose diagrams indicates the proportion of the observations occuring in each bin. Vectors indicate mean (μ) resultant length (R) of all detections. Lines radiating out from the circle edge indicate the number of detections in each bin. P-value from the Rayleigh Test of Uniformity.

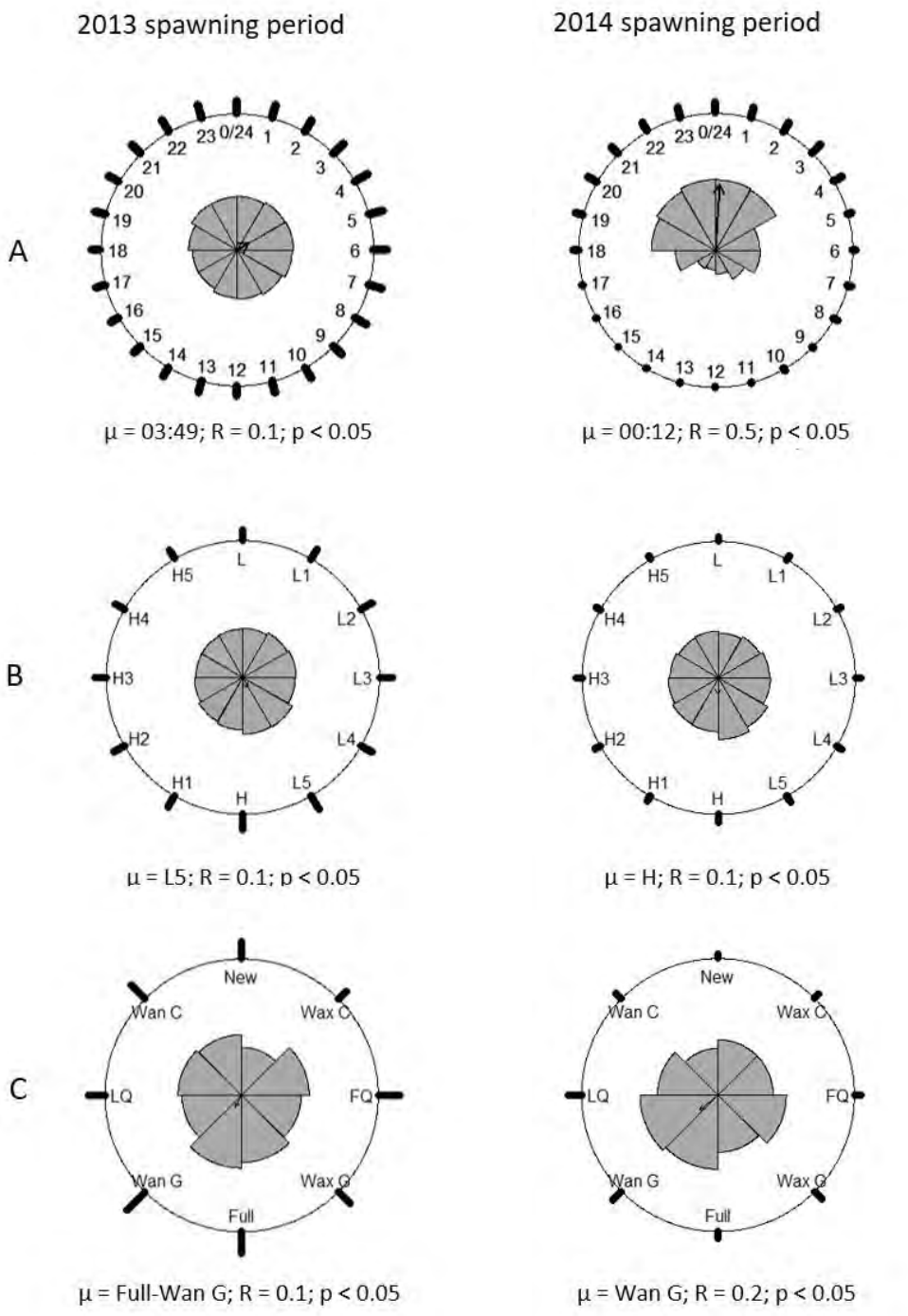


Figure 4.8: Temporal pattern of hourly number of fish detected at station F07 at the circadian scale (A), tidal scale (B) and moon phase scale (C), during the spawning period (November and December 2013 and 2014). Vectors indicate mean (μ) resultant length (R) of all detections. Surface area of rose diagrams indicates the proportion of total observations occuring in each bin. Lines radiating out from the circle edge indicate the number of detections in each bin. P-value from the Rayleigh Test of Uniformity.

4.4 Discussion

The presence of *A. coronus* at the inshore, mid-region of the Flamingo study site showed a significant relationship with temperature. This was evident in the GLM examining the relationship between temperature and the proportion of fish that were detected daily at this station, which predicts that the highest proportion of fish would be detected at lower temperatures (~16 °C). These results together with the findings in Chapter 3 show that this region of the Flamingo study site was an area of high-use, during 'cold' periods when the water temperature along this coastline is at its lowest due to the influx of cool, upwelled Benguela Current waters. The area evidently had a large draw for adult fish that were tagged close by (within 5 km) and further away (more than 5 km).

Viewing these results in isolation provided little evidence to facilitate our understanding of whether this concentration of *A. coronus* is an aggregation (i.e. independent of conspecifics) or a congregation (i.e. conspecifics were attractants to other individuals). Due to the seasonality of the phenomenon, and the significant relationship between their area use and water temperature, a physical concentration mechanism, such as a thermal niche, resulting in the fish aggregating at this region may be an appealing explanation. However, the temperature regime at this location differed by less than 1 °C from the other inshore regions during the same periods. If water temperature was the driver of this group formation, a north-south gradient in fish distribution may be expected, reflecting the north-south gradient observed in the water temperature. This was not the case, as the *A. coronus* concentration was flanked by low density to the north and the south. The remaining explanations then, are that it is an aggregation driven by habitat or other resource availability during cold periods, or that it is a socially-driven congregation. Although unequivocal differentiation is challenging with the current available data, the likelihood of both options is discussed further below.

It is possible that the seasonal increase in occupancy of this area by *A. coronus* is because of the seasonal abundance of their major food resource at this location. Large shoals of *Sardinella aurita* frequent the Flamingo coastline and regularly move close inshore during the austral winter (coinciding with cold periods in this study) at the mid-region of the Flamingo study site (station F07), particularly during the late afternoon and evening (Potts WM pers. comm.). These shoals are likely an important food source for *A. coronus* as 62% of the individuals examined by Potts et al. (2010) had *S. aurita* in their stomachs. Fish were detected more

frequently at this location during the early morning and late at night. This may lend support to the idea that this area is important for foraging, as this is when their dominant prey form dense groupings. As sciaenids have well-developed senses to detect vibrations (Taylor et al. 2020) they would be at an advantage hunting after sunset when prey may be less likely to detect their presence, in the absence of visual cues.

The period of group formation by *A. coronus* precedes the spawning season, which was indicated through gonadal staging to occur during the November-December period (Potts et al. 2010b). Spawning is an energetically costly process and this energy may be sourced directly from consumed food, or from energy reserves usually stored in muscle tissue, fat deposits, or in the liver (Craig et al. 2000; Lambert et al. 2003). Energy reserves have been shown to significantly decline during the spawning period, with increased food intake prior to this being a potentially important offset (Basade et al. 2000; Craig et al. 2000). Food intake may directly influence fecundity, as was found in captive haddock, *Melanogrammus aeglefinus* (Hislop et al. 1978) and captive European plaice, *Pleuronectes platessa* (Horwood et al. 1989). For *A. coronus*, the area around F07 may provide access to abundant food resources prior to spawning.

The sparsity of juvenile and sub-adult detections and the increasing seasonal residency with size (Figure 4.4) in the mid-region of the Flamingo study site may suggest that the group formation is associated with reproduction. However, relationships between the cyclical variables normally associated with spawning activity in sciaenids (Holt et al. 1985; Peters and McMichael Jr 1987, 1990; Johnson and Funicelli 1991; Erisman et al. 2012; Lowerre-Barbieri et al. 2013), and group formation at F07 were largely absent or very weak during the spawning period. However, a clear relationship with time of day emerged during the second spawning period, with more individuals being detected just after midnight than the rest of the day. Spawning activity in sciaenids has been associated with diel patterns. Peak spawning in the majority of species, including silver perch *Bairdiella chrysoura*, spotted seatrout *Cynoscion nebulosis*, red drum *Sciaenops ocellatus*, sand seatrout *C. arenarius*, king croaker *Menticirrhus* sp., Atlantic croaker *Micropogonias undulatus* and black drum *Pogonias chromis* occurs from three hours before to three hours after sunset (Holt et al. 1985). Spawning activity has been observed to occur around midnight in some sciaenids, through the use of passive acoustics (Mok and Gilmore 1983; Gilmore Jr 2002). Therefore, the increased presence of individuals at station F07 just after midnight is possibly spawning related. Spawning at night may be a successful strategy for *A. coronus* as it may reduce planktivore foraging, which occurs during

daylight hours, allowing the eggs time to disperse (Hobson and Chess 1978). The lack of cyclical patterns in the detection data may also be because the behaviour of the fish may not influence their detectability, if they remain in similar proximity to the receiver despite undergoing a behaviour change such as active spawning.

There was no relationship between the presence of adults at F07 and tidal cycle (Figure 4.7 B). The tidal cycle has been found to influence the feeding patterns of sciaenids. For example, foraging activity was focussed around shifting tides when the hydrodynamics suited the foraging strategy of blackspotted croaker *Protinibea diacanthus* (Semmens et al. 2010), and *A. japonicus* juveniles in an estuary in South Africa adopted a low-energy foraging tactic by moving with the tide to forage on passively drifting prey (Næsje et al. 2012). In these two studies, the tidal currents were important in either the movement of the predator for prey capture or for concentrating the prey and increasing their susceptibility to capture. However, as the tidal cycle is unlikely to drive currents or concentrate prey in the open environment around F07 in this study, it is less likely to play a role in determining when this area is suitable for feeding by *A. coronus*.

The lack of a relationship between the presence of adults at F07 and the tidal cycle does not necessarily preclude spawning activity as an explanation of the group formation. Several studies on sciaenids suggest that spawning occurs throughout the tidal cycle (Holt 2002; Aalbers 2008; Tellechea et al. 2011a). Typically, time of day is a stronger determinant of spawning in sciaenids (discussed above), regardless of tidal state.

There was no relationship between lunar phase and patterns in group formation in this study. Previous research on spawning periodicity in sciaenids found that spawning activity was timed around new and/or full moons during the spawning season in *S. ocellatus* (Peters and McMichael Jr 1987, 1990; Johnson and Funicelli 1991), Gulf weakfish *C. othonopterus* (Erisman et al. 2012) and *C. nebulosis* (Lowerre-Barbieri et al. 2013). However, in some instances the authors suggest that it was more likely the indirect lunar effect on tidal exchange rather than a direct lunar effect that spawning was cued to, as it was observed during new and full moons when tidal exchange was most pronounced (Peters and McMichael Jr 1990). However, a congregation may exist for a prolonged period, with spawning only occurring at certain lunar phases while the technique used in the current study did not detect this.

When considered together, the findings from this study provide some insight into the motivation for the group formation by *A. coronus* at station F07. The timing of the group formation ('cold' periods) appears to coincide with the inshore concentration of their dominant prey (*S. aurita*), specifically around F07 (Potts WM pers. comm.). The relationship with time of day could indicate that this may be a feeding aggregation, as the species (and most other sciaenids) does actively feed at night (personal observation). However, night-time spawning is a common feature of the sciaenid family and since the group formation at F07 was dominated by adult fish, with some evidence of increased presence at night, it is possible that this phenomenon may be a spawning congregation. While reproductively active fish have been largely absent from previous sampling efforts on the species, which relied on fishing with baited hooks or artificial lures, sampling bias due to reduced feeding activity during spawning periods may account for this absence, as sciaenids have been found to reduce their feeding activity during this time (Griffiths 1995). Spawning fish would also likely be located further offshore, away from the surf zone where the majority of sampling of the species has occurred, to prevent their pelagic eggs from washing onto the shore.

Additional research is needed to better understand the reason for this group formation. Possible future approaches could include using hydrophones to monitor the area for drumming sounds, which has been successful in identifying spawning behaviours in several sciaenid species (Luczkovich et al. 1999, 2008; Lagardère and Mariani 2006; Parsons and McCauley 2017); sampling the water for eggs to determine whether active spawning was occurring; or capturing individuals using nets, to eliminate the feeding bias from sampling techniques, and determining their gonad development state. Examining the movement ecology of *A. coronus* in relation to their major food resources, such as *S. aurita*, would inform the level to which their distribution is influenced by prey distribution, and indicate whether observed high densities of *A. coronus* can be attributed to high prey density. To provide further insight into the group formation identified in this chapter, Chapter 5 investigates the dynamics of the grouping behaviour and whether group membership is random over time or whether they may be socially structured.

Chapter 5: Network Analysis Suggests Persistent Sociality in *Argyrosomus coronus*

5.1 Introduction

Many animal taxa, including fishes, interact with conspecifics to varying degrees. These behaviours can be broadly referred to as 'sociality'. Sociality differs from simple group formation which may form through the mutual attraction to a resource or habitat (Johnson et al. 2002) and under such scenarios co-occurrences would be expected to be random over time, with no lasting pairing. Sociality infers an attraction to conspecifics in general, or on a more sophisticated level to particular individuals or types of individuals, perhaps characterised by sex, size or other features (Ward and Webster 2016).

Sociality exists along a spectrum ranging from the most basic transient grouping that may occur, for example, during reproductive behaviours (Lagardère and Mariani 2006; Semmens et al. 2010; Erisman et al. 2012; Rowell et al. 2012; Lowerre-Barbieri et al. 2013; Zarada et al. 2019) to the extreme of eusociality observed in restricted hymenopteran and isopteran insect taxa (Wheeler 1928; Alexander 1974). Sociality has evolved repeatedly in divergent animal taxa and influences various behaviours including foraging, locating mates, predator defence or evasion and rearing of offspring (Robinson et al. 2008).

Several social strategies are exhibited in fishes. The most classic of these is arguably schooling behaviour, which is thought to have been adopted primarily as a predatory defence mechanism (Kasumyan and Pavlov 2018). While schooling seems to be a complex behaviour, on a social level it is rather simple in that it is purely a highly coordinated group of conspecifics, and individual recognition is irrelevant (Kasumyan and Pavlov 2018). These groups may form through individual selfish responses in predator avoidance, with individuals positioning themselves relative to other individuals to reduce their chances of predation (Hamilton 1971). More complex social groupings include familial groups, harems, and colonial living (Kasumyan and Pavlov 2018).

A social approach to foraging has been adopted in some taxa. It may be an advantageous approach, depending on resource distribution and abundance, and forager group size relative

to resource availability (Harpaz and Schneidman 2020). An example of a social foraging interaction is the scrounger and producer dynamic, whereby one individual (producer) actively searches for a resource and the other individual (scrounger) responds to signs and behaviours it observes in the producer indicating resource acquisition (Barnard and Sibly 1981). This relationship may be fixed, in which case the producer gains nothing from the association. However, the roles may be facultative leading to gains for both parties and combined foraging rewards greater than what could be achieved from independent foraging efforts (Barnard and Sibly 1981).

Social behaviours are closely linked to genetics, endocrinology and physiology as certain internal processes moderate sociality. Stress, for example, has deleterious effects on standard behavioural interactions (de Abreu et al. 2020). Various hormonal pathways may moderate social interactions, as in the monogamous cichlid *Amatitlania nigrofasciata*, which exhibits affiliative behaviours to their preferred mate and agonistic behaviours to all other individuals (Oldfield and Hofmann 2011). Conversely, certain behaviours, or experimental inhibition of behaviours, may induce physiological changes; social interactions in several cichlid species have been found to affect reproductive physiology through influences on spermatogenesis and reproductive hormones (Scaia et al. 2020). While genetics plays an important role in sociality, social interactions have been found to influence brain gene expression, brain functioning and social behaviour itself (Robinson et al. 2008). Experimental isolation of naturally social fishes have been found to stunt their growth (Hesse and Thünken 2014), alter brain function and impair future social behaviour and interactions (Tunbak et al. 2020). In the harem adopting *Labroides dimidiatus*, dominance interactions by the largest individual, which is a male, supresses the smaller females from changing sex until the male is removed from the group (Robertson 1972).

Communication is a critical tool that has evolved to facilitate sociality among interacting individuals. The evolution of cooperative communication involving the sharing of information among individuals must either confer fitness advantages to those involved through relatedness, increasing familial level fitness (Floreano et al. 2007) or confer fitness benefits to the individuals involved through a reciprocal relationship (Barnard and Sibly 1981). Among fish taxa, sciaenids are highly adapted to generate sound. A pair of drumming muscles attached to the swim bladder enable these fishes to propagate drumming sounds through the manipulation of the swim bladder (Tower 1908). Studies have utilised the detection of drumming sounds in

sciaenids to infer reproductive behaviours (Saucier and Baltz 1993; Luczkovich et al. 1999; Lagardère and Mariani 2006; Ramcharitar et al. 2006; Tellechea et al. 2011b; Tellechea 2019). However, the role of sound communication in other behaviours, perhaps including foraging and territoriality, remains to be seen (Ramcharitar et al. 2006).

Grouping behaviour in sciaenids may have various benefits. It is common during spawning, as they are typically broadcast spawners with pelagic eggs (Watson 1982; Saucier and Baltz 1993; Griffiths 1996; Lowerre-Barbieri et al. 2013), therefore spawning in large groups increases the probability of egg fertilisation. Sciaenids also typically occupy turbid waters (Gray and McDonall 1993; Horodysky et al. 2008; Næsje et al. 2012) and may forage in groups, based on sporadically high CPUE for example in *A. coronus* (Potts et al. 2010b). Here group foraging would potentially increase individual foraging success when located resources are shared among group members, increasing individual foraging efficiency compared to solo foraging (Ranta et al. 1993).

This chapter aims to investigate whether the aggregations during 'cold' periods observed in Chapter 4 occur randomly in terms of the group constituents, or whether associations are indicative of preferential association and meet the criteria for sociality, rather than group formation. Network analysis was used to investigate the effects of ontogeny and season on associations within the network, and whether these associations persisted over time.

5.2 Materials and methods

The monitoring period was divided into the four periods: C1, W1, C2 and W2 (see Chapter 2 for more details on how periods were designated). The associations among monitored fish were analysed using separate network analyses for each of the four monitoring periods. Network analyses were conducted in *R* v 4.0.3 (R Core Team 2020). Pre-processing of data into time bins (10-minute sampling periods) was done using the **spatsoc** package (Robitaille et al. 2019). Thereafter the network analyses were conducted using **asnipe** (Farine 2013) and **igraph** (Csardi and Nepusz 2006) packages. Fish detected on the same receiver within a ten-minute sampling period were designated as co-located.

Relationships (co-locations) among pairs of individuals were described using the simple ratio index (*SRI*) (Cairns and Schwager 1987):

$$SRI = \frac{x}{x + y_{ab} + y_a + y_b}$$

where x is the number of sampling periods that both fish in a pair (dyad) were detected within a sampling period (within ten minutes of one another) on the same receiver, $y_{ab}$is the number of sampling periods that both fish in a dyad were detected on different receivers, y_a is the number of sampling periods that only fish *a* was detected and y_b is the number of sampling periods that only fish *b* was detected.

Mean SRIs were calculated for each fish, across all dyads. Mean SRIs were calculated during each period for each fish when part of a 'peer' dyad (both fish in the dyad were tagged at the same location) and when part of a 'strange' dyad (fish were tagged at different locations) and compared across periods, within life stages, using a Mann-Whitney test (*wilcox.test* function in *R* v 4.0.3 (R Core Team 2020)). Network graphs, with nodes representing the individual fish and edges connecting the nodes representing the SRI values, were then produced for each sampling period.

Several indices are commonly used to describe network characteristics. Three indices were used in this study (Table 5.1). All indices were calculated using the **igraph** package (Csardi and Nepusz 2006) in *R* v 4.0.3 (R Core Team 2020). 'Degree' (*D*) is a count of the number of dyads that a given fish was observed in. This was calculated using the *degree* function. A relatively small mean *D* across a network indicates low levels of inter-connectedness of nodes in a given network, while a large mean *D* indicates high levels of inter-connectedness. Values for *D* must be viewed relative to the total number of nodes (tagged fish) in the network. 'Strength' (*S*) is calculated by summing all *SRIs* for each individual. This was calculated using the *strength* function. Small mean *S* values across a network indicates that there are weak relationships between nodes in the graph, while large mean *S* values indicate strong relationships between nodes. 'Clustering coefficient' (*C*) is a measure of the probability of nodes connected to a focal node being connected to other nodes in the network. This was calculated using the *transitivity* function. Small mean *C* across a network describes a poorly inter-connected network, while large mean *C* is associated with a well-connected network.

The means of all three metrics (*D*, *C* and *S*) were calculated for each life stage (juvenile, sub-adult and adult) during each period (C1, W1, C2 and W2) and these values were used to compare the network structure between life stages across the monitoring periods.

Table 5.1: Summary of social metrics used to describe the networks.

Metric	Description	Interpretation
Degree (*D*)	Number of dyads a fish was observed in.	Indicates how connected (large *D*) or isolated (small *D*) an individual is within the network.
Strength (*S*)	Sum of *SRI* for each dyad for each individual.	Indicates the strength (over time) across all relationships for each individual. Small *S* indicates weak relationships. Large *S* indicates strong relationships.
Clustering coefficient (*C*)	Probability of nodes connected to a focal node being connected to other nodes.	Indicates level of sub-structuring within a network. Small *C* indicates a sub-structured network. Large *C* indicates well-connected network with low sub-structuring.

A series of randomisation tests was conducted whereby null models were used to test whether the observed network metrics differed significantly from those produced by randomly generated networks (Farine 2013). Null models were constructed for the strength metric, node degrees, SRI and the clustering coefficient using the *network_permutation* function in the **asnipe** package, with 10 000 permutations conducted for each analysis (Farine 2013), in *R* v 4.0.3 (R Core Team 2020). The *P*-values were calculated in each case by comparing the observed test statistic with the distribution of test statistics calculated from the null models. This was done by counting the number of occurrences where the observed test statistic was greater/less than (depending on the metric) the random test statistic generated in each null model and dividing that by the number of permutations generated for the comparison (Farine 2017). Comparisons of observed mean metrics against those from null models were used to provide insight into whether individuals are actively attracted to or avoid other individuals. For example, if the observed mean *SRI* were significantly greater than the random test statistic, then it is likely that the observed associations between pairs of fish were actively maintained and not through chance encounters. If the observed mean *D* were significantly less than the random test statistic, then it is likely that individuals were located with a lower number of

individuals than expected. If the observed mean *C* were significantly less than the random test statistic, then it is likely that there were sub-divisions of individuals within the network, and not homogeneous mixing among all individuals as would have been the case if observed mean *C* was significantly greater than the random test statistic. If the observed mean *S* were significantly greater than the random test statistic, it is likely that individuals actively favoured being co-located with select other individuals, while observed mean *S* significantly lower than the random test statistic suggests avoidance of co-location with other individuals.

Network analysis allows for the examination of structuring within the network. This allowed for the separation of individuals into groups. Groups, commonly referred to as 'communities' in the literature, consist of those individuals that are more connected with one another, than with individuals from outside of the group (Newman 2006a). Group assignment techniques that use a modularity approach compare the number of edges (which are the links between individuals within the network) within groups to the expected number of edges from a random group, and determines optimum groupings based on the strongest modularity (i.e. groups with the greatest difference from the random groups) (Newman 2006a).

In this study, groups were delineated using a spectral algorithm approach (Newman 2004, 2006b). This technique assigns a modularity score to a given community structure, with modularity ranging between 0 (indicating randomness) and 1 (indicating strong non-randomness) with values ~ 0.3 indicating well-supported community divisions (Newman 2004). This process was executed using the *cluster_leading_eigen* function in the **igraph** package (Csardi and Nepusz 2006) in *R* v 4.0.3 (R Core Team 2020). In some instances, groups of single individuals were output, isolated from other individuals. Once groups were assigned within each period, groups were examined for consistency of constituents across periods. Group identity was considered to be the same across periods if there was a minimum of 40 % persistence of individuals across periods. Groups were arbitrarily assigned a number to identify them across periods.

Finally, individuals and groups were classified according to their permanency. Individuals were classified as 'transient' if group membership lasted for a single period, 'semi-transient' if it lasted for two periods, 'semi-permanent' if it lasted for three periods and 'permanent' if it covered the full monitoring period. Juveniles were only monitored for two periods (C2 & W2) as they were tagged in the latter part of the study, and were thus never classified as 'semi-

permanent' or 'permanent'. Groups were classified by their consistency across periods. 'Dynamic' groups were those groups that consisted of >50 % transient or semi-transient individuals over the monitoring period. 'Static' groups were those groups that consisted of >50 % permanent or semi-permanent individuals.

5.3 Results

Dense networks were observed during all monitoring periods, with numerous strong associations (red and black lines) observed during period C2 (Figure 5.1). Visual inspection indicated that edges connected across tagging groups and life history stages. Higher weighted edges, which is based on the *SRI*, were observed more frequently among adults, particularly among 'peer' fish (individuals capture within 5 km of one another), although the pattern among 'peer' fish appeared to break down towards the latter period of the study. A notable, consistently observed dyad (pair of fish), with heavily weighted edges (strong associations) across all monitoring periods, was between fish 4 and fish 10, both of which were adults tagged at the same location (F07) on consecutive days.

Visual patterns observed in the social network were supported by the mean *SRI* (metric of the strength of individual associations), with lower associations among juveniles compared with adults (Figure 5.1). The mean *SRI* was lowest in juveniles over both periods that they were monitored (Figure 5.2 A) with values ranging between 0.0006 ± 0.0006 in W2 and 0.009 ± 0.01 in C2. The *SRI* of sub-adults ranged between 0.001 ± 0.001 during W2 and 0.04 ± 0.07 during W1, while that of adults ranged between 0.02 ± 0.05 during W1 and 0.07 ± 0.11 during C2. Adults typically had the highest mean *SRI*, except during W1 when it was highest in sub-adults. Adult mean *SRI* was relatively consistent during all periods except C2, when it was substantially higher. Variability in the mean *SRI* of the adults was also high. Mean *SRI* was significantly higher in adult relationships among peer fish (dyads comprising fish that were tagged at the same capture location) than strange fish (dyads comprising fish that were tagged at different capture locations), during C1 ($W = 200$, $p < 0.05$) and W1 ($W = 170$, $p < 0.05$), but not during the later periods C2 ($W = 120$, $p = 0.50$) and W2 ($W = 64$, $p = 0.21$) (Figure 5.3). Mean SRI among peer fish were not significantly different to strange fish in all other life stages, across all monitoring periods.

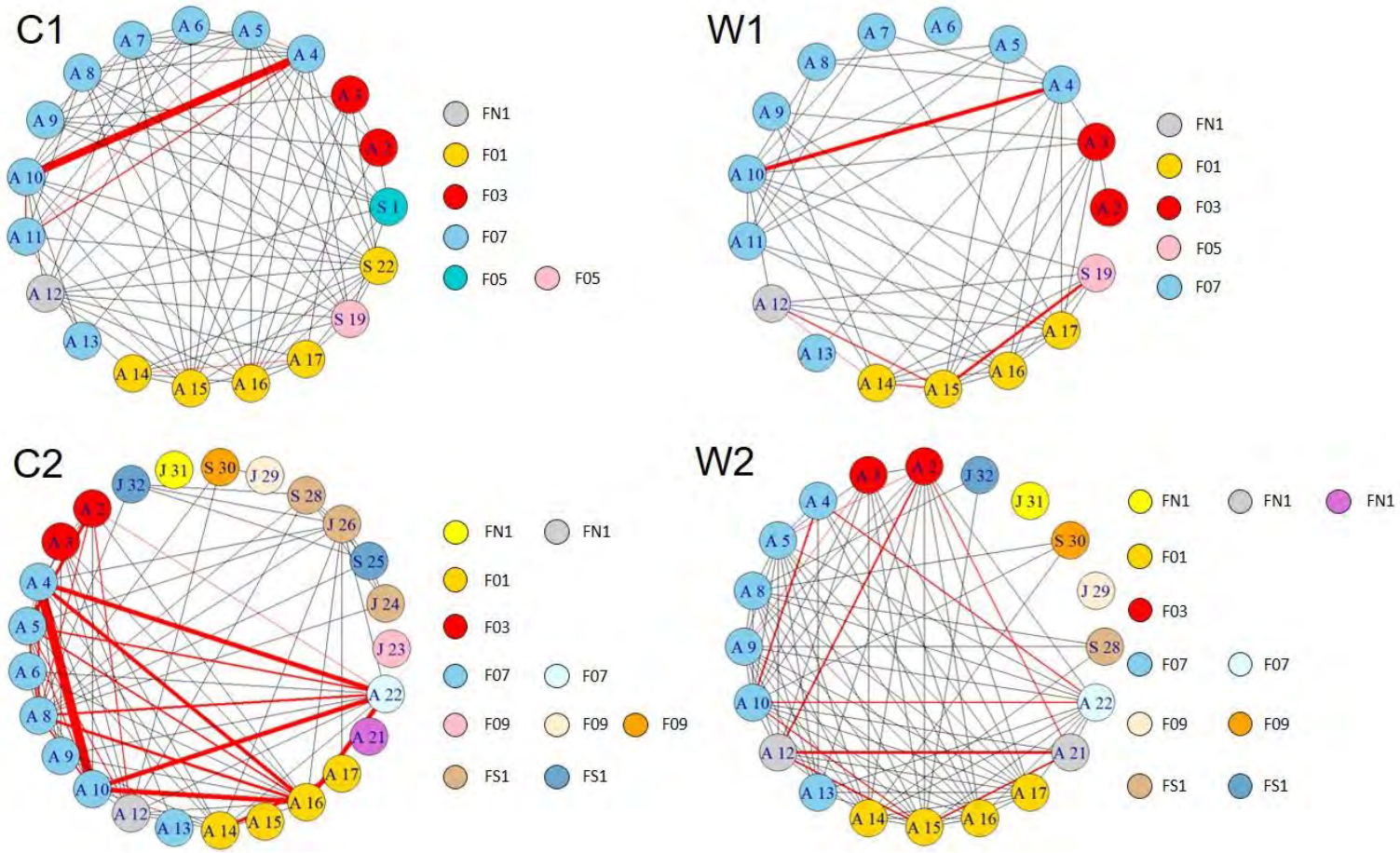


Figure 5.1: Social networks for the four monitoring periods C1, W1, C2 and W2. Nodes represent fish fitted with acoustic transmitters, with prefix letters in node labels indicating life stage of monitored fish (J: juvenile, S: sub-adult, A: adult). Node colours represent tagging location, with node labels in the legends indicating nearest receiver station to fish tagging location. Edges (black and red lines) between nodes indicate association of individuals during the monitoring period, with stronger associations indicated by red, thicker edges (based on the simple ratio index [*SRI*]).

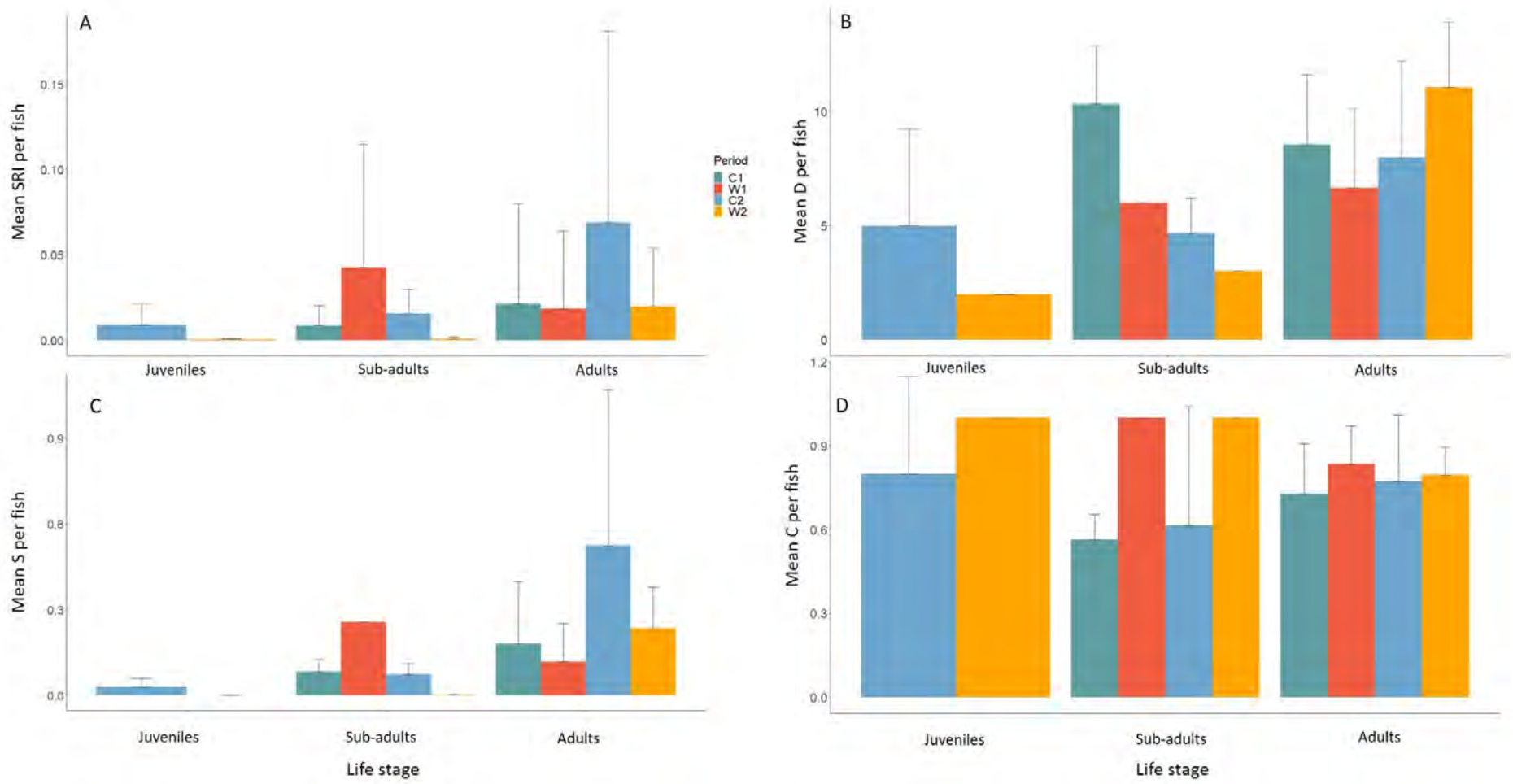


Figure 5.2: Mean (SD error bars) network metrics during each monitoring period for each life history stage of tagged *Argyrosomus coronus*. A: Simple ratio index (*SRI*) which is a metric of the strength of dyads, B: Degree (*D*) which indicates the number of dyads each fish forms part of, C: Strength (*S*) which is the sum of all *SRI* for all dyads a fish is part of, D: Clustering coefficient (*C*) which is a metric indicating sub-structuring of the network.

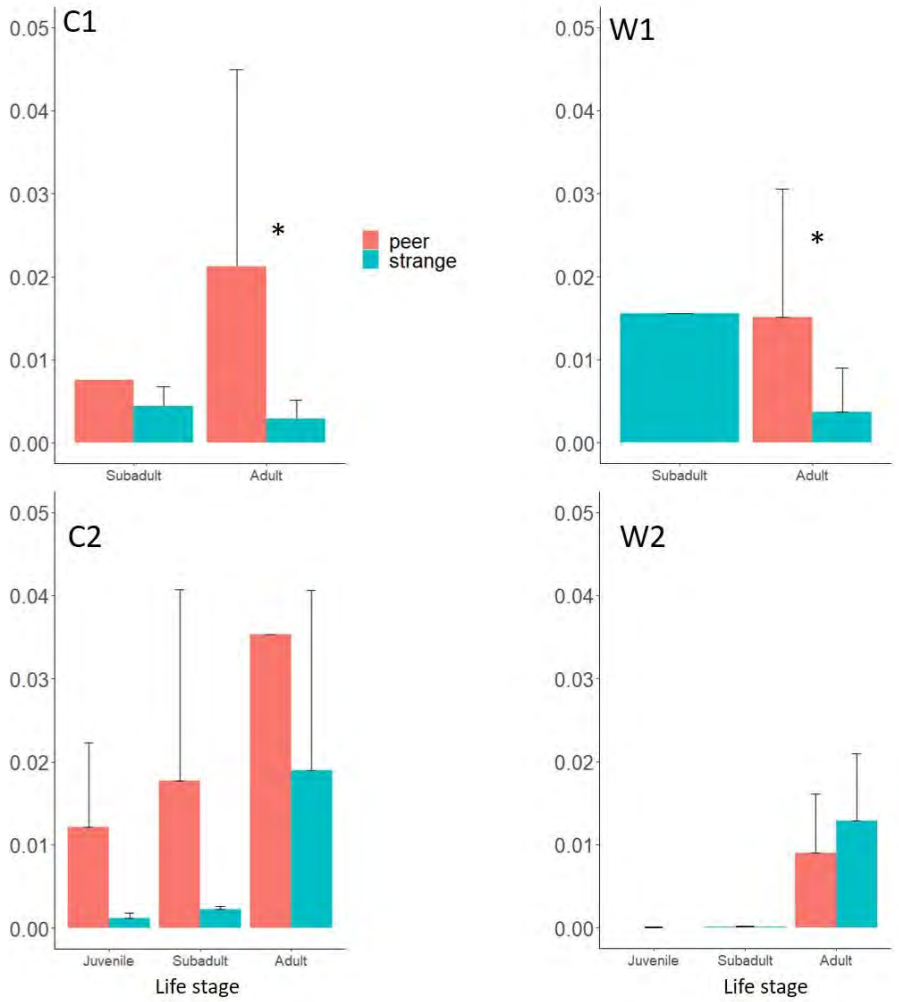


Figure 5.3: Mean simple ratio index (*SRI*; index of the strength of dyads) per life stage during each monitoring period for relationships between 'peer' (tagged at the same location) and 'strange' (tagged at different locations) fish. Asterisks indicate significant differences between peer-strange pairs ($p < 0.05$).

Visual patterns observed in the network were also supported by the mean *D* per fish (number of edges between nodes). It was variable but relatively low in juveniles, ranging between 2.0 ± 0 (n = 1) during W2 and 5.0 ± 4.24 during C2, higher in sub-adults, ranging between 3.0 ± 0 (n = 1) during W2 and 10.3 ± 2.5 during C1, and highest in adults, ranging between 8.0 ± 4.2 during C2 and 11.1 ± 2.8 during W2 (Figure 5.1, Figure 5.2 B).

Mean *S* (sum of *SRI* for each dyad that a fish was part of) per fish was low in juveniles, ranging between 0.002 ± 0.0007 during W2 and 0.090 ± 0.030 during C2, intermediate in sub-adults, ranging between 0.004 ± 0.002 during W2 and 0.510 ± 0 (n = 1) during W1 and highest in adults, ranging between 0.250 ± 0.134 during W1 and 1.120 ± 0.547 during C2 (Figure 5.2 C). Adults in the 'cold' periods (C1 & C2) exhibited higher mean *S* than the subsequent 'warm' periods (W1 & W2).

Mean *C* (which measures sub-structuring within the network, or how well the network is inter-connected) was greater during 'warm' periods (W1 & W2), than 'cold' periods (C1 & C2) for all life stages (Figure 5.2 D). Mean *C* for juveniles ranged between 0.80 ± 0.35 during C2 and 1 ± 0 (n = 1) during W2. Sub-adults' mean *C* ranged between 0.56 ± 0.09 during C1 and 1 ± 0 (n =1) during W1 and W2. The mean *C* for adults ranged between 0.73 ± 0.18 during C1 and 0.83 ± 0.14 during W1.

Randomisation test results indicated that mean *D* was significantly lower than random for all life stages and monitoring periods, indicating the occurrence of a smaller number of relationships among individuals than if associations were random, except in juveniles during W2 where *D* was indistinguishable from random association (Table 5.2). Randomisation tests indicated that the observed mean *SRI* was significantly higher than would be expected from random associations across all periods and life stages ($p < 0.05$; Table 5.2). Mean *C*, which indicates network sub-structuring, was significantly lower than expected from random associations for all periods and life stages, where there were sufficient observations for the analyses, indicating sub-structuring within the network (Table 5.2). Patterns in the overall association strengths, summarised by mean *S*, were varied (Table 5.2). Associations of juveniles were stronger than expected when compared with random association during both periods that they were monitored. Association of sub-adults were significantly weaker than expected when compared with random association during C1 and W2 but no different from random association during C2.

Table 5.2: Summary of the outputs from the randomisation tests. Metrics include the simple ratio index (*SRI*), cluster coefficient (*C*), strength metric (*S*) and degrees (*D*). These tests compared observed data to random null models to detect whether observations are process driven or similar to random association. Null models were constructed using 10 000 permutations for each analysis. Statistical significance was tested by comparing the observed test statistic to the distribution of test statistics calculated from the permutated models. Hypotheses tested were either that the observed statistic was greater (>) or less (<) than expected from random association. Statistics that differed significantly from random chance ($p < 0.05$) were designated as non-random (NR), while those that were indistinguishable from random associations were designated as random (R). Colours highlight the 'cold' (C1 & C2) and 'warm' (W1 & W2) periods.

		Simple ratio index (relationship strength between dyads)		Cluster coefficient (sub-structuring within the network)		Strength (cumulative measure of intensity of dyads per individual)		Degree (number of dyads per individual)	
Period	Life stage	Hypothesis tested	Test result (NR: Non-random [$p < 0.05$]) R: Random [$p > 0.05$])	Hypothesis tested	Test result (NR: Non-random [$p < 0.05$]) R: Random [$p > 0.05$])	Hypothesis tested	Test result (NR: Non-random [$p < 0.05$]) R: Random [$p > 0.05$])	Hypothesis tested	Test result (NR: Non-random [$p < 0.05$]) R: Random [$p > 0.05$])
C1	Juvenile	None tagged		None tagged		None tagged		None tagged	
	Sub-adult	>	NR	<	NR	<	NR	<	NR
	Adult	>	NR	<	NR	>	NR	<	NR
W1	Juvenile	None tagged		None tagged		None tagged		None tagged	
	Sub-adult	NA‡		NA		NA		NA	
	Adult	>	NR	<	NR	>	NR	<	NR
C2	Juvenile	>	NR	<	NR	>	R	<	NR
	Sub-adult	>	NR	<	NR	>	R	<	NR
	Adult	>	NR	<	NR	>	NR	<	NR
W2	Juvenile	>	NR	NA		>	R	<	R
	Sub-adult	>	NR	NA		<	NR	<	NR
	Adult	>	NR	<	NR	>	NR	<	NR

‡: NA = Insufficient observations during the period to allow for calculation

Associations of adults were significantly stronger than random during all four periods.

Ten different groups were identified by the community analysis, across all periods (Figure 5.4). The modularity values for the groups identified during each period were greater than the threshold of 0.3, indicating support for the group divisions identified. The observed values ranged from 0.3 during C1 and C2 to 0.4 during W1 and W2. Groups ranged in size from one individual, in which case there was no grouping with other fish (five groups), and only persisting for a single period (five groups), to ten individuals with the group spanning all periods (Figure 5.4, Table 5.3). All groups were classified as dynamic; consisting of >50 % transient or semi-transient individuals over the study period. Among the three larger groups that persisted across all periods (Grp 1 – 3), the transient (group membership lasting for a single period) and semi-transient (group membership lasting for two periods) proportions of the total group size ranged between 0.27 and 0.53, and between 0.30 and 0.45 respectively. The semi-permanent (group membership lasting for three periods) and permanent (group membership lasted for all four periods) components ranged between 0.07 and 0.10, and between 0.07 and 0.18 respectively. The group formation behaviour noted in Chapter 4 included individuals from multiple groups.

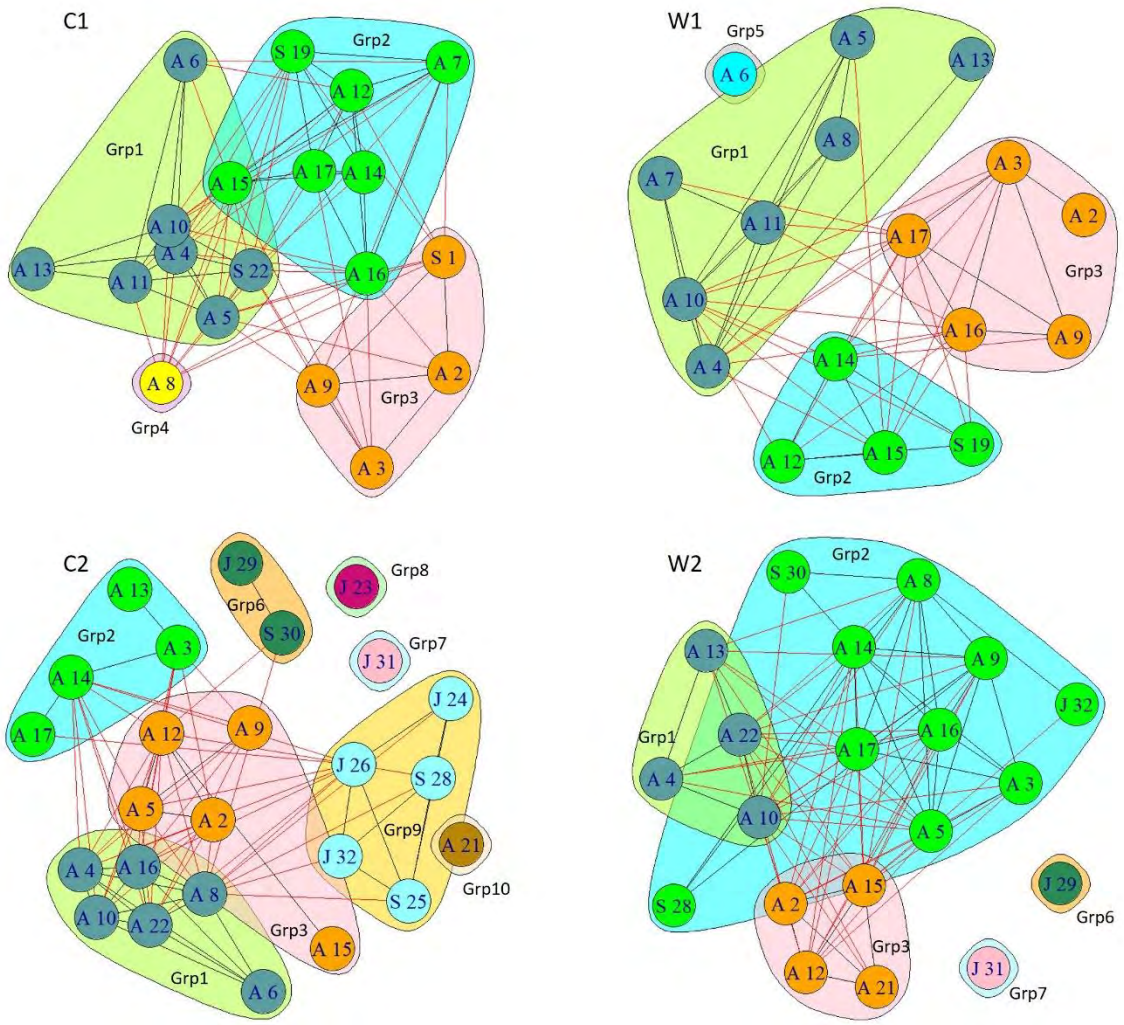


Figure 5.4: Community structure during each period identified using a spectral algorithm approach. Node colours and shading indicate a defined group, labelled Grp1 – 10. Defined groupings indicate patterns of co-location of individuals. Modularity values per period (with 0 indicating groupings are random and 1 indicating strong non-random groupings) calculated as 0.3 (C1); 0.4 (W1); 0.3 (C2); 0.4(W2).

Table 5.3: Dynamics of groups identified through community analysis. Individual member characteristics, type of group affiliations (transient, semi-transient, semi-permanent or permanent), longevity of groups and group category (static or dynamic) indicated. Table colour scheme references group colours in Figure 5.4.

Group number (colours reference Figure 5.4)	Individuals			Summary of individual affiliations per group			Periods group present	Group category
	Fish ID	Life stage	Total length (mm)	Type	N individuals	Proportion of group		
1	04	Adult	1 084	Transient	3	0.27	C1, W1, C2, W2	Dynamic
	05	Adult	960					
	06	Adult	1 150	Semi-transient	5	0.45		
	07	Adult	980					
	08	Adult	940	Semi-permanent	1	0.09		
	10	Adult	960					
	11	Adult	950	Permanent	2	0.18		
	13	Adult	900					
	16	Adult	1 155					
	22	Adult	1 100					

	03	Adult	950	Transient	8	0.53		
	05	Adult	960					
	07	Adult	980					
	08	Adult	940					
	09	Adult	960	Semi-transient	5	0.33		
	12	Adult	930					
	13	Adult	900					
2	14	Adult	1 000				C1, W1, C2, W2	Dynamic
	15	Adult	1 120	Semi-permanent	1	0.07		
	16	Adult	1 155					
	17	Adult	1 050					
	19	Sub-adult	845					
	28	Sub-adult	616					
	30	Sub-adult	765					
	32	Juvenile	490	Permanent	1	0.07		

3	01	Sub-adult	780	Transient	5	0.50	C1, W1, C2, W2	Dynamic
	02	Adult	950					
	03	Adult	950					
	05	Adult	960	Semi-transient	3	0.30		
	09	Adult	960					
	12	Adult	930					
	15	Adult	1 120	Semi-permanent	1	0.10		
	16	Adult	1 155					
	17	Adult	1 050					
	21	Adult	1 000	Permanent	1	0.10		
4	08	Adult	940	Transient	1	1.00	C1	Dynamic
5	06	Adult	1 150	Transient	1	1.00	W1	Dynamic
6	29	Juvenile	520	Transient	1	0.50	C2, W2	Dynamic
	30	Sub-adult	765	Semi-transient	1	0.50		
7	31	Juvenile	566	Semi-transient	1	1.00	C2	Dynamic
8	23	Juvenile	464	Transient	1	1.00	C2	Dynamic
9	24	Juvenile	595	Transient	5	1.00	C2	Dynamic
	25	Sub-adult	648					
	26	Juvenile	466					
	28	Sub-adult	616					
	32	Juvenile	490					
10	21	Adult	1000	Transient	1	1.00	C2	Dynamic

5.4 Discussion

Several studies have highlighted the benefits of sociality, which include optimising spawning (Domeier and Colin 1997), increased feeding efficiency (Alexander 1974; Ebert 1991b) and improved predator detection/avoidance (Hamilton 1971; Alexander 1974; Croft et al. 2006). Social attraction of an individual to a group has been found to be influenced by group size, size of individuals in the group, and familiarity of the individual with the group members suggesting the existence of individual recognition (Lachlan et al. 1998). Indeed, the network analysis results of this study indicated that *A. coronus* exhibit social attraction, with evidence for long-term relationships among individuals, and not simply group formation. The social dynamics were described by several metrics. The frequency of occurrence of dyads, described by the *SRI*, was higher than expected from random associations during all life stages and monitoring periods. This indicates that certain individuals favoured one another, occurring together with relatively high frequency. Individuals were found to associate with fewer others than expected under a random association scenario indicating the absence of complete mixing among all fish. At the group level, sub-structuring of the network was noted. Community analysis helped to better quantify this mixing; while groups were identified within each monitoring period, group dynamics were fluid with individuals frequently switching groups from one period to the next. There was, however, evidence of lasting association with one dyad in particular (between fish 04 and 10) exhibiting strong association throughout the study period.

Social foraging behaviours have been observed in several fish species (e.g. Ryer and Olla 1995; Day et al. 2001); however, this phenomenon does not appear to be documented for sciaenids. The lasting nature of sociality in *A. coronus* suggests that it is linked to an aseasonal behaviour, with foraging a likely possibility. Social foraging would benefit individuals when locating and capturing prey. Predators targeting schooling fish benefit from utilising an intra- or inter-specific group foraging approach to increase foraging efficiency by disorganising the school, following successive attacks on the school, or through confining their prey prior to capture (Thiebault et al. 2016; Sutton et al. 2020). In an apex predatory elasmobranch, the sevengill shark *Notorynchus cepedianus* (Ebert 1991b), their facultative social foraging ability expands the size-range of prey that they are able to exploit. It also enables them to collectively cover a wider search area when hunting, with the group benefitting once prey has been located or captured by one individual. Prey size would not necessitate a social foraging approach by large adult *A. coronus*, as their prey are small enough to be swallowed whole. The behaviour may,

however, increase foraging efficiency at the group level, and offer concomitant payoffs for individuals in the group. *Argyrosomus coronus* have been observed undertaking what appeared to be a coordinated hunting approach. This was observed on several occasions at the Flamingo study site, where adults exhibited coordinated group feeding behaviour to capture shoaling small pelagic fish, *S. aurita*. Here the shoals of *S. aurita* were chased to the surface by the group, before between three and ten adults darted through the shoal from below, jumping simultaneously out of the water (Potts WM pers. comm.). Feeding strategies such as this are undoubtedly more efficient than foraging individually (Ramcharitar et al. 2006).

Communication is a central component in any social interactions (Fine et al. 1977). The Sciaenidae are well known for their sonic communication ability, with individual recognition likely, but not confirmed for the family (Lagardère and Mariani 2006; Ramcharitar et al. 2006; Parsons and McCauley 2017). This ability to communicate would facilitate information sharing and group cohesion and the development and maintenance of associations. While other fishes may use visual (Fine et al. 1977) or electric (Macesic and Kajiura 2009) communication, the environments that *A. coronus* and several of its congeners favour are usually turbid (Griffiths 1996) and would thus make visual communication ineffective. In addition to being receptive to transmissions from conspecifics, a well-developed mechano-reception system has the added advantage of heightened prey detection in low-visibility environments (Deary et al. 2016) where this species tends to hunt. Further to its potential role in foraging behaviours, communication in sciaenids has widely been linked with reproduction (Luczkovich et al. 1999, 2008; Ramcharitar et al. 2006; Rowell et al. 2012; Lowerre-Barbieri et al. 2013; Tellechea 2019; Zarada et al. 2019), with the development of drumming muscles usually linked with maturation (Griffiths and Heemstra 1995). An increased ability to communicate as adults would facilitate a higher level of association compared to younger fish, as observed in this study.

An ontogenetic shift in sociality was noted with adult *A. coronus* generally having more, and stronger, associations with other individuals. This was evident from the *SRI* which, while highly variable in adults and sub-adults, the mean and maximum values were highest in adult fish. A similar pattern was observed in mean *S*, which is calculated from the *SRI*. In addition to the links between individuals being stronger in adults, they were also found to have relationships with a greater number of individuals, evident from the typically higher mean *D* in adults than in younger fish. Network metrics showed that the level of interactions among

individuals showed no trend with monitoring period, with similar patterns in randomisation tests observed during both 'cold' and 'warm' periods. While adults were found to be more social, suggesting a possible reproduction-based explanation, *A. coronus* are gonochoristic so are unlikely to have strong, sexually motivated social structures as is seen, for example, in harem forming hermaphroditic species (Petersen 1987; Welsh et al. 2013; Stier et al. 2013) and lek-breeding species (McKaye 1983; Oliveira and Almada 1998). Similar sociality was also observed across all monitoring periods and was not limited to peak spawning times and, therefore, was not an artefact of group spawning behaviour but rather a persistent feature of *A. coronus.*

These findings suggest that *A. coronus* have evolved to co-operate on some level with conspecifics, and are possibly able to recognise individuals, with relationships persisting over multiple years. While spawning may not be the primary driver of sociality in the species, sociality may improve spawning efficiency as reproductively mature individuals would not need to expend resources searching for mates during spawning season, as they are in close proximity year-round.

Sociality was not isolated to the aggregation periods observed in Chapter 4. While the metrics indicated similar patterns of sociality across monitoring periods, the number of strong dyads during period C2 was notable. Sub-structuring within the network was also lower during 'cold' periods, indicating higher levels of mixing. These metric patterns may be explained by the aggregation observed during 'cold' periods, which produced increased levels of sociality and mixing above the level occurring outside of this aggregation. Anecdotal evidence suggests that this is likely a feeding aggregation due to concentration of prey (see Chapter 4 for discussion). Persistent sociality may increase the susceptibility of *A. coronus* to exploitation. Continued fishing at the capture location of one fish may lead to the capture of many more associated fish.

The differences in sociality indices between different life history stages may, at least partially, be linked with sample-size and sampling approach. It was evident that fish that were tagged at the same location a relatively short time apart were more likely to spend a greater amount of time together, compared with fish tagged at different locations. This, together with the lower sample-size of juvenile and sub-adult fish, may contribute to the incongruence in observed sociality among the different life stages. To gain a better understanding of sociality among

younger *A. coronus,* further acoustic telemetry studies focussing on juvenile and sub-adult fish with larger sample-sizes and increased tagging effort at individual locations is suggested.

Caution should be exercised when inferring association from passive acoustic telemetry studies where the receiver array design does not facilitate fine-scale positioning, where detection ranges are large. Inferred associations may be, at least in part, explained by individuals utilising adjacent areas (Petersen 1987; Welsh et al. 2013; Stier et al. 2013; Wilson et al. 2014). While this cannot be unequivocally ruled out, the fact that many of the fish were captured prior to being tagged at the same location over a short period of time supports the fact that these fish do exhibit sociality. Additional research employing fine-scale positioning techniques would be required to investigate this aspect further.

This chapter found evidence of sociality in *A. coronus*. Individuals were frequently detected in groups, with group membership being fluid throughout the study period. Evidence suggests that some dyads may have relatively long lifespans. Due to the lack of strong seasonality in the associations, which were not centred around peak spawning periods, it is suggested that this sociality may primarily benefit the species in foraging efforts. A further, fine-scale positioning study would assist in deepening our understanding of this sociality.

Chapter 6: General Discussion

This study was located in rural southern Angola on a species of importance to local livelihoods that is harvested in multiple fishery sectors, from subsistence to industrial commercial. In addition to harvesting pressure, it is subjected to further threats within this climate change hotspot including climate change driven hybridisation with a congener that occurs within the region. In this context, understanding the space use of *A. coronus* is fundamental for understanding their ecology, and the influence that these stressors may have on the species as fish distribution and their movement ecology reflect a multitude of abiotic and biotic factors. The prevalence of different movement behaviours, from restricted movements resulting in a residency pattern, to large-scale movements such as longshore migration, are key aspects in movement ecology studies. Intra-specific interactions further shape population dynamics. Investigating how and when individuals have increased levels of interaction, whether it be through a concentrating effect due to resource or habitat availability, or through a social attraction also warrant consideration. Addressing this multitude of components typically requires a suitable multi-methods approach to fully understand population dynamics. Together this knowledge on spatial ecology, particularly in an important fishery species such as *A. coronus*, will allow for better informed decisions around conservation and fisheries management to be made.

The central hypothesis on the movement ecology of *A. coronus* prior to this study was that juvenile and sub-adult fish adopted a largely sedentary lifestyle, while adult fish underwent a seasonal longshore migration (Figure 6.1). This was based on convergent findings of an absence of adults from the shore-based fishery in southern Angola during summer ('warm' period) and recaptures in Namibia during the same season, of fish tagged in southern Angola (Potts et al. 2010b). This migration was thought to track the ABFZ as it shifted southwards during summer ('warm' period) into northern Namibia and northwards into southern Angola during winter ('cold' period). The shifting of the ABFZ exposes the southern Angolan coastline to drastic seasonal water temperature changes in the range of ~10 °C between 'warm' and 'cold' periods. This study, however, showed that although this migration may occur, it is likely a small proportion of the population that participates as the tagged individuals remained largely resident to their tagging location over the two-year monitoring period. While all life stages

were largely resident, juveniles and sub-adults utilised a smaller area compared to adults (Chapter 3), in agreement with prior hypotheses (Figure 6.1).

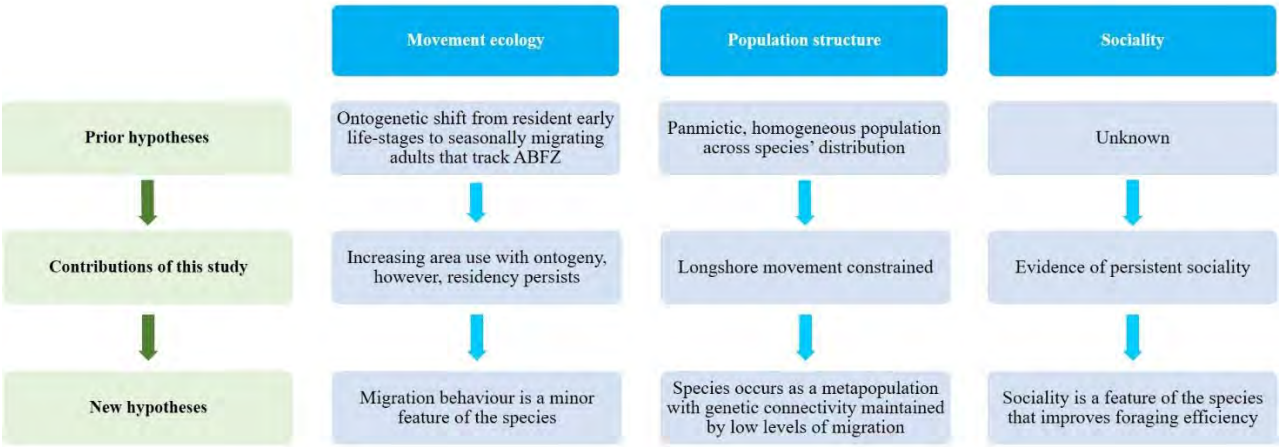


Figure 6.1: Contributions of this study to the knowledge of *A. coronus*.

This pattern of residency has implications for our understanding of the population dynamics of *A. coronus*. The species' primary distribution extends from its southern region in northern Namibia near to Cape Frio, northwards into southern Angola south of Lucira, covering ~540 km of coastline (Potts et al. 2010b). Genetically the population has been found to be panmictic across this distribution (Henriques et al. 2018). If the residency patterns observed in this study are widely representative of the species across their distribution and over time, then metapopulation theory applies (Kritzer and Sale 2004) whereby *A. coronus* exists as several sub-populations throughout their distribution (Figure 6.1). Connectivity among sub-populations, which is a feature of a metapopulation (Kritzer and Sale 2004), is maintained and reflected in the population genetics (Henriques et al. 2018). This connectivity may be through low levels of mixing by adults, for which there is evidence from conventional tagging data (Potts et al. 2018), during spawning periods. Connectivity may also be maintained through passive dispersal and settling of pelagic eggs, larvae and early juveniles. In Chapter 3, it was crudely estimated that dispersal distance during the pelagic phase (eggs and larvae) of *A. coronus* may be as high as 726 km, based on developmental stage durations of South African *A. japonicus* and the prevailing current speed. This distance is greater than half of the length of the Angolan coastline (~1 300 km) and would make maintaining genetic connectivity across their distribution an inevitability. More detailed studies on the pelagic phase duration of *A. coronus* and dispersal modelling is suggested to better understand this dispersal potential. A

similar metapopulation structure has been suggested for *A. japonicus* in South Africa (Childs 2013). This *A. japonicus* population has a similar life history and is a geographically close congener to *A. coronus* (Potts et al. 2010b). Movement studies of *A. japonicus* in South Africa (acoustic telemetry) (Childs 2013) and Australia (conventional tagging and acoustic telemetry) (Taylor et al. 2006; Hughes et al. 2022) found high levels of residency as well as a lack of genetic structuring similar to the present study (Barnes et al. 2016; Mirimin et al. 2016). Residency has also been observed in several other sciaenids. A study in an estuarine system in Florida, USA, on three sciaenids, *S. ocellatus*, *P. cromis* and *C. nebulosus*, found a high degree of residency with monitored fish spending 67 – 95 % of their time within a 33 km^2 area (Reyier et al. 2020). In a study on *Sciaena umbra*, 76 % (13 out of 17) of fish spent > 90 % of time within a stretch of coastline ~ 3 km long (Brazo et al. 2021).

Despite the high dispersal potential of the species during its early life stages, the residency observed, at least in the studied sub-population, indicates that sub-adults and adults are able to fulfil their resource requirements predominantly in a relatively short stretch of coastline. Anecdotal evidence suggests that the Flamingo study site has an abundant supply of small pelagic fishes year-round (Potts WM pers. comm.), which are their primary prey source (Potts et al. 2010b). This supports the notion that their resource requirements are met without having to traverse long distances in search of food. Residency in other predatory fish has been linked with food resources. Tiger sharks *Galeocerdo cuvier* in the Galapagos Marine Reserve were found to have a much-contracted area use, compared with individuals occurring elsewhere (Acuña-Marrero et al. 2017). This was linked with the presence of nesting sites of a prey species, green turtle *Chelonia mydas* within the reserve. This abundant prey resource enabled these sharks to forage over greatly reduced distances. At an atoll in French Polynesia, a seasonal spawning congregation of grouper was found to enable the existence of an inverted trophic pyramid, supporting a large biomass of predatory sharks, above levels that would have been possible in the absence of this resource (Mourier et al. 2016). These examples illustrate the strong influence that an abundant food resource can have on the movement behaviour of their predators.

Sciaenids are typically well-adapted to dealing with environmental variability. The southern Angolan region is characterised by a highly variable oceanography, as the ABFZ cycles seasonally up and down the coastline, exposing the region to warm, clear water during ‘warm’ periods and cool, turbid water during ‘cold’ periods (Meeuwis and Lutjeharms 1990). While it

was initially hypothesised that *A. coronus* adults migrated with the movement of the front, this study showed that this was not the case. An increased offshore area use during 'warm' periods (beyond the reach of shore-based fishers) (Chapter 3) explained the lack of adults from the shore-based fishery that was previously observed (Potts et al. 2010b). The year-round presence of *A. coronus* in the region indicates that they are physiologically and behaviourally adapted to this dynamic environment. Resident sub-populations that are exposed to large seasonal environmental variability such as *A. coronus* must be able to deal with the associated physiological challenges. This residency may make them more vulnerable to changes in local environmental conditions. However, they are resilient in dealing with large seasonal fluctuations, at least in terms of water temperature, as they are able to tolerate a wide range of temperatures (Chapter 4), and possibly other environmental variability. The ability to deal with environmental variation has made the sciaenids generally successful in using estuaries, which are typically dynamic physico-chemical environments, where this environment occurs within their range (Alvarez-Borrego 2001; Catalán et al. 2006; Lamberth et al. 2008; Cowley et al. 2008). Other *Argyrosomus* spp. have also been observed modifying their area use in relation to seasonal water temperature changes. Adult *A. inodorus* in Namibia, based on conventional tagging data, was found to undertake annual spawning migrations linked with seasonal water temperature patterns, although a component of residency was also noted (Kirchner and Holtzhausen 2001). The distribution of *A. inodorus* in South Africa was found to respond to local oceanographic conditions (Griffiths 1997b). There, cooler water restricted their distribution closer inshore during summer, while the recession of cooler water offshore during winter enabled them to expand their range into deeper water, with no notable longshore movement observed (Griffiths 1997b).

Group formations in fishes serve various functions including reducing predation risk, increasing foraging efficiency and facilitating successful spawning. The literature on group formations in sciaenids focusses on those associated with spawning behaviours (Erisman et al. 2012; Lowerre-Barbieri et al. 2013; Tellechea 2019; Zarada et al. 2019). Spawning in *A. coronus* has been shown to be seasonal, occurring in November (end of 'cold' period/early 'warm' period delineated in this study) based on gonad development (Potts et al. 2010b). However, this study noted some level of group cohesion during all monitoring periods (Chapter 5) (Figure 6.1) and a more pronounced group formation during 'cold' periods (Chapter 3). While group formation in this broadcast spawning species is undoubtedly important during spawning periods, it does not account for the lasting groups that were noted outside of peak

spawning periods. During these periods, social cohesion likely facilitated improved foraging efficiency, particularly for small pelagic fish prey. Through this process, resources are more easily located by a group, and where shoaling prey is concerned, group foraging improves capture efficiency (Thiebault et al. 2016; Sutton et al. 2020). Indeed, group foraging behaviour by *A. coronus* has been observed on several occasions at the Flamingo study site, with groups seen chasing shoals of small pelagic fishes to the surface before darting through the shoal in concert in attempts to capture them (Potts WM pers. comm.).

In addition to the southern Angolan coastline experiencing drastic seasonal fluctuations in water temperature, due to the shifting ABFZ, it also occurs in a region classified as a climate change hotspot due to the rapid rate of sea water warming that is occurring here (Hobday and Pecl 2014). The findings from Chapter 3 showed that *A. coronus* are largely resident despite a seasonally dynamic environment. This may suggest that the species is able to tolerate a broad range of environmental conditions. A recent study, however, documented a distributional shift by *A. coronus* further south into Namibia (Potts et al. 2014b). These authors suggested that a decrease in the size of fish caught in southern Angola may indicate an intra-generational distribution shift by adult life stages, although it was acknowledged that the effects may be fishery-related. It was, however, advocated that the former was most likely. These acoustic telemetry results challenge this hypothesis, primarily because of the high degree of adult residency. Based on this, it is possible that the successful settlement of eggs and larvae increasingly further south may be the mechanism driving this environmentally-mediated range expansion. However, considering that individuals previously conventionally tagged at the Flamingo study site did move long distances south into Namibia, where they were recaptured during the 'warm' period (Potts unpublished data). This suggests that there is a possibility that a proportion of the sub-population does undertake migrations. As waters at the southern edge of the species' distribution-limit warm through climate change processes, these migrants, as well as individuals that are resident at the southern extent, may be able to extend the species' southern range. This is particularly true if these migrating individuals typically occur further offshore and were missed by the capture techniques used in this study, and hence were not monitored alongside the resident, inshore individuals. The present study did, however, use the same techniques during a similar time of year as the conventional tagging study that detected a migration, so it seems more probable that these migrants make up a very low proportion of the sub-population, and due to the small sample size of this study, none were included.

Regardless of the mechanism driving the distribution shift, the outcome has been the hybridisation of *A. coronus* and *A. inodorus* in the area of overlap of the two species (Potts et al. 2014b). If the warm water continues moving further south, *A. inodorus* (which is typically a cooler-water dwelling species compared to *A. coronus*) may be pushed into an ever-shrinking habitat, and under threat of extinction. Laboratory-based physiology experiments showed that *A. inodorus* are adapted to cooler waters with declining aerobic scope, indicative of physiological stress, in water temperature > 21 °C, while *A. coronus* are adapted to warmer waters with an increasing aerobic scope in water temperatures > 21 °C (Pringle et al. in review). However, the existence of the Lüderitz Upwelling Cell, which bounds the southern extent of this population of *A. inodorus* (Kirchner and Holtzhausen 2001) may offset the warming of the Namibian coastline in the region of the upwelling, through the constant influx of cold, upwelled water, maintaining a refuge with suitable water temperatures for the species.

Hybridisation in some instances results in 'hybrid vigour' whereby offspring demonstrate increased fitness relative to either parent lineage (Barton 2001; Birchler et al. 2006). If the hybrids can tolerate the rapidly warming temperatures beyond that of *A. inodorus*, it is possible that hybridisation may be a mechanism to retain at least part of the *A. inodorus* gene pool. If the hybrids are able to tolerate a wider range of temperatures than the parental species, then it is possible that both species may be replaced by hybrids. While this may seem detrimental as it would result in the loss of two currently distinct species, it may be advantageous as the hybrid would ensure the continuation of both lineages, in a form better adapted to the changing climate. Hybridisation between species does not always result in hybrid vigour, but may produce less fit hybrids, or hybrids with fitness similar to parental lineages (Barton 2001; Montanari et al. 2017). While investigations on the consequences of this hybridisation are still in their infancy, preliminary physiology investigations on the hybrids of *A. coronus* and *A. inodorus* have suggested that the hybrids outperform both parental lineages at warmer water temperatures (> 18 °C), based on their aerobic scope (Pringle et al. in review). If this hybrid vigour translates to increased fitness then the hybrids may replace these species, particularly in a warming environment.

Social behaviours facilitate organisms' responses, for example to the threat of predation or during foraging (Ward and Webster 2016). The resident nature of *A. coronus* perhaps facilitates the existence of sociality among individuals observed in this study (Chapter 5) (Figure 6.1). The nature of the sociality varied, with some pair-wise associations observed throughout the

monitoring period, while others were more fluid. This could be explained through individual variability in sociality (Jacoby et al. 2014), although it may also be an artefact of the small sample size and greater sociality of some tagged individuals with untagged individuals which were obviously undetected. Despite the relatively low sample size of the study, there was evidence that the species is gregarious in nature, with relatively high numbers of pair-wise associations for each individual. While sociality plays a role in foraging and reducing predation risk at the individual level, it has the ability to influence metapopulation structure. Using simulated data, Blanchard et al. (2021) found that sociability was predicted to reduce dispersal distance, as individuals were less likely to disperse from conspecifics, resulting in increased density of sub-populations. Reduced sociability was predicted to increase dispersal distance and reduce sub-population density.

Communication is acknowledged as an important component in social interactions and sciaenids are known for their ability to produce sound as a means of communication (Fine and Parmentier 2015). The evolution of this ability in sciaenids has occurred through adaptations to existing anatomy which initially produced involuntary sound but evolved to become a voluntary feature, a process known as exaptation (Parmentier et al. 2017). In the case of *A. coronus*, it is likely that social behaviour developed in an ancestral lineage, and an ability to communicate evolved to facilitate this through exaptation. The ability for non-visual communication would allow these fishes to maintain sociality beyond visually limiting environments, including turbid waters and at night or in depths beyond the photic zone (Parmentier and Fine 2016). In southern Angola, this may be particularly necessary during the cold periods, where the water from the Benguela Current is generally more turbid. The use of turbid environments has the advantage of reducing vulnerability to predation, particularly by visual predators. Habitat use by sciaenids does indicate that they favour turbid waters, and tend to be more active during crepuscular and nocturnal periods in clearer waters when vision would be less effective (Johnson and Funicelli 1991; Gannon 2003; Luczkovich et al. 2008; Horodysky et al. 2008; Næsje et al. 2012).

Several results from this study are relevant to the management of *A. coronus*. From a fisheries perspective, although sciaenids are a popular target globally, their populations are susceptible to exploitation (Cisneros-Mata et al. 1995; Griffiths 1997c; Holtzhausen et al. 2001; Sadovy and Cheung 2003; Silberschneider et al. 2009; Ferrer Montaño and Morales 2013; dos Santos and Velasco 2021). An incidental finding of the present study was the extremely high

vulnerability of *A. coronus* to capture in the local fisheries. Of the first batch of 20 tags deployed, four (20%) were returned to the author by fishers within seven months of deployment, indicating that those fish were harvested. An additional two reports were received of tagged fish being captured (a total of six recaptures from 33 tag deployments – 18% recapture rate for the study); however, their tags were never retrieved from the fishers due to logistical/communication challenges. Three of the fish from which tags were returned were sub-adults (760 – 850 mm TL) and one was an early adult (950 mm TL) at the time of tagging. High recapture rates have been reported in other *Argyrosomus* telemetry studies. Juvenile *A. japonicus* in acoustic telemetry studies in South Africa experienced very high recapture rates (between 20 and 41 %) (Cowley et al. 2008; Childs et al. 2015). In a study on juvenile and sub-adult *A. japonicus* in southern Australia, a recapture rate of 54 % was reported (Lieschke 2019). Together, these findings suggest that smaller, and hence younger, *A. coronus* are more vulnerable to local fisheries, and raises concern for the possibility of growth overfishing. This phenomenon has been linked with the population depletion of *A. japonicus* in South Africa (Griffiths 1997c). Like other large sciaenids, the trends in CPUE (Potts et al. 2014b) and population-status evaluation (Beckensteiner et al. 2016) have provided evidence for a population decline, and certainly the evidence from this study suggests that this decline may largely be attributed to exploitation.

Fisheries management needs to consider various ecological, social and economic factors in developing management strategies. The objectives of fisheries managers themselves may be addressed using various approaches. From the perspective of the fish stock, fisheries management primarily considers biomass conservation, while genetic (Benestan 2019) and behavioural diversity (Conrad et al. 2011; Bergseth et al. 2016) have largely been ignored, but are increasingly acknowledged as important considerations for conservation. Fisheries impacts on fished populations are managed through output and input controls. Output controls are measures that directly limit the quantity of fish harvested by a fishery and include various types of catch limits (to limit the total harvest) and size limits (to reduce the harvest of vulnerable life stages) (Liu et al. 2016). Input controls are imposed to restrict how the fishery operates, thereby indirectly influencing the quantity and demographics of the fish that are harvested. These include limiting the amount of effort in a fishery (Anderson et al. 2019) and limiting the types and quantities of gear and vessels in use (Liu et al. 2016). Spatial management measures may be used to permanently protect designated areas of importance for target species, in the form of marine protected areas (MPAs), or to seasonally protect vulnerable behaviours such as

spawning congregations (Holland 2003), or vary access rights and the distribution of effort across a managed area (Rassweiler et al. 2012). For such measures to be effective, the spatial ecology of a species as well as the threats it faces are critical areas of knowledge.

Three classes of fisheries account for the majority of the catch of *A. coronus* in southern Angola (Potts et al. 2010b). Two of these are the subsistence and artisanal fisheries – both being critical livelihood-sustaining fisheries in an area with little economic alternatives (Sowman and Cardoso 2010). The third class is the recreational fishery. This fishery is typically enjoyed by wealthier fishers, a large proportion of whom are foreign visitors (Potts et al. 2009). Management measures should consider these fisheries in terms of the livelihood support that they provide. While restricting catch in the artisanal and subsistence fisheries may have drastic impacts on those relying on the resource, doing so in the recreational fishery may have very little, if any, negative effects on the fishery or on its attractiveness as an angling destination to foreign tourists. Priority aspects of the population that warrant management consideration include reduced population levels, high levels of capture of immature fish and the conservation of genetics, particularly in light of the hybridisation observed in this species (Potts et al. 2014b).

Current evidence suggests that *A. coronus* exists as a genetically mixed population (Henriques et al. 2018), while information from this study (see Chapter 3) (Figure 6.1) supports the hypothesis that the species occurs as a metapopulation comprised of a number of sub-populations whose adults are primarily resident. The lack of geographic genetic divergence simplifies conservation considerations, as the single gene pool precludes the necessity for genetic-unit based management efforts. There are currently no management measures in place for the species in Angola, and existing measures in Namibia are directed at the smaller and earlier maturing *A. inodorus* and are thus ineffective for *A. coronus* (Potts et al. 2010b). In the south of Angola, 20 km north of the Namibian border extending 125 km northwards, just inland from the shore, lies the Iona National Park. This park greatly reduces coastal access to people, keeps human population density in the area low, and therefore fishing effort low. The northern region of Namibia also falls inside the Skeleton Coast National Park, where shore-based fishing is greatly restricted. Together, these parks already provide some refuge to this species. Reducing ease of access to fishing grounds, whether intentionally or not, is an effective way to reduce fishing effort with benefits to targeted fish stocks. A beach driving ban in South Africa was found to have unintended positive consequences for shore-based fishery species after only

ten years (Mann et al. 2016). This without banning fishing in these areas but simply by making it more difficult to access them as anglers would have to walk long distances to reach them.

As a management measure, MPAs are only effective if the target species remains in the protected area for a large proportion of time. The spatial dynamics of *A. coronus* most closely resembles the "movement within a home range" area use category defined by (Grüss et al. 2011), so a targeted MPA may be an effective measure in protecting a proportion of the metapopulation from fishing. Alternative spatial management approaches to protecting fished populations include protecting vulnerable stages such as spawning, when there is a high concentration of spawner biomass (Grüss et al. 2011), with spawning congregations being a common behaviour of sciaenids (Johnson and Funicelli 1991; Luczkovich et al. 2008; Lowerre-Barbieri et al. 2013; Tellechea 2019). This could either be done through spatial fishery exclusions, referred to as "targeted MPAs", if the spawning area(s) can be identified and clearly bounded and if they are consistent over time (Grüss et al. 2011), or it could be done through temporal fishery closures over the spawning period. These measures would help to ensure a continued existence of sufficient spawner biomass to maintain the population.

Considering the vulnerable nature of the subsistence and artisanal fishers in the region, it would be logical to mitigate the impacts of the recreational fishery on *A. coronus* first. A simple management measure that would not have negative consequences for the vulnerable fishers and which would relatively easily increase protection of the species from the current state, would be to designate the area currently used largely by the tourist-based recreational shore-based fishery along the Flamingo coastline, as a strictly catch-and-release zone. This predominantly international tourist-based fishery has great economic value for the region (Potts et al. 2009). Reducing the impact of this fishery on its target species would also benefit the fishery itself, through maintaining healthy fish populations and likely allowing fish to reach bigger sizes, which are favoured by anglers. This measure would be a good first management step, as it does not threaten livelihoods of local fishing communities, who are already largely impoverished, and could improve the catches in the subsistence and artisanal fishery in the region as well as in the recreational fishery itself. This recreational fishery should be viewed in the context of the local social, ecological and economic context (Arlinghaus et al. 2017). Efforts that optimise the economic benefits of the fishery directly to the local human population, by adopting strategies that minimise economic leakage out of the local economy,

may grow support for measures that maintain healthy fish stocks and sustain this fishery (Butler et al. 2020).

The risk of growth overfishing of *A. coronus* is one that should be carefully managed. With younger fish seemingly more vulnerable to capture in the fisheries, a consideration for management would be the setting of a minimum size limit of 870 mm (length-at-50% maturity) to provide juveniles and sub-adults with increased protection from overfishing before being able to spawn, and reduce the risk of growth overfishing. An alternative may be to introduce fishing exclusion zones in areas where the catch predominantly comprises juveniles and sub-adults, for example adjacent to the Cunene River mouth (Potts et al. 2010b). While these may be tough measures in the short term to implement for those whose livelihoods depend on the resource, in the long term a sustained resource and improved catches would be advantageous to all stakeholders.

The hybridisation that is occurring between *A. coronus* and *A. inodorus* (Potts et al. 2014b) is an imminent risk to both species and should be carefully monitored, both in terms of the spread of hybrids further north, and in terms of the biology and ecology of the hybrids. As a mitigation measure, prioritisation of protection of *A. coronus* further north beyond the current hybrid zone should be considered. Monitoring of the northern limit of these hybrids, through frequent genetic testing of fish captured immediately north of their current northern distribution, should be a priority to inform best management practices. This would provide an early warning of any northward expansion of the hybrid zone and enable management to react accordingly.

Further to biomass preservation, fisheries management measures should prioritise additional conservation objectives. These may include genetic diversity, particularly with the aim of maintaining resilience to climate change; complex sociality, for example in reproductive biology as seen in harem-forming hermaphrodites; and other social behaviours such as foraging. Social foraging, which may be a strategy utilised by *A. coronus*, could be hampered by removing individuals through fishing as the behaviour may rely on a critical group size to be effective. Several management objectives can be addressed simultaneously by closing certain areas of the coastline to fishing, including the preservation of genetic diversity and resilience, and behavioural complexity (von der Heyden 2009; Bergseth et al. 2016). Utilising MPAs as part of a management strategy would be prudent to mitigate the risk that such behaviours are interrupted.

Following on from this study, there are a few avenues that warrant further exploration. The metapopulation hypothesis could be further tested using acoustic telemetry, by tagging several batches of *A. coronus* along a longer stretch of coastline, with batches of arrays similar to that used at the Flamingo study site, deployed at the tagging areas. This would indicate the replicability of the observations in this study, in terms of area use, by multiple batches along the coast, perhaps representing multiple sub-populations. Additionally, effort should be focussed on tagging fish caught further offshore to investigate the possibility of there being an offshore contingent that may be segregated from the inshore oriented fish sampled in the present study. A concurrent study to the present one, on *Lichia amia* in southern Angola, identified the existence of at least two contingents – one of which underwent an annual, southerly migration in summer ('warm' period), returning to the Flamingo study site during winter ('cold' period) (Winkler 2018). The restriction of tagging effort on *A. coronus* to the inshore, and during relatively constricted periods during the 'cold' period, may mean that any potential spatial segregation would not have been detected.

The sociality component in *A. coronus* could also be more deeply interrogated. Continuing with a passive telemetry approach, a denser network of acoustic receivers and using low-power transmitters (this study used high-power transmitters) would facilitate fine-scale positioning of individuals to confirm whether they are co-located or simply have similarly positioned core areas. An active telemetry approach could also be adopted to get even finer-scale positions of tagged animals; however, this approach is limited in the number of tags that can be monitored concurrently, both technologically as the number of frequencies is limited, and logistically in terms of the ability to track multiple fish.

Spawning behaviours in the majority of sciaenids remain poorly understood, despite the typically high levels of exploitation of species belonging to this family. Environmental acoustic monitoring, either using passively-moored hydrophones or boat-based mobile hydrophones, has been successfully used in locating spawning sciaenids, as they tend to use acoustic communication during these periods and form large congregations (Johnson and Funicelli 1991; Luczkovich et al. 2008; Lowerre-Barbieri et al. 2013; Tellechea 2019). As their eggs tend to be floating, they can be easily collected at the water's surface to confirm a spawning event (Johnson and Funicelli 1991). Locating and protecting spawning areas would be an effective conservation measure for the species at a vulnerable time, as concentrations of very large fish in a small area are an appealing target of any fishery.

It is prudent to note caveats of any study, and ideas for improvement that are generated after conducting a study. A common challenge in acoustic telemetry studies is small sample sizes of tagged animals, due largely to the costly nature of acoustic transmitters, and oftentimes constrained research budgets particularly in developing countries. Efforts should always be made to have effective sample sizes in acoustic telemetry studies. Despite the small sample sizes in this study, valuable insights have still been gained. This study collected a very low number of detections from juveniles and smaller sub-adults, typically over a very restricted area. At the onset of this study it was hypothesised that juveniles and small sub-adults utilised small areas. In such a case, smaller 'sub-arrays' should be considered, within the larger array. This sub-array should increase the density of receivers at the tagging site(s), to monitor small-scale movements or account for a lack of movements by tagged fish. The larger array would account for movements outside of this sub-array. While the possibility cannot be ruled out that these smaller fish were removed from the study site by fishers or predators, the four juveniles and one small sub-adult that were detected over a period > 100 days (range: 128-300 days) only logged between 9 and 1417 detections. Mortality from the tagging procedure also cannot be excluded, particularly in two fish that were never detected, but this was unlikely in the remaining fish as they were detected for at least 16 days post-release.

This study contributes significant knowledge on the movement ecology of *A. coronus*. It challenges the hypothesis that the species is migratory in nature, shifting with the annual movement of the ABFZ, and shows them to rather be a largely resident species. This modifies the way that the population structure is viewed. The species likely occurs as a metapopulation, consisting of localised, resident sub-populations. While the species has been found to be panmictic across its distribution, this is likely maintained through low levels of connectivity which is achieved either through genetic contributions during spawning periods, or through passive dispersal during the early pelagic life stages, or a combination of these two mechanisms. The high levels of residency will make sub-populations vulnerable to overexploitation and environmental stressors, but also increases the likelihood of spatial management measures being effective. While conserving this top predator is important from an ecological perspective, it is also of value to several livelihood-sustaining fisheries, in an impoverished region. Although this study highlights the value of acoustic telemetry in studying movement ecology, it also shows the importance of drawing on multiple methods to fully understand a species' spatial ecology, including conventional tagging, genetics, and fishery catch and effort data. Sound knowledge of a species' spatial ecology facilitates efforts for

managing fished populations and mitigating the interactive risks imposed by climate change on fished populations.

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Appendix

Table A1: Summary of detection data of tagged fish for juveniles (< 600 mm), sub-adults (600–870 mm) and adults (>870 mm) during the 'cold' and 'warm' periods throughout the study.

	Cold 2013			Warm 2013-14			Cold 2014			Warm 2014-15		
	Flamingo	**Tombua Bay**	**Baia dos Tigres**	**Flamingo**	**Tombua Bay**	**Baia dos Tigres**	**Flamingo**	**Tombua Bay**	**Baia dos Tigres**	**Flamingo**	**Tombua Bay**	**Baia dos Tigres**
Number of fish tagged												
Juveniles	-	-	-	-	-	-	7	-	-	-	-	-
Sub-adults	3						3					
Adults	17						2*					
Number of tag returns												
Juveniles	-	-	-	-	-	-	0	0	0	0	0	0
Sub-adults	2	0	0	0	0	0	0	0	0	0	0	0
Adults	0	0	0	1	0	0	0	0	0	0	0	0
Number of fish detected												
Juveniles	-	-	-	-	-	-	6	0	0	3	0	0
Sub-adults	3	0	0	1	0	0	3	0	0	2	0	0
Adults	16	2	0	15	1	0	16	0	0	15	3	0
Number of days at least 1 fish detected												
Juveniles	-	-	-	-	-	-	110	0	0	25	0	0
Sub-adults	91	0	0	59	0	0	82	0	0	38	0	0
Adults	100	2	0	151	3	0	153	0	0	212	36	0
(number of monitoring days)	(100)	(100)	(100)	(151)	(151)	(151)	(153)	(153)	(153)	(212)	(212)	(212)

Average ± SD number of receivers each fish detected by												
Juveniles	-	-	-	-	-	-	3.2 ± 2.6	0	0	2.7 ± 1.5	0	0
Sub-adults	9.3 ± 4.2	0	0	6 ± 0	0	0	2.3 ± 0.6	0	0	3.5 ± 0.7	0	0
Adults	5.9 ± 4.4	1 ± 0	0	9.1±5.4	4 ± 0	0	5.6 ± 3.9	0	0	13.4 ± 4.8	3.7 ± 0.6	0
(number of receivers at site)	(19)	(4)	(16)	(19)	(4)	(16)	(19)	(4)	(16)	(19)	(4)	(16)
Number of days each fish detected (median; min-max)												
Juveniles	-	-	-	-	-	-	12; 0–96	0	-	0; 0–19	0	-
Sub-adults	43; 40–49	0	0	29.5; 0–59	0	0	25; 0–60	0	0	0; 0–27	0	0
Adults	56.5; 6–97	1; 11	0	60.5; 1–143	3; 3–3	0	71; 0–153	0	0	88; 0–170	3; 2–31	0
(number of monitoring days)	(100)	(100)	(100)	(151)	(151)	(151)	(153)	(153)	(153)	(212)	(212)	(212)
Longshore displacement at Flamingo (Median; min-max km)												
Juveniles	-	-	-	-	-	-	0; 0–10.5	NA	NA	2; 0–3.1	NA	NA
Sub-adults	13.7; 11.6–23.5	NA	NA	13.2; 2.9–23.5	NA	NA	2; 0–4.7	NA	NA	2;2–2	NA	NA
Adults	5.3; 0–43	NA	NA	11.7; 3.1–23.5	NA	NA	5.3; 0–23.5	NA	NA	23.5; 2.9–23.5	NA	NA
Zeroes indicate detections at a single line.												

*: tags reused after previously tagged fish had been captured