Reproductive behaviours, drivers of activity, and effects of wildlife tourism on yellowtail kingfish (*Seriola lalandi*) in southern Australia

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By

Thomas Michael Clarke

(BSc. Mar Biol, Hons)

Thesis

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CONTENTS

THESIS SUMMARY

Understanding the behaviours and physiology of free-ranging animals, and the ecological processes driving them is a fundamental goal of studies in ecology. However, insights into these behaviours and responses to human impacts are poorly understood for large-bodied pelagic fish, despite these species being ecologically and economically important. Yellowtail kingfish (*Seriola lalandi*, family Carangidae) can be used as a model species to develop techniques to identify ecologically-important behaviours and the effects of anthropogenic pressures on the movements and physiology of large pelagic fishes. This thesis aimed to examine kingfish spawning behaviours, impacts of wildlife tourism, and drivers of activity in southern Australia.

Accelerometers and a machine learning model were used to describe behavioural classes of captive kingfish based on 624 hours of accelerometer data paired with visual observations. The model was subsequently used to predict behaviours from eight free-ranging kingfish to identify naturally-occurring reproductive behaviours (Chapter 2). Paired with environmental information and geographic location, my results show that accelerometers and machine learning provide an opportunity to identify spawning aggregations, and advise the implementation of spatial management efforts of large pelagic fish, when required.

The effects of feeding during white shark cage-diving tourism on kingfish residency and space use (Chapter 3), along with activity and physiological status (Chapter 4) were assessed through acoustic tags fitted with accelerometer sensors over two years. Kingfish were residential to the cage-diving site, with individuals detected up to 79% of days. Daily time spent at the site increased by ~27% when operators were present, and individuals were 62% closer to food-based compared to acoustic-attractants. Kingfish activity and burst events also increased during operations, by 18% and 60% respectively. However, I found that physiological condition of kingfish at the tourism site (measured using bioelectrical impedance analysis) was similar to individuals from eastern Australia that were not exposed to wildlife tourism (*n* = 113). Therefore, behavioural changes from tourism-interactions did not reflect a decrease in physiological status, suggesting that consumption of food-based attractant may be compensating for raised energetic expenditure.

A national network of acoustic-tracking receivers was used to identify environmental drivers of activity from 65 kingfish throughout south-eastern Australia (Chapter 5). Generalised Linear Mixed Models revealed that activity increased with temperature and was inversely correlated with moon illumination, with variable responses to tide height and time of day. Additionally, I demonstrated that continental-scale acoustic networks can be used to not only identify large-scale movements of individuals, but also evaluate activity over long-term and large-scale datasets.

Overall, kingfish provided a model species to showcase the power of multiple electronic tags to reveal important behaviours and environmental drivers of large pelagic fish energetics. My results make an original contribution by identifying the reproductive behaviours and describing the movements of kingfish in southern Australia, and by developing widely-applicable techniques suitable across large pelagic fishes globally. In a time of shifting and unstable marine climates, and human-induced pressures, identifying drivers of movements and activity of large pelagic fish is essential to detect shifts and to employ effective and adaptable management strategies.

DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Signed..

Date: 17/09/2021

AUTHOR CONTRIBUTIONS, PERMITS AND FUNDING

The following outlines the author contributions and acknowledgements for each chapter:

Chapter 2

T Clarke, S Whitmarsh and C Huveneers were involved in the conception and design of the research. **T Clarke** was responsible for data collection, analysis, and interpretation of the research data. S Whitmarsh and C Huveneers contributed to data collection and earlier drafting of the manuscript. J Hounslow, A Gleiss and N Payne aided with analysis and significantly contributed to revisioning drafts of the manuscript.

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I thank staff from Cleanseas Aquaculture Hatchery, Arno Bay, who assisted with captive kingfish trials. Volunteers from the Southern Shark Ecology Group at Flinders University assisted in capture and tagging of free-ranging kingfish at the Neptune Islands. The white shark tourism operators: Rodney Fox Shark Expeditions, Calypso Star Charters, and Adventure Bay Charters staff and crew provided ongoing support and in-kind contributions, facilitating field work at the Neptune Islands. Commercial scale fishers assisted with the capture and tagging of kingfish in Coffin Bay.

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T Clarke, S Whitmarsh, and C Huveneers were involved with the conception and design of the research, and acquisition of field data. **T Clarke** was responsible for analysis and interpretation of research data. R Dwyer, V Udyawer and H Pederson substantially aided to the analysis and interpretation of the data. All authors were involved in drafting and revising drafts of the chapter.

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OTHER PAPERS OR CONTRIBUTIONS

I was also able to contribute to all of the following papers during my thesis period:

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Chapter 1

General Introduction

1.1 Movement and behavioural ecology: Connections between animals and the environment

Animal movements occur across multiple scales and can influence the density of individuals and populations, regulate community and ecosystem structure, and influence evolutionary processes and patterns of biodiversity (Dickinson et al. 2000, Nathan 2008). Species' movements can be directly influenced by a variety of environmental factors, which are often related to reproductive behaviours or resource needs (Harrington & Taylor 1990, Skov et al. 2013), e.g., acquisition of food (Shivik et al. 1996, McIntyre & Wiens 1999, Marable et al. 2012), predation avoidance (Hoey & McCormick 2004, Hammerschlag et al. 2017), and mating opportunities (Chapman et al. 2012, Espinoza et al. 2016, Robertson et al. 2018). Consequently, the movements of animals are a fundamental aspect of ecological and evolutionary processes, with the study of the size and use of core areas (i.e. home range size, habitat association; McNab 1963, Börger et al. 2006) and extent of movements (residency versus distant migrations; Simpfendorfer et al. 2002, Pedersen et al. 2011) revealing important information of how animals interact with their surrounding environment (Nathan 2008, Hussey et al. 2015). An understanding of animal movements and of factors influencing them, can therefore contribute crucial knowledge of a species ecology, as these behaviours account for large portions of energetic budgets, and underpin critical components of behavioural characteristics and processes, e.g., feeding and reproduction.

Estimating the rates at which free-ranging animals expend energy is also essential to basic and applied ecology, and to understand how individuals physiological responses are influenced by natural (Briggs & Post 1997, Payne et al. 2013, Watanabe et al. 2019) and human-induced effects (Christiansen et al. 2013, Barnett et al. 2016, Huveneers et al. 2018). The energetic cost associated with behaviours innately influences individual fitness, measured via survival, growth, and reproductive success (Brown et al. 2004, Cooke et al. 2004a), and so provides critical information to understand ecological processes (Cooke et al. 2004a). The study of animal behaviours and activity in relation to ecological and environmental constraints (i.e., behavioural ecology; Danchin et al. 2008, Davies et al. 2012), is often investigated in parallel to movement ecology when attempting to characterise a species' movement strategies and physiological responses in the context of its surrounding environment. Given that the movements and behaviours of animals are so intrinsically linked to fitness of individuals and populations, there is a need to identify and study ecologically-important behaviours and energetic strategies to infer responses to biotic and abiotic factors in nature.

Impacts from human activities on natural ecosystems have become so pervasive that the current epoch of immense human influence has come to be known as the Anthropocene (Crutzen 2006, Lewis & Maslin 2015). Anthropogenic stressors have been identified across almost every ecosystem, with putative impacts on the functional diversity of organisms (e.g., terrestrial vertebrates and invertebrates; Dirzo et al. 2014, coral reefs; Woodhead et al. 2019, marine megafauna; Pimiento et al.

2020), dramatic changes in biogeography (Worm & Tittensor 2011, Darling & Carlton 2018, Tucker et al. 2018), and a need to revise conservation targets in the face of climate change (Hannah et al. 2002, Rilov et al. 2020). Yet, while there is strong evidence of anthropogenic stress, identifying and quantifying causative human impacts with the intention of developing appropriate intervention strategies is extremely difficult given the almost overwhelming pace at which change is occurring (Halpern et al. 2008, Hobday & Lough 2011, Schimel et al. 2013, but see:, Nabe-Nielsen et al. 2018). One of the greatest challenges affecting animal movements, is the increasing level of human impacts on ecosystems, which drives ecological change and has the potential to lead to widespread disruptions of animal movement and behavioural ecology (Halpern et al. 2008, Doherty et al. 2021). For example, changes as a result of anthropogenic impacts can create physical barriers that reduce the organisms movements and contract movement ranges (Worm & Tittensor 2011, Tucker et al. 2018), reduce prey abundance leading to increased foraging efforts (Graham et al. 2005), or disturb natural conditions that leads to changed behaviour, therefore reducing foraging performance and fitness (DeRuiter et al. 2013, Francis & Barber 2013). Identifying the factors that contribute to an animal's movement and behaviour is important for predicting change and prioritising effective management or conservation strategies for ecological communities under threat (e.g., Hobday et al. 2011, Doherty & Driscoll 2018, Katzner & Arlettaz 2019). For instance, movement data from animal tracking studies have been used to predict overlap of terrestrial mammal migration routes with proposed oil and gas developments (Sawyer et al. 2009), manage interactions between modelled avian movements with human recreational activities and wind turbine locations (Braunisch et al. 2011, Perona et al. 2019), and modelled habitat preference of marine (Hobday et al. 2011) and freshwater fishes (Lamouroux et al. 1999) to inform spatial fisheries management decisions. The capacity to quantify and describe the movements of animals in the Anthropocene is therefore essential to strategies effective conservation and management and detecting changes in species ecology attributed to human impacts.

1.2 Large pelagic fishes in the Anthropocene

Pelagic ecosystems are highly dynamic environments, characterised by complex relationships between physical, chemical, and biological phenomena. Movements and behaviours of individuals within these ecosystems are therefore largely regulated by the interactions between environmental conditions, and physiological needs of species (Humston et al. 2000, Bakun 2006, Robinson et al. 2015). Large-bodied pelagic fishes are influential predators in pelagic ecosystems that have high ecological, economic, and social value (Hobday et al. 2009, Macfadyen et al. 2016, van Denderen et al. 2018). They are dominant predators which occupy upper positions in food webs, regulating lower trophic levels through direct and indirect interactions (Bornatowski et al. 2018, Roesti et al. 2020), in addition to playing an important role as prey for larger marine animals (e.g., Grainger et al. 2020). These interactions can influence the functioning within ecosystems (Kitchell et al. 2006, Baum & Worm 2009), and so the prevalence of large pelagic fish in these environments is crucial to the functioning and energy flow within pelagic food webs. In addition to their role as ecologically-important mesopredators, large pelagic fishes contribute substantial economic benefits through commercial and recreational fishing, and social significance to local coastal communities (Henry & Lyle 2003, Macfadyen et al. 2016). Large pelagic fishes are more profitable for fisheries than their smaller-bodied counterparts (Sethi et al. 2010), with financial contributions from global tuna fisheries alone contributing $42 billion annually (Macfadyen et al. 2016). However, despite their importance for the structuring of pelagic ecosystems and significant socio-economic value, stocks of many large pelagic species are declining, and have been the focal point of many concerns about sustainability and performance of management strategies (Ceo et al. 2012, Pons et al. 2018). Although, development of robust and adaptable management strategies has displayed the potential to promote recovery of overfished stocks of pelagic fishes (e.g., tuna and billfishes; Pons et al. 2017, Pons et al. 2018). This further emphasises the importance for knowledge about the movement and behavioural ecology of these species during the Anthropocene to prioritise effective conservation measures (Galland et al. 2018).

Movements of large pelagic fish are diverse and widespread across open ocean and coastal environments, with the capacity to occur over large spatial scales (hundreds to thousands of kilometres; Gillanders et al. 2001, Galuardi et al. 2010, Hobday et al. 2016). The high mobility of these species throughout pelagic habitats and association with coastline environments often results in high levels of spatial overlap with human interactions, resulting in increasing pressures from anthropogenic effects (Halpern et al. 2008, Petrik et al. 2020). Impacts from these interactions can be either direct, through exploitation via fishing pressures leading to species being categorised as overfished or unsustainable (Pauly & Watson 2003, Ceo et al. 2012), or indirect impacts leading to alterations in range and space use via decreased mobility and dispersal, or changes to habitat preferences (Worm & Tittensor 2011, Champion et al. 2018, Pecl et al. 2019). While research has aimed to address pressures on economically-important species (e.g., tuna, billfishes, sharks) due to ongoing and increasing fishing pressures (Crossin et al. 2017, Pons et al. 2018), and climate change (Robinson et al. 2015, Petrik et al. 2020), there has been comparatively less focus into human-induced drivers of movement on less frequently targeted pelagic species (e.g., carangids, mackerel) due to changing environmental conditions.

With reproductive behaviour being one of the key animal behaviours driving population dynamics, spawning events also influence the fitness and survival of large pelagic fishes (Rowe & Hutchings 2003, Bakun & Parrish 1991). Fertilisation success, transport of fertilised eggs and larvae, food availability, and suitable conditions for growth of offspring ultimately regulate the recruitment success of spawning events and the abundance of populations (Cury & Roy 1989). For example, reproductive behaviours of small pelagic species is reliant on spawning events in optimal conditions triggered by boundary currents and upwelling intensity (Roy et al. 1992, Brochier et al. 2013), or timing with tidal cycles (Foster 1987), whereas spawning events in unfavourable conditions potentially lead to poor larval growth and survival (Lasker 1981, Bergenius et al. 2002). This is particularly problematic in marine ecosystems that are under increasing pressures from shifting climatic conditions and associated alterations to environmental conditions. Yet, the patchy distribution, diversity of reproductive strategies, and extensive movements of large pelagic fishes, paired with logistical difficulties associated with working in the marine environment have made the study of naturally occurring spawning behaviours of many large pelagic species challenging (Costa 2015, Richardson et al. 2016). As a result, there is a need for effective, and efficient methods to predict geographic location and timing of spawning aggregations of large pelagic fish in the wild.

1.3 Tracking movements and behaviours of mobile fauna

Functional understandings about the movements and behaviours of free-ranging (i.e., wild) pelagic fishes and the factors driving them largely relies on the capacity to accurately track individuals as they move through the natural environment. Early studies of pelagic fish movements used mark-recapture approaches; where species are caught, tagged, and released so that they can be identified when recaptured later (e.g., Pepperell 1985, Schaefer & Fable Jr 1994, Gillanders et al. 2001). The effectiveness of this method has continued to grow through collaborative efforts between recreational anglers, commercial fishing sectors, and researchers, by means of engagement in cooperative tagging programs which increase spatial scale and sampling efforts (e.g., Pepperell 1985, Saul & Holdsworth 1992, Begg et al. 1997, Gunn & Block 2001, Block 2005, Hutson et al. 2007). While these studies provide coarse estimates of movement patterns and distribution, they are limited to only providing knowledge of tagging location and recapture site, failing to account for movements and behaviours between captures. Since the early 1990s, electronic tagging has emerged as a more effective technique to remotely monitor the detailed movements, behaviours, and physiology of marine animals as they move freely through the environment, and provide crucial information for management and policy makers (Cooke et al. 2004a, Crossin et al. 2017, Taylor et al. 2017).

Acoustic telemetry has advanced as a tool to remotely monitor the fine-scale habitat use and extent of species' movements (Hussey et al. 2015, Heupel et al. 2018). This method involves placing electronic transmitters (tags) on animals, that autonomously transmit data to logging or relay-receiver stations to identify the presence of an animal as it moves from one location to another (Arnold & Dewar 2001, Hussey et al. 2015). Early applications of acoustic tracking in the marine realm required researchers to follow the sounds emitted from tags using a directional hydrophone, with positions recorded regularly (e.g., every minute, hour) to represent the movement tracks of individuals (e.g., Holland et al. 1985, Block et al. 1992a, Morrissey & Gruber 1993). These studies led to more effective and efficient tracking of mobile marine fauna, revealing the potential to remotely monitor movements of animals as they move freely through the environment, however, were limited in temporal and spatial resolution as it was required that researchers actively tracked individuals near-continuously. In more recent years, technological advancements in battery engineering, and software and hardware development have enabled acoustic tracking to expand in applicability, through fixed, strategically-positioned acoustic receiver stations that passively monitor the movements of tagged animals without requiring researchers to actively track individuals (Brousseau et al. 2004, Egli & Babcock 2004). The incorporation of remotely-positioned receivers and collaborative tracking systems (e.g., Brodie et al. 2018, Hoenner et al. 2018, Lédée et al. 2021) has broadened the geographical and temporal extent of studies of marine animal movements, permitting characterisation of horizontal and vertical movements over broad spatial (meters to thousands of kilometres) and temporal scales (hours to several years) (Orbesen et al. 2008, Brodie et al. 2018). Additionally, long-term tracks of individuals movements can be combined with extensive environmental variables (e.g., temperature, depth, light levels) and reveal movements in response to changing conditions (Donaldson et al. 2014). Insights into movements collected via acoustic telemetry have resultingly contributed to design and management of marine protected areas around core ranges of movements, seasonal closures of fisheries, and assessing the impacts of fisheries management strategies (Crossin et al. 2017, Taylor et al. 2017). Movement information collected through acoustic telemetry therefore allows studies to accurately track the movement and distribution of animals in response to surrounding conditions and variables, and provides researchers with the ability to assess the implications on human interactions and environmental parameters on the movements of highly mobile large pelagic fishes.

In addition to tracking movement ecology of marine animals, electronic tags can be used to identify infrequent behaviours and interactions that occur at scales too small (spatially or temporally) to be detected through tracking methods such as acoustic telemetry. Tri-axial accelerometer loggers (accelerometers) can infer behaviours of unrestrained animals by measuring characteristics of acceleration and body position (e.g., Watanabe et al. 2008a, Moreau et al. 2009, Broell et al. 2012). The applicability of accelerometers to describe behaviours based on acceleration provides a novel opportunity to characterise naturally-occurring behaviours of large pelagic fishes, such as spawning events, which have previously been difficult to study and often require destructive sampling methods (e.g., euthanising and gonad removal; Yasuda et al. 2013) or direct observations (Sakaji et al. 2018). Additionally, advanced statistical software and programming capabilities has enabled researchers to model these complex datasets and use described behavioural profiles to remotely predict naturally-occurring behavioural classes in the wild (Carroll et al. 2014, Ladds et al. 2017). In addition to deducing the occurrence of ecologically-important behaviours, acceleration features collected through accelerometers provide a useful method to estimate energetic status of free-ranging animals, through the association of accelerations with oxygen consumption, and resulting metabolic rate (Wilson et al. 2006, Gleiss et al. 2011a, Murchie et al. 2011). Acceleration measured through these tools allows researchers to estimate field-based measures of metabolic rate and energy expenditure (Wilson et al. 2006, Murchie et al. 2011), and identify effects of environmental conditions (Whitney et al. 2007, Gleiss et al. 2011b, Payne et al. 2016), or anthropogenic stressors on energy budgets and resulting health and fitness of these individuals (Fitzpatrick et al. 2011, Barnett et al. 2016, Huveneers et al. 2018). Overall, different scales of electronic tagging can be combined to complement one another and identify and describe drivers of movements (telemetry), behaviours, and activity budgets (accelerometers). Together, these tools provide a unique opportunity to be used in unison and address the complex movement and behaviour ecology of large pelagic fishes, identify the timing and occurrence of important behavioural events, and help to identify consequences from human impacts on natural movements.

1.4 Wildlife tourism: An industry on the rise

The wildlife tourism industry is one form of human-animal interactions that is growing globally, steadily increasing in the number and diversity of operations and targeted species (Orams 2002, Trave et al. 2017). As a result, interacting with wildlife is one of the main drivers influencing travel decisions, particularly within Australia, where 43% of international visitors seek experiences through wildlife tourism (Ballantyne et al. 2009). Globally, estimates of participants are between 79 and 440 million (Moorhouse et al. 2015, Trave et al. 2017), with the industry expected to further double in the next 50 years (French et al. 2011, Trave et al. 2017, note: prior to COVID-19 crisis halting international travel). These operations contribute substantial economic benefits, accounting for 9% of global gross domestic product (Moorhouse et al. 2015), in addition to also supporting local businesses and infrastructure (Scheyvens 1999, Huveneers et al. 2017a). Wildlife tourism also supports conservation through preservation of natural resources by supporting the creation and maintenance of protected areas, financially contributing to governing organisations, and providing education opportunities (Higginbottom & Tribe 2004, Apps et al. 2018). Additionally, wildlife tourism can provide psychological benefits to participants (Muloin 1998, Curtin & Kragh 2014) through providing a unique opportunity to connect tourists with wildlife in a situation that otherwise would not be possible (Curtin & Kragh 2014).

The sustainability and success of wildlife tourism ventures are dependent on reliable and consistent encounters with animals. However, ensuring predictable and dependable interactions with wild animals for tourists can be challenging, and is exacerbated by many focal species being highly mobile, elusive, and vastly dispersed (Knight 2009, Gallagher & Huveneers 2018). Wildlife tourism operators therefore often use various forms of attractant to maximise the likelihood of reliable and up-close encounters for tourists (i.e., provisioning; Meyer et al. 2021b). Some of the attractants used do not involve direct feeding; e.g., minced fish or fish oil (also called berley or chum; Bruce & Bradford 2013, Clarke et al. 2013), bait inside a crate or box that cannot be accessed by the focal animals

(Dicken & Hosking 2009, Fitzpatrick et al. 2011), visual stimuli to attract natural prey sources and subsequently focal animals (Osada 2010, Needham et al. 2017), or auditory stimuli to mimic the vibrations of injured prey items (Rizzari et al. 2014). However, other types of wildlife tourism directly feed the focal animals to draw them closer to tourists (direct feeding, e.g., Samuels et al. 2000, Brookhouse et al. 2013, Pini-Fitzsimmons et al. 2018). Many studies have shown that provisioning from wildlife tourism can lead to short- and long-term impacts (Orams 2002, Higginbottom et al. 2003, Meyer et al. 2021a) by generating unnatural conditions, inherently altering the environmental and ecological cues that control natural feeding and movement patterns of animals. Direct feeding in particular has been shown to have various effects including on abundance and species composition (Clarke et al. 2013, Brunnschweiler et al. 2014, Whitmarsh 2019), site occupancy (Brookhouse et al. 2013, Bruce & Bradford 2013, Huveneers et al. 2013), swimming behaviours and movements (Laroche et al. 2007, Fitzpatrick et al. 2011, Pini-Fitzsimmons et al. 2018), and physiological responses (Barnett et al. 2016, Huveneers et al. 2018) of focal animals targeted by tourism, and is therefore an important concern for development of sustainable tourism management frameworks (Francis & Barber 2013, Meyer et al. 2021a).

Despite feeding being intended for focal species, indirect or unintentional feeding of non-focal (i.e., non-targeted) individuals can also occur (e.g., Laroche et al. 2007, Brena et al. 2015, Rizzari et al. 2017). In the terrestrial realm for example, non-focal species which are indirectly provisioned can consume up to 98% of food intended for game wildlife (Donalty et al. 2003, Inslerman 2006). While some of these operations have designed food-based attractant that is inaccessible to focal species (e.g., in a box; Dicken & Hosking 2009, Fitzpatrick et al. 2011) or withdrawn before feeding (Huveneers et al. 2017b, Meyer et al. 2020), non-focal species are often still able to access food sources meaning that feeding of these species might even be more ubiquitous than for focal species. As a result, effects of indirect feeding from wildlife tourism on non-focal species can mirror, and even exacerbate those effects on targeted individuals. For example, shark tourism using baits and berley has been shown alter dietary profiles (Meyer et al. 2021b), increase parasite infestation (Vignon et al. 2010), and change behaviour of movements (Milazzo et al. 2006, Rizzari et al. 2017) of non-target fish and ray species, as well as and changing community assemblages at tourism sites (Whitmarsh 2019). However despite the potential for negative implications from wildlife tourism on non-focal individuals, only 7% of studies assessing the effects of wildlife provisioning examined non-focal or ecosystem-wide effects (Trave et al. 2017). These interactions of wildlife provisioning with non-focal species are often not accounted for by tourism management frameworks and policies (Higginbottom et al. 2003, Gallagher & Huveneers 2018, Meyer et al. 2020) and could have implications on populations by disrupting important natural movements and ecosystem processes.

1.5 Study species and region

Yellowtail kingfish (*Seriola lalandi*, kingfish, Valenciennes 1833) is a large-bodied (up to 2.5 m, ~70 kg) pelagic carangid, distributed throughout temperate and sub-tropical waters of the southern hemisphere and northern Pacific (Gomon et al. 2008, Ben-Aderet 2018). Kingfish typically occur in large schools, especially around deep rocky reefs and seamounts (Hobday & Campbell 2009), offshore islands (Brookhouse et al. 2013), and adjacent sandy areas of coastal waters in depths of up to 300 m, but on some occasions entering shallower estuaries (Gomon et al. 2008, Brodie 2016). Due to their large size and fighting ability, kingfish have established a strong reputation among recreational anglers, in addition to contributing towards expanding finfish aquaculture industry with 4,000 t annual production with a market value of $60 million/year (Donohue et al. 2021). This industry is estimated to further increase to reach 5,000 tonnes of production by 2022 (Poortenaar et al. 2001, Symonds et al. 2014). Kingfish are seasonal, pelagic-broadcast spawners that are triggered by increasing water temperature expected to coincide with natural conditions between spring/summer months (Gillanders et al. 1999, Poortenaar et al. 2001, Moran et al. 2007). However, despite intensive research into optimal spawning conditions for kingfish in a captive environment for production purposes (Gillanders et al. 1999, Poortenaar et al. 2001, Moran et al. 2007), natural spawning behaviours and aggregations of kingfish in the free-ranging environment have not been identified, yet provide crucial information about the frequency, timing, and location for these events.

In Australia, kingfish are distributed across the southern coastline from Queensland to Western Australia and eastern Tasmania. Genetic analyses have revealed on large south-eastern population found from Queensland (QLD), New South Wales (NSW), Victoria (VIC), South Australia (SA), Tasmania (Tas) and New Zealand (Patterson & Swearer 2008, Miller et al. 2011, Green et al. 2020), which is genetically distinct from kingfish in Western Australia. As such, Australian kingfish stocks are categorised into two jurisdictions: Eastern (Commonwealth, NSW, QLD, SA, Tas and VIC) and Western Australian stocks (FRDC 2020). Despite catches of kingfish recorded across several states, the ‘Eastern Australian’ biological stock is assessed using data primarily from the NSW fishery, with most recent commercial catch estimates of 76 t in 2018–19 (FRDC 2020), compared to 2.89 t from the Western Australian jurisdiction. Recreational catch estimates are expected to exceed commercial catch, with Eastern Australian catch estimated at 129 t in 2017–18, and 7 t in Western Australia (Murphy et al. 2020). The persistence of kingfish along Australia’s south-eastern coast is driven by oceanographic condition regulated by temperature, with increased prevalance along the east coast during summer and Autumn months in response to shelf incursions from the East Australian Current (EAC; Brodie et al. 2015, Champion et al. 2018). Though, climate-driven shifts increasing the poleward extent of the EAC (Hobday & Lough 2011, O’Kane et al. 2011) are predicted to lead to a decline in temporal persistence of kingfish in northernmost areas of their eastern distribution, leading to southward shifts in the distribution along eastern Australia (Champion et al. 2018).

In spite of being a favoured target among seafood consumers , mark-recapture is popular among anglers targeting kingfish, accounting for 10% of all tagged fish in the cooperative New South Wales (NSW) Department of Fisheries Game Fish Tagging Programme since 1973, in addition to being the most abundantly recaptured species (34% of all recaptures, 8% recapture rate; Gillanders et al. 2001, Hutson et al. 2007). Movement data from these tags support previous descriptions of one distinct south-eastern population, with substantial long-range and bi-directional movements between SA and NSW ranging up to 1,500 km (Gillanders et al. 2001, Hughes & Stewart 2020), as well as between eastern Australia and New Zealand (Saul & Holdsworth 1992, Gillanders et al. 1999). These large-scale movements mostly occur in large individuals (> 1000 mm TL), however high levels of site-fidelity is also observed for both large and smaller individuals with a majority of recaptured fish occurring within 50 km of the original tagging location (Gillanders et al. 2001, Hutson et al. 2007, Hobday & Campbell 2009), in addition to individuals frequently recaptured at the same location as the original tagging even after 442 days at liberty (Gillanders et al. 2001). While tagging efforts from these cooperative tagging programs have revealed large-scale movements of kingfish, a majority of the information about kingfish movements is based on tag-and-recapture data with limited information about movements and activity between capture events, leaving detailed understanding of spawning aggregations and energetic strategies poorly understood (Baxter 1960, Pepperell 1985, Saul & Holdsworth 1992).

The Neptune Islands Group (Ron and Valarie Taylor Marine Park) in South Australia is a group of temperate offshore granite islands situated 60–70 km south-east of Port Lincoln (Figure 1.1a). The Neptune Islands are comprised of the North and South Island groups, situated ~12 km apart (Figure 1.1b), and accommodate breeding and feeding opportunities for many local and migratory sea birds (e.g., Osprey *Pandion haliaetus*, Cape Barren goose *Cereopsis novaehollandiae*), Australian sea lions (*Neophoca cinerea*) and long-nosed fur seals (*Arctocephalus forsteri*), as well as hosting diverse communities of fishes (Whitmarsh 2019, Figure 1.2b). The importance of the islands for such a diverse range of transient and residential taxa resulted in its inclusion in the South Australian Marine Parks program implemented in 2014, including a no-take sanctuary zone (North Neptune Islands), Habitat Protection Zone (South Neptune Islands), and Restricted Access Zones (North and South Neptune Islands; Figure 1.1b).

The Neptune Islands Group is additionally home to Australia's only white shark (*Carcharodon carcharias*) cage-diving tourism operation (Figure 1.2), where three operators run charters to the island groups with the objective of ensuring a close encounter for tourists with sharks. While operators are permitted to visit both North and South Neptune Islands, tourism mostly occurs at the North Neptune Islands (85% of operating days; C Huveneers unpublished data), where operators typically anchor in the bay on the south-eastern side of the islands, and on the northern side of the islands group (Figure 1.1c). At the South Neptune Islands, operators usually frequent the eastern side of the islands (Figure 1.1d). Two cage-diving operators use a near-constant plume of food-based attractant (chum; mixture of minced southern bluefin tuna *Thunnus maccoyii*) and tethered baits to entice sharks into the field of view of tourists (Huveneers & Lloyd 2017, Huveneers et al. 2017, Meyer et al. 2020b), while an additional third company uses acoustic stimuli (music played through underwater speakers) to attract sharks. The industry is regulated to reduce the prevalence of focal white sharks from being fed (DEW 2016), but non-focal kingfish are often observed in the chum plume behind food-based operators, feeding on smaller particles of bait and chum that enter the water (Figure 1.2). Even though white sharks are not intentionally fed, these operations have been found to influence the fine-scale activity and time spent of sharks (Bruce & Bradford 2013, Huveneers et al. 2013, Huveneers et al. 2018), and smooth stingrays (*Bathytoshia brevicaudata*; Rizzari et al. 2018), as well as changes in the dietary composition and abundance of several pelagic and demersal fish species (Whitmarsh 2019, Meyer et al. 2020). While it has been revealed that these operations have the potential to influence the dietary profiles of non-focal fish species, it is unknown whether these practices may have additional implications on natural behaviours and movements of these individuals as has been observed from larger rays and sharks. Cage-diving at the Neptune Islands has the potential to alter the movement ecology of kingfish by impeding the environmental cues that trigger natural movements and behaviours, and may have implications for the health and fitness of individuals and at a population level.

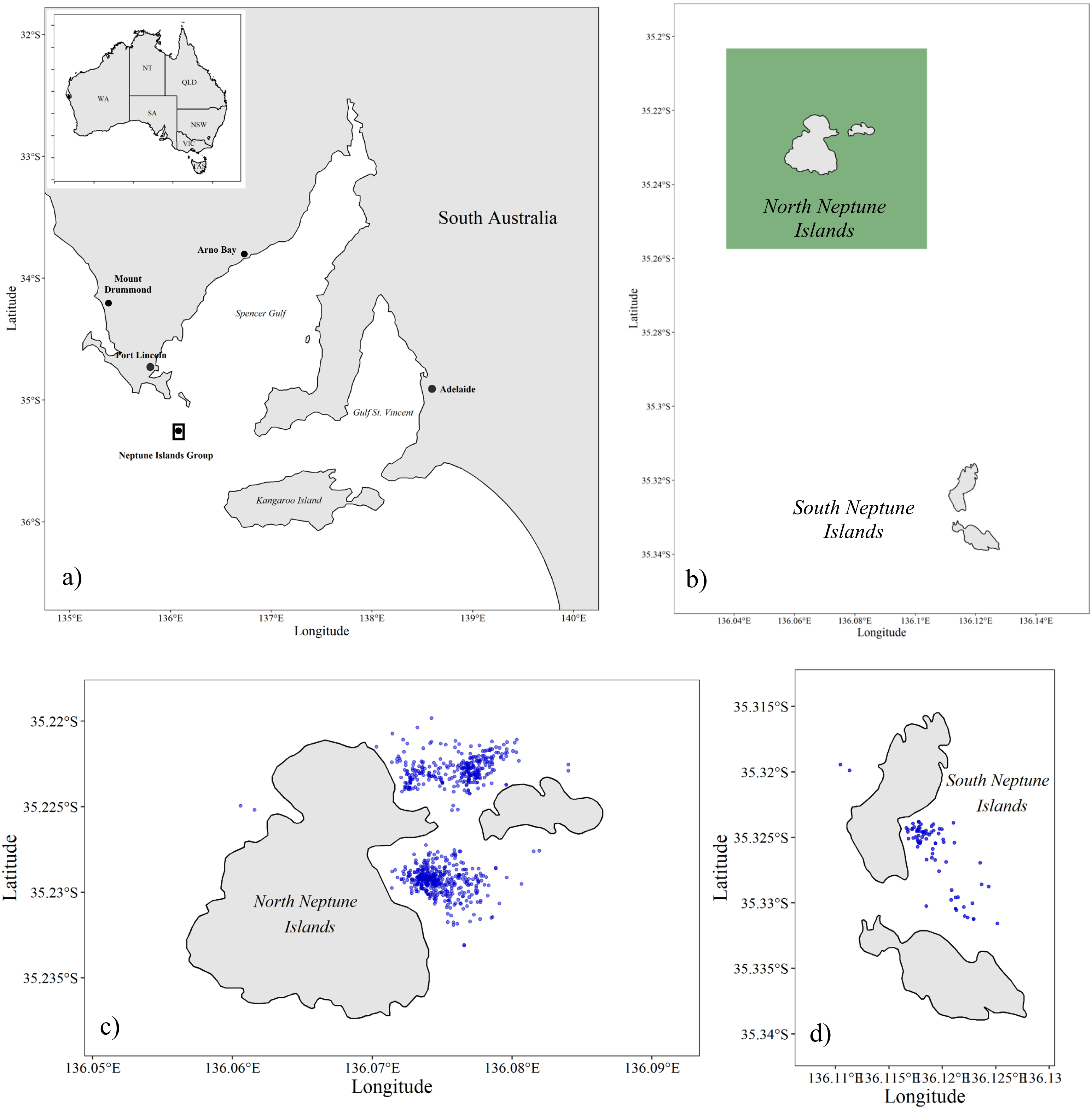


Figure 1.1. Location of the a) Neptune Islands Group within South Australia, b) Sanctuary Zone boundaries (green), and locations of cage-diving anchorages (blue) at the North (c) and South (d) Neptune Islands Groups between August 2018 – August 2020. Source: https://www.marineparks.sa.gov.au

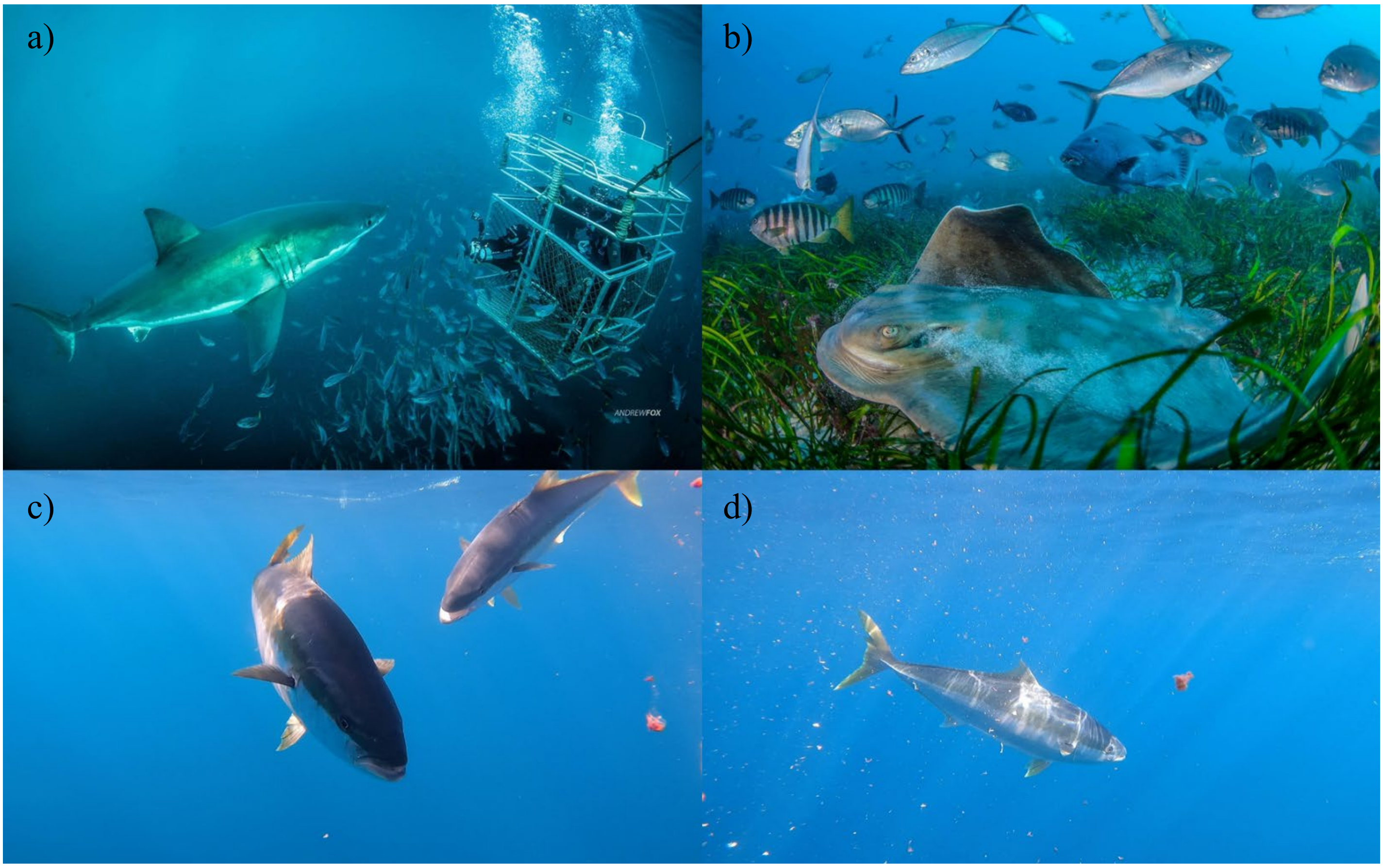


Figure 1.2. Examples from the Neptune Islands Group showing a) shark cage-diving operations, b) diverse fish assemblages (provided by Rodney Fox Shark Expeditions), and c), d) kingfish interacting with food-based attractant (provided by Calypso Star Charters).

1.6 Research objectives

The main objective of this study was to increase the understanding of the reproductive behaviour, and activity patterns of yellowtail kingfish in southern Australia, and investigate the potential impacts of wildlife tourism on kingfish. This objective stems into three overarching aims to:

1) Characterise and identify courtship and spawning behaviour of kingfish
2) Assess the effects of white shark cage-diving tourism on kingfish
3) Identify drivers of kingfish activity across south-eastern Australia

To address these aims, I have compiled four thesis chapters (excluding this introductory [1] and general discussion [6] chapters, each with specific aims and goals which link to the overall objective of this study (Figure 1.3).

Thesis structure

Chapter 1 provided an introduction about movement and behaviour ecology, the study species, and wildlife tourism, in particular the white shark cage-diving industry in South Australia. Interactions of kingfish with cage-diving tourism are introduced, highlighting the potential for negative implications on kingfish movements and physiology. This chapter represents a brief introduction to the key topics included in the thesis as more details are provided within each data chapter.

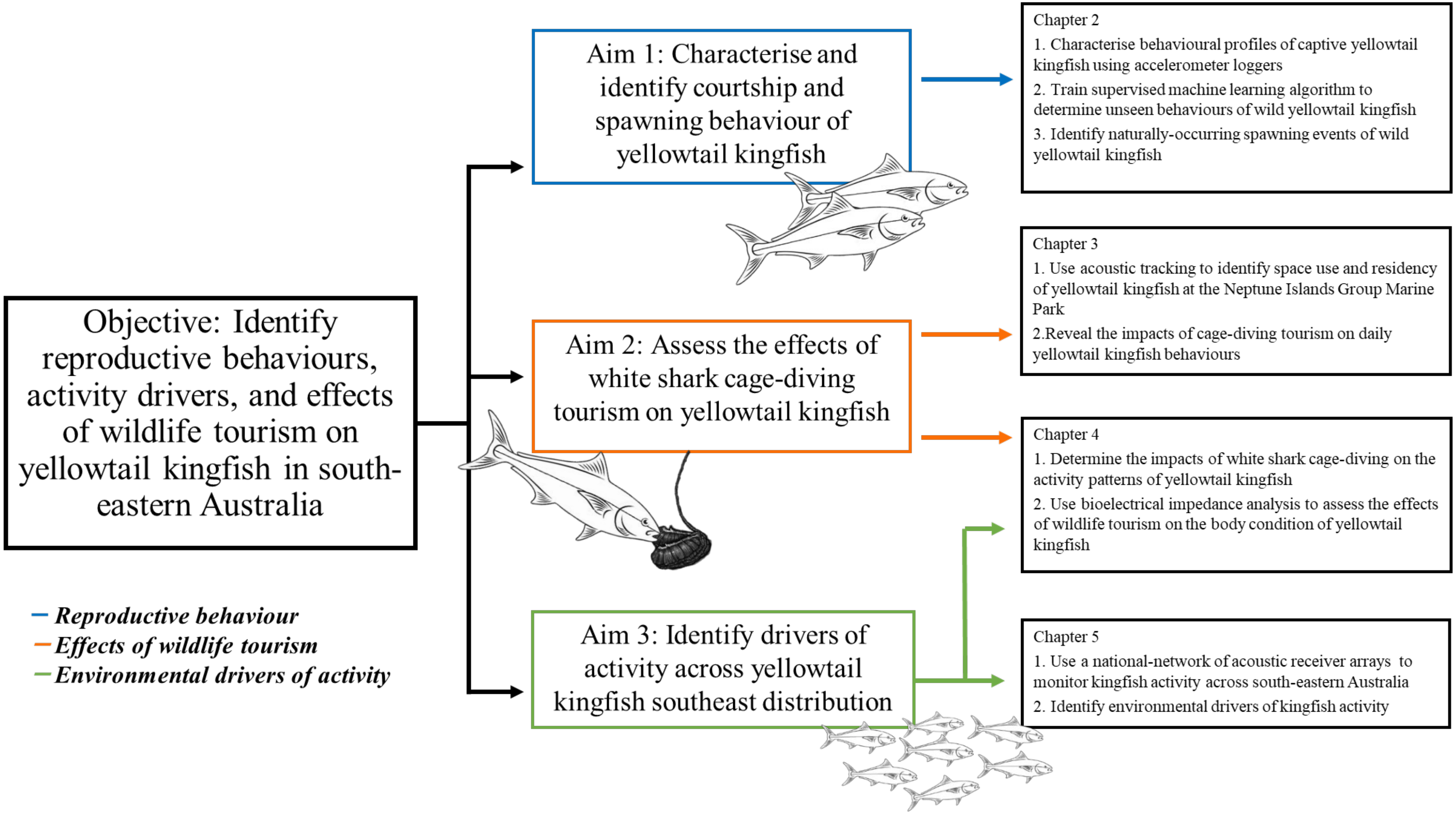
Chapter 2 used accelerometer loggers and machine learning to identify spawning behaviours of kingfish. This included 1) characterising and describing behaviours of kingfish in a captive environment, and 2) subsequently applied behavioural profiles on unseen data from free-ranging kingfish to detect naturally-occurring reproductive behaviours. This chapter fits within aim 1 (Figure 1.3) and has been published in *Movement Ecology*.

Chapter 3 examined the influence of white shark tourism on the movements of kingfish at the Neptune Islands. Kingfish residency and space use was assessed over a two-year period, and the weekly number of operating days and type of operator attractant (food-based, acoustic, no operator) was tested to measure the effects of tourism on kingfish movements. Findings from this chapter align with aim 2 and is under review in *Marine Ecology Progress Series*.

Chapter 4 assessed the influence of white shark tourism on the physiological responses of kingfish. Activity of kingfish was compared during times that food-based, acoustic, or no operators were present to reveal effects of chumming operations on activity. Body condition (measured through Bioelectrical Impedance Analysis) of kingfish at the Neptune Islands was assessed to further divulge if feeding on a provisioned food source was reflected by poorly physiologically conditioned individuals. These findings relate to aim 2.

Chapter 5 accumulated data of kingfish activity from their distribution across south-eastern Australia through a national network of acoustic tracking receivers to reveal environmental drivers of kingfish activity, and included a case-study of activity patterns over a small spatial scale (~120 km^2) within a semi-enclosed embayment system in Coffin Bay. This chapter built on the understanding of kingfish energetic strategies between interconnected sites from one largely distributed population, and aligns with aim 3.

Chapter 6 synthesised results from chapters 2 – 5 and discussed major findings and inferences for the wider understanding of kingfish ecology in southern Australia. This highlights the power of multiple electric tagging methods to reveal reproductive behaviours and energetic budgets of large pelagic fish, and emphasises the potential effects from shark tourism on non-focal mobile species.



Objective: Identify reproductive behaviours, activity drivers, and effects of wildlife tourism on yellowtail kingfish in south-eastern Australia

Aim 1: Characterise and identify courtship and spawning behaviour of yellowtail kingfish

Aim 2: Assess the effects of white shark cage-diving tourism on yellowtail kingfish

Aim 3: Identify drivers of activity across yellowtail kingfish southeast distribution

Chapter 2

1. Characterise behavioural profiles of captive yellowtail kingfish using accelerometer loggers
2. Train supervised machine learning algorithm to determine unseen behaviours of wild yellowtail kingfish
3. Identify naturally-occurring spawning events of wild yellowtail kingfish

Chapter 3

1. Use acoustic tracking to identify space use and residency of yellowtail kingfish at the Neptune Islands Group Marine Park
2. Reveal the impacts of cage-diving tourism on daily yellowtail kingfish behaviours

Chapter 4

1. Determine the impacts of white shark cage-diving on the activity patterns of yellowtail kingfish
2. Use bioelectrical impedance analysis to assess the effects of wildlife tourism on the body condition of yellowtail kingfish

Chapter 5

1. Use a national-network of acoustic receiver arrays to monitor kingfish activity across south-eastern Australia
2. Identify environmental drivers of kingfish activity

Figure 1.3. Overall objective and aims of thesis with each chapter's contribution to those aims

Chapter 2

Using tri-axial accelerometer loggers to identify spawning behaviours of large pelagic fish

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2.1 Abstract

Tri-axial accelerometers have been used to remotely describe and identify *in situ* behaviours of a range of animals without requiring direct observations. Datasets collected from these accelerometers (i.e., acceleration, body position) are often extensively large, requiring development of semi-automated analyses to classify behaviours. Marine fishes exhibit many ‘burst’ behaviours (e.g., feeding, escape, etc.) with high amplitude accelerations that are difficult to interpret and differentiate. This has constrained the development of accurate automated techniques to identify different burst behaviours occurring naturally, where direct observations are not possible. Here, I developed a trained random forest machine learning algorithm based on 624 hours of accelerometer data from six captive yellowtail kingfish (*Seriola lalandi*) during spawning periods. Five distinct behaviour classes (swim, feed, chafe, escape, and courtship) were described, which were used to train the model based on 58 predictive variables. Overall accuracy of the model was 94%. Classification precision of each behavioural class was variable; predictive accuracy (F_1 scores) ranged from 0.48 (chafe) – 0.99 (swim). The model was subsequently applied to accelerometer data from eight free-ranging kingfish, and all behaviour classes described from captive fish were predicted by the model to occur, including nineteen events of courtship behaviours, ranging from 3 seconds to 108 minutes in duration. Our findings provide a novel approach of applying a supervised machine learning model on free-ranging large pelagic fish, which has previously been predominantly constrained to direct observations of behaviours, and not predicted from free-ranging individuals. Additionally, our findings identify timing and location of typically ambiguous spawning and courtship behaviours of a large pelagic fish as they naturally occur.

2.2 Introduction

In the past decade, the field of biologging has increasingly enabled remote monitoring of many aspects of the lives of some of the most enigmatic animals (Block 2005, Rutz & Hays 2009, Hussey et al. 2015). Devices such as tri-axial acceleration data loggers (hereafter accelerometers) allow for remote *in situ* assessments of animal movements and are often used in the marine realm (Shepard et al. 2008a; Suzuki et al. 2009). Accelerometers measure acceleration across three axes (e.g., dorso-ventral [heave], anterior-posterior [surge], and lateral [sway] axes; Shepard 2008a) to generate a time-series characterising movement and activity. Accelerometers, therefore, provide an opportunity to describe acceleration profiles related to movement and energetic expenditure in an environment that is otherwise difficult to directly observe (Foerster et al. 1999, Tsuda et al. 2006, Moreau et al. 2009). Additionally, accelerometers also provide an opportunity to quantify kinematic profiles of animals, enabling the inference of unique behavioural classes based on distinctive characteristics. For example, accelerometer data may be used in combination with spatio-temporal data (e.g., depth, geographic location, season) to identify ecologically-important behaviours, such as spawning (Tsuda et al. 2006, Sakaji et al. 2018, Schlenker et al. 2021), or feeding (Tanoue et al. 2012; Brownscombe et al 2014; Gleiss et al. 2013; Kadar et al. 2020). Remotely inferring occurrences of such behaviours from accelerometer data also allows for further insight into movement strategies (Gleiss et al. 2011a, Wang et al. 2015, Watanabe et al. 2019), and energy budgets (Ladds et al. 2017, Lear et al. 2020) of animals in free-ranging environments. Studies have used visual observations of animals in nature to relate acceleration profiles to particular behaviours such as different modes of travelling and feeding/drinking in Adélie penguins *Pygoscelis adeliae*, domestic cat *Felis catus* (Watanabe et al. 2005), and polar bears *Ursus maritimus* (Pagano et al. 2017). However, validation from time-synchronised accelerations with direct observations, referred to as ground-truthing, is required to accurately infer behaviours from accelerometer data and create labelled datasets. Other research efforts have employed animal-borne video to ground-truth behaviours of free-ranging animals, time-synchronised to accelerometer data (Watanabe & Takahashi 2013, Watanabe et al. 2019), but validating behaviour *in situ* using animal-borne cameras is limited due to cameras either being too large for small organisms, short battery life incapable of recording for long periods, or insufficient lighting to accurately infer some behaviours that occur during less illuminated hours of the day.

To characterise fine-scale behaviours of taxa beyond binary classification (e.g., active vs inactive), studies using accelerometers are required to use high temporal resolution sampling rates (Noda et al. 2013, Noda et al. 2014). Consequentially, datasets collected from accelerometers are exceptionally large, consisting of millions of rows of data, ands a result, manually analysing accelerometer datasets is time-consuming and often one of the limiting tasks of behavioural studies using these devices (Müller & Schrader 2003, Shepard et al. 2008a). To overcome these limitations, more recent studies have used machine learning (ML) algorithms to train models based on patterns in the collected data allowing predictions from unseen data (Valletta et al. 2017, Brewster et al. 2018, Hounslow 2018, Hounslow et al. 2019). Machine learning approaches address these complex, large datasets that would otherwise be intractable using classical statistical techniques (Leos-Barajas et al. 2017, Valletta et al. 2017). In particular, supervised machine learners, such as random forest models, are trained on a labelled data-sets to recognise unlabelled or 'unseen data' (Valletta et al. 2017). Random forest (RF) algorithms are an ensemble classifier designed to mitigate the issues associated with overfitting in decision trees through using multiple unpruned classification or regression trees (Breiman 2001). These RF models are particularly popular with behavioural classification data (e.g., Nathan et al. 2012, Wang et al. 2015, Pagano et al. 2017, Hounslow et al. 2019) because of they often produce higher classification accuracy than other models (e.g., k-nearest neighbour, support vector machine, naïve Bayes, adaptive boosting; Breiman 2001, Tatler et al. 2018, Mansbridge et al. 2018). Random Forest models can handle thousands of mixed categorical and continuous predictions with robustness to outliers (Valetta et al. 2017) and have relative ease of execution. In the case of behavioural classification of acceleration data, training an RF model to predict from unseen data means first ground-truthing to 'train' the model, by confirming the behaviour of the animal carrying an accelerometer to match acceleration data with the corresponding behaviour class of the individual (Watanabe et al. 2005, Shepard et al. 2008b). Thus, a well-trained algorithm can predict the behaviour of a wild ('unseen') individual across ecologically-important times or areas.

Understanding courtship and spawning behaviours of large pelagic fish is vital to predict population responses to environmental and fishing pressures, and develop suitable and adaptable management strategies (Rowe & Hutchings 2003, Sakaji et al. 2018). However, observations of spawning behaviours of most free-ranging fish in pelagic environments is often difficult due to their patchy distribution, large-scale movements, occurrence in low light conditions, and the logistical difficulties associated with working in the marine environment. In marine fishes, accelerometers have been used to characterise a number of behavioural classes such as foraging (Brownscombe et al. 2014), feeding (Tanoue et al. 2012, Kawabata et al. 2014), and escape behaviours (Noda et al. 2013) based on acceleration profiles. Accelerometers have also been used to characterise complex reproductive behaviours, such as chum salmon (*Oncorhynchus keta*; Tsuda et al. 2006), flounder (*Paralichthys olivaceus*; Yasuda et al. 2013), and greater amberjack (*Seriola dumerili*, Sakaji et al. 2018), as well as showing potential to describe mating strategies of nurse sharks (*Ginglymostoma cirratum*; Whitney et al. 2010), by confirming reproductive status via either destructive gonad sampling or direct visual observations. Random forest models developed through data collected via accelerometers therefore offer an opportunity to build on this past research to address the typically challenging task of detecting natural spawning events by training a predictive model based on acceleration characteristics during visually-confirmed events, and subsequently identify naturally-occurring reproductive events on unseen data from free-ranging individuals.

Yellowtail kingfish (*Seriola lalandi*; hereafter referred to as kingfish) is a large migratory pelagic carangid, found globally in temperate and sub-tropical coastal waters (Gomon et al. 2008). In addition to being commercially and recreationally targeted, kingfish are highly palatable and as a result, part of an expanding aquaculture sector in Japan and southern Australia (PIRSA 2014). Access to kingfish in a captive aquaculture environment has permitted the description of optimal conditions and kinematics during reproductive behaviours (Gillanders et al. 1999, Moran et al. 2007). Spawning most often occurs between dawn and dusk (A Miller; pers. comms, Moran et al. 2007), and typically involves long periods of high-speed pursuit of a female by one male, interspersed with stalling, nipping, and touching of bodies followed by the male nipping the female gonoduct, presumably to initiate spawning (Moran et al. 2007). Kingfish movement and body position during these events should, therefore, be suitably different to other behaviours, providing a unique opportunity to use accelerometers to characterise acceleration profiles of spawning behaviours (Sakaji et al. 2018) and develop a RF model to identify these behaviours from free-ranging kingfish.

This study aimed to describe and quantify behaviours of captive kingfish by developing a supervised ML algorithm (RF model) based on ground-truthed accelerometer data, and subsequently apply this to data collected from free-ranging kingfish to identify naturally-occurring spawning behaviour.

2.3 Methods

Captive kingfish trials

Captive trials were undertaken at the Cleanseas Aquaculture Hatchery Facility, in Arno Bay, South Australia (33°56.222‘S, 136°34.4918‘E; Figure 1.1). Here, sexually mature broodstock kingfish are housed in large tanks for the purpose of ongoing production runs and egg stocking. Broodstock kingfish in production tanks are originally sourced from wild kingfish caught locally in South Australia. Between August 2018 and February 2019, two tracking sessions where undertaken where six captive brood stock kingfish (three each tracking session - 1 female and 2 males; Table 2.1) were tagged with tri-axial accelerometer data loggers (Technosmart Europe srl, Axy-Depth, Rome, Italy) scheduled to record at 50 Hz and ± 4G. Loggers were programmed to record in three-axes of acceleration; surge (x), heave (y), sway (z) corresponding to dorsal-ventral, anterior posterior, and lateral orthogonal body axes.

Fish were removed from holding tanks and placed inside a ‘knock-out tub’ containing AQUI-S (10 ppm) for tagging. The logger was affixed to a padded base plate, which was attached to the fish by passing 45 kg breaking-strain monofilament leader through the dorsal musculature using sharpened embroidery needles, which had the monofilament passed through the eyelet and held secure firmly with a small crimp and heat shrink tubing. The monofilament was then cut to remove the needle and passed through a padded button (one per strand of monofilament) to act as an anchor. To identify tagged individuals, accelerometers were designed with different coloured buttons, different patterns (for night-time), as well as different numbered base plates that could be identified through video footage. Once the logger was secured, the fish was returned to the housing tank. A recovery period of 3 hours following tagging was allowed prior to trials to allow fish to resume regular behaviours. Following trials, tagged individuals were recaptured, and loggers were manually removed.

Over 5-day periods, four video cameras (GoPro Hero 7 and Concord CCTV infrared cameras) were placed inside the tank to enable constant recording over the trial period. Cameras were secured in waterproof acrylic housings, while running from a charging power bank battery pack to allow cameras to record for ~8-hour periods. Time on the video recording was synchronised to the same time as the accelerometers, so that acceleration data could be directly related to the video footage for a given point in time. Trials were carried out in regular production brood stock tanks to ensure natural spawning events would occur, so there were 27 (tracking session 1) and 60 (tracking session 2) additional untagged fish within each tank over the trial periods. Fish were fed to satiation twice per day by spreading 1,400–2,000 g of pellet into the tank over 3 – 5 minutes. Escape behaviour was also induced during the second tracking session and consisted of a 5-minute period where an extendable pole was held inside the tank with the pole moving behind tagged fish and used to instigate an escape behaviour until individuals were out of reach. Times of initiated feeding and induced escape behaviour were noted for synchronisation with acceleration data. During winter months (April–October; Trip 1) spawning in the tanks is initiated through manipulation of tank water temperatures, but during warmer months (November – March; Trip 2) tanks are kept at ambient seawater temperatures and spawning occurs naturally. As not all fish engage in spawning events within the tank, confirmation of courtship from tagged individuals was required and obtained through direct observation or video footage.

Free-ranging kingfish trials

Between October 2015 and November 2019, eight free-ranging kingfish (98 – 151 cm TL) were caught and tagged with accelerometers (Little Leonardo, ORI400-D3GT, Tokyo, Japan or Technosmart Europe srl, Axy-Depth, Rome, Italy) for 2–3 days (Table 2.1). An additional ninth kingfish was tagged with an accelerometer that prematurely released after 2 hours and so was excluded from the analysis. Only fish > 80 cm total length (TL) were tagged, as this is expected to be the minimum size that both male and female kingfish are mature and to coincide with spawning behaviours (Gillanders et al. 1999). Additionally, an effort was made to ensure that free-ranging fish were of similar size to the tagged captive fish to minimise any potential influence of fish size on acceleration profiles (Webb 1976, Webb 1978). Free-ranging fish (98 – 151 cm, mean = 122.9 cm TL) in this study were, however, slightly larger than captive fish (90 – 105 cm, mean 96.5 cm TL). Kingfish were tagged during the Austral spring and summer months to coincided with expected natural spawning events, that are expected to be triggered by increasing water temperature and occur between spring/summer months i.e., November through April (Gillanders et al. 1999, Poortenaar et al. 2001, Moran et al. 2007).

Table 2.1. Description of yellowtail kingfish (*Seriola lalandi*) used for captive (C) and free-ranging (FR) accelerometer trials. Free-ranging kingfish were not checked for sex (shown as '-'). Location refers to tagging location.

Fish ID	Location	Date tagged	Sex	Total length (cm)	Logger recording time (hours)
C1	Arno Bay	21/08/2018	M	91	115
C2	Arno Bay	21/08/2018	F	105	115
C3	Arno Bay	21/08/2018	M	95	115
C4	Arno Bay	8/2/2019	M	90	93
C5	Arno Bay	8/2/2019	F	97	93
C6	Arno Bay	8/2/2019	M	101	93
FR1	Neptune Islands	28/10/2015	-	99	45.5
FR2	Neptune Islands	28/10/2015	-	98	37
FR3	Neptune Islands	30/10/2015	-	114	16.7
FR4	Neptune Islands	13/2/2019	-	120	10.7
FR5	Neptune Islands	15/2/2019	-	119	16.6
FR6	Coffin Bay	10/11/2019	-	151	51.2
FR7	Coffin Bay	10/11/2019	-	142	33.7
FR8	Coffin Bay	10/11/2019	-	140	30.3

Accelerometers were attached to free-ranging kingfish using the same protocol as detailed above (section 2.1) but were modified to self-detaching recoverable packages, containing an accelerometer (Axy-Depth, Technosmart Europe srl, Rome, Italy), radio transmitter (MM100, Advanced Telemetry Systems Inc, Isanti, USA), and Smart Position and Temperature (SPOT) transmitting tag (258, Wildlife Computers, Redmond, USA), and were deployed with corrodible links to allow for recovery after 2–3 days. Logger packages (138–150 g, 15 x 4 x 5.5 cm) were designed to be as small and streamlined as possible and of similar size to logger plates used in captive trials.

Data analysis

Accelerometer data were downloaded and visually observed through IGOR Pro (WaveMetrics Inc., Lake Oswego, OR, USA, version 8.0.3) with add-on software Ethographer (Sakamoto et al. 2009). Data from periods where fish could not be directly observed or identified from the video footage due to low light conditions, or out of view of cameras were removed from further analysis.

Static acceleration (as a result of Earth's gravitational field) and dynamic acceleration (representing body movement) were calculated for all three acceleration axes (X, Y, and Z) to filter the dominant signal caused by tail beating and body attitude, and to isolate behaviours with high amplitude acceleration (Table 2.2, Wilson et al. 2006, Shepard et al. 2008b). Continuous wavelet transformations were then applied to the lateral acceleration data (sway axis [Z] as a measure of tail beating undulations; Rioul & Vetterli 1991, Sakamoto et al. 2009) to derive acceleration wavelets representing amplitude (maximum displacement from equilibrium position) and cycle (stroke frequency) of tail beat sequences. The vector of the three axes of dynamic body acceleration (VeDBA) was calculated as a metric of activity level, whereby behaviours associated with increased levels of activity and metabolic rate correspond to higher values of VeDBA (e.g., Qasem et al. 2012, Broell et al. 2016; Ladds et al. 208; Lear et al. 2020). Pitch and roll values were calculated based on orientation of the logger (Table 2.2). Absolute values for roll were used to represent the roll without influence of directionality (i.e. -90 ° and +90 ° resulting in running mean average roll of 0 °, or minimum value equalling 90°). A set of descriptive predictor variables was produced characterising kingfish behaviour for subsequent ML classification (*n* = 64, Table 2.2), by calculating the mean, standard deviation, skewness, kurtosis, minimum, and maximum for each of these values from 1 second increments (Shepard et al. 2008a) matched to known behaviour labels. Summarising acceleration data into 1-second increments was chosen as longer increments would not encompass short burst behaviours such as chafe (which only lasts 1–2 seconds; Hounslow 2018, Robert et al. 2009, Campbell et al. 2013), in addition to it not being possible to make sub-second manual observations of behaviour.

Table 2.2. Definitions and formulae for each predictor variable measured through the accelerometer data

Variable	**Formula**	**Definition**
Static acceleration	Filtered 0.06, 0.6	1 second means for static acceleration representing body posture in each axis
Dynamic acceleration	Raw (g) – Static (g)	1 second means for dynamic acceleration representing body movement in each axis
Vector of Dynamic Body Acceleration	$\sqrt{}$Dynamic (X axis)^2 + Dynamic (Y axis)^2 + Dynamic (Z axis)^2	Square root of the sum of squares of absolute dynamic body acceleration in each axis
Cycle		Cycle for the dominant frequency obtained through the continuous wavelet transformation generated spectrogram. Represents the inverse of tail-beat frequencies.
Amplitude		Amplitude for the dominant frequency obtained through the continuous wavelet transformation generated spectrogram.
Pitch	atan(X axis/(sqrt(Z axis*Z axis)+(Y axis)*(Y axis))) *180/pi	Body inclination of the fish (Watanabe et al. 2008b) during ascending (+) or descending (-)
Roll	atan2(Z axis, Y axis)*180/Pi	Spinning movements of an individual around the main axis of the fish (Sfakiotakis et al. 1999). Absolute values for roll were used to alleviate influence of roll direction.

Standard deviation	Standard deviation of static and dynamic acceleration, VeDBA, pitch and roll in each axis.
Skewness	A measure of the symmetry of the variable
Kurtosis	A measure of the tail shape of the variable
Minimum	Minimum value of static and dynamic acceleration, VeDBA, pitch and roll in each 1 second increment
Maximum	Maximum value of static and dynamic acceleration, VeDBA, pitch and roll in each 1 second increment

Time-series acceleration data were inspected to identify potential burst-behaviours. Behaviours that exceeded ± 1 g acceleration in the sway axis (indicative of behaviours with high acceleration amplitude associated with tail beat), had substantial changes in roll, or periods of rapid changes in acceleration were inspected in the video footage. This conservative threshold was expected to be sufficient to detect successful spawning events based on previous descriptions of spawning in *Seriola dumerili* exceeding ± 2 *g* (Sakaji et al. 2018). Feed and escape behaviours were identified based on events during times that fish were fed, or escape trials were undertaken. Behaviours were then coded (using the Ethographer mask feature) as one of five behavioural classes observed from the video: feeding, swim, escape, courtship, or chafe (Table 2.3).

Table 2.3. Definitions of behaviours coded from video footage that were attributed to acceleration data. Behaviours that were initiated by researchers are marked with *.

Coded behaviour	Definition
Feed*	Between 1,400–2,000 g of pellet feed was dispersed into the tank from the surface and fish were observed accelerating towards and consuming pellets. Typically lasted 3–5 minutes, until pellets were exhausted.
Escape*	Five trials per individual of 5-minutes in length where a researcher used a long pole to initiate burst swimming behaviour by following tagged fish with the pole until fish was out of reach. Only events where fish were visually observed to react to the presence of the pole were included as escape.
Courtship	Included both typical chase preceding spawning and actual spawning events, due to low sample size of visually confirmed spawning events (*n* = 8). A typical chase was identified from the tagged individual(s) chasing another kingfish by closely following behind or next to another fish with increase in swim speed, often rubbing nose on the underside of the body or nipping at pelvic or caudal fins (Moran et al. 2007). Spawning was identified by a group of individuals (including tagged fish) closely rubbing bodies, followed by large burst swimming by involved individuals lasting <10 seconds, and with gametes observed in the water column.
Chafe	Individual rolls to face one side of the body to the surface either in mid-water or to the bottom of the tank. Roll motion where dorsal side contacts surface or substrate in an effort to remove unwanted parasites or foreign bodies (Myrberg Jr & Gruber 1974, Hounslow 2018)
Swim	Typical swim behaviours with no burst or roll events, steady lateral undulatory locomotion (Maia et al. 2012, Hounslow 2018). 1,500 seconds of swimming behaviour was allocated during periods where fish could be directly observed regularly swimming around the tank with no bursts in acceleration amplitude observed. These periods were allocated as five random, 5-minute periods with good visibility, and not within 30 minutes of feed- or escape trials.

Development of a machine learning classification algorithm

Random forest classification was performed using the *randomForest* function from 'randomForest' package in R (version 1.1.453). Values from each predictor variable was pooled for all captive individuals into a single dataset, before being randomly split into two datasets; 70% for training the model and 30% as a test dataset to assess the performance of the model. This partitioning of data is commonly used in machine learning applications to ensure a suitably sized test dataset, enabling high accuracy of error estimates from acceleration data studies (Nathan et al. 2012, Sur et al. 2017). A range of number of trees (*ntree* values) were tested starting at 500 and increasing in increments of 500 up to 2,000 trees. Additionally, the number of variables randomly sampled at each split (*mtry*) were tested (in increments of 5, from 5 to 20) to assess influence on error rate of the model. It was deemed that a *ntree* value of 1,000 with *mtry* default value (square root of the number of predictor variables) was sufficient based on the low range of Out-Of-Bag (OOB) error variation (5.54%), that showed minimal change when the number of trees increased beyond 1,000. An attempt was made to account for the unbalanced size of behaviour class data (due to more frequently occurring behaviours) through stratified sampling with equal probabilities (function: *strata*, package: 'sampling' version 2.8). However, while this stratified sampling improved precision accuracy of behaviour classes with smaller sample sized (e.g., chafe), precision of courtship class was decreased and so this function was not included in the final model. The 64 predictor variables were checked for relative importance to the overall class predictive performance of the classification model with the function '*varImpPlot*' within the 'randomForest' package in R, measures the mean decrease in overall accuracy if a predictor variable is removed from the model (Figure S1) (Wang et al. 2015, Sur et al. 2017, Valletta et al. 2017).

Evaluation of model performance

Performance metrics were calculated from the RF confusion matrix as indicators of the performance of the model for classifying kingfish behaviours (Chen et al. 2004, Brewster et al. 2018). A confusion matrix was created using the *confusionMatrix* function from the 'caret' package in R (version 6.0.88). This matrix provides a table of actual observations from each behaviour class (rows) versus the behaviour class predictions of the model (columns). Performance metrics were calculated from the true positive (TP), false positive (FP) and false negative (FN) observations determined by the confusion matrix (Brewster et al. 2018). True positives are observations which have successfully been assigned to the correct class by the model (Brewster et al. 2018). False Positives are observations which have been incorrectly assigned to a behaviour class. False Negatives (FN) are values that belong to a particular class but have been incorrectly assigned to another behaviour. To evaluate performance of the model for predicting distinct kingfish behaviour, evaluation metrics (Pr), recall (Re), and the F-measure (F_1) were used:

Recall: Proportion of predicted behaviours from each class that were correctly classified.

$$R = TP/TP + FN$$

Precision: Proportion of predicted behaviours from each class that were that behaviour.

$$P = TP/(TP + FP)$$

F_1 Score: The harmonic mean of recall and precision. Value of 0–1, where values near 0 have low classification performance, while values closer to 1 have best classification performance

$$F_1 = 2PR/(P + R)$$

Predicting free-ranging kingfish behaviours

The RF algorithm developed using ground-truthed data from captive kingfish was subsequently applied to unseen data from eight free-ranging kingfish using the *predict.randomForest* function in R. The first 60 minutes of data once each fish was released was removed from the dataset, to avoid incorrect allocations of capture-induced behaviours (Roberts et al. 2011). As kingfish are physiologically robust fish (Moran et al. 2008) and anaesthetic was not used during the tagging procedure of free-ranging individuals, I assumed 60 minutes to be sufficient time for resuming regular behaviours. Each one-second running mean increment of time-series data (recorded at 50 Hz) was allocated a predicted behavioural class, based on values and the same predictor variables calculated from captive fish to train the RF. To minimise misallocations of free-ranging behaviour class predictions, 1 second increments that were predicted differently to the behaviour in adjacent increments was instead allocated as the same behaviour as that which preceded it. For example, if behaviours were classified in order as: swim, swim, feed, swim, swim; feed would be reclassified as swim. Given the improbability of behaviours occurring in a duration <1 second, it is more likely that a predicted behaviour is the same as that which precedes that second, rather than transitioning to a new behavioural class for only one second. Courtship predicted from the model were categorised as either spawning events or reproductive behaviours. Spawning events were labelled as each portion of free-ranging data that courtship was predicted to occur(Figure S2). Reproductive behaviours included time periods where several spawning events were predicted over a 30 – 90-minute period, based on descriptions from (Moran et al. 2007; Figure S2). Time-series data were then allocated into selected time-bins using the *getSunlightTimes* function (package 'suncalc' version 0.5.0), apportioned as dawn, day, dusk, and night based on data of 1-hour periods either side of sunrise (dawn) and sunset (dusk). Values of swimming depth (m) was also recorded once every five seconds for free-swimming fish, and values for each 1 second running-mean were allocated based on the previously filled value.

2.4 Results

Captive Kingfish behaviour classes

A total of 624 hours of acceleration data was obtained from six kingfish during captive trials over two tracking sessions at times of controlled spawning. Fertilised eggs were collected from trial tanks from 4 out of 5 (Tracking session 1) and 3 out of 4 nights (Tracking session 2), confirming that successful spawning occurred on seven nights while kingfish carried accelerometers. Over 11,600 seconds of accelerometer data were ground-truthed and categorised as one of five behavioural classes: feed (1,332 seconds), escape (398 seconds), courtship (766 seconds), chafe (113 seconds), and swim (Figure 2.1). Total events (1-second increments) allocated to behavioural classes per individual varied between 1,674 (C2) to 2,490 (C4) seconds (Figure 2.1).

Twenty-five minutes (1,500 seconds) of regular swim behaviour was manually coded for each captive fish (9,000 seconds total). Feed events were observed for all captive individuals, apart from C3. Feed classes varied between 30 – 614 seconds per individual, and a total of 1,332 seconds across all fish (Figure 2.1). Courtship behaviours were observed from five fish, varying between 128 – 172 seconds in total per individual (Figure 2.1) and a cumulative total of 776 seconds. Escape behaviours were variable between individuals, with only 2 seconds of this class observed for C1 and C3, with up to 182 seconds for C6 (Figure 2.1). No escape behaviours were observed for C2. A total of 398 seconds of escape behaviours were collected across all fish. Chafe was the least represented behavioural class, with 113 seconds of this behaviour observed varying between 5 (C2) and 45 (C6) seconds in continuous length (Figure 2.1).

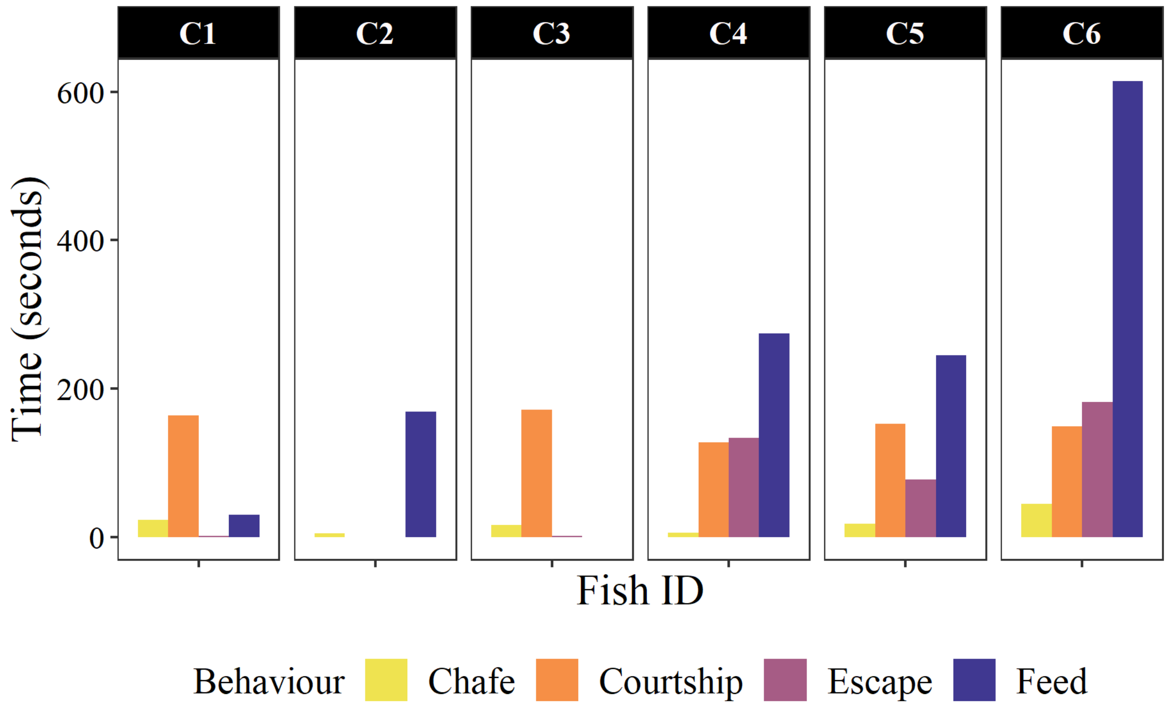

Figure 2.1. Number of 1-second increments spent performing observed behaviours for captive kingfish tagged with accelerometers, (*n* = 6, recording time = 115 hours C1, 2, 3; 93 hours C4, 5, 6). Swim behaviours are not included as the same amount of time swimming (1,500 seconds) was used for each individual.

Acceleration characteristics of behaviour classes

Chafe behaviours were typified by a short burst (1 – 3 seconds) where fish dove to the bottom of the tank represented by a descend in depth and pitch (mean Pitch = -6° ± 2.21), with large values of roll as fish would turn onto their sides (Figure 2.2, Figure S3). Chafe included medium-strength bursts of acceleration, characterised by increased VeDBA (0.31 G ± 0.01) and tail beat (amp = 0.14 ± 0.02, cycle = 0.54 ± 0.01 s). Courtship behaviours were typically extended periods (up to 1 – 2 minutes) of increased cycle and amplitude, interspersed with short bursts of roll and pitch (Figure 2.2, Figure S3). Courtship events displayed the highest intensity acceleration of all behaviours (mean VeDBA = 0.48 ± 0.002 g), though tail beats were slightly slower and less strong than during feeding (amp = 0.19 ± 0.01, cycle = 0.43 ± 0.004 s). Escape behaviours had acceleration signatures that were lower in intensity compared to other burst behaviours (e.g., feed, courtship) but higher than typical swimming (mean VeDBA = 0.15 ± 0.002G). Fish remained mostly upright (pitch = 2 ± 0.50 °), with intermittent small roll values (34.4 ± 0.73 °; Figure 2.2, Figure S3). Feed behaviours were identifiable by several large peaks in amplitude and VeDBA values with several large events over 3 – 5 minutes periods (Figure 2.2, Figure S3). These large peaks corresponded to observed moments that fish would increase acceleration to feed on a pellet in the tank. Feed had the second highest intensity of acceleration (mean VeDBA = 0.43 ± 0.003 G), with the fastest tail beat cycles (0.42 ± 0.003 s) and highest amplitude (0.21 ± 0.006). Pitch was slightly positive (mean = 5 ± 0.38 °) due to fish ascending towards the surface to consume pellets. Swim behaviours were characterised by steady, low values of acceleration, pitch, roll, and cycle, and consistent low peaks of cycle demonstrative of the regular occurring tail beat of the individual (Figure 2.2, Figure S3). During swim, VeDBA was lowest out of all classes (mean VeDBA = 0.04 ± 0.44 G), which was due to slow, long-duration tail beats (amp = 0.02 ± 0.006, cycle = 0.9 ± 0.003 s). During swimming, body position of fish remained upright, resulting in roll values close to zero (mean roll = 0.34 ± 0.7).

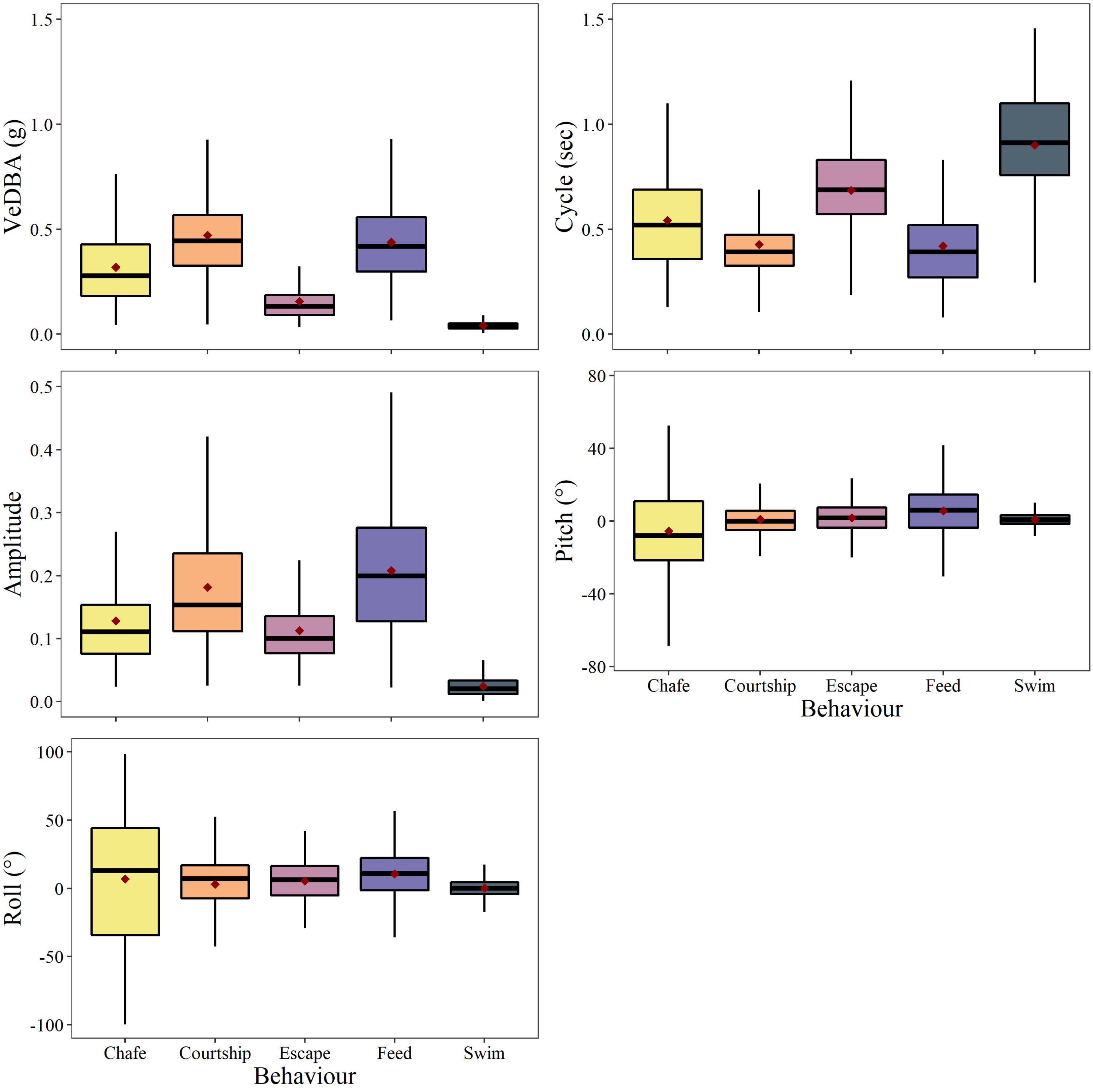

Figure 2.2. Characteristics of observed behavioural classes from captive kingfish tagged with accelerometer loggers. Mean values shown as red diamonds. Black horizontal bars represent median values. Black boxes encompass the interquartile range, and vertical black lines represent the maximum and minimum values.

Model classification performance of behavioural classes

Overall model accuracy of the RF model was 94%. The RF model predicted behaviour classes with variable performance (F_1 ranging from 0.46 – 0.99). Classification performance (F_1) was highest for swim and feed classes (> 84% accuracy, Table 2.4), followed by courtship, with lower allocation scores for escape and chafe classes (Table 2.4). Swim class had the highest correct allocation of all behavioural classes, with all performance metrics exceeding 0.99 (Table 2.4). Swim was correctly predicted for all 1 second increments, except for 9 seconds which were incorrectly allocated as escape. Feed was the next highest performing behavioural class. Somewhat low precision for the feed class (0.75) caused by feeding behaviours being predicted by courtship, chafe, and escape, was complemented by high recall (0.93), resulting in an F_1 score of 0.84. Courtship had a high level of correctly allocated predictions (precision = 0.93), on only 11 occasions was incorrectly allocated as feed, chafe, or escape. Courtship had a lower score for recall (0.57) as a result of misallocations of actual courtship events being predicted incorrectly, predominantly as feed. This resulted in an F_1 score for the courtship class of 0.70. Escape was largely correctly allocated (precision = 0.69), though 17% and 12% of escape behaviours were incorrectly allocated as swim and feed classes, respectively. The model incorrectly predicted courtship (9%) and feed (12%) occurrences as escape resulting in a recall score of 0.70, and an overall F_1 of 0.69. Chafe was the poorest performing behavioural class, with only 31% of chafe behaviours correctly allocated as this class. Most of these behaviours (48%) were incorrectly predicted as the feeding class. Although chafe had a high result for precision (0.90) representative of the model only incorrectly predicting chafe to occur once, as feeding. These values resulted in a F_1 score of 0.46.

Table 2.4. Performance metrics of behavioural classes from captive kingfish calculated from random forest algorithm on the test data (30% overall). Grey boxes represent number of correctly allocated behaviour increments from test data set.

Reference behaviour	**Predicted behaviour**					**Performance metrics**		
	Chafe	**Courtship**	**Escape**	**Feed**	**Swim**	**Precision**	**Recall**	**F_1**
Chafe	9	2	3	14	1	0.90	0.31	0.46
Courtship	0	142	12	96	1	0.93	0.57	0.70
Escape	0	1	83	14	21	0.69	0.70	0.69
Feed	1	8	14	379	2	0.75	0.93	0.84
Swim	0	0	9	0	2671	0.99	0.99	0.99

Free-ranging Kingfish behaviours

The model trained using the entire ground-truthed dataset was used to predict naturally-occurring behaviours from eight free-ranging kingfish (Figure 2.3). All five behavioural classes observed and coded in the captive trials were predicted to be performed by free-ranging individuals. Five of the eight free-ranging fish spent most of the recording period swimming (67–97%; Figure S4), however the remaining three fish (FR4, FR5 and FR7) mostly displayed escape behaviour, accounting for 81, 58, and 45% of behaviour class allocations, respectively. Courtship was predicted to occur from five free-ranging fish, three from the Neptune Islands and two from Coffin Bay in temperatures between 16.5 – 19.5°C. A total of 48 spawning events were predicted and classified into 19 expected reproductive behaviours. Reproductive behaviours were typically made up of between 1 to 6 spawning events, with one reproductive behaviour containing 18 spawning events, lasting 108.6 minutes (Figure 2.3b). Of the 19 behaviours, 12 included only single spawning events. Of these single occurrence events, duration ranged from 3 to 14 seconds (Figure 2.3c). Reproductive behaviours occurred between 12 – 103 m of depth at the Neptune Islands (n = 16 events, mean = 35.8 ± 3.84 m) and 1 – 6 m in depth at Coffin Bay (n = 5 events, mean = 2.98 ± 0.42 m). During courtship, fish exhibited minimal changes in depth, generally propelling slightly towards the surface 0.74 ± 0.18 m in Coffin Bay, 1.81 ± 0.38 m at the Neptune Islands (Figure 2.3a). Courtship predominantly occurred at dawn and day, with 17 and 18 events (accounting for 35 and 38% of all spawning events respectively). Comparatively, 7 (15%) and 6 (13%) of the events occurred at night and dusk (Figure 2.3c).

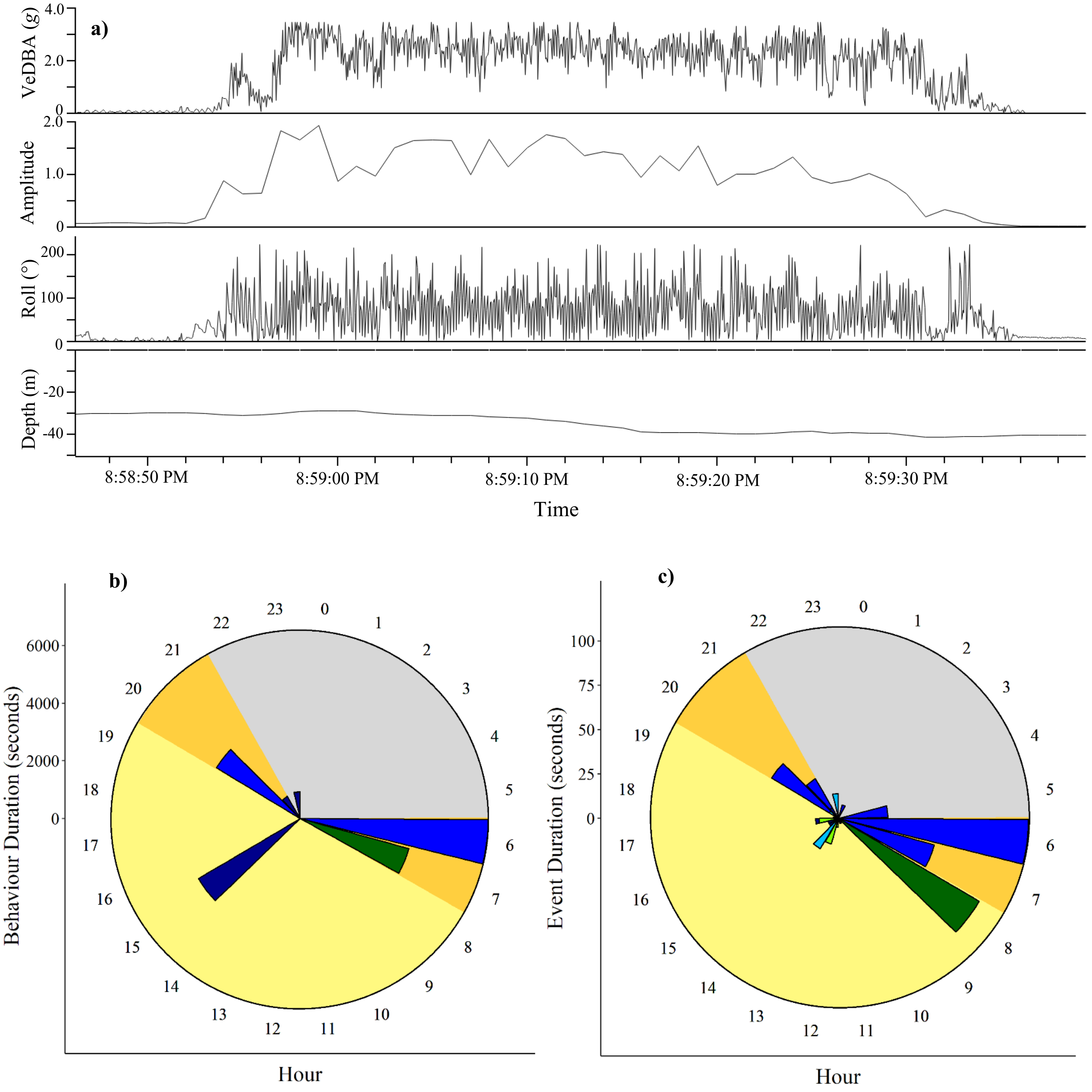

Figure 2.3. Example of one free-ranging kingfish reproductive event predicted from the random forest model (a), and total duration in seconds of b) reproductive behaviours and c) spawning events predicted from free-ranging yellowtail kingfish individuals at the Neptune Islands (blue) and Coffin Bay (green) as predicted from a supervised machine learning model. Time of day is indicated by dawn (orange), dusk (orange), day (yellow) and night (grey).

2.5 Discussion

This study used accelerometers and machine learning to describe reproductive behaviours of yellowtail kingfish in a captive environment, differentiate these from other behaviours, i.e., swimming, feeding, escape behaviours, and identified these behaviours in free-ranging kingfish. These results showed that free-ranging kingfish displayed all behaviour classes , with swimming and escape behaviours being most common. Evidence of courtship was observed from five free-ranging kingfish, supporting anecdotal descriptions of occurrence of reproductive behaviour and spawning events at both the Neptune Islands and Coffin Bay, and further encouraging the combined use of accelerometers and machine learning as a tool to identify naturally-occurring behaviours of large pelagic fish.

Accelerometers provide an opportunity to record *in situ* movements of free-ranging organisms to infer behaviours based on changes in acceleration, body position, and tail beat signatures (Kawabe et al. 2003, Whitney et al. 2010). Previous applications of this method to verify ecologically-important behaviours of large pelagic fishes have been limited to identifying and describing spawning events of marine fishes based on visualisation of tail beat acceleration signatures (Yasuda et al. 2013, Sakaji et al. 2018). However, accelerometers have not yet been used to distinguish spawning from other naturally-occurring burst behaviours. This chapter successfully identified and described five behavioural classes of yellowtail kingfish, including courtship, based on variables characterising acceleration profiles, body position, and tail beat signatures. While visual observation of data obtained from accelerometer loggers was sufficient to identify bursting behaviours (e.g., courtship, feed, escape), the random forest algorithm was necessary to differentiate among these high-acceleration events.

Swimming behaviour in pelagic fish is represented by regular, low intensity cyclic patterns in sway acceleration which is more regular and consistent compared to infrequent, high intensity burst behaviours (Gleiss et al. 2009, Broell et al. 2016). These predictable waveform signals are typical in pelagic fish and sharks (Gleiss et al. 2009, Hounslow 2018), contributing to forward propulsion and is commonly the most highly allocated behaviour in machine learning studies differentiating behaviours of swimming marine organisms given that these behaviours are the most frequently performed behavioural class (Hounslow 2018). These expectations were met by our model, with consistent high levels of successful allocations for swimming behaviour. However, differentiating behavioural classes with more complex kinematics, and high and variable frequency and amplitude such as burst behaviours, has been a challenge for most accelerometer-based studies of behavioural predictions (Brownscombe et al. 2014, Sakaji et al. 2018).

While courtship and spawning were visually confirmed from five of the six tagged captive kingfish, low light levels when courtship and spawning mostly occurred, i.e., at night, dusk, and dawn (Poortenaar et al. 2001, Moran et al. 2007), limited the number of spawning events which could be visually confirmed via video footage. Induced spawning through hormone injections could have been used to increase the number of spawning events observed (e.g., Sakaji et al. 2018), but the acceleration signature from such events may not be representative of kinematics exhibited during naturally-occurring spawning (i.e., less courting or chasing), limiting its use to infer spawning events in free-ranging fish. Likewise, the use of additional artificial lighting to improve visibility in low light conditions (e.g., at night, dawn) could affect fish behaviour and prevent spawning from occurring (Bromage et al. 1984, Hansen et al. 2001, Kissil et al. 2001). Instead, increased observation effort during dawn and dusk when spawning is expected to occur would likely increase the number of reproductive behaviours observed and improve predictive capacity of naturally-occurring courtship in the future.

The most frequently predicted behaviour of free-ranging kingfish at both the Neptune Islands Group and Coffin Bay was swimming, providing some support for the predictive power of this approach, given it would be expected that swimming should be occurring a majority of time by free-ranging individuals. However, escape was the most frequently occuring behaviour in three free-ranging fish, but it is unlikely that these fish spent more time escaping predators than swimming across 1 – 2 days. Acceleration signatures are also influenced by body size and locomotion of pelagic schooling fish (Noda et al. 2016), which may result in misclassification of behavioural classes between differently sized individuals. In addition to body size, free-ranging kingfish may exhibit larger tail strokes than captive fish constrained in tanks, resulting in fast regular swimming in free-ranging fish being allocated to escape behaviours. While I attempted to minimise these effects by attaching loggers to fish of similar size in both captive and free-ranging environments, free-ranging fish were slightly larger than captive individuals (91 – 105 *vs*. 99 – 151 cm). Escape behaviours invoked by pursuing individuals with a pole in the captive environment may also not be sufficiently comparable to natural escape responses in a free-ranging environment. For example, movements exhibited while escaping predators would likely differ from manoeuvres performed in tanks. Therefore, this may lead to the escape behaviours from the captive fish poorly translating in the model, contributing to high allocations of escape in some free-ranging individuals. Although this approach is effective for identifying some behaviours (e.g., courtship, feeding), the constraints of validating naturally-occurring behaviours in tanks can affect the accuracy of detecting others (i.e., escape) that are not well translated from captive to natural environments.

Access to captive kingfish from the aquaculture industry has previously enabled research describing spawning and reproduction in captivity (Poortenaar et al. 2001, Moran et al. 2007). Our study reveals, for the first time, information about the timing and locations of kingfish spawning in the wild. A total of 19 reproductive behaviours were identified in five of the eight free-ranging fish, although thirteen behaviours lasted less than 1 minute and might be misallocated behaviours. The six remaining behaviours lasted 14 – 109 minutes which is of similar duration to reproductive behaviours described by Moran et al. 2007. All but two of these behaviours occurred at dawn or dusk, resembling theories of spawning occurring predominantly during low light levels, e.g., dawn (Poortenaar et al. 2001, Moran et al. 2007) and supporting the validity of my results here. As tagging periods were targeted in Austral spring and summer conditions, temperature during free-ranging reproductive events (16.5 – 19.5°C) additionally met descriptions of hatching success in captive environments (15 – 26°C; Moran et al. 2007). Courtship was identified from fish tagged at both study sites, the Neptune Islands and Coffin Bay. While it is possible that the kingfish left the vicinity of the Neptune Islands or Coffin Bay after tagging, the location of the loggers upon recovery and high residency of kingfish at both these locations (Chapters 3, 5) suggest that the spawning observed occurred in areas within Coffin Bay and around the Neptune Islands. While these findings of courtship are encouraging, courtship events which do not match the described spawning profiles of kingfish (i.e., short duration, occurring in the middle of the day or night) may have been misclassified from other burst event behaviours with similar acceleration profiles. This reiterates that behaviours predicted by the RF model should be carefully reviewed and ground-truthed where possible regardless of the high accuracy and performance of the model (Valletta et al. 2017). It is also possible that the identified courtship events did not result in the successful release of gametes, which affects the suitability of using accelerometers to infer spawning events (Graham & Castellanos 2005). However, even if the tagged fish does not release gametes, the indication that courtship or spawning attempts are taking place is a reliable indication of timing and areas used for reproductive events (Graham & Castellanos 2005) and that accelerometers can help identify when spawning is occurring. Integrating additional sensors (e.g., depth sensor) or tags (e.g., acoustic or satellite tags) means studies may also use accelerometers to infer patterns in migrations, as well as spatial and habitat use to determine spawning location and depth for spatial and temporal management efforts to protect spawning aggregations (Flavelle et al. 2002, Pecl et al. 2006, Rowell et al. 2015).

A limitation of behavioural studies such as this present chapter using accelerometers is the individual variation in behaviours, movements, and swimming performance between captive and wild individuals. Captive environments are space-limited and often have manipulated conditions which may skew its performance for use on datasets from free-ranging individuals. In addition, ML algorithms such as the RF model developed in this study do not account for the temporal auto-correlation expected in timeseries (Brewster et al. 2018, Leos-Barajas et al. 2017). While there are very few ways to combat these issues (e.g., Hidden Markov models; Leos-Barajas et al. 2017), future studies may attempt to ground-truth data in the wild environment through means of animal-born video cameras. However, these technologies come with a trade-off of limited battery-life, low visibility under poor lighting, and additional weight to accelerometer packages potentially influencing behavioural profiles.

2.6 Conclusions

Combined use of accelerometers and supervised machine learning algorithms has become prevalent as a method of characterising behaviour classes from both terrestrial and marine taxa. This study is the first to use a trained classification model to identify behaviours of free-ranging pelagic fish.. Through direct observations of courtship and spawning behaviours, these findings provide the first study to predict naturally-occurring courtship of a large pelagic fish, yellowtail kingfish, via the use of accelerometers and ML. These findings contribute to more detailed approaches of identifying naturally-occurring behaviours, which in the past have been only inferred through increase in general activity patterns, or destructive sampling approaches. This method may contribute to a detailed understanding of timing and location of important reproductive aggregations of large pelagic fish, and in turn the effective spatial and temporal management strategies required to protect spawning populations.

Chapter 3

Investigating the effects of shark tourism on the daily residency and movements of a non-focal pelagic fish

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3.1 Abstract

Marine wildlife tourism is increasing in popularity, with operations targeting a wide range of taxa globally. While previous studies have mostly focused on assessing the effects of provisional feeding from tourism on focal species of such operations, non-focal species that unintentionally feed upon provisioned food sources have largely been overlooked. This study improves our understanding of the effects from provisioning shark cage-diving tourism on the movements and behaviours of a non-focal pelagic fish. I used acoustic tracking to determine the effects of shark cage-diving tourism on the residency and space use of yellowtail kingfish (*Seriola lalandi*) at the Neptune Islands, South Australia. I revealed that while cage-diving did not affect the weekly residency and space use of kingfish, daily time spent at the islands and location of kingfish was influenced by the presence of operators. Acoustic attractant did not influence kingfish behaviours, but operators using food-based attractant increased the average daily time spent at the Neptune Islands by ~27% (from 230.6 ± 6.8 to 293.8 ± 5.5 minutes). Similarly, kingfish were observed closer to operators using food-based attractant (217 ± 4.82 m from vessel) compared to acoustic operators (412 ± 29.5 m from vessel). Findings from this chapter identify changes in the daily behaviour of kingfish at the Neptune Islands as a result of food-based provisioning from shark cage-diving, which demonstrates that non-focal large pelagic species can be affected by shark diving tourism. These results highlight that food-based attractant used from tourism may also lead to longer-term effects on the physiological condition and energetic budgets of these individuals.

3.2 Introduction

Wildlife tourism is gaining popularity globally, and is one of the fastest growing sectors of the tourism industry (Wearing & Neil 2009, Barnes et al. 2019). These practices often provide substantial socio-economic benefits by offering an alternative to the consumptive use of wildlife (e.g., hunting, fishing) that results in assorted conservation and economic benefits to local communities (Huveneers et al. 2017a, Apps et al. 2018). The focal-species of most wildlife tourism ventures are often large, charismatic animals which can occur infrequently and sporadically. As a result, tourism operations often use a food-based attractant (i.e., provisioning, Meyer et al. 2021b) to aggregate these targeted individuals and increase the chance of a consistent and up-close encounter for tourists (Knight 2009; Meyer et al 2021a). However, food-based provisioning from these operations can modify the movements and behaviour of focal species (Chateau & Wantiez 2008, Bruce & Bradford 2013), and affect their health and condition by changing their diet (Brena et al. 2015, Trave et al. 2017, Patroni et al. 2018, Meyer et al. 2020). While provisioning practices are aimed at attracting targeted animals, other non-focal species are frequently observed feeding on the food provided (often termed indirect feeding, Meyer et al. 2020). Consequences for these non-focal individuals have been found to replicate effects on focal species, with altered movements (Rizzari et al. 2017), increased risk of predation (Milazzo et al. 2006), nutrient loading (Turner & Ruhl 2007), parasite infestations (Vignon et al. 2010), and shifts in diet reflected through fatty acid and stable isotope profiles (Meyer et al. 2020). However, despite the potential impacts on non-focal species, literature surrounding implications from provisioning tourism has been largely skewed towards focal species (93% of studies, Trave et al. 2017), with no studies investigating these impacts for non-focal large-pelagic fishes (Trave et al. 2017). The need for further research to assess impacts of provisioning from wildlife tourism on non-focal species has also been highlighted in recent reviews (Gallagher and Huveneers, 2018; Gallagher et al., 2015) and management frameworks (Higginbottom et al. 2003, Meyer et al. 2021a)..

White shark (*Carcharodon carcharias*) cage-diving is a popular form of wildlife tourism, which occurs in five countries worldwide, i.e., Australia, South Africa, the United States of America, Mexico (Guadalupe Island), and New Zealand. In Australia, the Neptune Islands Group Marine Park (South Australia), is the only location where white shark cage-diving is permitted (Figure 1.1). At this site, two companies use a near-constant plume of food-based attractant (chum; mixture of minced fish, usually southern bluefin tuna *Thunnus maccoyii*) and tethered baits to attract sharks into the field of view of tourists (Huveneers et al. 2017b, Meyer et al. 2020). A third company uses acoustic attractant (music played through underwater speakers) to attract sharks. The industry is regulated to ensure that operators are not permitted to deliberately feed sharks (DEW 2016), however, baits may be consumed if the handler is not fast enough to react and withdraw the tether (Huveneers et al. 2013). Although white sharks are not intentionally fed, a number of small, non-focal species (e.g., yellowtail kingfish *Seriola lalandi*, trevally *Pseudocaranx* spp.) are often observed feeding on smaller particles of chum and bait that disperse into the water column.

Yellowtail kingfish (*Seriola lalandi*, kingfish hereafter) are a large-bodied coastal pelagic fish distributed globally in temperate and sub-tropical environments (Gomon et al. 2008). Kingfish are a highly-valued focal for recreational and commercial fishers (Stewart et al. 2004, Hughes & Stewart 2020), and contribute to an expanding aquaculture industry (Tanner & Fernandes 2010, Symonds et al. 2014). Mark-recapture tagging programs have identified that kingfish are capable of migrating large distances (up to 1000's of kilometres; Brodie 2016, Gillanders et al. 2001, Saul & Holdsworth 1992), but have also revealed high levels of site-fidelity with individuals often recaptured within 5 km of their original tagging location (Hutson et al. 2007, Hobday & Campbell 2009). Movements of kingfish along Australia's south-eastern coastline are predominantly driven by suitability of oceanographic conditions, with increased movements to offshore island groups during warmer months, and high residency and site-fidelity in shallow estuaries during cold months (Brodie 2016). At the Neptune Islands, kingfish are often observed behind cage-diving tourism vessels year-round, feeding on smaller particles of bait and chum which enter the water column to attract white sharks.

This indirect feeding from cage-diving operations has the potential to change the frequency of important behaviours, e.g., spawning (see Chapter 2), in addition to changing movements and space use associated with natural foraging and crepuscular patterns (Myers et al. 2016, Rizzari et al. 2017), or halting migrations associated with habitat selectivity (Brodie et al. 2016, Champion et al. 2020) by leading kingfish to remain at the Neptune Islands for longer than they would naturally. As a result, the chumming occurring during white shark cage-diving may lead to kingfish spending more time at the tourism site even when the habitat becomes less optimal from a physiological or fitness perspective, e.g., less suitable oceanographic conditions (Champion et al. 2020).

In this study, I used implanted tags and an array of acoustic receivers to examine how kingfish residency and space use is affected by the white shark cage-diving industry. Cage-diving in the Neptune Islands typically operates on most days (i.e., 261 days of the year, 6 days per week), with the number of operators present varying between zero and three operators per day (two food-based, one acoustic attractant). Furthermore, the temporary halt in cage-diving operations in mid-2020 due to COVID-19-related travel restrictions provided a unique opportunity to investigate the behaviour of kingfish when operators were absent over longer periods (Huveneers et al 2021). Specifically, I hypothesised that 1) weekly residency of tagged kingfish increases and space use contracts to within proximity of cage-diving operations as the number of days operators were present increased; 2) daily time spent by kingfish at the Neptune Islands increases when food-based operators were present; and 3) kingfish occur closer to food-based operators than acoustic-based operators when present.

3.3 Materials & Methods

Study site

The Neptune Islands Group (Ron and Valarie Taylor Marine Park; Figure 1.1) is a group of offshore granite islands 60 – 70 km towards the southeast from Port Lincoln, South Australia. The islands group consists of the North Neptune islands (35°13.944’S; 135°03.834’E) and South Neptune islands (35°19.518’S; 135°06.762’E), located 12 km south from the North Neptune Islands. While shark tourism operators run trips to both groups, approximately 85% of the trips occur at the North Neptune Islands (C. Huveneers, unpublished data) due to its closer proximity to Port Lincoln where vessels depart. Operations run year-round, with tourism vessels permitted to run trips ten days every fortnight, with four ‘operator-free days’ to reduce tourism pressure and minimise any potential effects on focal white sharks (DEW 2016).

Capture of Kingfish

Between August 2018 and May 2020, 18 kingfish (> 80 cm total length) were captured with hook and line at the Neptune Islands and tagged with V16A 98 x 16 mm (17.3 g; 1090 days battery life) or V13A 48 x 13 mm (6.5 g; 368 days battery life) acoustic activity tags (Innovasea, Nova Scotia, Canada, innovasea.com). Fish were inverted upside down in a padded cradle, maintaining water flow over the gills using a hose inserted in the mouth, inducing a tonic immobility reflex where the fish do not respond to external stimuli (Wells et al. 2005). A small incision was made, and the acoustic tag was inserted in the peritoneal cavity, before being stitched with absorbable sutures (Monosyn 2-0/3-0, B. Braun, Hessen, Germany). Acoustically tagged individuals were also tagged with an external identification tag to avoid double-tagging, if recaptured.

Receiver Deployments

An array of 16 V2AR acoustic receivers (Innovasea, Nova Scotia, Canada, innovasea.com) were deployed in November 2018, with 15 receivers positioned at the North Neptune Islands (Figure 3.1) and 1 positioned at the South Neptune Islands. Due to the infrequency of operators to visit the South Neptune Islands, only data from receivers at the North Neptune Islands group were included (hereafter North Neptune Islands is referred to as Neptune Islands). Prior to deployment of the acoustic receiver array, range testing was undertaken to assess detection range. Receivers were positioned ~350 m from each other to ensure simultaneous tag detection by 2 – 3 receivers and enable to estimate high-precision fish positions throughout the study period. Receivers were deployed in 10 – 40 m water depth on low-profile moorings ~2 m high with 70 – 100 kg of anchor chain as weight and sub-surface floats. Receivers were strategically positioned where cage-diving boats anchor which is also the side of the island most protected from dominant winds and swell (Figure 3.1). The array was deployed for nearly two years with downloads occurring annually. Acoustic receivers also recorded water temperature hourly, enabling calculation of daily and weekly mean temperature (Figure 3.2).

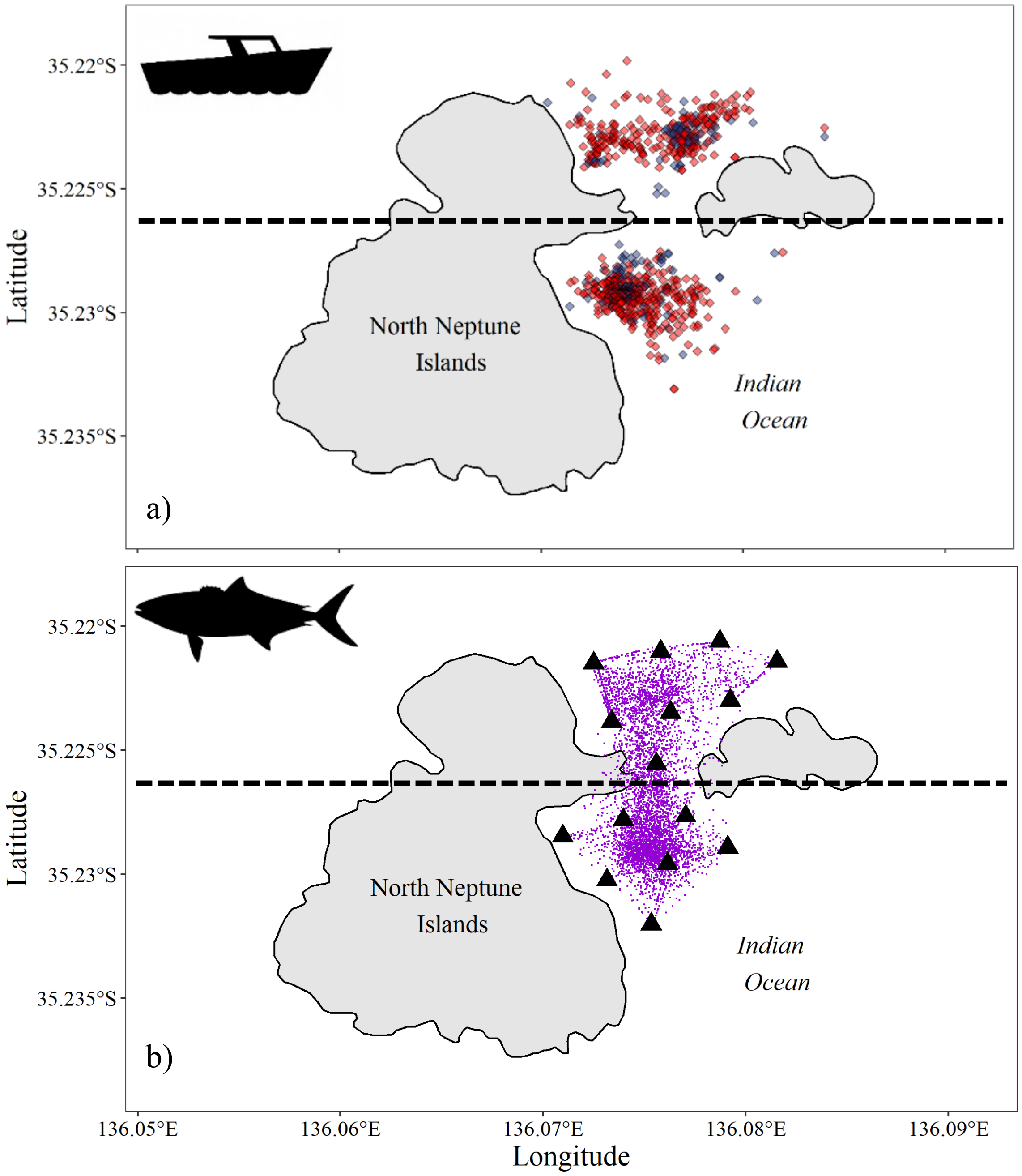

Figure 3.1. Map of the Neptune Islands Group showing a) operator anchoring locations (acoustic attractant in blue, food-based attractant in red); and b) kingfish positions within the array during daylight hours (60-minute center of activities). Horizontal dashed line represents 'north-' and 'south-eastern' sides of the island. VR2AR acoustic receivers are presented as black triangles. See Figure 1.1 for location of the Neptune Islands in South Australia.

Data analysis

Daily operator position was collected through a customised daily e-logbook (Fulcrum^{TM} from November 2018 to February 2019 and White Shark Cage-Diving app from March 2019 to August 2020; Nazimi 2018). For each day of operation, cage-diving operators recorded time at the Neptune Islands using food or acoustic attractant and anchor location (coordinates). Weekly sums of the number of 'operating days' were calculated based on the iso-week calendar (beginning on Monday of each week) using the *isoweek()* function from the 'lubridate' (version 1.7.9) package in R (R Core Team 2020). Daily 'operator types' were determined based on the configuration of operators present on a given day: one food-based, two food-based, acoustic only, one food-based + acoustic, all operators, or no operators. To identify spatial effects of operators across the island, the group was categorised as the north-eastern and south-eastern sides (latitude ≥ 35°13.680'S) based on the two distinct groupings of operating locations (Figure 3.1).

Analyses of kingfish residency and space use were performed in the R statistical environment (version 1.2.5033). The 'VTrack' package (version 1.21) with Animal Tracking Toolbox extension (Udyawer et al. 2018) was used to calculate position in the array, residency, and space use. Residency (days detected divided by days at liberty) was calculated using the *detectionSummary* function, with overall residency (i.e., for the full period of tag operation) and weekly subsets calculated. Residency calculations from the first and last week of the recording period were removed, due to shortened weeks during receiver deployment and collection. Approximate kingfish positions within the acoustic array were estimated through 60-minute centres of activity (COAs) using the *COA* function in VTrack, to enable sufficient signal receptions from transmitters for accurate location estimates (Simpfendorfer et al. 2002).This method assumes that detection probability is a linear function of distance, and calculates the position based on the mean of receiver detections weighted by the number of detections at each receiver within the array. Although COAs provide a mean-weighted estimate of an individual's position, and are conventionally used to infer spatial and temporal patterns of movement within acoustic arrays, an attempt to calculate refined positioned through a Vemco Positioning System (VPS) was made based on the 3-receiver time-difference-of-arrival algorithm (Espinoza et al. 2011). However, there was low success of conversion from detections to position estimates reduced detection range during high noise periods and fish positioned around the fringe of the array. As a result, COAs were used in this study to infer kingfish positions while maintaining abundant position estimates to infer change due to tourism operations. Estimates of space use (weekly and overall) were calculated using 50% contour of Brownian-Bridge Kernel Utilisation Distributions (BBKUD-50) based on COAs, using the *HRSummary* function. The Brownian-Bridge approach was used rather than other metrics of space use (i.e., fixed KUD) as it accounts for autocorrelation between sequential location estimates by incorporating movement paths, and more accurately represents space use in highly mobile animals such as kingfish (Horne et al. 2007, Udyawer et al. 2018). Choice of smoothing parameter associated with relocation error (σ_2) for the Brownian-bridge movement model was undertaken using an *ad hoc* approach (Kie 2013), with the smoothing parameter associated with animal speed (σ_1) estimated using a maximum likelihood estimator (see Horne et al. 2007).

To identify the acute responses of kingfish to the provisioning from cage-diving operations, daily metrics of residency (time spent) and space use (distance to closest vessel) were calculated. Daily time spent by tagged kingfish within the array was calculated as the difference in time (minutes) between the first and last detection for each individual detected on that day. Distance between kingfish and the closest operator vessel were estimated using the *distHarversine* function (package: ‘geosphere’ version 1.5.10) which measures the shortest distance between two points, using coordinates of kingfish COAs and operator anchor locations. Sunrise and sunset times were estimated using the *getSunlightTimes* function (package: ‘suncalc’ version 0.5.0), and only detections occurring between the end of sunrise and the beginning of sunset were used for analyses as the operators only ran trips and were present on the Island during daylight hours.

Generalised linear mixed models (GLMMs) were used to test the effects of cage-diving operations on kingfish residency and space use at weekly and daily scales using the *lmer* or *lme* function in the ‘lme4’ R package (Bates et al. 2014). Individual fish (Transmitter) was included as a random effect ($_{\text{rand}}$) to account for potential lack of independence in behaviour within fish. Potential effects of temporal autocorrelation on the residency and space use of kingfish were accounted for by using an AR1 correlation structure in the weekly models (form = ~WeekNumber|Transmitter; $_{\text{corr}}$). As AR1 correlation structure is not possible through the *lmer* function with repeated samples for the same time increment, daily models included week number as a random factor with slopes and intercepts randomised by the weekly number of operating days. Number of operating days (0 – 7; weekly GLMM) and operator type (no operators, acoustic only, one/two food-based, food-based + acoustic, all operators; daily GLMM) were included as fixed factors, along with temperature recorded by the acoustic receivers to test for the potential effects of operators and temperature on kingfish movements. The most appropriate statistical family, transformation, and validity of the model was determined by examining the distribution of the response variable and visual inspection of residuals. A square-root transformation was deemed appropriate for daily time spent and distance from operator values, while a $\log_{10}$ transformation was required for the weekly models to maintain normality of residuals. All model combinations of fixed-effect terms were run using the *dredge* function (package: ‘MuMIn’; version 1.43.17; Barton 2020) and ranked using Akaike’s information criterion corrected (AIC_C) for small sample size (Burnham & Anderson 2002). The *r.squaredGLMM* function was then used to estimate marginal (fixed-factor) and conditional (all factors) R^2 values for each model. Full models used for GLMM's were:

Weekly model:

$$\text{detection index/BBKUD-50} = \text{Operator days*Temperature} + \text{Operator Days|Transmitter}_{rand} + \text{WeekNumber|Transmitter}_{corr}$$

Daily model:

$$\text{time spent/distance to operator} = \text{Operator Type*Temperature} + \text{Operator Type|Transmitter}_{rand} + \text{Operator Type|WeekNumber}_{corr}$$

3.4 Results

Operator Days

Between November 2018 and August 2020, white shark cage-diving operators were present at the Neptune Islands on 435 / 637 days (68%) of the study period. Operators were most often present on 6 / 7 days of the week (n = 32 weeks; 35% of all weeks; Figure 3.2), but there were some weeks where operators visited the islands on all days (n = 5 weeks, i.e., 5% of all weeks). The period with the least tourism activity was a 6-week period between March and August 2020 when COVID-19 controls and travel restrictions were in place and no cage-diving operators visited the Neptune Islands (Figure 3.2).

Kingfish detections

Between November 2018 and August 2020, the number of detections per kingfish ranged from 35 to 58,771 (mean = 14,320 ± 3,959 detections). Kingfish were detected at all fifteen receivers deployed at the North Neptune Islands. A total of 13,398 kingfish positions were calculated in the acoustic array based on 60-minute COAs (Figure 3.1b), with positions mostly occurring on both north-eastern (44% of locations) and south-eastern sides (56% of locations) of the North Neptune Islands.

Residency and space use summary

Mean kingfish residency at the Neptune Islands over the near two-year period was 0.52 ± 0.04 (range: 0.29 – 0.79; Figure S5, Table S1) which is representative of individual fish being present within the array on 52% of all days. Monthly residency of all kingfish was highest during January (0.59 ± 0.06) and December (0.59 ± 0.06) and lowest during July (0.39 ± 0.06) and August (0.35 ± 0.06), but persistence of kingfish at the islands remained consistent throughout the year (0.35 – 0.59). Brownian-

Bridge Kernel Utilisation Distribution estimates were estimated from 16 kingfish based on 6 to 2,233 COA positions (mean = 788 ± 145.6 positions). One kingfish (Transmitter ID 4310) was only detected 35 times (Figure S5) from 11 receivers, thus, a reliable space use metric could not be estimated for this individual. Space use (50% BBKUDs) of tagged kingfish ranged from 0.15 to 1.97 km^2 (mean = 0.59 ± 0.05 km^2; Figure S6). Space use was smallest during July (0.41 ± 0.06 km^2) and August (0.40 ± 0.05 km^2), and the largest during the months of March (0.54 ± 0.02 km^2) and April (0.53 ± 0.07 km^2) but remained consistent with kingfish using all areas inside the array across all months (range: 0.40 – 0.53 km^2; Figure 3.2).

Weekly residency and space use

Weekly residency of tagged kingfish at the Neptune Islands ranged from 0.14 (1 day detected) to 1 (present on all 7 days; 0.56 ± 0.03). Water temperature or the number of operator days did not influence the weekly residency of kingfish, as the top-ranked model was the null model that only included the random effect, Transmitter ID (wAIC_c = 0.76; Table 3.1; S3.5; Table S2). Only 12% of the variation was explained by this model, with some variation in residency between years. Weekly space use of kingfish ranged from 0.11 to 1.05 km^2 (mean = 0.32 ± 0.01 km^2). The top-ranked model was again the null model (wAIC_c = 0.60; Table 3.1), indicating that the number of operating days nor the temperature was influencing weekly space use of kingfish, with the individual Transmitter ID explaining more of the deviance than the weekly residency model (R_c = 0.46 *vs*. 0.12).

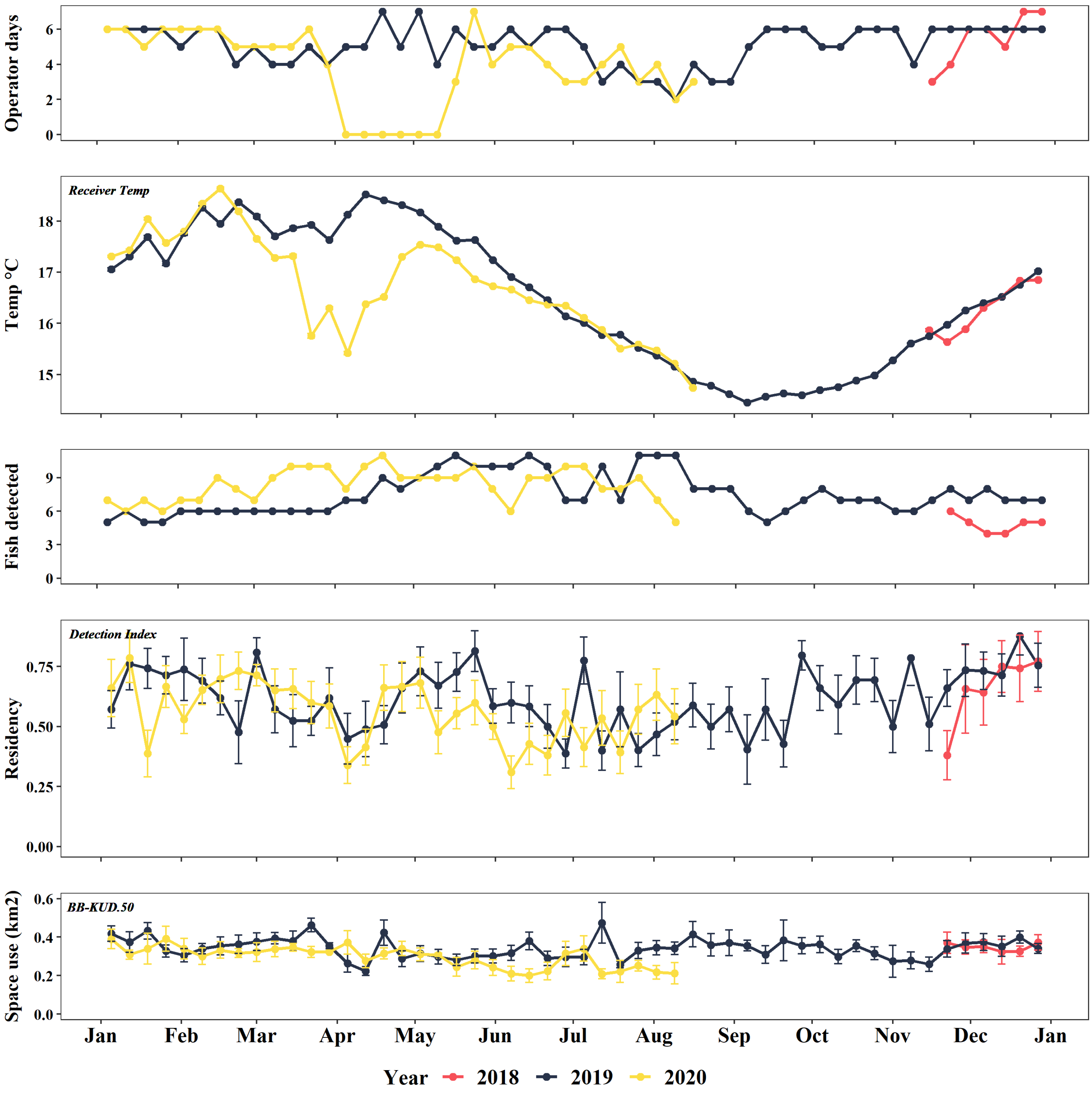

Figure 3.2. Weekly summaries of operator and kingfish residency and space use at the Neptune Islands Group Marine Park; a) number of operating days; b) water temperature (temp) ± se; c) number of fish detected; d) residency ± se; and e) space use (BBKUD-50 ± se).

Table 3.1. Summary of models estimating effects of cage-diving operations (weekly operator days; opdays) on kingfish a) residency and b) space use (BBKUD-50). df, degrees of freedom; AIC$_c$, Akaike's information criterion corrected for small sample size; ΔAIC$_c$, difference in AIC$_c$ between the current and the top-ranked model; wAIC$_c$, model probability; R$_m$, marginal (fixed effects) R^2; R$_c$, conditional (fixed and random effects) R^2.

Model	**df**	**logLik**	**AIC$_c$**	ΔAIC$_c$	**wAIC$_c$**	**R$_m$**	**R$_c$**
a) Weekly residency (days detected/days at liberty)							
Residency ~ 1 (intercept only)	**4**	**-14.9**	**37.8**	**0**	**0.76**	**0**	**0.116**
Residency ~ Temperature	5	-15.7	41.4	3.64	0.12	0.014	0.122
Residency ~ Opdays	5	-15.8	41.6	3.85	0.11	0.017	0.105
Residency ~ Temperature + Opdays	6	-17.1	46.4	8.65	0.01	0.029	0.117
Residency ~ Temperature * Opdays	7	-20.8	55.7	17.91	0.00	0.031	0.121
b) Weekly space use (Brownian-bridge Kernel Utilisation Distribution, 50%)							
Space use ~ 1 (intercept only)	**4**	**490.4**	**-972.7**	**0**	**0.97**	**0**	**0.465**
Space use ~ Temperature	5	487.7	-965.3	7.43	0.02	0.006	0.483
Space use ~ Opdays	5	486.1	-962.1	10.66	0.01	0.000	0.479
Space use ~ Temperature + Opdays	6	483.4	-954.7	18.06	0.00	0.006	0.497
Space use ~ Temperature:Opdays	7	478.6	-942.9	29.84	0.00	0.006	0.495

Daily time spent at the North Neptune Island

The daily time that tagged kingfish spent at the North Neptune Islands acoustic array ranged from 1 second (i.e., one detection) to 922 min (mean = 68 ± 13.3 min) and was influenced by temperature and operator type (wAIC$_c$ = 0.84; Table 3.2; Figure 3.3a). While the total variance explained was 24%, most of this was from the random factor (fish ID, 22%), with only 2% explained by the fixed factors. Daily time spent within the acoustic array at the North Neptune Islands was shortest on those days when no operator was present (230 ± 6.8 mins) and on days when only an acoustic attractant was used (222 ± 19.4 mins; Figure 3.3). Comparatively, kingfish spent more time within the acoustic array on days when food-based attractant was present, regardless of whether it was one (276 ± 8.4 mins) or two operators present (276 ± 12.7 mins; Figure 3.3a; Table S2). Daily time spent in the receiver array was highest on days when all three operators were present at the islands (329 ± 11.7 mins; Figure 3.3a). Temperature had a small, but positive influence on daily time spent of kingfish (Figure 3.3a), with kingfish spending more time within the array on warmer days.

Distance between fish and cage-diving operations

During times that cage-diving vessels frequented the Neptune Islands, kingfish were on average 202.6 ± 6.2 m from the closest operator. The distance that tagged kingfish occurred in proximity to operator vessels was influenced by operator type (top-ranked model $wAIC_c = 0.37$; Table 3.2). While the second and third best model had similar $wAIC_c$ (0.34 and 0.28 respectively) and included either temperature (third best model) or the interaction between operator type and temperature (second best model), the variance explained did not substantially increase when including these factors (from 44% for the top-ranked model to 46% and 45% for the second and third best model respectively). Most of that variance was attributed to the random effect (individual fish ID, $R_c = 40\%$). Distance between kingfish and cage-diving operator vessels was greatest on days when only acoustic attractant operator was present (mean = 412 ± 29.6 m; Figure 3.3b). Kingfish came closer to cage-diving operations when a food-based attractant was used (Figure 3.3b), but there was no effect from an increased number of these chumming operators (180 ± 9.22 m [when acoustic and food-based present] - 234.4 ± 8.5 m; Figure 3.3b). The influence of the food-based operators on kingfish position in the Neptune Islands array was supported by increase in likelihood of fish to be detected on the same side of the island as chumming operators (Figure 3.4a). When no operators frequented the islands, kingfish showed a slight preference to the southern side of the island, occurring here 54% of the time (Figure 3.4a). Kingfish position was similar when only acoustic-attracting operators were present on the northern or southern sides of the island (Figure 3.4b, c). In comparison, this likelihood of kingfish to occur on the southern side of the island increased to 75% when food-based operators were present on this side (Figure 3.4e). The same effect was observed when operators where anchored on the northern side, with 71% of detections occurring on this side of the island during these times (Figure 3.4d).

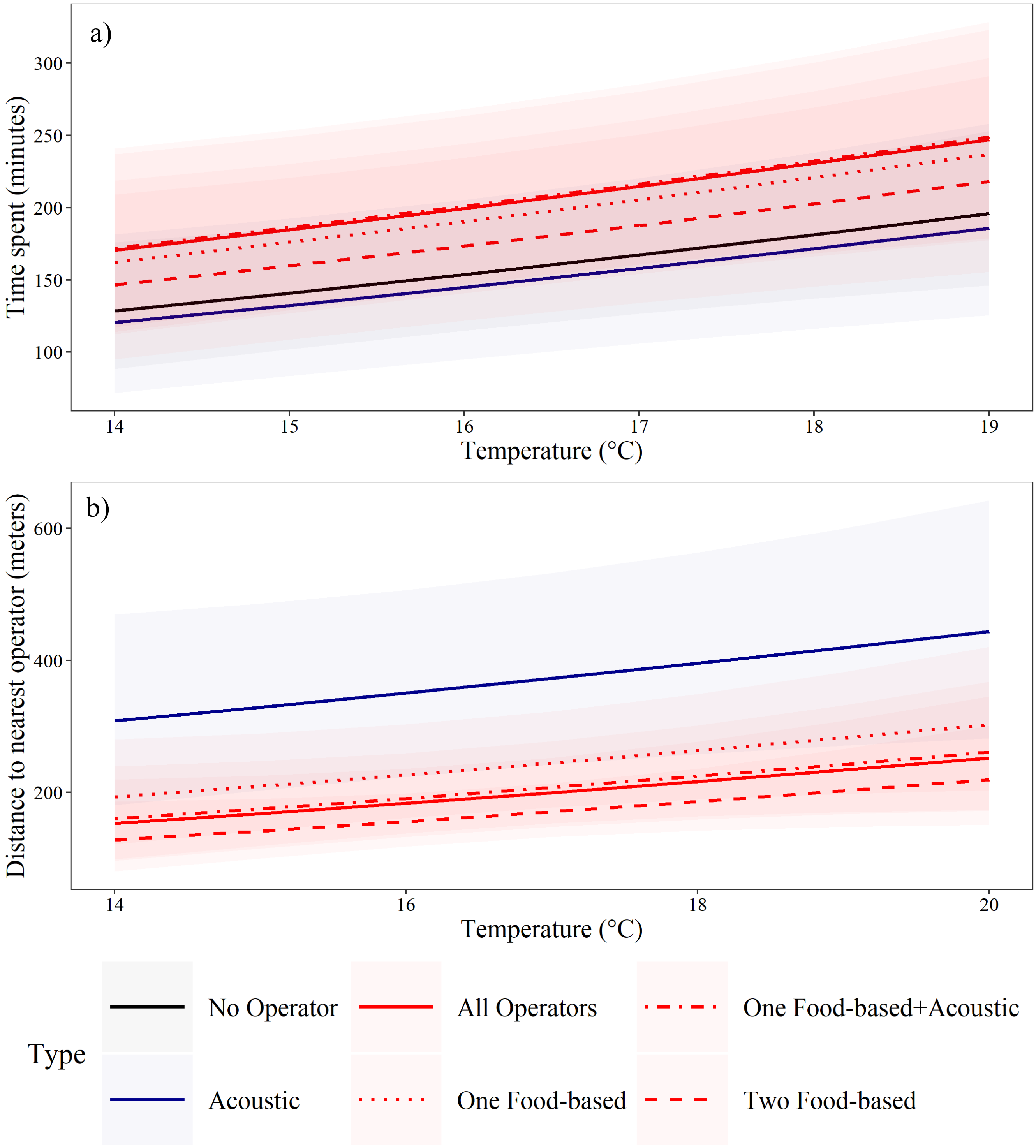

Figure 3.3. Interaction between the predicted a) time spent and b) distance to the closest cage-diving operator with temperature at the Neptune Islands across temperatures from Generalised Linear Mixed Models. Operating types using food-based attractant are shown in red, acoustic attractant in blue, and no operator days in black.

Table 3.2. Summary of models estimating effects of operator type (type) on daily time spent and proximity of kingfish to the closest operator vessel. df, degrees of freedom; AIC_c , Akaike's information criterion corrected for small sample size; ΔAIC_c , difference in AIC_c between the current and the top-ranked model; $wAIC_c$, model probability; R_m, marginal (fixed effects) R^2; R_c, conditional (fixed and random effects) R^2.

Model	**df**	**logLik**	**AIC_c**	**ΔAIC_c**	**$wAIC_c$**	**R_m**	**R_c**
a) Daily time spent (time between first and last detection)							
Time ~ Type + Temperature	**50**	-9575.2	19252.4	0	0.78	0.02	0.26
Time ~ Type	49	-9578.1	19256	3.69	0.12	0.01	0.26
Time ~ Temperature	45	-9583.1	19257.8	5.42	0.05	0.01	0.27
Time ~ Type + Temperature + Type*Temperature	55	-9573.1	19258.4	6.07	0.04	0.02	0.26
Time ~ 1 (intercept only)	44	-9586	19261.4	9.0	0.01	0.00	0.27
b) Distance to nearest operator (m)							
Distance ~ Type + Temperature	37	-4019	8115.2	0	0.43	0.04	0.46
Distance ~ Temperature + Type + Temperature*Type	41	-4015	8115.7	0.49	0.34	0.04	0.46
Distance ~ Type	36	-4021	8116.6	1.35	0.22	0.03	0.44
Distance ~ 1 (intercept only)	32	-4029	8124.2	8.92	0.01	0.00	0.44
Distance ~ Temperature	33	-4029	8124.9	9.66	0.00	0.01	0.45

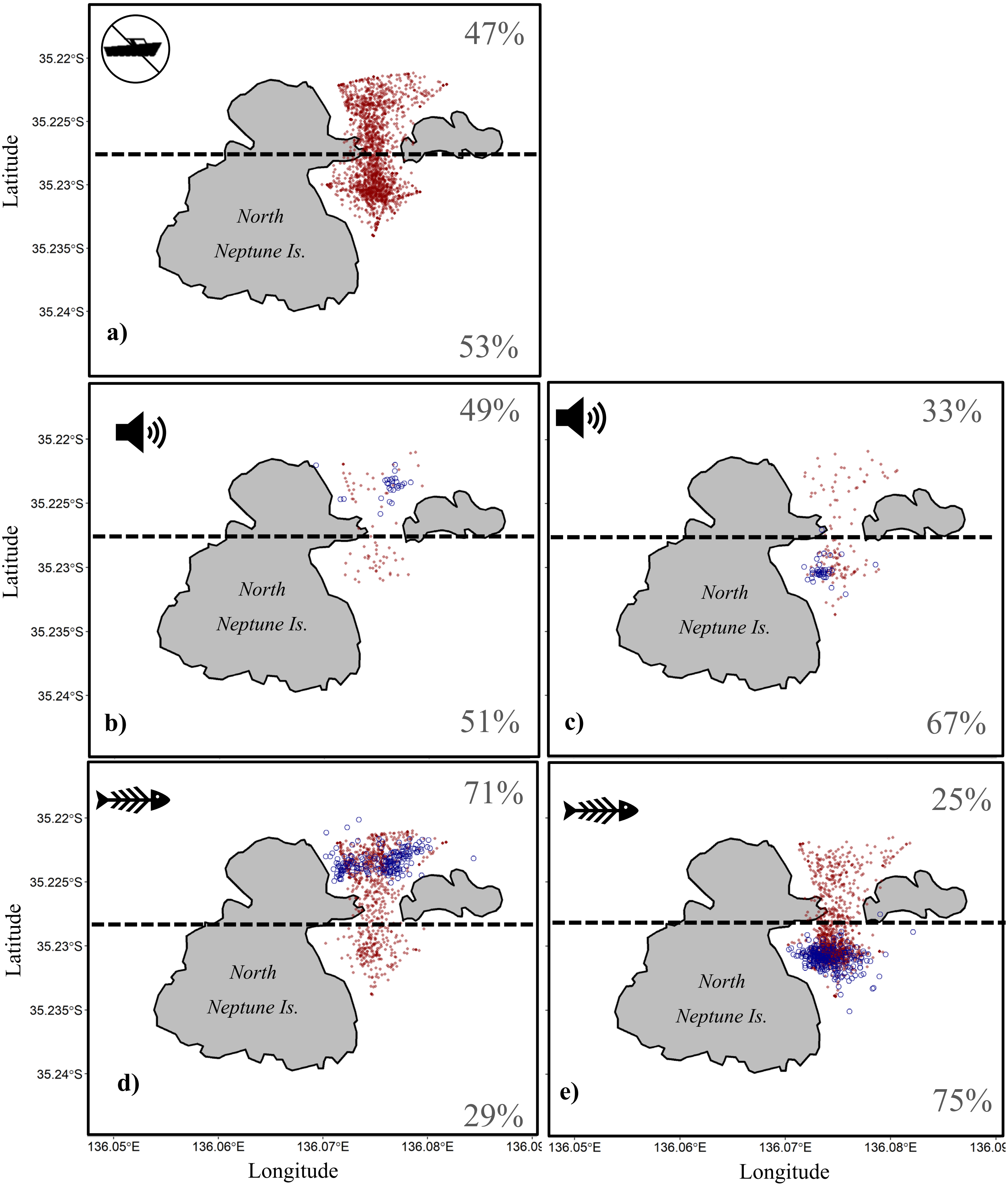

Figure 3.4. Estimated hourly COAs of kingfish (red) in relation to the location of cage-diving operators (blue). Positions on days when no operators were present (a), on days when operators were

using acoustic (b, c) or food-based (d, e) attractant (b, d) shows days when operators where anchored on the northern side of North Neptune Island; (c, e) shows days when operators were anchored on the southern side. Percentage of positions occurring on the respective half of the island during operator treatments are provided.

3.5 Discussion

This study improves the understanding of kingfish residency and space use at a temperate offshore island group and reveals the impacts of shark cage-diving tourism on a non-focal large pelagic fish. Findings show that kingfish can be year-long residents of the North Neptune Islands, with tagged individuals exhibiting a high residency index within the array throughout the year and some individuals spending up to 79% of days at the islands. While cage-diving tourism did not affect the weekly residency and space use of kingfish, the time that kingfish spent within the North Neptune Islands acoustic array each day increased when food-based attractant are used. This shift in daily residency therefore delays the time of day when kingfish naturally left, which could be linked to diurnal behaviours linked to foraging and minimising predation risk. The use of acoustic attractant did not have the same effect. In addition, kingfish daily space use was also affected by the presence of bait and chum, with kingfish occurring closer to cage-diving vessels using food-based attractant than acoustic attractant and shifting its position to match anchoring locations of chumming operators.

Kingfish are highly mobile and migratory pelagic fish, with movements and residency largely driven by changing oceanographic conditions (Gillanders et al. 2001, Brodie 2016, Champion et al. 2018). Such seasonal migrations are common in many coastal-pelagic fishes, with movements tracing optimal conditions to access resources and increase recruitment opportunities (Golovanov 2006, Walli et al. 2009, Briscoe et al. 2017). Previous descriptions of kingfish movements have demonstrated northerly latitudinal changes in winter, with increased residency around offshore islands in summer when water temperature is warmest, often with an complete exodus at these islands during winter (e.g., Lady Julia Percy Island [J Rizzari pers. obs.], Coffin Bay [see Chapter 5], Brodie 2016). In contrast, most kingfish tagged at the Neptune Islands remained inside the array throughout most of the year, with fish residing at the islands during all months. This opposing trend in the residency of kingfish at the Neptune Islands compared to observations at other offshore islands may be indicative of an effect of cage-diving tourism, where a reliable supply of an provisioned food source is altering the cues that kingfish naturally use to select optimal habitat (Meyer et al. 2020, Semeniuk 2021). As a result, kingfish may choose to remain at the Neptune Islands for extended periods, rather than moving away from the islands in response to seasonal fluctuations in food availability and preferable habitat conditions (Champion 2019, Champion et al. 2020b). However, despite the tendency of kingfish to be detected at the Neptune Islands year-round, all kingfish occasionally left the area for extended periods throughout the year (from several weeks up to 5 months; Figure S5). Additionally, three individuals were detected at the South Neptune Islands (~12 km from North Neptune), and two individuals were detected over 1,800 km away in Narooma, Batemans Bay and Manly in New South Wales between August, and December 2020. One of these individuals was also detected off Victor Harbor, South Australia, ~230 km from the Neptune Islands further contributing information about the spatial movements of kingfish across south-eastern Australia. While the year-round residency of kingfish at the Neptune Islands is high compared to previous studies (e.g. Brodie 2016, Udyawer et al. 2018), large-scale movements to other offshore island groups and interstate show that even if the cage-diving industry may be contributing to high residency, it does not stop kingfish from occasionally undertaking large-scale movements which may be attributed to prey availability (Nøttestad et al. 1999), or spawning migrations (Axenrot & Hansson 2004, Barbaro et al. 2009) and pursuing optimal environmental conditions (Champion et al. 2018).

Despite no effect from the number of operating days on the weekly residency of kingfish, the amount of time that kingfish spent at the North Neptune Island array each day increased by 17% (63 ± 5 minutes) when food-based operators occurred, compared to days that no operators or only acoustic-attractant were present. The lack of effect when acoustic attractant was used by operators suggests that kingfish were attracted to bait and chum input, rather than simply the presence of the operator vessels. Diurnal undulations in persistence and movements across habitats in coastal-pelagic fish such as kingfish are common, with many species adapting habitat use strategies that favour optimal foraging conditions (i.e., light availability) and prey availability (Horwood & Cushing 1978; Buckley et al. 1994). Prolonged time spent by kingfish at the Neptune Islands because of provisioning from cage-diving operations therefore has the potential to disrupt natural foraging behaviours, leading to more reliance on the food-source supplied from cage-diving operations and less time foraging for natural prey items. However, kingfish maintained high residency even during COVID-19 lockdown restrictions in April – May 2020, when no operators frequented the Neptune Islands. Although, it is difficult to infer whether this high residency is attributed to provisioning or natural residency due to the lack of historical data prior to the onset of tourism operations. The prolonged daily duration of kingfish at the Neptune Islands may contribute to the documented shift in dietary profiles where kingfish diets more closely resemble *T. maccoyii* used as bait rather than natural prey items observed at control sites (Meyer et al. 2020), and has the potential to reduce kingfish physiological condition and fitness (Bessa et al. 2017, Semeniuk et al. 2021). In addition to influencing nutritional profiles, extended exposure to cage-diving vessels has the potential to lead to alterations in energetic budgets of kingfish due to increasing fast swimming behaviours through chasing baits and feeding on chum around the surface. Previous examples from provisioning wildlife tourism has revealed shifts in the activity budgets of whitetip reef sharks (Fitzpatrick et al. 2011, Barnett et al. 2016), white sharks (Huveneers et al. 2013, Huveneers et al. 2018), and whale sharks (Barry 2020) due to an increase in strong accelerations and vertical movement behaviours associated with pursing bait resources at tourism sites. These changes in activity are reflective of shifts in metabolic rate (Wilson et al. 2006, Payne et al. 2011), and have the potential to lead to long-term effects on the biological processes and survival on individuals that is not reflected from behavioural and dietary shifts (Brown et al. 2004).

Movements and space use of upper trophic level pelagic fish such as kingfish are often associated with foraging and feeding on small mobile preys like fish, squid, and crustaceans (Gomon et al. 2008). However, provisioned feeding from wildlife tourism can influence the space use of mobile marine species, with individuals aggregating where the feed is provided (Clua et al. 2010, Corcoran et al. 2013, Thomson et al. 2017). I therefore anticipated that the chum and bait used during food-based cage-diving operations would contract the space use of kingfish around operator vessels rather than moving around the islands seeking prey. Previous studies at the Neptune Islands have shown similar effects on the focal species of operations, i.e., white sharks (Huveneers et al 2013) and benthic non-focal species, i.e., smooth stingray *Bathytoshia brevicaudata* (Rizzari et al. 2017). Although such reduction in the weekly space used of kingfish in response to the number of operating days was not observed, the daily location of kingfish was affected, with kingfish more likely to occur on the side of the island that chumming operators occurred. Additionally, provisioning from food-based operators resulted in kingfish occurring on average ~200 m closer to operators using food-based attractants than the operator using acoustic attractant. Attracting kingfish within close proximity to tourism operations can negatively affect kingfish, e.g., injuries through interaction with vessels or passengers, predation from white sharks (Grainger et al. 2020), increased stress hormone levels (Semeniuk et al. 2008, Bessa et al. 2017), changes in hierarchical structure (Pini-Fitzsimmons et al. 2021, Brookhouse et al. 2013), and heightened risk from parasite infestation through increased transmission rates (Semeniuk & Rothley 2008, Clua et al. 2010, Brookhouse et al. 2013). Additionally, implications may be extended to broad ecosystem-wide effects by shifting the environmental services that kingfish play in the ecosystem. As large-bodied pelagic fish, kingfish are meso-predators that occupy high positions in pelagic food webs in addition to playing a role in regulating concentrations of small-bodied prey items as well as being an important prey-source for larger predators (Navarro et al. 2017, Grainger et al. 2020). Therefore, altering movements of kingfish at the Neptune Islands away from natural foraging areas has potential flow-on effects by disrupting both prey and predator interactions that would otherwise occur throughout unmodified daily movement patterns.

Wildlife tourism at the Neptune Islands can also positively affect kingfish. The significance of the islands for focal white sharks along with the biological importance of diverse habitat and fauna that inhabit the area have led to the implementation of a marine protected area around the islands (Neptune Islands Group (Ron and Valarie Taylor) Marine Park; Department of Environment and Water https://www.environment.sa.gov.au/marineparks/). This includes a no-take sanctuary zone around the North Neptune Islands, where commercial and recreational fishing practices are prohibited (Figure

1.1). As a commonly targeted species for recreational and commercial fisheries across south-eastern Australia (Lowry et al. 2016), an increase in the time spent and occurrence close to operator vessels within the no-take zone may therefore have positive effects for the kingfish population residing at the Neptune Islands. However, effectiveness of these no-take zones for aggregated populations are dependent on compliance efforts to ensure illegal fishing does not occur (Read et al. 2011, Campbell et al. 2012, Arias & Sutton 2013). Wildlife tourism can also assist in maximising the efficacy of marine protected areas, by increasing conservation awareness and having a presence reducing illegal fishing activities for both focal and non-focal species (McKeon & Drew 2019, Meyer et al. 2021a).

3.6 Conclusions

Findings from this chapter reveal that the behavioural effects of wildlife tourism extend beyond the targeted species (i.e., white sharks) and have the potential to influence the residency and space use of an upper-trophic level pelagic fish. Despite the weekly movements of kingfish not being affected by cage-diving vessels, food-based operators increased time spent at the Neptune Islands during the day and moved kingfish core space use. Potential flow-on effects from these behavioural changes may lead to reduced individual and population fitness, highlighting the importance for marine wildlife tourism management to expand beyond focal species and account for non-focal species.

Chapter 4

Influence of shark tourism on the activity and physiological status of a non-focal pelagic fish

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4.1 Abstract

Wildlife tourism can have adverse effects on the behaviours and movements of animals, leading to physiological consequences and impacts to the health and fitness of individuals and populations. I used activity data collected through acoustic telemetry to show that the food-based provisioning used in shark tourism increases activity in yellowtail kingfish (*Seriola lalandi*, kingfish, *n* = 18), a large-bodied pelagic fish often associated with shark tourism vessels. Kingfish activity was 18% higher on days when operators using bait and berley were present compared to days with no operators, or when only acoustic (i.e., non-food-based, 17% higher). Increased activity in response to berleying was restricted to periods when kingfish were on the same side of the island group as tourism vessels, but decreased after provisioning stopped and operators left the area. The incidence of burst swimming events was also affected, with the ratio of burst behaviours increasing by 60% during operations when food-based tourism operators were present. Kingfish activity and burst events also increased in warmer temperatures. Despite this increase in fish activity and the frequency of burst swimming events, likely associated with pursuing and feeding on baits and berley particles, the physiological condition of kingfish (measured using bioelectrical impedance analysis) at the tourism site remained consistent with kingfish from a control site that was not exposed to tourism (*n* = 113). This suggests that kingfish were able to compensate their increased energy expenditure by feeding on bait and berley used by operators or through natural foraging. These findings highlight that the effects of provisioning from wildlife tourism can extend beyond changes in behaviours and movements and can additionally influence the energetic condition of non-focal animals through increased activity. However, supplemental food-sources provided through wildlife tourism, or changes in natural foraging, may be sufficient to compensate for the increased energy expenditure and lessen the effects of tourism on individual fitness and health.

4.2 Introduction

Knowledge of the activity of free-ranging organisms is essential to understand species' behavioural ecology and examine how energy expenditure is influenced by abiotic factors (Brown et al. 2004, Payne et al. 2011). The energetic cost associated with different activities can influence growth, reproductive success, and ultimately survival (Brown et al. 2004), and subsequently provides vital information for management and the understanding of ecological processes (Brown et al. 2004, Cooke et al. 2004b). Suitability of the surrounding environment contributes to regulating the energetic balance of animals, through prey availability and the subsequent energetic costs of finding and consuming prey items. Changes to environmental conditions via natural (Pörtner et al. 2008, Payne et al. 2011, Payne et al. 2013) or anthropogenic drivers (Pörtner & Peck 2010, Kreiss et al. 2015, Barnett et al. 2016) can, therefore, impact predation efficacy, affecting energy budgets and innately have implications for health and fitness. Identifying drivers of activity from free-ranging animals therefore contributes to determining energetic expenditure and assessments of how environmental changes or anthropogenic pressures influence animal behaviour at a functional level (Payne et al. 2010). Despite the importance of understanding the energy costs associated with different activities, many methods used to determine metabolic rate only provide a limited temporal resolution (e.g. doubly-labelled water; Butler et al. 2004), or require loggers that need to be retrieved (e.g. heart-rate monitoring methods; Butler et al. 2004). More recently, proxies of activity calculated from tri-axial accelerometers (e.g. Overall Dynamic Body Acceleration; ODBA) has gained traction as a useful method to estimate energetic status of free-ranging animals due to the positive relationship between movement and oxygen consumption, inherently linked to metabolic processes (Yoda et al. 2001, Wilson et al. 2006, Payne et al. 2011). Such activity proxies can help study relative changes in energy expenditure in a range of taxa, including those in the marine environment which are often logistically difficult to study, and identify factors contributing to shifts in the energetic strategies of these individuals (Watanabe & Goldbogen 2021).

In addition to acute physiological responses of animals measured through activity metrics, physical body condition is also broadly used to assess the nutritional and physiological status of fishes (Bolger & Connolly 1989, Stevenson & Woods 2006, Brosset et al. 2015) and has been used as an indicator of growth (Critchell & Hoogenboom 2018), reproductive condition (Trippel 2003), and mortality (Hoey & McCormick 2004, Brosset et al. 2015). Metrics used to measure the body condition of fish, including length-weight relationships (Fulton's K; Nash et al. 2006), height (Richter et al. 2000), hepatosomatic and gonadosomatic indices (Chellappa et al. 1995, Tierney et al. 1996, Lenhardt et al. 2009), and energy density (Hartman & Brandt 1995, Johnson et al. 2017) are typically insensitive, lethal, or costly and time-consuming, or are restricted to laboratory procedures that measure specific physiological parameters. More recently, sub-lethal methods of measuring body condition of fishes *in situ* have been established. One such method is through electrical phase angle, which measures the ratio of resistance and reactance of tissue to applied electrical current, measured through bioelectrical impedance analysis (Cox & Heintz 2009). Phase angle allows for in-field measurements of body condition from live individuals by combining a prompt field-based measurement, with the intricacy of laboratory analysis by measuring both extra- and intracellular water distribution within the tissues of an live individual (Cox & Heintz 2009). Phase angle has been applied to detect differences in condition of fish at different stages (e.g. fed *vs*. fasted, and *post mortem*; Cox & Heinz 2009, Champion et al. 2020a), changes attributed to preferable environmental conditions (e.g. wild *vs*. hatchery, and winter *vs*. spring; Cox & Heintz 2009), and optimal oceanographic conditions (Champion et al. 2020b). Body condition may therefore be used to reveal long-term changes in physiological status due to ongoing effects from changes in activity budgets and energy expenditure (Willis & Hobday 2008), and changed diets due to provisioned food sources.

Wildlife tourism is a form of human-animal interaction that can lead to lead to behavioural (Laroche et al. 2007, Clua et al. 2010, Heinrich et al. 2021) and physiological (Barnett et al. 2016, Huveneers et al. 2018) effects on focal- and non-focal species at tourism sites. The use of food-based attractant is often required during tourism operations to aggregate focal species which are often sparsely distributed, in low densities, and undertake large-scale movements, making it challenging to ensure reliable and consistent interactions (Knight 2009, Gallagher & Huveneers 2018). When provisioned food is provided in small quantities and at unpredictable times and places, feeding from wildlife tourism can be an efficient technique for tourism operators to increase the likelihood of up-close encounters for tourists (Knight 2009, Meyer et al. 2021b). However, frequent use of food-based provisioning at tourism sites can have a multitude of detrimental effects on species occupying these areas. For example, direct feeding of nocturnal species can invert diel behaviours, such as southern stingrays *Hypanus americanus* at Stingray City Sandbar in the Cayman Islands (Corcoran et al. 2013). Similarly, habituation towards supplemental food sources can restrict core area space use of some marine species due to increased time spent within the vicinity of operators, rather than undertaking natural behaviours such as searching for food (Huveneers et al. 2013, Rizzari et al. 2017). However, assessment of species movement and residency patterns may not be sufficient to comprehensively assess the impacts of provisioning tourism operations on the health and fitness of animals (Semeniuk et al. 2009, Burgin & Hardiman 2015, Barnett et al. 2016). Food-based provisioning has also been shown to alter the energetic responses and physiological condition of individuals at tourism sites (Semeniuk et al. 2009). Frequent (i.e., near-daily) supply of supplemental food can increase activity and frequency of burst events associated with pursing baits and fragmented particles in the water column (Barnett et al. 2016, Huveneers et al. 2018), reflecting changes in metabolic efficacy that ultimately influence critical biological and ecological processes (Brown et al. 2004). Food-based attractant used by tourism operators is also often different to naturally-occurring prey items, particularly for non-focal species which are indirectly fed, and is often consumed in much higher quantities than regular prey due to ease of access. Persistent feeding on these unnatural food types can lead to high parasite loads (Semeniuk et al. 2009, Brookhouse et al. 2013), raised stress hormones (Semeniuk et al. 2009), and excessive fat deposits (Brookhouse et al. 2013). While few studies have delved into the energetic and physiological responses of sharks (Barnett et al. 2016, Huveneers et al. 2018) and rays (Semeniuk et al. 2009), the effect of food-based wildlife tourism operations on the energetic responses and physiology of highly-mobile large pelagic fish have rarely been quantified (but see Brookhouse et al. 2013).

White shark cage-diving at the Neptune Islands, South Australia, provides an opportunity to assess energetic and physiological responses to provisioning feeding practices on non-focal mobile pelagic fish. Here, two companies use a near-constant plume of food-based attractant (berley; mixture of minced southern bluefin tuna *Thunnus maccoyii*) and tethered baits to entice sharks into the field of view of tourists (Huveneers & Lloyd 2017, Huveneers et al. 2017b, Meyer et al. 2020). A third company uses acoustic stimuli (music played through underwater speakers) to attract sharks. While sharks are not fed bait intentionally, small particles from bait and berley plumes in the water column are eaten by smaller, non-focal species (e.g., smooth stingrays *Dasyatis brevicaudata*; Rizzari et al. 2017, trevally *Pseudocaranx* spp., horseshoe leatherjacket *Meuschenia hippocrepis*; Meyer et al. 2020). This indirect feeding has altered the diets of some of these fish, with a shift in fatty acid profiles to more closely resemble the *T. maccoyii* baits rather than naturally-occurring prey sources (Meyer et al. 2020), as well as contributing to changes in local assemblage abundance (e.g. *Pseudocaranx* spp., *M. hippocrepis*, Whitmarsh 2019), and altered daily movements of some mobile species (e.g., *D. brevicaudata*; Rizzari et al. 2017, kingfish; see Chapter 3). However, it remains undetermined whether these changes contribute to physiological effects on the energetic balance and physiological condition of non-focal species, as changes in space use and diet do not necessarily lead to a change in the health or fitness of individuals (Gill et al. 2001, Beale & Monaghan 2004).

The yellowtail kingfish (*Seriola lalandi*, hereafter referred to as kingfish) is a large-bodied coastal-pelagic fish, frequently occurring at the Neptune Islands Group. Kingfish are typically considered to be mobile piscivores, capable of large-scale movements (i.e., up to 1000s of kilometres; Saul & Holdsworth 1992, Gillanders et al. 2001), but individuals at the Neptune Islands are highly residential throughout the year (Chapter 3) and are often observed feeding on the food-based attractant (Meyer et al. 2020). It is possible that the occurrence of kingfish around cage-diving vessels pursuing baits and feeding on bait and berley could translate to an increase in activity (Fitzpatrick et al. 2011, Barnett et al. 2016), and that reliance on an unnatural prey source might limit natural foraging or lack nutritional quality, resulting in poorly conditioned individuals (Meyer et al. 2020). Kingfish therefore provide a model species to assess the potential effects of shark tourism on the activity and physiological status of a non-focal, large pelagic fish. This study aimed to identify if cage-diving tourism influences the activity and physiological status of kingfish at the Neptune Islands. Specifically, I hypothesised that a) activity of kingfish increased when food-based cage-diving operators were present at the Neptune Islands, and increased further when kingfish were in close proximity to the vessels, and b) body condition of kingfish at the Neptune Islands was reduced due to increased activity and diet modification from feeding on an unnatural prey item.

4.3 Methods

Site description

This study was undertaken at the North Neptune Islands group (hereafter referred to as Neptune Islands), located ~30 km from mainland South Australia (Figure 1.1; 35°13.944'S; 135°03.834'E). An array of 15 VR2-AR acoustic receivers (Innovasea, Nova Scotia, Canada, innovasea.com) was deployed in November 2018 for a 2-year period. Receivers were positioned ~350 m from each other in areas where cage-diving vessels anchor to ensure simultaneous tag detection by 2 – 3 receivers and enable to estimate high-precision fish positions throughout the study period. This is also the side of the island most protected from dominant winds and swell (Figure 1.1). Acoustic receivers also recorded water temperature hourly, which was used to calculate daily mean water temperature.

Capture of kingfish

Between August 2018 and May 2020, 18 mature kingfish (> 80 cm total length; Gillanders et al. 1999, Poortenaar et al. 2001) were caught via hook and line at the Neptune Islands, and tagged with V16A 98 x 16 mm (17.3 g; 1090 days battery life) or V13A 48 x 13 mm (6.5 g; 368 days battery life) acoustic activity tags (Innovasea, Nova Scotia, Canada, innovasea.com). Acoustic tags were equipped with acceleration sensors, which records measurements of acceleration (hereafter referred to as activity). These tags are less sensitive than accelerometers used in Chapter 1, enabling long-term monitoring of relative activity rather than fine-scale characteristics of behaviours (i.e., 12.5 Hz for one second every 30 – 90 seconds *vs*. 50 Hz continually). Acceleration (± 4.9 m/s^2 range) was sampled for each transmission cycle and converted to a value by the onboard microprocessor using the root mean square value of all three axes (activity = $\sqrt{[X^2 + Y^2 + Z^2]}$). The static contribution to the overall acceleration (g) was filtered out prior to root mean square calculation. Root mean square acceleration resolution was 0.0191 m/s^2 (Payne et al., 2011).

Body condition measurements: bioelectrical impedance analysis

Kingfish body condition was quantified using Bioelectrical Impedance Analysis (BIA) following the protocols detailed by Cox & Heintz et al. (2009) and Champion et al. (2020a). Bioelectrical Impedance Analysis measures two paths of electrical current, resistance (R) and reactance (X_c). Resistance is a reflection of extracellular material (i.e., fat) which is nonconductive and is indicated by higher measurements of R (Cox & Heintz 2009, Cox et al. 2011) in poorly conditioned individuals. Reactance is measured as the total volume of healthy cells, indicated by the ability of a substance to hold a charge (Gabriel et al. 1996, Hartman et al. 2015). Measurements of R and X_c were used to derive values of electrical phase angle, which is an index of the metabolic condition of fishes (Willis & Hobday 2008) and has been previously used to assess the body condition of kingfish through the eastern Australian distribution of this species (Champion et al. 2020a):

$$\text{phase angle } (°) = \left(\arctan\left(\frac{X_c}{R}\right)\right) \times \frac{180°}{\pi}$$

Phase angle provides a measurement of the angle between the R and X_c vector components of impedance, ranging from 0 to 90°, where higher values represent good body condition as a result of high readings of X_c which are indicative of a high proportion of intact cell membranes (Foster & Lukaski 1996).

Phase angle measurements were taken from kingfish at the Neptune Islands between August 2018 and July 2021 using BIA. Individuals were captured using the hook and line methods described above. Three replicate BIA measurements were taken along the dorsal musculature of kingfish on a nonconductive surface using the Seafood Analytics Certified Quality Reader (Certified Quality Foods, Inc., United States of America, certifiedqualityseafoods.com), and mean of replicate measurements was calculated for each kingfish. As body length does not influence phase angle measurements taken for kingfish (Champion et al. 2020a), a direct comparison across individuals of different size classes was not necessary. Although variation in reproductive status has the potential to influence phase angle measurements due to increased lipid and moisture content during spawning periods (Jonsson et al. 1997, Domínguez-Petit et al. 2010), previous research has found no effect from reproductive status on Dolly Varden (*Salvelinus malma*) sampled along the dorsal musculature, despite gonads being on average 30 times larger in spawning *vs*. non-spawning individuals (Stolarski et al. 2014). Rather, by sampling across dorsal tissue that doesn't intersect with gonadal tissue, comparisons across different class size is further justified (Stolarski et al. 2014). Data were compared with phase angle values sampled for wild kingfish throughout the species' eastern Australian distribution, where values >28° (i.e., the median of 113 fish sampled) reflects individuals within the population that are in relatively good physiological condition (Champion et al. 2020a).

Kingfish activity in response to cage-diving operations

Coordinates of anchored locations and time of cage-diving operations were collected through a customised daily e-logbook (named Fulcrum^{TM} from November 2018 – February 2019 and White Shark Cage-Diving app from March 2019 – August 2020; Nazimi et al. 2018). Boat position was allocated to either north-eastern (latitude ≥ 35°13.68'S) or south-eastern (latitude ≤ 35°13.68'S) side based on daily coordinates, and activity measurements were then assigned as 'same side' if the detection occurred on the same side of the island as cage-diving operators were anchored, or 'different sides' if the detection occurred on the opposite side. To reduce the effect from crepuscular patterns influencing the activity of kingfish, only detections during the day were used by filtering for daytime only using the *getSunlightTimes* function (package 'suncalc' version 0.5.0). Activity measurements were also classified based on whether the detection occurred before, during, or after cage-diving operations based on time of operation recorded on the White Shark Cage-Diving app. For days when operators did not visit the islands, the average arrival (09:04:00) and departure (16:21:00) times were used to assign a before, during, or after cage-diving operation category. Activity measurements exceeding 4 m/s^2 were identified as ‘burst events’, as this was the threshold expected to correspond with burst feeding events in kingfish of similar size (see Chapter 2, Clarke et al. 2021). Daily ‘burst ratios’ were calculated for each individual based on the number of burst events divided by the number of detections for that day.

Statistical models

A series of generalised linear mixed models (GLMMs) were used to test the effects of cage-diving operations on the behaviour of kingfish at the Neptune Islands. All models were constructed using the *lmer* function in the ‘lme4’ package (version 1.1.23, Bates et al. 2015) in the R statistical environment (version 4.0.2). The first model tested the effect of six different daily operator types (one food-based, two food-based, acoustic only, acoustic + food-based, all operators, no operators) on kingfish activity, while controlling for temperature and unobserved heterogeneity by adding temperature and Transmitter ID to the model as fixed and random effects (slope + intercept), respectively. Absolute temperature values collected from receivers were used instead of temperature anomalies, as sea temperature has previously been linked to kingfish spawning behaviours (Moran 2007, Miller et al. 2011), persistence across oceanographic habitats (Champion et al. 2018), and physiological condition (Champion et al. 2020). Study week (i.e., week since the start of the project, when first fish was tagged) was included as a random effect to account for temporal autocorrelation. The most appropriate statistical family, transformation, and validity of the model was determined by examining the distribution of the response variable and visual inspection of residuals. Activity values were log-transformed for models measuring effects from operator type, side of the island, and time of the day.

A second model tested for the effect of food-based *vs*. no provisioning on tagged kingfish activity. Here, no-operator days and days that only acoustic attractant were present were classes as ‘no provisioning’ and any operator type containing food-based attractant as ‘provisioning’. This model included a before/after effect (i.e., whether activity measurements were taken before, during, or after operators were present), a second control/impact effect (i.e., if detection occurred on the same ‘side’ of the island as cage-diving operations), and an interaction between these three terms representing the Before After Control Impact (BACI) effect. Temperature (receiver temperature, °C) and Transmitter ID were included as a random effect with randomised slope and intercept to account for potential lack of independence in behaviour within fish. Activity values were again log-transformed prior to the analysis.

A third model was used to test the effect of berleying operations on the burst ratio of kingfish during hours of operation. This model included only measurements during cage-diving operations, and a control/impact effect (i.e., if food-based or. no-food provisioning was used). Only detections during food-based operations on the same side of the island as cage-diving operations were included as provisioning days to assess burst ratio. Temperature and Transmitter ID were also included as a random effect with randomised slope and intercept. A square-root transformation were deemed necessary for burst ratio model due to the occurrence of 0 values when no burst events exceeding 4 m/s^2 was recorded on a particular day.

All combinations of factors were run, with the most parsimonious model selected using Akaike's information criterion corrected for small sample size (Burnham & Anderson 2002) via the *dredge* function from package 'MuMIn' (version 1.43.17). Deviance explained from all model factors (conditional R^2; R_c) and from only fixed-factors (marginal R^2; R_m) were then estimated by subtracting the deviance explained from the null-model from each alternative model. The *ggpredict* function (package 'ggeffects' version 1.0.1) was used to estimate marginal means (predicted values) for fixed effects included in top ranked models. Full models were:

$$\text{Type: activity} = \text{Operator type} + \text{Temperature} + \text{Transmitter}_{\text{rand}}$$

$$\text{Interaction: activity} \sim \text{Provisioning*Side*Time of day} + \text{Temperature} + \text{StudyWeek}|\text{Transmitter}_{\text{rand}}$$

$$\text{Burst ratio: burst ratio} \sim \text{Provisioning} + \text{Temperature} + \text{Transmitter}_{\text{rand}}$$

4.4 Results

Activity measurements were obtained from 243,440 detections at the Neptune Islands. Over 95% of detections (232,928 detections) occurred during daylight hours, with 3% at night and < 1% for dawn and dusk. Between August 2018 and November 2020, cage-diving operators were present on 62% of days (397 out of a possible 639 days). Activity of kingfish at the Neptune Islands was influenced by operator type (2% deviance explained) and temperature (3%), with both factors included in the top-ranked model and together explained 5% of the model deviance (Table 4.1a). Activity was lowest on days when no operators were present (0.96 ± 0.04 m/s^2) and on days with only acoustic attractant (0.97 ± 0.04 m/s^2; Figure 4.1a). Food-based operations led to an increase in kingfish activity, with activity higher on days when one (1.06 ± 0.04 m/s^2), or two (1.09 ± 0.04 m/s^2) food-based operators were present (Figure 4.1a; Table S3). Activity of kingfish increased with water temperatures with this effect slightly larger than operator type (Figure 4.1b, Table S3). Activity also varied between individual kingfish, which explained 7% of the model deviance.

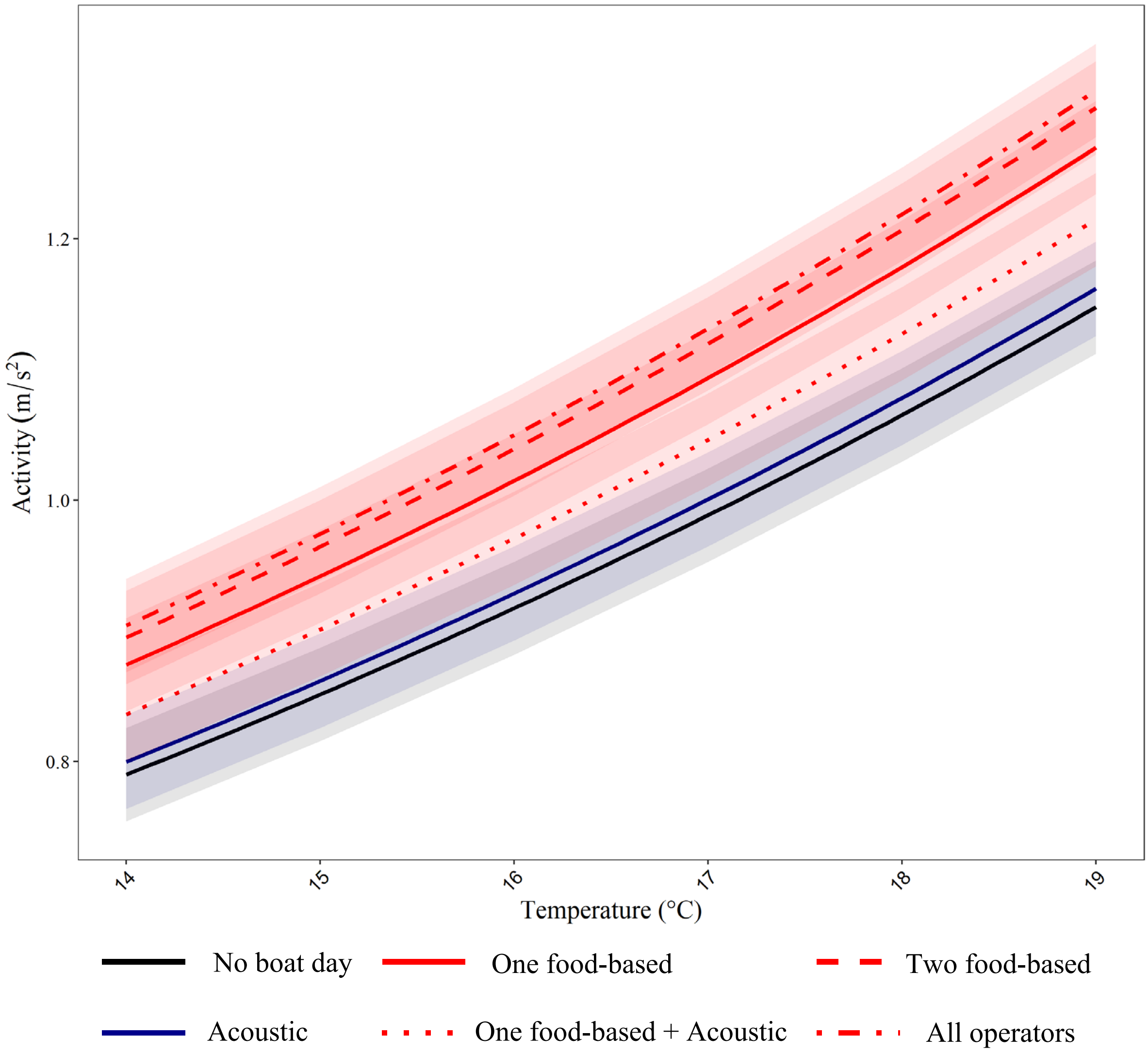

Figure 4.1. Predicted activity (m/s^2; marginal means) from Generalise Linear Mixed Model of kingfish at the Neptune Islands with different tourism operator types (food-based = red, acoustic attractant = blue, no operator days = black).

Provisioning, time of day, side of the island

The effect of food-based attractant on kingfish activity was influenced by all three fixed-effects (provisioning, side of the island, and time of day) and each of their two-way interactions (Table 4.1b) as well as a positive relationship with temperature for all interactions (Figure 4.2). The top-ranked model also included the interaction between all three factors (Table 4.1). Interactions explained 4% of the model variation, but there was also high variability between individuals, with random factors explaining 33% of the total variation (Table 4.1). When kingfish were detected on the same side of the island as food-based operators, activity was 18% higher during operations than when non-food-based operators were present (0.92 ± 0.05 – 1.1 ± 0.05 m/s^2). There was, however, no effect on kingfish activity when kingfish were on opposing side to the operators (1.01 ± 0.04 – 1.05 ± 0.05 m/s^2; Figure 4.2). The effect of operators on kingfish activity was also supported by the difference in activity being greatest during tourism operations, with little differences observed prior to the operators arriving (Figure 4.2, Table S4). After operators left the Neptune Islands, activity on days that food-based operations occurred returned to levels that resembled days that no food-based attractant was present on the same side of the island, but was higher than after operations when operators were on both the same and opposing sides of the island (Figure 4.2, Table S4).

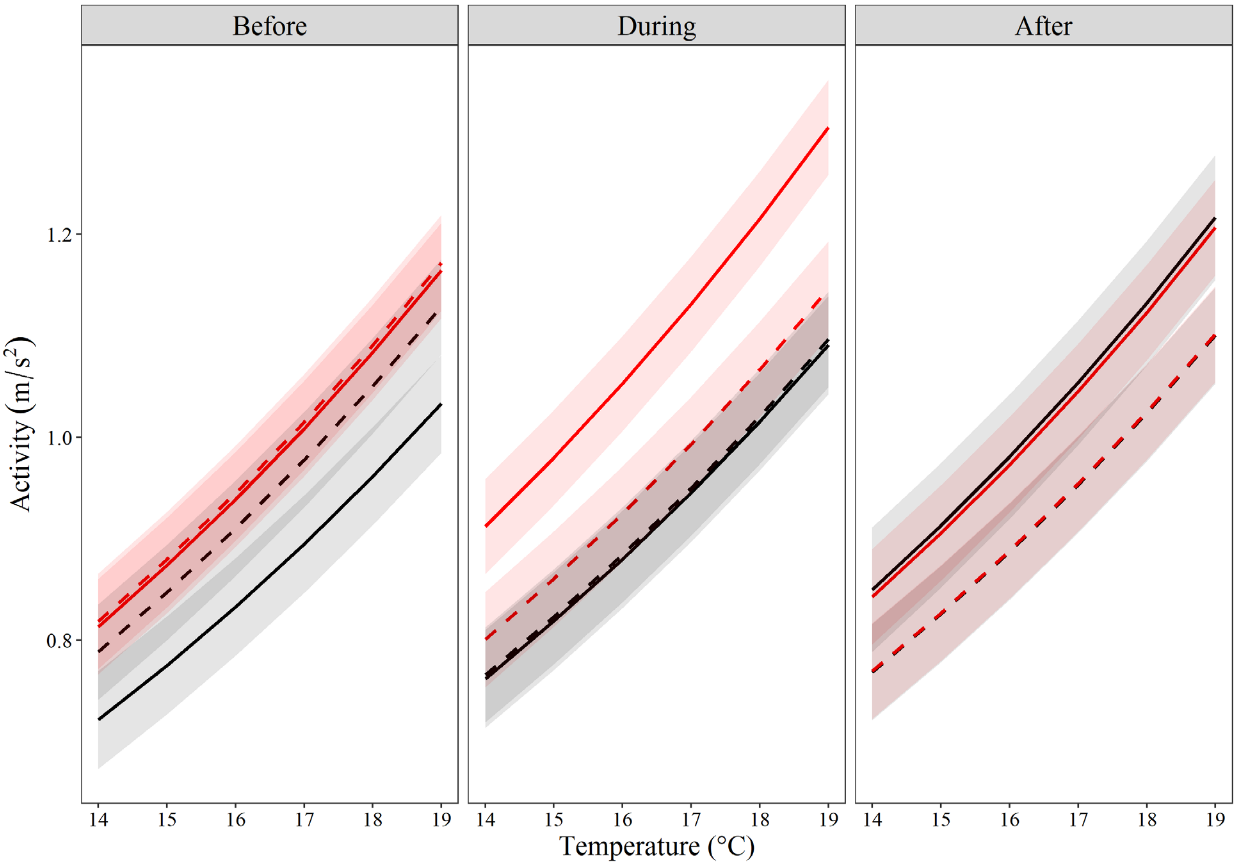

Figure 4.2. Predicted activity (marginal means ± SE) from Generalised Linear Mixed Model of kingfish at the Neptune Islands showing the interaction between same (solid) and different (dashed) sides of the island with food-based (red) and non-food-based (black) operations across sampling temperature. Panels represent different times of day.

Burst events

Across the sampling period, 3,366 burst events exceeding 4 m/s^2 were detected, ranging between 1 to 26 events per day by individual kingfish. Burst ratio (number of burst/number of detections) for each day ranged from 0 to 0.5 (mean = 0.02 ± 0.0008). Food-based operations (3% of variance) and temperature (2% of variance) affected burst ratio, however, there was also a large amount of variation in burst events amongst individuals with 14.1% of the variance of the model explained by individual Transmitter ID (Table 4.1c). Burst behaviours increased by ~60% with the presence of food-based operators (from 0.0048 ± 0.01 m/s^2 to 0.003 ± 0.12 m/s^2; Table 4.1, Figure 4.3).

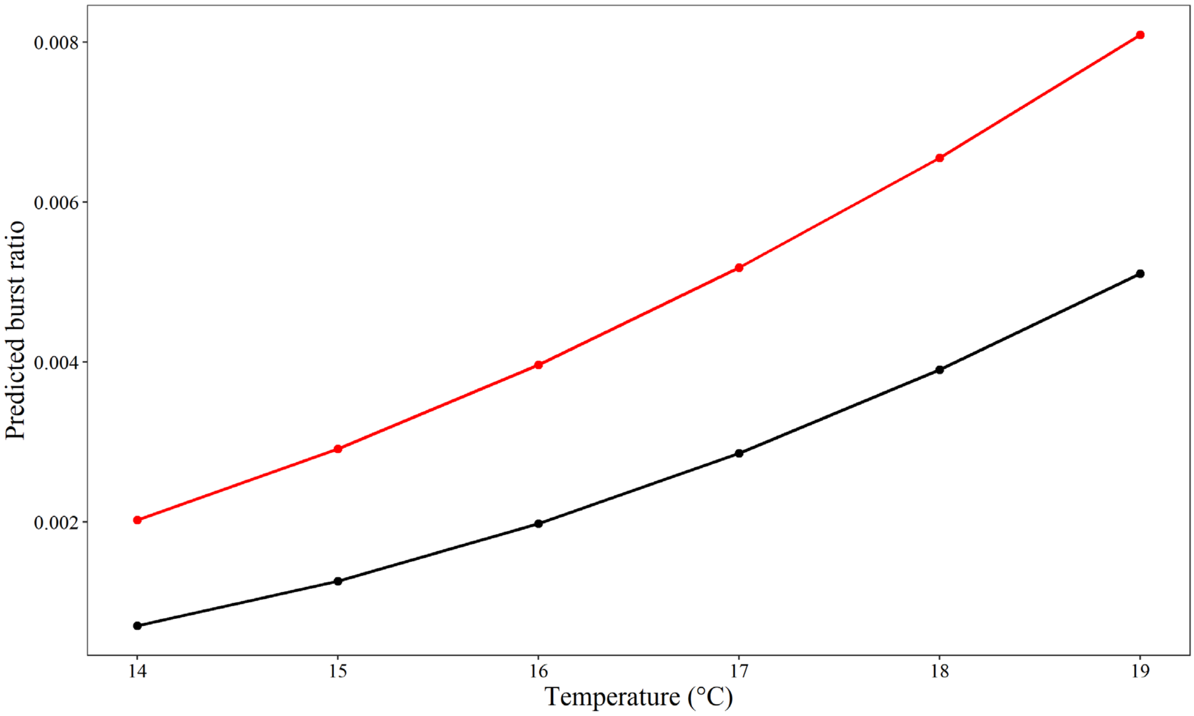

Figure 4.3. Predicted burst ratio (events exceeding 4m/s^2/total daily detections) from Generalised Linear Mixed Model of kingfish on days with food-based operators (red) and no food-based attractant present (black).

Table 4.1. Summary of models to estimate effects of cage-diving operations on kingfish activity. df, degrees of freedom; AICc , Akaike's information criterion corrected for small sample size; degrees of freedom (df); log-likelihood (logLik); ΔAICc , difference in AICc between the current and the top-ranked model (ΔAIC_c); $wAIC_c$, model probability; R_m, marginal (fixed effects) R^2; R, conditional (fixed and random effects) R^2. Only the top 5 ranked models are presented for table clarity.

Model	df	logLik	AIC_c	ΔAIC_c	$wAIC_c$	R_m	R_c
a) Operator type							
Activity ~ Operator Type + Temperature	**9**	**-161400**	**322818.1**	**0**	**1**	**0.04**	**0.12**
Activity ~ Temperature	4	-162679	325366.3	2548.21	0	0.03	0.11
Activity ~ Operator Type	8	-164688	329392.8	6574.71	0	0.02	0.08
Activity ~ 1 (intercept only)	3	-166510	333025.1	10207.02	0	0.00	0.07

Model	df	logLik	AICc	ΔAIC_c	$wAIC_c$	R_m	R_c
b) Interaction							
Activity ~ Provisioning + Time + Side + Temperature + Provisioning*Time + Provisioning* Side + Time*Side + Provisioning*Time*Side	**17**	**-159505**	**319043.9**	**0**	**0.75**	**0.037**	**0.366**
Activity ~ Provisioning + Time + Side + Temperature + Provisioning*Time + Provisioning* Side + Time*Side	15	-159508	319046.1	2.22	0.25	0.037	0.359
Activity ~ Provisioning + Time + Side + Temperature + Provisioning* Side + Time*Side	13	-159515	319056	12.11	0.002	0.037	0.359
Activity ~ Provisioning + Time + Side + Temperature + Provisioning*Time + Time*Side	14	-159577	319180.9	137.07	0	0.037	0.353
Activity ~ Provisioning + Time + Side + Temperature + Provisioning* Side	12	-159585	319193.2	149.37	0	0.037	0.355

Model	**df**	**logLik**	**AICc**	**ΔAIC_c**	**$wAIC_c$**	**R_m**	**R_c**
a) Burst ratio							
Burst ratio ~ Provisioning + Temperature	**5**	**1677.5**	**-3344.9**	**0**	**0.884**	**0.019**	**0.180**
Burst ratio ~ Temperature	4	1674.1	-3340.1	4.84	0.078	0.012	0.168
Burst ratio ~ Provisioning	4	1673.3	-3338.6	6.31	0.038	0.010	0.158
Burst ratio ~ 1 (intercept only)	3	1667.2	-3328.4	16.57	0	0.000	0.141

Kingfish body condition

Body condition was calculated from 39 kingfish caught at the Neptune Islands. Kingfish were 52 – 165.5 cm total length and sampled from water temperatures between 16.01 – 19.8°C. All acoustically-tagged kingfish showed high levels of residency (0.42 – 0.69 residency index [days detected/days at liberty], mean = 0.55 ± 0.04; Figure 4.4a). Phase angle ranged from 26.17 – 35.83° (mean = 30.20 ± 0.38°, Figure 4.4b) and was not influenced by water temperature at the time of sampling or body length, with the top-ranked model not including any fixed effects (wAICc = 0.53). Of the 39 fish sampled, 77% (including three acoustically-tagged individuals) had phase angle values similar to kingfish considered in good body condition (i.e., > 28° as per Champion et al. 2020a).

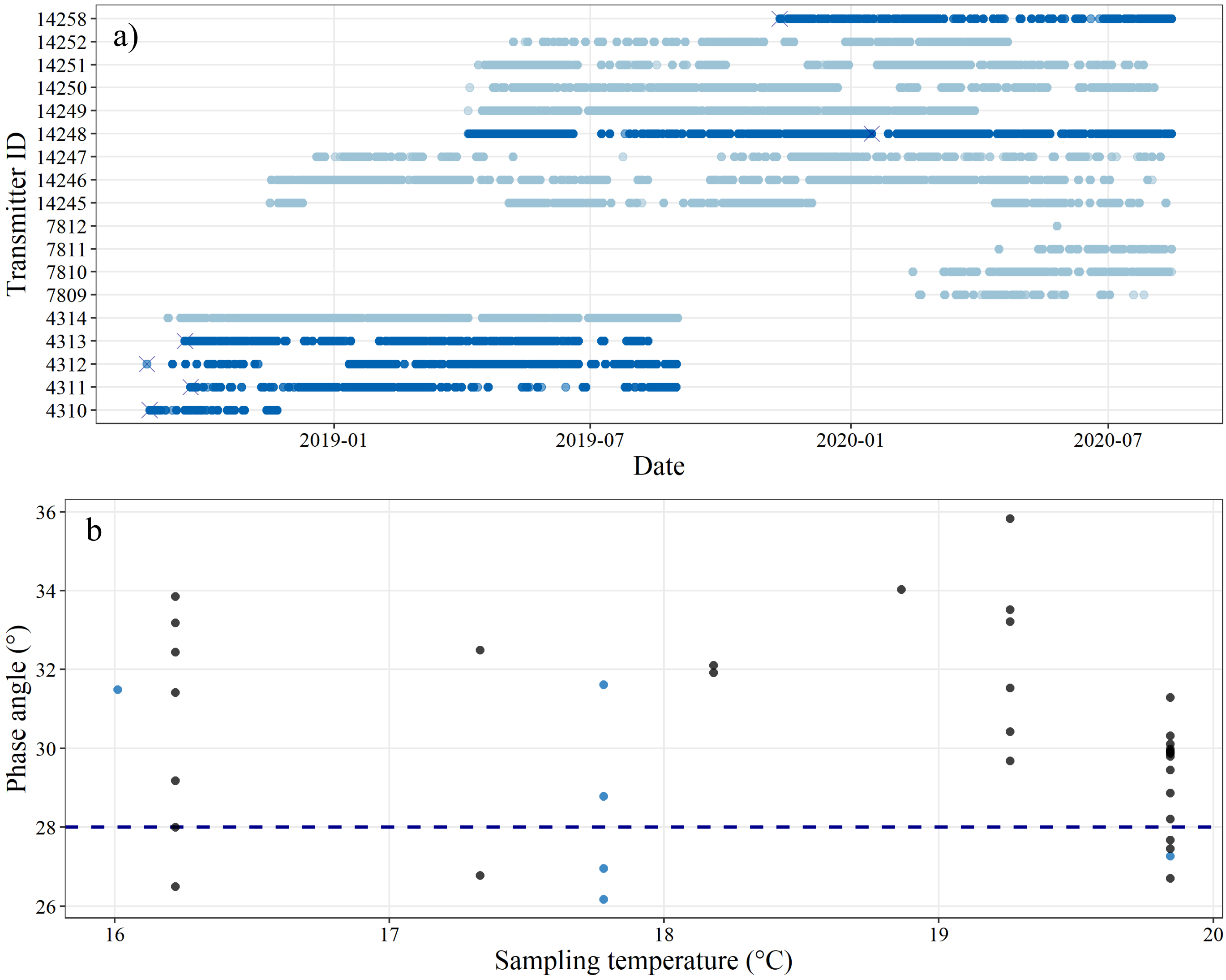

Figure 4.4. a) Residency of acoustically-tagged kingfish at the Neptune Islands, with individuals sampled using Bioelectrical Impedance Analysis in dark blue, unmeasured individuals in light blue. Crosses represent date that body condition measurements were taken. b) Body condition (electrical

phase angle) of kingfish sampled at the Neptune Islands during food-based provisioning operations. Blue circles represent acoustically-tagged individuals, black circles are untagged kingfish. The horizontal dashed line (y = 28) represents value above which kingfish are considered in good body condition based on phase angle measurements from 113 kingfish sampled throughout eastern Australia (provided from Champion et al. 2020b).

4.5 Discussion

This study revealed that the use of bait and berley during white shark cage-diving increased kingfish activity and frequency of burst events, which could potentially affect the energy budget, health, and fitness of these individuals. Activity increased on days when food-based operators were present at the islands, but not when sound was the only attractant used. The increased activity was only identified when fish were on the same side of the island as operators using food-based attractant, suggesting that the effects from these operators were restricted to within ~500 m to vessels. Activity of kingfish also fluctuated throughout the day, being at their highest during berleying activities when operators were on the same side of the island. In comparison, activity remained consistent and lower throughout the day when operators using food products were not present, or when they were on opposite sides of the island to the kingfish at the time of the detection. However, the observed activity increase did not lead to low body condition of these individuals, suggesting that the changes incurred by the cage-diving tourism does not result in reduced physical condition or fitness.

Kingfish activity was 18% higher during operations on days when food-based operators were at the Neptune Islands compared to days when these operators were not present. In comparison, no change was observed when the acoustic operator was present, suggesting that the increased activity is associated with the use of bait and berley rather than the mere presence of the cage-diving vessels. Changes in activity are reflective of raised energetic expenditure, and is linked to shifts in metabolic rate (Wilson et al. 2006, Gleiss et al. 2011b, Lear et al. 2017). Raised activity cost during cage-diving operations might raise kingfish energy expenditure above that incurred during naturally-occurring behaviours, which can lead to ongoing effects on growth, reproductive health, and ultimately fitness and survival (Videler & Weihs 1982). Mobile pelagic fish such as kingfish are capable of high-speed burst behaviours to capture fast-swimming prey and avoid predation (Block et al. 1992b), but the high frequency of bursts of activity during cage-diving activities (60% increase) might further affect kingfish energetic budgets, as well as increases risk of physical injury though collisions with vessels, cages, or interspecific species (Brookhouse et al. 2013). These high-acceleration behaviours likely occur when freshly tethered baits are thrown in the water, resulting in individuals dashing towards the food-source. Such burst events in pelagic fish require anaerobic effort and can result in decreased blood pH and oxygen uptake for several hours (Jones 1978, Randall et al. 1987). As a result, increased frequency of burst swimming behaviours has the potential to disrupt essential biological functions that require oxygen (e.g., respiration, feeding, locomotion, predatory avoidance, reproduction; Kramer 1987). Additionally, kingfish are highly residential to the Neptune Islands (residency of some individuals reaching 80%, Chapter 3), with food-based tourism practices further increasing the number of hours spent at the tourism site. These compounding effects could lead to kingfish exhausting anaerobic energy stores which are required to capture prey items, reproduce, or avoid predators (Payne et al. 2011), and in the long-term limit growth and reproductive success of individuals and populations (Brown et al. 2004, Tomlinson et al. 2014).

The increase in kingfish activity when food-based operators were present was limited to occasions when kingfish were detected on the same side of the Neptune Islands as operators. The geological formation of the Neptune Islands essentially segregates the north- and south-eastern sides of the island, with a small gap in-between (~250 m in width; Figure 1.1). The bait plume and berley particles might therefore be restricted to the side of the Neptune Islands where it is used and disbursed, not being transported to the other side and influencing kingfish there. While might be appealing to restrict cage-diving operations to one side of the Neptune Islands to minimise the impact of shark tourism on kingfish, mobile pelagic species like kingfish (Chapter 3), trevally (J Dennis, unpublished data), and white sharks (C Huveneers, pers obs.) can move between the north- and south-eastern sides of the Neptune Islands within a few minutes and have been observed to interact with vessels on both sides of the Neptune Islands on the same day. Therefore, restricting operators to one side of the Neptune Islands is unlikely to be an effective approach to reduce the impact of the cage-diving industry on kingfish activity. Management efforts, if required, should instead focus on temporal restrictions (i.e., daily operating hours, number of days of operation) or limiting bait and berley quantities, both of which are already in effect (DEW 2016).

Some wildlife tourism ventures strive to combat negative effects from operations by enforcing strict operating time limitations to reduce the degree of interaction of wildlife with companies (Trave et al. 2017). However, behavioural shifts from supplemental feeding practices can additionally extend beyond operating hours, inverting naturally occurring diel activity patterns (Corcoran et al. 2013). Findings from this study suggest that kingfish activity remained slightly elevated after operators have left the islands, however this was apparent for both food-based and non-food-based days but only when operators were on the same side of the island as operators. This poses additional difficulties when attempting to quantify the effect of wildlife tourism on the health of animals, given that physiological effects can extend beyond times that fish are interacting with tourism operators. Diurnal rhythms in activity and associated energy budgets are common amongst pelagic piscivores and are often associated with feeding behaviours and prey availability (Arostegui et al. 2020). Like most large-bodied pelagic fish, kingfish are visual diurnal predators which actively search to find prey during the day (Pankhurst 1989, Silvano 2001). Observed changes in kingfish activity during berleying operations could therefore disrupt natural activity patterns attributed to foraging, increasing the reliance of these individuals on the provisioned food sources from operators.

Although food-based operations increased the activity and burst events of kingfish which has the potential to negatively affect the health and fitness of individuals, this study showed that these changes did not translate to a decrease in physiological condition. Based on body condition of kingfish in eastern and southeast Australia, individuals at the Neptune Islands were of relatively good physiological status (Cox & Heintz 2009, Champion et al. 2020a) and of similar condition to kingfish from a highly suitable habitat (Champion et al. 2020b). Body condition is inherently linked to the composition of healthy cells and permeability of cell membranes, and has previously been used to detect unfavourable environmental conditions (Champion et al. 2020b), risk of predation (Hoey & McCormick 2004), and effects from anthropogenic stressors (Cavraro et al. 2019). The lack of reduced body condition despite increased activity might be due to the provisioned food source provided by the food-based operators (bait and berley) which is fed upon by kingfish (Meyer et al. 2020) and is of high nutritional value. The southern bluefin tuna used as bait and berley by cage-diving operators are acquired locally from aquaculture operations in Port Lincoln, less than 50 km from the Neptune Islands. Tuna are fed locally sourced baitfish i.e., sardines *Sardinops* spp., that are high in natural proteins and oils, and as a result contain high levels of nutritional fatty acids, including omega-3 fatty acids (Glencross et al. 2002, Gregory et al. 2010, Pethybridge et al. 2015). While not a naturally-occurring prey item for kingfish, this dietary shift to southern bluefin tuna may, therefore, be comparable, if not more nutritious than the common prey items of kingfish (e.g., small pelagic fish, squid, crustaceans; Gomon et al. 2008, Meyer et al. 2020). This subsidised food source may be compensating for increasing the energy cost during and following cage-diving operations (Barnett et al. 2016), resulting in a lack of effect on body condition. The consumption of food-based attractant could in fact be necessary to compensate for the increased energy expenditure during interactions with cage-diving vessels. A similar instance of food-based wildlife tourism influencing activity budgets has been described, whereby the activity and associated metabolic rate of whitetip reef sharks (*Triaenodon obesus*) increased by 6.37% on feeding days, with sharks required to increase food consumption (e.g., baits) to compensate and maintain constant body mass (Barnett et al. 2016). However, reliance on tuna as a food source may also decrease kingfish dietary diversity, which can influence gut microbiome communities and disease control (Bolnick et al. 2014) and resultingly affect health and reproductive output (Kowalczyk et al. 2014). There may also be other health impacts for kingfish that is not measured through BIA. For example, kingfish fed with bread and aquaculture pellets at a fish-feeding site at Lord Howe Island (NSW, Australia) demonstrated dependency on supplemental food, raised aggression, frequent skin lesions and stomach ulcers, and heightened parasite loading (Brookhouse et al. 2013). Kingfish that fed on bread and pellets at Lord Howe Island had excessive fat deposits, which would be expected to be represented by poorly conditioned fish indicated through bioelectrical impedance values. Kingfish at the Neptune Islands, however, were found to have comparable body condition to individuals from a control site. The relatively good condition of kingfish at the Neptune Islands compared to those fed on Lord Howe Island further suggests that *T. maccoyii* is a nutritionally high-quality supplemental diet (in comparison to bread, aquaculture pellets) which may be compensating for the increased energy expenditure during cage-diving operations. The sensitivity of this method to detect subtle changes in physical condition from varying food intake and environmental conditions, suggests that phase angle should be suitable to detect physiological change due to unfavourable dietary sources. However future research into physiological shifts in response to provisioning wildlife tourism would benefit from more sensitive measurements of physiological changes (e.g., increased stress hormones; Iwama et al., 1998, Peter 2011, changes in blood glucose, lactate build up; Barton et al. 2002) to be paired with energetics inferred through activity metrics, but these methods are more intrusive and time-consuming for field-based studies.

4.6 Conclusions

Findings from this study identified impacts from white shark cage-diving tourism on the physiological responses of kingfish, highlighting potential implications for the daily energy budgets and resulting consequences for the health and fitness of these individuals. These results reveal that impacts on activity from food-based wildlife tourism can extend beyond focal-species, and additionally have effects on non-focal individuals, which is particularly pervasive for highly mobile and active individuals such as mobile pelagic fish. Future research would benefit from quantifying the calorific value and quantity of bait and berley consumed by kingfish, in combination with to respirometry data (Brodie et al. 2016) to help provide a clearer estimation of metabolic processes reflected through energetic status of effected individuals (Brunnschweiler et al. 2018), but these practices are often expensive and logistically difficult to execute on mobile pelagic fish. Such information of these implications is important for the development of adequate management wildlife tourism frameworks which often largely focus only on impacts to focal-species (Higginbottom et al. 2003, Meyer et al. 2020, Meyer et al. 2021a), with little consideration for highly mobile non-focal animals such as pelagic fish.

Chapter 5

Environmental drivers of yellowtail kingfish activity across south-eastern Australia inferred through a national network of acoustic tracking arrays

Image removed due to copyright restriction. Original can be viewed at:

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5.1 Abstract

Environmental conditions (natural or influenced by humans) can affect the behaviours and movements of organisms in marine ecosystems. Identifying species response to variations in environmental conditions and the relationships between the environment and species ecology can contribute to proactive and adaptable management, but can also be logistically challenging. Activity (measured via acceleration) provides an insight into energetic expenditure of animals which is linked to movement, behaviour, and physiological processes. This study used a network of acoustic tracking receivers ($n = 93$) across south-eastern Australia to identify the effects of environmental conditions on the activity of yellowtail kingfish (*Seriola lalandi*, $n = 63$). Activity, calculated through accelerometer sensors via acoustic tracking, was tested against geographical (latitude, bathymetry, distance to land), environmental (sea surface temperature, tide height, moon fraction, hour of the day), and biological (individual length) factors to identify drivers of kingfish activity. Sea surface temperature, hour of the day, and bathymetry strongly influenced the activity of kingfish, while activity slightly decreased during high tide height and moon fraction. Differences in activity and movement (residency and space use) within a small temperate estuary (120 km^2) were further investigated in a case study of a seasonal kingfish aggregation in Coffin Bay, South Australia. Kingfish remained in Coffin Bay during warm months (September – April), with a complete exodus from the estuary in winter. While residing in Coffin Bay, activity varied between interconnected areas, with temperature, hour of the day, tide height, and moon fraction also influencing kingfish activity. These results reveal that energetic responses of kingfish are sensitive to long-term (i.e., seasonal sea surface temperature) and diurnal; (time of day, photoperiod) changes in the environment, which can regulate behaviours and physiological processes. Findings from this study have implications for the energetic budgets of large pelagic fish in sub-tropical and temperate regions, which are facing rapidly changing climates. This is also the first study to highlight the potential for national-scale acoustic tracking to go beyond quantifying residency and movements, and describe physiological responses to changing environments for highly mobile and broadly-distributed species.

5.2 Introduction

Environmental processes in marine environments are complex and highly variable, and can have substantial impacts on the behaviours and movements of animals (Pörtner & Peck 2010, Udyawer et al. 2013, Heupel & Simpfendorfer 2014). Such changes can occur across different temporal scales, from acute behavioural responses over daily cycles (e.g., daily cycles of tidal currents, moon periods; Naylor 1999, Brownscombe et al. 2014) to chronic changes in movements due to more gradual environmental shifts (e.g., phenological temperature changes, photoperiod; Schlaff et al. 2014, Udyawer et al. 2015). These behavioural shifts can lead to positive outcomes such as increased access to nutrients or productive thermal shifts to increase recruitment (e.g., Morrongiello et al. 2014), or in some cases can have negative outcomes such as reduced resource availability, unfavourable thermal conditions, and increased energetic demands (Magnuson et al. 1990, Sorte et al. 2013). While the spatial movements and temporal persistence of some species linked to environmental conditions have been identified (Ackerman et al. 2000, Block et al. 2001, Udyawer et al. 2015), there has been a paucity of information in the effects of environmental drivers on the energetic status of free-ranging animals. Identifying how environmental variability can influence the activity of animals can therefore contribute towards understanding the effects of natural and anthropogenic-driven changes on the physiology of marine species (Udyawer et al. 2015).

While some marine fishes are endothermic (e.g., tunas, lamnid sharks), most marine teleosts are ectotherms that cannot thermoregulate internally (Wright & Cooper 1981, Johnston & Dunn 1987). To compensate, behaviours and movements of ectothermic fish are inherently linked to temperature changes in their surrounding environment, as individuals seek favourable areas to facilitate essential physiological processes (i.e., metabolism, oxygen uptake, immune response; Wright & Cooper 1981, Pörtner et al. 2001, Whitney et al. 2007). As a result, most mobile temperate pelagic species are typically more active or mobile during warm periods or within warm areas, due to increased energetic expenditure generated through active behaviours (e.g., swimming, foraging, spawning; Brodie et al. 2016, Payne & Smith 2017, Matley et al. 2020). Additionally, warm temperatures provide conditions that facilitate breeding opportunities and the survival and growth of early life-stage marine animals (Schofield et al. 2009, Payne et al. 2011, Matley et al. 2020). However, warming temperatures can exceed thermal tolerances, reaching levels at which physiological processes and energetic gains can decline (Johansen et al. 2015, Payne et al. 2016, Payne & Smith 2017). As temperate ecosystems continue to face fast-warming conditions (Müller et al. 2009, Hobday & Lough 2011), energetic budgets of ectothermic species are at risk of exposure to unfavourable conditions that can lead to implications on frequency and functioning of important behaviours and associated physiological processes. Identifying the activity responses of ectothermic pelagic fish across varying temperature conditions, therefore, offers valuable insights to inform climate and environmental variability models (Malishev et al. 2018). While temperature is arguably the most notable driver of activity, various other environmental parameters have the potential to influence behaviours and movements of ectothermic fish species. Shifts in salinity (Collins et al. 2008, Bernal et al. 2012), tidal patterns (Medved & Marshall 1983, Ackerman et al. 2000, Embling et al. 2013), bathymetry (Maravelias 1999, Hobday & Campbell 2009, Embling et al. 2013), current velocity and direction (Gaspar et al. 2006, Sleeman et al. 2010, Brodie et al. 2015), among a number of other abiotic factors (Schlaff et al. 2014) have the potential to influence movements and behaviours of marine ectotherms and subsequently has implications for energetic budgets. Revealing spatial patterns of activity associated with environmental factors can untangle interactions between highly mobile taxa and their surrounding environment, beyond traditional tracking methods (e.g., acoustic telemetry, mark-recapture) which only quantify geographical movements of animals.

Yellowtail kingfish (*Seriola lalandi*; hereafter referred to as kingfish), is a large-bodied carangid distributed circumglobally across coastal pelagic environments in temperate and sub-tropical oceans (Gillanders et al. 2001, Gomon et al. 2008). As a palatable table fish, kingfish support large recreational and commercial fisheries in Australia (Henry & Lyle 2003, Lowry et al. 2016), but are additionally recognised as a popular catch and release target amongst game fishers which has resulted in a large input of movement information from government supported tagging programs (e.g., New South Wales Game Fish tagging program). The south-east Australian distribution of kingfish (from southern Queensland [QLD], through New South Wales [NSW], Victoria [VIC], and Tasmania [Tas], to the western boundary of South Australia [SA]) is comprised of one, single population which is genetically distinct from Western Australia (WA; Miller et al. 2011). Kingfish abundance in east Australia's coastal areas increases in summer and autumn in response to warming conditions generated through shelf incursions from the East Australian Current (Brodie et al. 2015). Sea level anomalies, eddy kinetic energy, and oceanographic conditions around topographic features are also significant environmental predictors for the distribution of kingfish in southern Australia (Hobday & Campbell 2009, Brodie et al. 2015). This distribution and occurrence of kingfish along Australia's eastern coast has shifted poleward over the past 20 years in response to climate-driven shifts, changing the environmental conditions and habitats that individuals may naturally be exposed to (Champion et al. 2018). Kingfish in Australia can also undertake large-scale movements (up to 1000s of kilometres) between Australian state boundaries (Gillanders et al. 2001), and internationally with some individuals travelling between Australia and New Zealand (Saul & Holdsworth 1992). Throughout shifts in the distribution and large-scale movements across temperate (i.e., SA – southern NSW) and sub-tropics (i.e., northern NSW), kingfish in the south-eastern population are exposed to a range of environmental conditions which have the potential to influence energetic expenditure. Despite studies of movement compiled through recreational tagging programs (Gillanders et al. 2001, Hutson et al. 2007, Brodie et al. 2015) and studies investigating the site-specific habitat use of kingfish (Hobday & Campbell 2009, Roberts et al. 2011, Brodie 2016), environmental drivers of activity and energetic performance across south-eastern Australia have not been investigated.

This study assessed the activity (inferred through acceleration) of kingfish in south-eastern Australia (western SA to northern NSW) to determine chronic and acute environmental drivers of activity. Specifically, I collated acoustic tracking data from a national-scale animal tracking database and collaborative tagging projects to assess changes in kingfish activity in response to environmental, geographical, and biological factors. This study also included a case study within a small semi-enclosed estuary system (Coffin Bay, South Australia) to determine fine-scale activity changes within different interconnected areas across a small geographic scale (~ 120 km^2).

5.3 Methods

Study sites

South-eastern Australia

Acoustic tracking receiver arrays were deployed across > 2,500 km of coastline in south-eastern Australia (Figure 5.1a), encompassing temperate to sub-tropical habitats in NSW, VIC, and SA through a collaboration across three locally-focused projects (Figure 5.1b, Table S5). Raw detections and activity metadata was sourced through the Integrated Marine Observing System (IMOS) Australian Animal Acoustic Telemetry Database (animaltracking.aodn.org.au; Hoenner et al. 2018). Acoustic arrays included a combination of VR4, VR2W, and VR2AR acoustic receivers (Innovasea, Nova Scotia, Canada, innovasea.com) with kingfish detections collected from 96 receivers (Figure 5.1; NSW = 51, SA = 45). Receivers in VIC detected too few individuals for sufficient analyses of activity (*n* kingfish = 1, detections = 10) and, thus, were not included. Receiver installations within each state included the North and South Neptune Island Groups and Coffin Bay (SA), and Narooma, Sydney (coastal), Sydney Harbour, and Coffs Harbour (NSW) (Figure 5.1). Due to potential influence from cage-diving operations on kingfish activity at the Neptune Islands (see Chapter 4), detections on days that shark cage-diving operators visited the islands were not included.

Coffin Bay

Coffin Bay is a shallow (< 9 m) inverse estuary system comprised of interconnected bays located on the southern tip of the Eyre Peninsula, South Australia (34°37’18.84”S, 137°27’ 59.76”E; Kämpf & Ellis 2015; Figure 5.1b). Mean bathymetry in the system is ~2.6 m and total length is ~25 km (Kämpf & Ellis 2015). The mouth of the bay is a narrow opening created from a long (~5 km) spit of sand which limits exchange of estuarine water with ambient shelf water. This main body of the bay narrows to smaller interconnected sections (hereafter referred to as areas; Fig 5.1b), with two smaller islands named the Brothers. Long beach is an extended stretch of sand on the southern side of Coffin Bay, with a deep channel (8 – 9 m) that connects the outer areas to the inner bays of the system (Figure 5.1b). Dutton and Kellidie Bays are inner areas to the north and east of Long Beach, respectively. Each of the interconnected areas of the estuary have variable depths, flushing time, oceanographic conditions, and biota (Kämpf & Ellis 2015), in addition to unique assemblages of fauna (Whitmarsh et al. 2020). An array of 28 VR2W acoustic receivers (Innovasea, Nova Scotia, Canada, innovasea.com) were deployed throughout Coffin Bay in November 2019 prior to tagging of kingfish. Receivers were deployed throughout the estuary with a maximum distance of ~700 m apart, to form acoustic gates at the entrance to each area, enabling the detection of individuals moving between each area (Huveneers et al. 2016). Receivers were fixed into the benthos on galvanised star-pickets and serviced annually.

Capture and tagging of kingfish

Between March 2009 and March 2020, 59 kingfish were captured via hook-and-line and tagged with V9/V13/V16 AP64 acoustic activity tags (64/126 – 369/1090 days battery life, respectively; Innovasea, Nova Scotia, Canada, innovasea.com) in Sydney Harbour (n = 34), Coffs Harbour (n = 7), and the Neptune Islands (n = 18). Acoustic tags were equipped with acceleration sensors, which take measurements of acceleration (hereafter referred to as activity). Acceleration (± 4.9 m/s^2 range) was sampled for each transmission cycle and converted to a value by the onboard microprocessor using the root mean square value of all three axes (activity = $\sqrt{[X^2 + Y^2 + Z^2]}$). The static contribution to the overall acceleration (g) was filtered out prior to root mean square calculation. Root mean square acceleration resolution was 0.00139 – 0.01922 m/s^2 (Payne et al. 2011). An additional four individuals were tagged in western Victoria (38°24'41.1"S, 142°00'32.7"E; Lady Julia Percy Island [*Deen Maar*]), but only one individual was detected (10 detections) 21 km from tagging location (Fitzroy River entrance; 38°16'03.3"S 141°50'48.9"E) and so was not included in activity analyses. Total length of individuals ranged from 465 – 1,510 mm (mean = 865 ± 38 mm), though fish tagged in NSW were generally smaller (465 – 890; mean = 637 ± 15.8 mm TL) compared to individuals tagged in South Australia (800 – 1510; mean = 1,195 ± 39.9 mm TL). In November 2019, six additional kingfish were caught via seine net in Coffin Bay. All kingfish were tagged within the Kellidie Bay area, from two shots of the seine net. All fish were internally tagged with transmitters following standard surgical techniques (Taylor et al. 2013).

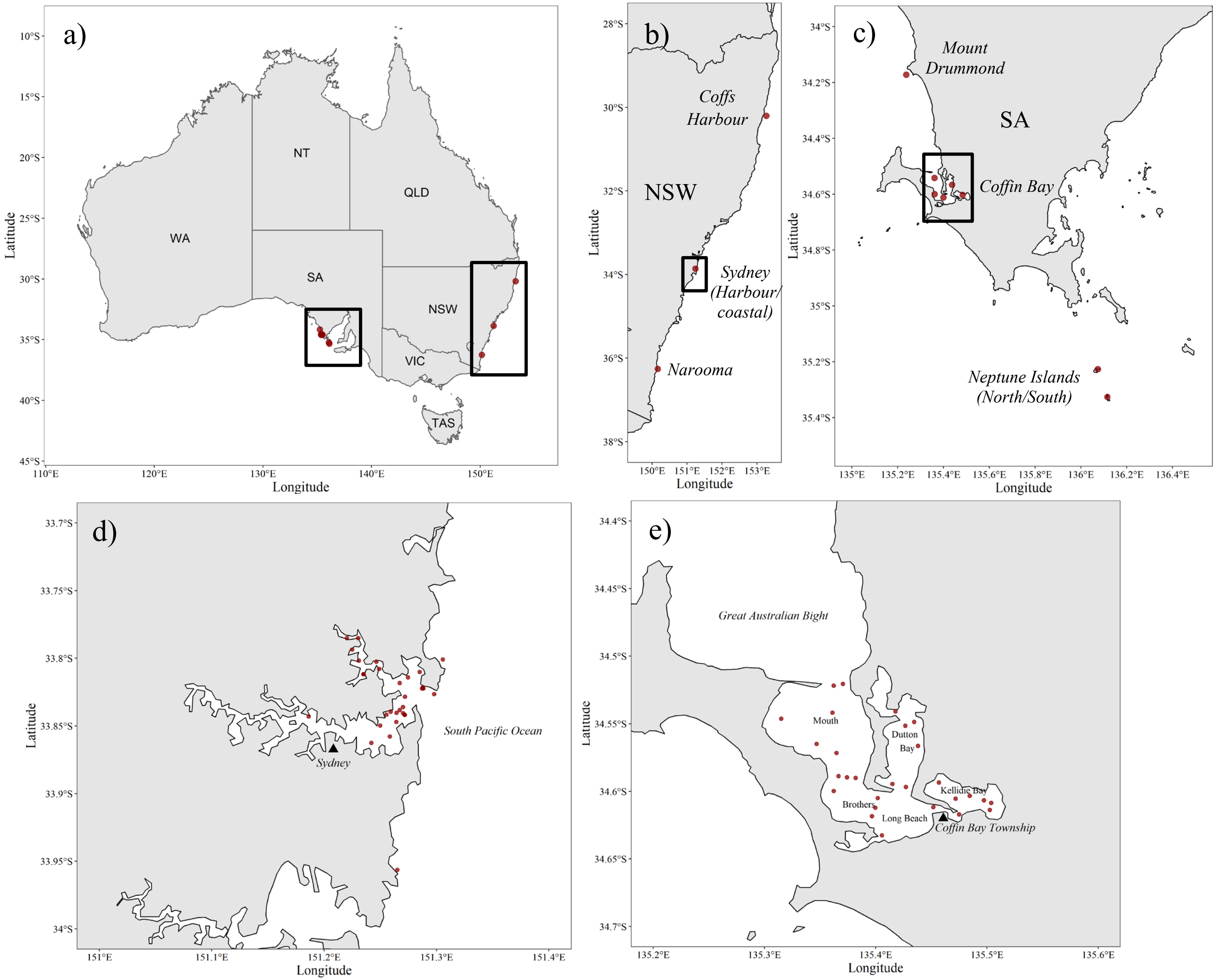

Figure 5.1. Map showing location of acoustic receiver arrays (red circles) in a) Australia, state subsets showing acoustic installations for b) New South Wales and c) South Australia (Coffin Bay inset), and detailed installation arrays in d) Sydney Harbour and e) Coffin Bay.

Extraction of environmental parameters

Analyses of kingfish activity was performed in the R statistical environment (version 1.2.5033). Measurements of interpolated daily sea surface temperature (GHRSST data, 15 km resolution), bathymetry (m; Geoscience Australia, 250 m resolution), distance to nearest landmass (km), combined current velocity (m/s^2) and bearing (°) were extrapolated using the *env_extract* function from the package 'IMOSTrack' (in development; Table 5.1). For locations that were missing derived environmental information, nearest pixel averages were calculated to assign approximate values (see Table 5.1 for geographical extent of interpolation). Hourly predictions of tide height derived from global models based on nearest tide gauge observations and supplied from the Bureau of Meteorology. Moon fraction (as a fraction of 0.0 [new moon] – 1 [full moon]) was calculated from the *getMoonIllumination* function from the package 'suncalc' (version 0.5.0). Fortnightly mean temperature and salinity data for Coffin Bay was obtained from the Primary Industry and Regions of South Australia Shellfish Quality Assurance Program (SASQAP) across three locations due to poor spatial resolution from satellite data.

Residency times and space use in Coffin Bay

Residency time in each area (time in days spent by kingfish in each area receiver array) was calculated using the *residency* function in the 'actel' package (version 1.2.1; Flávio & Baktoft 2021) based on time between first and final detections from receivers within the area array. Monthly utilisation distributions (UDs) were estimated for each kingfish using the *dynBBMM* function from the 'Refined Shortest Path' (RSP) package (version 1.0.1.9003; Niella et al. 2020). This function uses the Brownian-bridge approach to account for variable temporal windows between detections across all individuals (Horne et al. 2007). Contours were calculated for 50% (BBKUD-50; core) and 95% (BBKUD-95; extent) space use estimates, representing where animals spent 50 and 95% of the tracking time respectively.

Statistical analyses

To assess environmental drivers of kingfish activity across south-eastern Australia, activity measurements were examined in response to environmental parameters. The relationship between environmental variables (Table 5.1) and activity were tested using a Generalised Additive Mixed Model (GAMM), through the *gam* function (package 'mgcv', version 1.8.33). Fish length was included as an additional biotic factor but was highly correlated with sea surface temperature (r = -0.80) due to discrepancies in fish size between sampling locations and removed from the model. Factors were tested for correlation using *UncertCoef* (categorical factors, package: 'DescTools' version 0.99.42) and *cor.test* (numeric factors, package: 'stats' version 3.6.2). A hierarchical cyclic cubic spline was fit to account for ordinal cyclical features of hour of the day (i.e., 1 – 23). Four individuals from NSW were detected fewer than 10 times and were removed from subsequent analyses. The full south-eastern Australia activity model was:

$$\text{activity} \sim \text{Latitude} + \text{SST} + \text{Bathy} + \text{Tide} + \text{Moon} + \text{Dist2land} + \text{Hour} + \text{Transmitter}_{rand} + \text{Year}_{rand}$$

A second GAMM was used to test the effect of environmental factors (temperature, tide, moon fraction, hour) on the activity of kingfish in different areas of the Coffin Bay estuary system. Interactions between each area of Coffin Bay with environmental factors were tested to identify differences in kingfish responses in each area. Bathymetry was highly correlated with area ($r = 0.96$; i.e., all receivers within each area were of similar bathymetry) and was not included in mixed-effect models. The full Coffin Bay activity model was:

$$\text{activity} \sim \text{Temperature*Area} + \text{Tide*Area} + \text{Moon*Area} + \text{Hour*Area} + \text{Transmitter}_{rand} + \text{Weeknumber}_{rand}$$

Generalised Linear Mixed Models (GLMM, function *lmer*; package 'lme4' version 1.1.23) were used to predict the monthly residency and space use of kingfish in Coffin Bay. Month and temperature were highly correlated, so categorical month was removed from GLMMs. Models for residency time in each area of the system were tested in response to temperature. Core (50% BB-KUD) and extent (95%) range of movements were also modelled in response to temperature, but as BB-KUD's were not calculated for individual areas, interaction with area was not included. Months and areas with no detections were allocated as 0. Fish ID was additionally included in all models as a random intercept to account for individual variation in behaviours between kingfish, and study month (month of the study in ascending order from 1 – 15) was included for each fish to account for temporal autocorrelation across the study period. The full Coffin Bay movement models were:

$$\text{Residency: residency time} \sim \text{Area*Temperature} + (\text{Studymonth}|\text{Transmitter})_{\text{rand}}$$

$$\text{Space use: BBKUD-50/95} \sim \text{Temperature} + (\text{Studymonth}|\text{Transmitter})_{\text{rand}}$$

The most appropriate statistical family, response variable transformation, and validity of each model was determined by examining the distribution of the response variable and visual inspection of residuals. All model combinations of fixed-effect terms were run using the *dredge* function (package: 'MuMIn'; version 1.43.17, Barton 2020) and ranked using Akaike's information criterion corrected for small sample size (AIC_c; Burnham & Anderson 2002). The r.*squaredGLMM* function was then used to estimate marginal (fixed-factor; R_m) and conditional (all factors; R_c) R^2 values for each model.

Predicted values were extracted for each factor included in the top performing model using the *ggpredict* function from package ‘ggeffects’ (version 1.0.1).

Table 5.1. Summary of Generalised Additive Mixed Model covariates used to test environmental drivers of kingfish activity in south-eastern Australia.

Covariate	Description	Source	Units	Range
latitude	Location south of the equator; measured in decimal degrees	IMOS ATF (IMOSTrack R package)	Decimal degrees; S	30.20 – 35.33
SST	Sea surface temperature; one day composite remotely interpolated across 15 km radius; composite of multi-swath multi-sensor (L3S); derived from the Group for High Resolution Sea Surface Temperature (GHRSST)	IMOS ATF (IMOSTrack R package)	°C	13.2 – 25.75
bathy	Australian Bathymetry and Topography Grid; 250 m resolution	Geosciences Australia (IMOSTrack R package)	m	1.5 – 38
dist2land	Distance from nearest shoreline; derived from high-resolution Open Street Map shoreline product	IMOS ATF (IMOSTrack R package)	km	1 – 31.0
hour	Hour of the day (local time) extracted from activity detection	IMOS ATF (IMOSTrack R package)	h	0 – 23
tide	Hourly predictions of tide height derived from global model based on nearest tide gauge observations	Bureau of Meteorology	m	-0.69 – 2.2
moon	Illuminated fraction of the moon; varies from 0.0 (new moon) to 1.0 (full moon)	getMoonIllumination function (suncalc R package)		0 – 1
length	Total length		mm	465 – 1510

5.4 Results

Summary of south-eastern Australia results

A total of 211,713 activity measurements were collected from 59 individuals via six receiver installations and across 5.124 degrees of latitude (30.202 – 35.326°S) in south-eastern Australia (Table S5). Average sea surface temperature was 18.9 ± 0.01°C (Table S6), ranging from 16.1 ± 0.01°C (Coffin Bay) to 23.4 ± 0.02°C (Coffs Harbour). These installations were also at the extremities of bathymetry (mean = 13.1 ± 0.02 m), with bathymetry in Coffin Bay being the shallowest (mean = 5.5 ± 0.01m) compared to deepest at Coffs Harbour (20.8 ± 0.08 m). Distance to the mainland ranged from 1 km (Sydney Harbour and Sydney Costal) to 31 km (South Neptune Islands), with an average distance of 10.1 ± 0.03 km. Full cycles of tide (mean = 0.321 – 0.001 m), moon fraction (0.385 – 0.001), and hour of the day were observed (Table 5.1). Even on days that shark cage-diving operators did not frequent the area, kingfish activity was highest at the North Neptune Islands installation (mean activity = 1.09 ± 0.003 m/s^2; Figure 5.2a), followed by coastal Sydney (1.06 ± 0.01 m/s^2) and Coffs Harbour (0.95 ± 0.007 m/s^2). Kingfish activity decreased in Sydney Harbour (0.77 ± 0.002 m/s^2) and Coffin Bay (0.7 ± 0.003 m/s^2) and was lowest at the South Neptune Islands (0.53 ± 0.02 m/s^2).

Environmental drivers of kingfish activity in south-eastern Australia

Except for distance to land, all environmental parameters in the GAMM had significant effects on activity of kingfish (Table S7) and were included in the top-ranked model (wAIC$_c$ = 0.523, Table 5.2), however, the second best model included distance to land and had a similar wAIC$_c$ (0.477), but did not improve the variance explained by the model (i.e., 23 *vs*. 22%). Latitude and temperature had the largest influence on activity (Figure 5.2b, Table S7). Activity increased southwards (Figure 5.2a), despite activity being lowest at the most poleward installation South Neptune Islands (0.53 ± 0.02 m/s^2; Figure 5.2b) and third highest at the northernmost installation Coffs Harbour (5.1b 0.95 ± 0.01 m/s^2). This trend was likely attributed to activity being highest at the North Neptune Islands (1.09 ± 0.003 m/s^2) and coastal areas of Sydney (1.06 ± 0.01 m/s^2; Figure 5.2b). Temperature had a large, positive relationship with activity irrespective of latitude (Figure 5.2), with individuals being less active at low temperatures (~0.55 ± 0.2 m/s^2 at 15°C *vs*. 1.1 ± 0.01 m/s^2 at 24.5°C). Kingfish had strong diurnal activity patterns, being largely inactive at night (0.5 – 0.6 m/s^2 from 1900 – 0600 *vs*. 0.7 – 0.8 m/s^2 at ~12:00; Figure 5.2b). Kingfish activity was negatively correlated with bathymetry (Figure 5.2b). Tide height and moon fraction had a slight inverse relationship with activity (Figure 5.1). Random model effects also influenced kingfish activity, with Fish ID explaining 17% of the model variation, while study year explained less of the variance (3%, Figure S7).

Large-scale movements

In addition to exposure to local environmental conditions, three individuals (13%) tagged in South Australia undertook large-scale movements away from their tagged location. One individual (ID 14251), tagged at the North Neptune Islands group in April 2019, remained at the Neptune Islands until July 2020 and was then detected ~250 km away at Victor Harbor (Granite Island, -35°33’24.48"S, 138°38'11.4"E) in September 2020. This individual was then detected 11 days later over 1,400 km away in Narooma, New South Wales (36°15'46.4"S 150°09'52.1"E), then three days later ~ north of Manly (Sydney, NSW; ~300 km north of Narooma). This individual was again detected near Manly two months later and at the entrance of Sydney Harbour in December 2020. In total, this individual moved ~1,800 km, and across four Australian state boundaries. A second individual (ID 7809) tagged at the North Neptune Islands was detected in Batemans Bay, NSW (35°47'42.1"S 150°14'13.3"E) 56 days after being detected last at the Neptune Islands, and was then detected in Manly six days later (two months prior to ID 14251). One kingfish (ID 14253) tagged in November 2019 inside Coffin Bay was detected outside of the estuary system at Mount Drummond (34°10'21.4"S 135°14'16.1"E; Figure 5.1) in September 2020, over ~60 km from tagging location in Coffin Bay. This individual was detected here one day before being detected back inside the Coffin Bay array, where it continued to reside for the following 4 months. During all large-scale movements, brief occurrences of individuals at receivers (i.e., < 5 detections) were accompanied by high activity values (1.2 – 2.04 m/s^2), suggesting that these individuals are more active while travelling compared to when residing in installation areas.

Table 5.2. Summary of top five models estimating effects of environmental parameters on kingfish activity in south-eastern Australia. df, degrees of freedom; AIC_c, Akaike information criterion corrected for small sample size; ΔAIC_c , difference in AIC_c between the current and the top-ranked model; $wAIC_c$, model probability; R_m, marginal (fixed effects) R^2; R_c, conditional (fixed and random effects) R^2.

Model	**df**	**logLik**	**AIC_c**	**ΔAIC_c**	**$wAIC_c$**	**R_m**	**R_c**
Activity (m/s^2) ~ Bathy + Latitude + Moon + Hour + SST + Tide	**89**	**-8323.3**	**16825.3**	**0**	**0.523**	**0.064**	**0.23**
Activity (m/s^2) ~ Bathy + Dist2land + Katitude + Moon + Hour + SST + Tide	89	-8322.9	16825.5	0.18	0.477	0.059	0.22
Activity (m/s^2) ~ Bathy + Latitude + Hour + SST + Tide	88	-8343.8	16864.3	38.93	0	0.059	0.22
Activity (m/s^2) ~ Bathy + Dist2land + Latitude + Hour + SST + Tide	88	-8343.5	16864.6	39.29	0	0.059	0.22
Activity (m/s^2) ~ Bathy + Dist2land + Moon + Hour + SST + Tide	89	-8351.4	16881.2	55.9	0	0.058	0.22

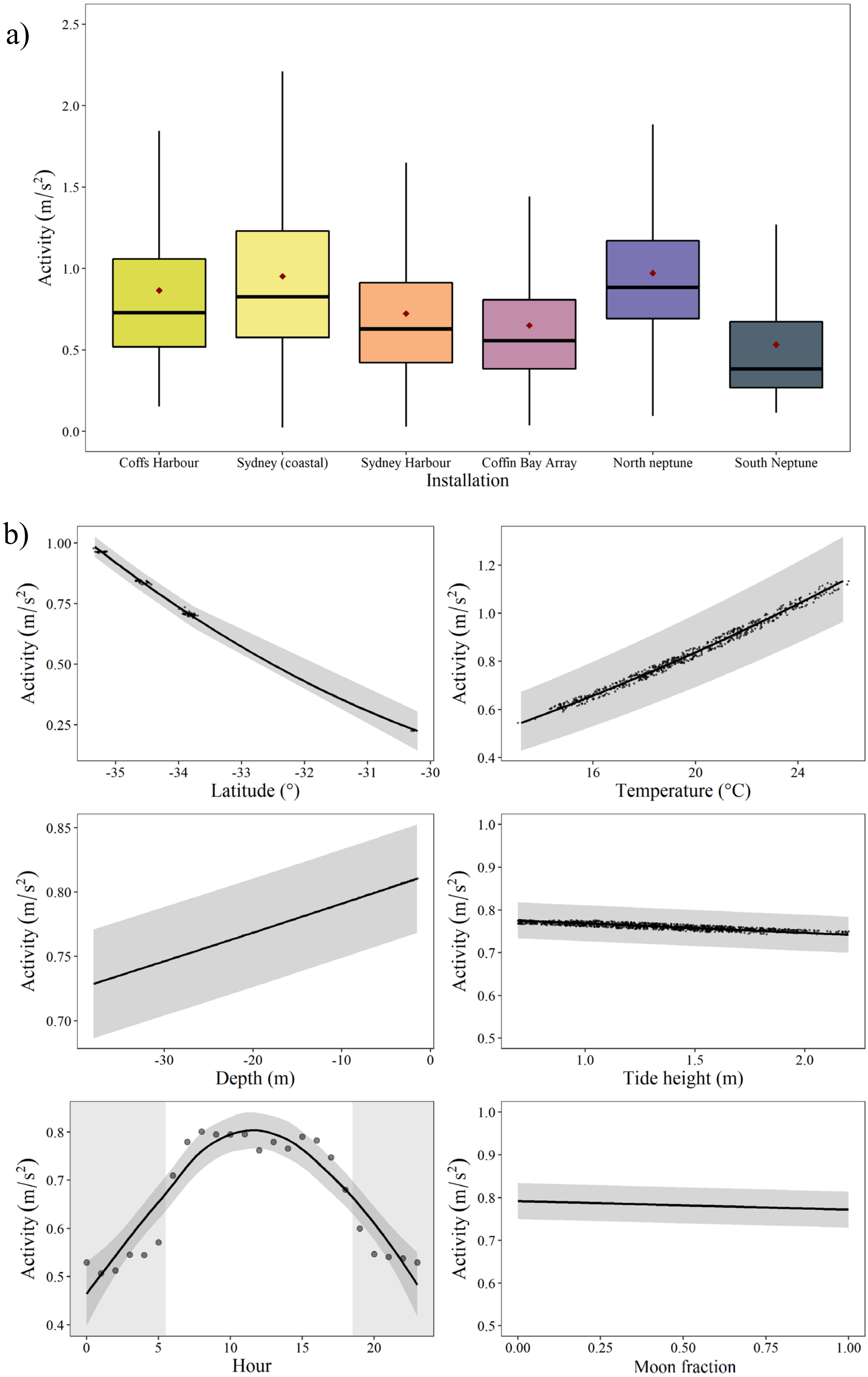

Figure 5.2. a) Estimated means of kingfish activity at different installations in south-eastern Australia. Mean values shown as red diamonds. Black horizontal bars represent median values. Black boxes encompass the interquartile range, and vertical black lines represent the maximum and minimum values. b) marginal means (predicted values ± SE) of kingfish activity in response to environmental variables from Generalised Additive Mixed Model.

Coffin Bay case study: Drivers of movement and activity in a seasonal aggregation within a semi-enclosed embayment

Kingfish (*n* = 6) were detected 33,371 times in the Coffin Bay array between November 2019 and January 2021 (mean = 5,562 ± 33.5 per fish). The most frequented area of Coffin Bay was Mount Dutton Bay, comprising 71% of all detections (Figure 5.3, Figure 5.4). There was a complete exodus of kingfish from the estuary during winter, with no fish detected between the 30th of April and 8th of August 2020 (Figure 5.3). Three tagged kingfish returned to Coffin Bay in September, all returning within a three-day window (8 – 12th September; Figure 5.3).

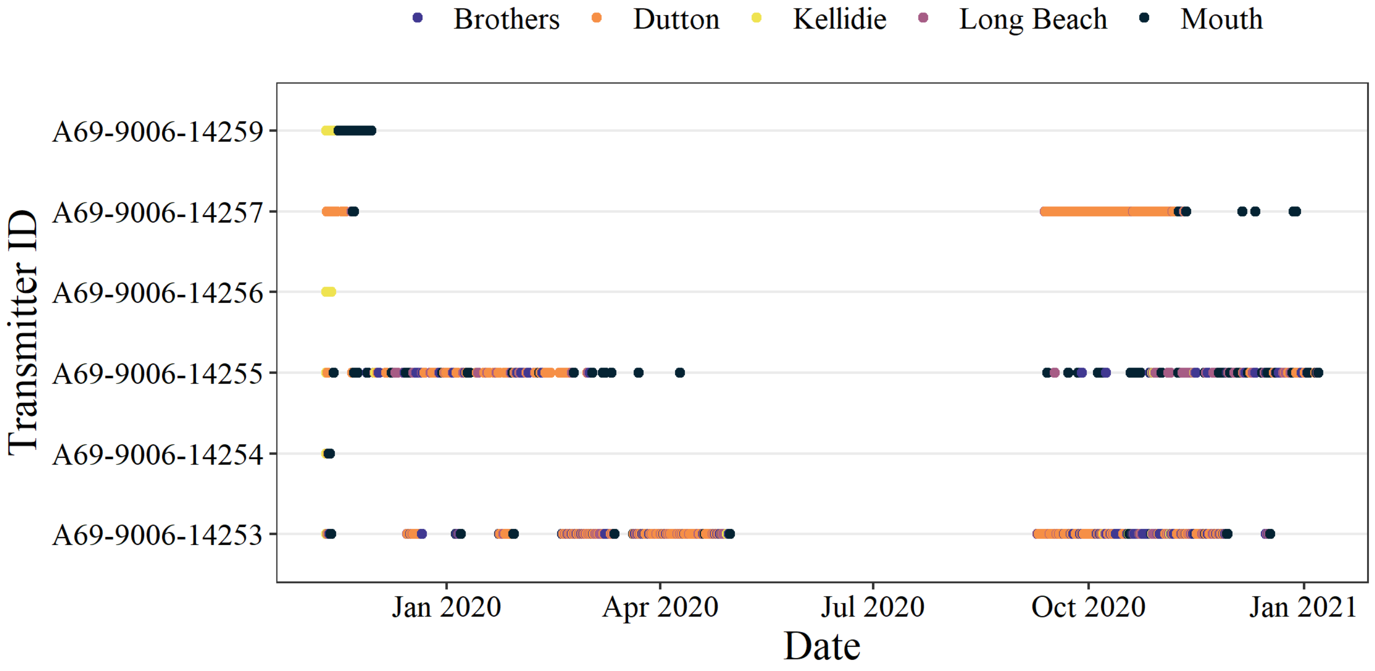

Figure 5.3. Residency of kingfish in Coffin Bay between November 2019 – January 2021, colours correspond to interconnected areas of the system. Darker colours represent areas closer to the mouth (entrance of the system), lighter colours represent areas further into the estuary.

Residency and space use in Coffin Bay

The top-ranked model for residency time in Coffin Bay only included area and was not affected by temperature, or the interaction between temperature and area (Figure 5.4a; Table 5.3). Kingfish spent the most time in Dutton Bay (1.58 ± 0.27 days per month), which was substantially higher than in any other areas (0.06 – 0.12 days; Figure 5.4a). Average core (BBKUD – 50) space use by individual kingfish in Coffin Bay was 5.84 ± 1.45 km^2, and extent (BBKUD – 95) of space use was 30.68 ± 6.83 km^2. Core and extent of kingfish space use was influenced by temperature, with the most space occupied during warm periods (Table 5.4, Figure 5.4). In contrast to residency behaviours, individual Transmitter ID contributed to the variation of the space use model (19% core, 13% extent *vs*. 4% for time spent), indicating that space use was variable between individuals. Predicted core space use was highest in warm temperatures > 18°C (October – February, 4.4 – 7.83 km^2, Figure 5.3, Figure 5.4), but decreased when temperature was < 15°C (March and April), coinciding with the exodus of fish from Coffin Bay between May – August when space use shifted towards the entrance of Coffin Bay (< 12.5°C, 0.01 – 0.0.02 km^2, Figure 5.3, Figure 5.5). When fish returned to Coffin Bay in August, core space use gradually increased and individuals occupied areas deeper into the estuary system, until it peaked in November – February (Figure 5.5). This trend was mirrored from the extent of space use, with kingfish occupying the most space during summer months when temperature was above 18°C (November – February, 26.45 – 45.07 km2, Figure 5.5), decreasing when kingfish left the bay between May and June.

Table 5.3. Summary of Generalised Linear Mixed Model estimating effects of month on residency time (time within each area) in Coffin Bay. df, degrees of freedom; AIC$_c$, Akaike information criterion corrected for small sample size; ΔAIC$_c$, difference in AIC$_c$ between the current and the top-ranked model; wAIC$_c$, model probability; R$_m$, marginal (fixed effects) R^2; R$_c$, conditional (fixed and random effects) R^2.

Model	**df**	**logLik**	**AIC$_c$**	**ΔAIC$_c$**	**wAIC$_c$**	**R$_m$**	**R$_c$**
Time spent ~ Area	**9**	**-380.5**	**779.8**	**0**	**0.97**	**0.14**	**0.19**
Time spent ~ Area + Temperature	10	-382.8	786.8	6.94	0.03	0.14	0.19
Time spent ~ 1 (Intercept only)	5	-396.1	802.3	22.51	0	0	0.04
Time spent ~ Area + Temperature + Area*Temperature	14	-388.6	807.3	27.46	0	0.14	0.19
Time spent ~ Temperature	6	-398.3	809.1	29.28	0	>0.01	0.04

Table 5.4. Summary of Generalised Linear Mixed Model estimating effects of month on kingfish core (BBKUD – 50) and extent (BBKUD – 95) space use at Coffin Bay. df, degrees of freedom; AICc , Akaike's information criterion corrected for small sample size; ΔAICc , difference in AICc between the current and the top-ranked model; wAICc , model probability; Rm, marginal (fixed effects) R^2; Rc, conditional (fixed and random effects) R^2.

Model	**df**	**logLik**	**AIC_c**	**ΔAIC_c**	**$wAIC_c$**	**R_m**	**R_c**
a) BBKUD – 50							
Temperature	**6**	**-81.625**	**177.5**	**0**	**0.986**	**0.24**	**0.46**
Intercept	5	-87.233	186.0	8.54	0.014	0	0.19
b) BBKUD – 95							
Temperature	**6**	**-116.89**	**248.0**	**0**	**0.995**	**0.26**	**0.43**
Intercept	5	-123.53	258.6	10.62	0.005	0	0.13

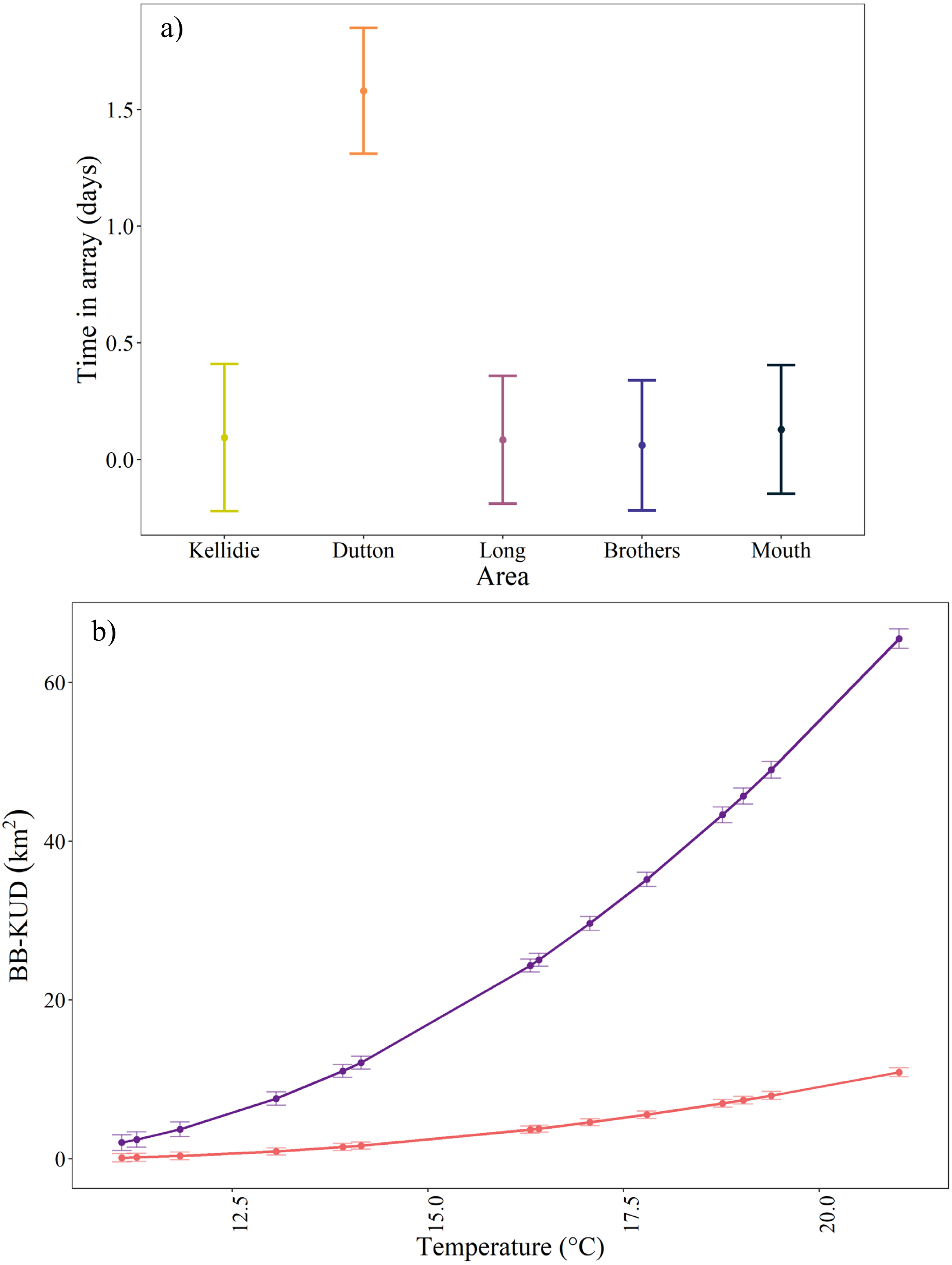

Figure 5.4. Generalised Linear Mixed Model predicted effects (marginal means) of a) residency time in each area, and b) core (pink: 50%) and extent (purple: 95%) space use ± standard error space use in response to temperature of kingfish in Coffin Bay.

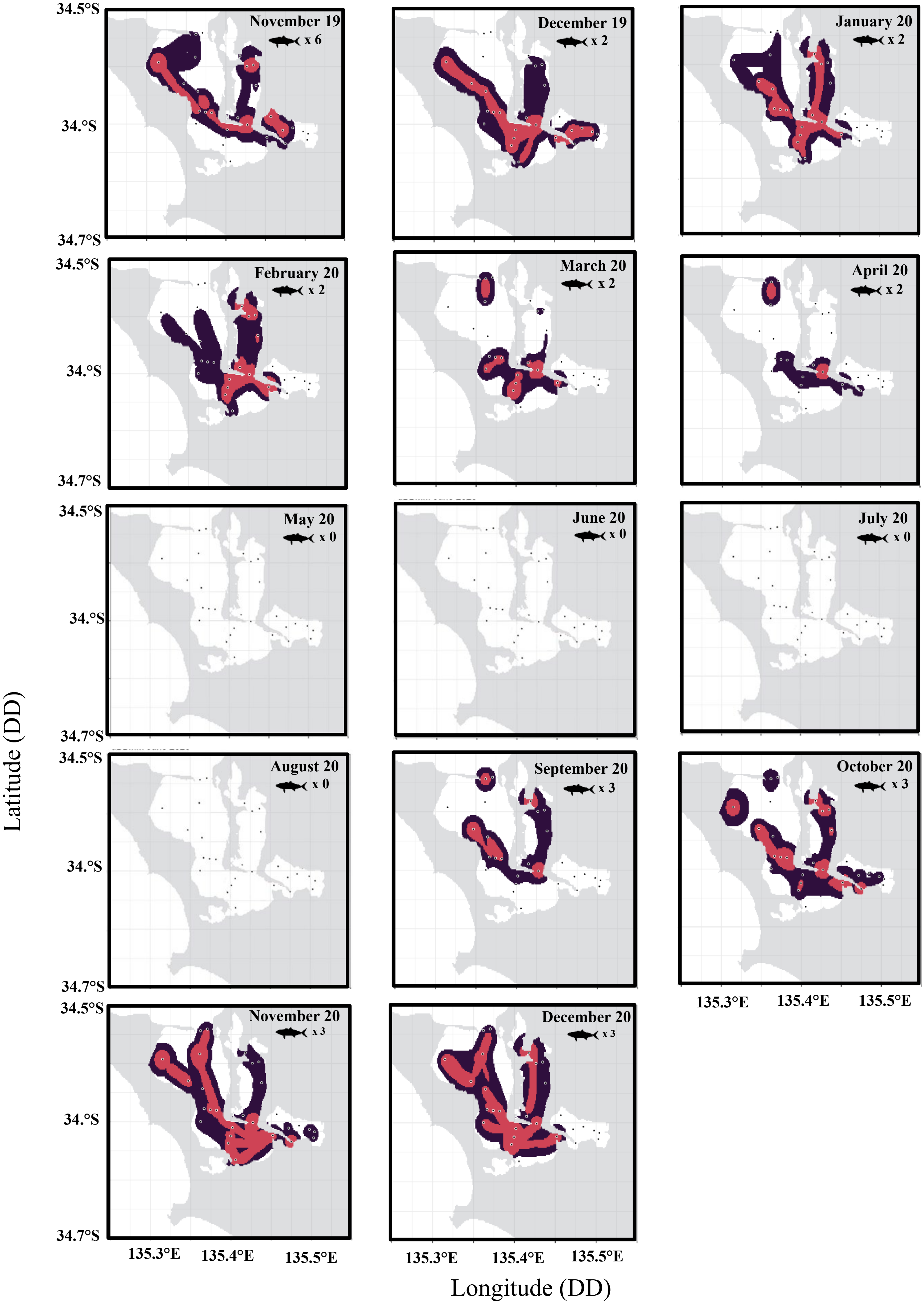
November 19
x 6
December 19
x 2
January 20
x 2
February 20
x 2
March 20
x 2
April 20
x 2
May 20
x 0
June 20
x 0
July 20
x 0
August 20
x 0
September 20
x 3
October 20
x 3
November 20
x 3
December 20
x 3
34.5°S
34.°S
34.7°S
135.3°E
135.4°E
135.5°E
Latitude (DD)
Longitude (DD)

Figure 5.5. Monthly core (pink: 50%) and extent (purple: 95%) of space use in Coffin Bay. Grey areas represent land. Acoustic receivers shown as black circles. Number represents number of fish detected in the array that month

Activity drivers in Coffin Bay

Interactions between area and temperature, hour of the day, tide height, and moon fraction were all included in the top-ranked model and influenced the activity of kingfish in Coffin Bay ($wAIC_c = 0.99$, 19% of variance explained, Table 5.5, Table S8). The effects of environmental drivers on kingfish activity were also variable between individuals and across the temporal period, with 6% of model deviance linked to the random effects (i.e., 5% Transmitter ID, 1% study week number).

In all areas of Coffin Bay, activity of kingfish was lowest at night and increased during the day, except for the Mouth which remained consistent across all hours of the day (Figure 5.6a). In the morning, activity was highest in the Brothers area (0.96 ± 0.04 m/s^2) but was highest in the Long Beach area in the afternoon (1.02 ± 0.02 m/s^2). Despite spending the most time in Dutton Bay (Figure 5.4), activity was consistently lowest in this area all hours of the day (0.44 – 0.68 m/s^2, Figure 5.6a). Temperature in Coffin Bay ranged from 10.1 – 21.9°C, but kingfish were only detected in the system above 13.2°C. Kingfish activity increased with warming temperatures in all areas, but the intensity of the response was variable (Figure 5.6). At low temperatures (<15°C), kingfish were most active in Brothers (0.77 ± 0.02 m/s^2) and Long Beach (0.77 ± 0.02 m/s^2; Figure 5.6b). However, activity in Kellidie Bay rose rapidly with temperature and became higher than all other areas in warm conditions (Kellidie = 1.44 ± 0.12 m/s^2). Activity in Dutton Bay also increased with temperature but was the area of lowest activity across all temperatures (from 0.38 – 0.87 m/s^2, Figure 5.6b). The influence of tidal height on activity varied between areas of Coffin Bay (Figure 5.6c). Kingfish were most active at low tide heights and decreased as tide heights increased in all areas, except for Dutton Bay where activity slightly rose with tide height (0.46 – 0.48 m/s^2, Figure 5.6c). At both low and high tide heights, activity was highest in the outer bays (i.e., Brothers [0.92 ± 0.03 m/s^2], Long Beach [0.89 ± 0.02 m/s^2]; Figure 5.6c). Activity in Kellidie and the Mouth dropped noticeably with tide heights, to the point of activity at the Mouth being similar to activity in Dutton Bay at tide heights higher than 1.2 m (~0.54 m/s^2, Figure 5.6c). Kingfish activity was negatively correlated with moon fraction in Kellidie, Dutton, and the Mouth, but increased at the Brothers and Long Beach areas (Figure 5.6d).

Table 5.5. Summary of the top five models estimating effects of environmental drivers on kingfish activity in Coffin Bay. df, degrees of freedom; AIC_c , Akaike's information criterion corrected for small sample size; ΔAIC_c , difference in AIC_c between the current and the top-ranked model; $wAIC_c$, model probability; R_m, marginal (fixed effects) R^2; R_c, conditional (fixed and random effects) R^2.

Model	**df**	**logLik**	**AIC_c**	**ΔAIC_c**	**$_wAIC_c$**	**R_m**	**R_c**
Area + Moon + Temperature + Tide + Hour*Area + Area*Temperature + Area*Tide + Area*Moon	88	-25376.2	50929.6	0	0.99	**0.193**	**0.249**
Area + Moon + Temperature + Tide + Hour*Area + Area*Temperature + Area*Tide	85	-25394.7	50960.8	31.25	<0.01	0.0192	0.248
Area + Moon + Temperature + Hour*Area + Area*Temperature + Area*Moon	83	-25398.5	50964.2	34.63	<0.01	0.0192	0.248
Area + Moon + Temperature + Tide + Hour*Area + Area*Temperature + Area*Moon	84	-25398.1	50965.3	35.74	<0.01	0.0192	0.248
Area + Temperature + Tide + Hour*Area + Area*Temperature + Area*Tide	84	-25402.1	50972.9	43.30	<0.01	0.0192	0.248

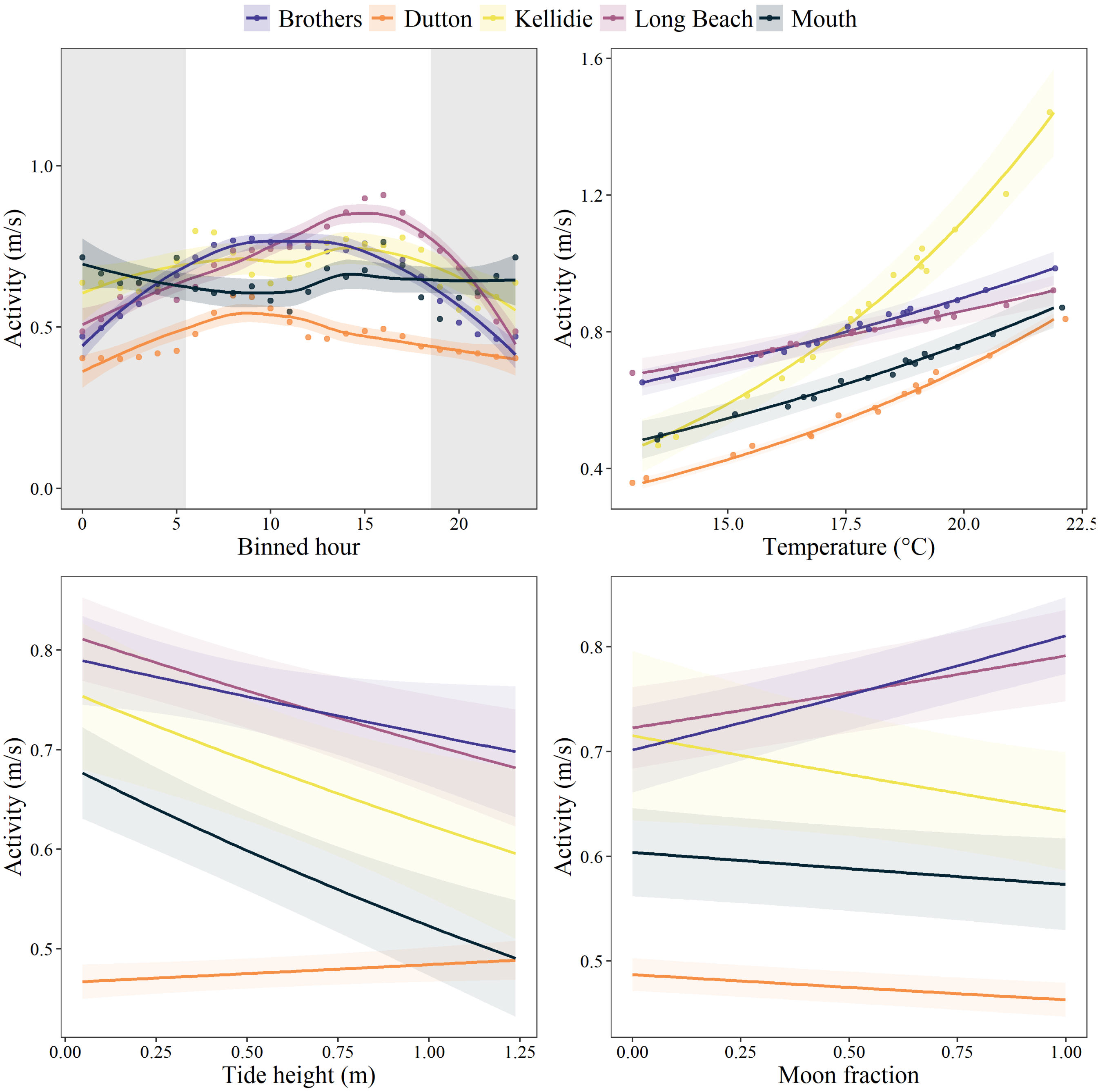

Figure 5.6. Activity of kingfish predicted from Generalised Additive Mixed Model in different areas of Coffin Bay through interactions with environmental parameters. Darker colours represent areas closer to the mouth of the estuary, lighter shades are areas further into the system.

5.5 Discussion

The capacity to infer the behaviours and energetic budgets of highly mobile pelagic fish, and their responses to environmental conditions has historically been logistically challenging. While past applications of standard telemetry methods have been used to quantity environmental drivers of horizontal and geographic movements of mobile marine species, linking these drivers to activity and energetic expenditure of mobile species has been limited. This study identified several environmental drivers of kingfish activity in south-eastern Australia, while demonstrating the capability of a national network of acoustic-tracking receivers to identify important drivers of energetic budgets for a highly mobile pelagic fish across a large geographic footprint. Acoustic transmitters, equipped with accelerometer sensors, revealed that sea surface temperature had a large positive influence on kingfish activity across south-eastern Australia, with activity also increasing in areas of shallower bathymetry and during daylight hours. Activity of kingfish decreased during higher tides and with increasing moon fraction. In addition, the Coffin Bay case study highlighted that activity and movements are influenced by environmental conditions within a small spatial scale less than ~120 km^2 and can vary between interconnected areas of a shallow estuary system. I also identified large-scale movements of kingfish in southern Australia through acoustic tracking, which has previously been reliant on tag-and-recapture or habitat modelling through fisheries catch data (e.g., Hutson et al. 2007, Brodie et al. 2015, Champion et al. 2018). Describing the relationship between activity and environmental conditions across south-eastern Australia provides a novel understanding of the ecology of kingfish, which is increasingly important in the Anthropocene (Steffen et al. 2015, Aswani et al. 2018) in an area where changes to the oceanographic conditions of water bodies has already been identified (i.e., poleward extension of the East Australian Current; O'Kane et al. 2011, Oliver & Holbrook 2014).

This study found that kingfish activity was strongly correlated with sea surface temperature, whereby fish spent more energy when under warm conditions. This relationship mirrors previous descriptions of thermal-dependent energy expenditure for ectothermic teleosts (Wright et al. 2014, Payne et al. 2016) and cephalopods (Payne et al. 2011), where raised temperatures facilitate active behaviours such as increased intensity and frequency of foraging and feeding, reproductive behaviours, or predator avoidance strategies. Previous activity comparisons from eastern Australia found that kingfish were more active in warm coastal *vs*. estuarine environments (Brodie 2016), but my findings build on a sub-tropical acoustic telemetry dataset and extend to the temperate distribution of kingfish in south-eastern Australia. Thermal conditions have significant implications for the movements and behaviours of marine ectotherms (Udyawer et al. 2015, Payne et al. 2016). Optimal thermal conditions for kingfish physiology along Australia's eastern coastline is expected to be ~22°C, which corresponds to optimal growth in captivity (Fielder & Heasman 2011, McKenzie et al. 2014) and preferable physiological status (Champion et al. 2020b). In this current study, kingfish were sampled across a broad temperature range (13.2 – 25.75°C), revealing a linear relationship with activity extending beyond the 22°C limit for optimal growth and condition (Fossette et al. 2012, Payne & Smith 2017). Furthermore, coastal and pelagic environments adjacent to areas of south-eastern Australia in this study are warming 3 – 4 times more rapidly than the global average, due to the poleward extension of the southward flowing East Australian Current (EAC) (Cai et al. 2005, Ridgway 2007). Transportation of warm, tropical water from the EAC to cooler temperate climates has led to this region being within the top 10% of fastest warming areas of the global ocean, with projections expected to continue to increase (Hobday & Lough 2011, O'Kane et al. 2011, Hobday & Pecl 2014). As a result, habitat suitability of northernmost areas of kingfish distribution are predicted to contract, leading to a poleward shift in the distribution and persistence of kingfish in south-eastern Australia (Champion et al. 2018). With the thermal habitats of kingfish in south-eastern Australia facing climate-driven shifts, it is possible that kingfish could be unable to efficiently manage energy expenditure, and deplete anaerobic energy stores which are required to capture prey, reproduce, or avoid predators (Payne et al. 2011).

Given that northern areas (i.e., tropics) of Australia are warmer than southern regions, it was expected that activity would decrease with southward latitudes due to poleward areas being cooler. However, despite a strong positive relationship with temperature, kingfish activity was predicted by the GAMM to increase in poleward latitudes. This is likely explained by the highest activity being at the North Neptune Islands and Sydney coastal areas, which are both further south of Coffs Harbour where kingfish had low activity. Activity was highest at the North Neptune Islands, even though only activity measurements when cage-diving operators were not present were used. This indicates that kingfish activity at the Neptune Islands remains elevated even on days that tourism operators do not frequent the islands, making activity at this location more comparable to regions or periods of warm water temperature. Kingfish from Sydney coastal waters had higher activity than kingfish from Sydney Harbour and Coffs Harbour, despite these two locations having comparable, if not warmer, water temperatures. Higher activity in coastal areas may be due to fish using Sydney coastal waters as migratory corridors compared to estuaries like Sydney Harbour or offshore island groups (i.e., Coffs Harbour – South Solitary Islands, South Neptune Islands) where kingfish might be more resident and use the area as a low-activity refuge away from strong currents like the EAC (Brodie 2016). Findings from the Coffin Bay estuary further show that activity can vary over a small spatial scale (i.e., between different areas of the system). These findings highlight that the energetic responses of kingfish can be acute in response to local environmental drivers (i.e., habitat in different areas of the system, prey availability; Whitmarsh 2019) even within similar geographic conditions.

Bathymetry plays an important role in facilitating the vertical and horizontal distributions and activity of coastal-pelagic species (Maravelias 1999, Collins et al. 2012). Shallow coastal environments often provide warm, highly productive habitats that promote high levels of activity in mobile fish (Watson et al. 2014, Tanner et al. 2019). Although the distance to the nearest landmass did not influence activity, kingfish were most active in shallow areas, which is likely associated with individuals using these areas for active behaviours possibly linked to foraging or reproduction, often facilitated by high levels of primary production and resource availability. Shipley et al. (2018) described a similar trend from Caribbean reef sharks (*Carcharhinus perezi*), where activity increased when closer to the reef-shelf, expected to coincide with important foraging areas for this species. Although an effort was made to include measurements of primary productivity (daily chlorophyll-a concentration) in mixed models, insufficient measurements from satellite-derived platforms was obtained for areas close to landmasses or in estuarine systems (i.e., Sydney Harbour, Coffin Bay), exposing a limitation of using satellite-derived environmental information across marine landscapes and highlighting the need for *in-situ* observations. In addition to shallow coastal environments, large pelagic fish are often also associated with bathymetric features on continental shelves, seamounts, and mid-ocean ridges which are used as aggregation areas (Maravelias 1999, Hobday & Campbell 2009). For example, in Western Australia 80% of recaptured tagged kingfish were associated with these features (Hobday & Campbell 2009). While these associations suggest high site-fidelity, it would be expected that activity surrounding these deeper, offshore bathymetric structures would resemble lower activity estimates as observed at the South Neptune Islands and Coffs Harbour (Solitary Islands) as fish are less active while residing. Future research should examine the roles of such offshore bathymetric formations in the energetic budgets and physiological processes of kingfish in southern Australia. Findings from this chapter highlighted that in addition to being important areas for movements and aggregations, bathymetry played an important role in the energetics of kingfish in south-eastern Australia.

One of the most notable drivers of kingfish activity was hour of the day, with strong diurnal patterns indicating a 30% increase in activity during the day (0700 – 1800; 0.75 ± 0.1 m/s^2). Diel patterns of movement are a common trait that have been observed in many large pelagic fish (e.g., bigeye tuna *Thunnus obeseus*; Musyl et al. 2003, sailfish *Istiophorus platypterus*; Chiang et al. 2013, sunfish *Mola mola*; Chang et al. 2020, dolphinfish *Coryphaena hippurus*; Lin et al. 2020), coinciding with availability of prey items and associated foraging opportunities during daylight hours. As active mobile feeders that feed during the day on cephalopods, smaller mesopelagic fish, and crustaceans (Gomon et al. 2008, Meyer et al. 2020), increased activity of kingfish during the day likely corresponds with energetically-costly movements and behaviours associated with foraging and feeding. In Coffin Bay, diurnal activity trends varied between areas of the estuary system. Despite spending the greatest time in Dutton Bay, activity was lowest here of all areas, with a small increase in activity during the day. This low activity, paired with elevated residency suggests that kingfish are using this area to reside and rest, with energetically-costly behaviours taking place in other areas of Coffin Bay. Unlike other areas of the system, activity was consistent throughout all times of the day at the mouth, with no diurnal peaks or troughs. These areas near the entrance of the estuary are more likely used as transportation areas in and out of the system, rather than residing areas by fish while inside of Coffin Bay where diurnal trends are more prevalent.

Tide height and moon phase also influenced kingfish activity, although to a lesser extent than other abiotic factors (e.g., temperature, bathymetry, hour). Kingfish were exposed to a range of tidal heights (-0.69 – 2.20 m), with highest activity identified at lower tides. Lower tide height concentrates prey resources (Mackinson et al. 1999, Hoare et al. 2004, Robinson et al. 2004), so higher activity during shallower tides may be linked to foraging and feeding behaviours of kingfish maximising access to prey items. The effect of tide height was stronger in Coffin Bay when compared to south-eastern Australia overall, with activity in all areas of the system decreasing considerably with higher tides, except for Dutton Bay where activity remained low regardless of tides. In inner-areas of the Coffin Bay, kingfish are often observed traveling along shallow banks and sandbars, where they can be visually observed with caudal fins out of the water. Mobility in shallow bathymetries creating additional drag requires more powerful movements and would likely explain why activity was higher in shallow areas at low tide (i.e., Kellidie Bay, < 2 m bathymetry) compared to deep areas (e.g., Dutton Bay, 4 – 6 m bathymetry). Relationships with lunar cycles are often observed in the movements, feeding, and reproductive behaviours of marine and freshwater fishes (Di Natale & Mangano 1995, Naylor 1999, Milardi et al. 2018). Kingfish in south-eastern Australia were most active when moon fraction was lowest i.e., new moon, with a small decrease coinciding with moon fullness. Moon fraction and tide changes are inherently linked, where newer moons are associated with large tide cycles, so it is likely that the relationship between tide heights and the effects on kingfish activity are most prevalent at new and full moons where tidal influence is greatest. This relationship was replicated in Coffin Bay, except for Long Beach and Brothers areas where activity increased with moon fraction. Previous descriptions in the pelagic domain have associated periods of full moons to increased schooling behaviours (Thomas & Schülein 1988) and occupying greater depths in the water column (Gaudreau & Boisclair 2000) which are reflective of decreased movement and associated activity levels. Increased fraction from the moon raises light levels in the water column, which for nocturnal animals would be expected to translate to higher activity levels during periods of increased fraction due to increased foraging and mobility (Milardi et al. 2018, Merciai et al. 2020). However, I found kingfish were not more active during periods of increased moon fraction, suggesting that they are not using nights of increased moon light to increase foraging and movements and might instead be visual feeders that predate and forage during daylight hours (Gomon et al. 2008). In other circumstances, raised activity during darker periods (i.e., less moon fraction) have been suggestively linked to reducing predation risk during reproductive behaviours or eggs being laid (Hammerschlag et al. 2017). For example, reef associated damselfish (Pacific sergeant major *Abudefduf troschelii*) have been described to synchronise hatching of eggs near the new moon, expected to coincide with timing of tidal cycles to transport eggs away from higher risk of predation

(Foster 1987). Raised activity of kingfish near the new moon may be indicative of kingfish using these times for reproductive behaviours, especially in inner areas of Coffin Bay (i.e., Kellidie Bay, Dutton Bay) where the largest effect of moon fraction was observed, and spawning aggregations have been described (DEW 2018). The relationship between tide and moon characteristics and the activity of fishes such as kingfish is of particular interest to fishers, who produce lunar calendars charts, and applications which strive to optimise fishing strategies (Sharma & Dhenuvakonda 2019, Di Natale & Mangano 1995). This additional insight into the effects of moon and tide for species such as kingfish could be linked to catchability, and fishers could direct the timing and location of fishing activities to reduce or increase catches of large pelagic species' such as kingfish (Hammerschlag et al. 2017).

Detections from the national acoustic tracking network revealed long-range movements of individual kingfish up to ~1,800 km, with three individuals tagged in South Australia displaying large-scale movements > 50 km away from tagging location. Throughout these broad movements, individuals were exposed to a range of temperatures (15.6 – 20.6°C) and other environmental factors that can influence activity. These movements occurred within relatively short temporal scales (i.e., 56 – 80 days), so the physiological performance of these individuals is dependent on the ability of kingfish to cope with variable conditions. These migrations of kingfish across the south-eastern coast of Australia are supported by mark-and-recapture data (Gillanders et al. 2001) and genetic population structure that has identified one large south-eastern Australian population that is genetically distinct from Western Australia (Patterson & Swearer 2008, Miller et al. 2011). This study shows that a national network of acoustic tracking receivers can not only monitor large-scale movements of mobile species, but also provides an opportunity to assess how animals are partitioning energetic budgets across large spatial scales. In addition to identifying environmental drivers of activity, this nation-wide network of acoustic receivers may also be used by future studies to provide an insight into how human impacts may effect species energetic expenditure on a broad spatial scale (Huveneers et al. 2021a) and contribute to area management strategies for mobile large pelagic fish.

5.6 Conclusions

Environmental processes play vital roles in the functioning and structure of pelagic ecosystems, and so it is critical to recognise animals' energetic responses to variable conditions to infer the relationships between species and their surrounding environment. This study found that kingfish were most active during the day, in warm and shallow areas, and expended slightly less energy with rising tide height and increased moon fraction. Effects from increasing temperature were not reproduced by a decrease in activity poleward, with kingfish predicted to be most active in southern regions, most likely attributed to raised activity due to lag effects from feeding during shark tourism at the North Neptune Islands, and lower activity in Sydney Harbour and offshore islands around Coffs Harbour where individuals are residing. These findings advance our understanding of kingfish activity in south-eastern Australia, providing valuable information about the energetic responses of an ectothermic pelagic fish under changing environmental conditions. Additionally, this study highlights the potential for national-scale acoustic receiver arrays to accumulate long-term and broadly-distributed information not only about animal movements, but also combine detections with environmental conditions to identify spatially-important areas and timing of raised energetic expenditure. In the current climate of increased pressures from human impacts, this is a valuable approach to predict population responses to changing environmental conditions, particularly for highly mobile and vastly-distributed large pelagic fishes such as kingfish.

Chapter 6

General discussion

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6.1 Thesis overview

Yellowtail kingfish (*Seriola lalandi*) is an important predator in pelagic ecosystems (Gomon et al. 2008), in addition to contributing to significant economic and social gains through commercial and recreational fisheries (Henry & Lyle 2003, Lowry et al. 2016). However, there is a paucity of research into reproductive behaviours and factors driving activity of kingfish across southern Australia. In this thesis, I used kingfish as a model species of large pelagic fish to develop methods to identify ecologically-important behaviours, and reveal effects from human pressures on fine-scale movements and activity. My findings demonstrate that biologging can be used to identify timing and locations of spawning events, and has potential to be conditioned to identify spawning behaviours of other species of large pelagic fish, and reveal natural and anthropogenic drivers of residency, space use, and energetic expenditure. Throughout this thesis, I addressed the understudied reproductive behaviours, effects of wildlife tourism, and environmental drivers of kingfish activity in south-eastern Australia. Specifically, I applied a machine learning algorithm to characterise courtship and spawning behaviours of kingfish, and subsequently applied the model on unseen data to predict naturally-occurring spawning events (Chapter 2); revealed impacts of white shark tourism on the residency and space use (Chapter 3); and physiological responses (Chapter 4) of kingfish; and identified environmental drivers of kingfish activity across a south-eastern Australia dataset (Chapter 5). Outcomes from this thesis contribute essential knowledge about the ecology of kingfish in southern Australia, but also demonstrated novel methods and approaches that are applicable to other species of large-bodied and mobile pelagic fish (e.g., scombrids, carangids, billfish).

6.2. A new method to identify spawning behaviour of large pelagic fish

Reproductive success of large pelagic fish is vital for preserving viable populations in the wild, but identifying spawning events in a pelagic environment in the past has been logistically challenging (Balon 1984, Ware 1984). My thesis developed a non-destructive and efficient method to describe kinematics and acceleration during spawning behaviours and remotely predict the occurrence of these events in the wild (Chapter 1). Prior to these findings, identifying these events was limited to destructive approaches (e.g., gonad staging or gonadosomatic indixes; DeMartini et al. 2000, Karakulak et al. 2004, Richardson et al. 2018) or required high-effort sampling in spawning areas (e.g., ichthyoplankton tows for fertilised eggs; Davis et al. 1990, Paine et al. 2008, Richardson et al. 2016). My results build on previous use of accelerometers, which have been used to characterise reproductive behaviours based on acceleration and body posture during visually-confirmed events (Tsuda et al. 2006, Yasuda et al. 2013, Sakaji et al. 2018). I used a machine learning algorithm to characterise behaviour classes, and additionally demonstrated the potential for these methods to be applied on free-ranging individuals to remotely identify naturally-occurring spawning aggregations, among other ecologically-relevant behaviours (i.e., feeding, escape, chafing). Accelerometers in this study successfully confirmed 776 seconds of courtship from captive kingfish, in addition to 772 seconds of courtship and spawning behaviour from free-ranging individuals, and thus should be considered for application on other large-bodied marine taxa. Reproductive behaviours from wild individuals predominantly occurred at dawn (35% of events) and during the early hours of the morning (38% of events), and between temperatures of 16.5 – 19.5°C, which aligns with previous examples of kingfish spawning from anecdotal and aquaculture-based descriptions (Gillanders et al. 1999, Poortenaar et al. 2001) and thus further reinforces the reliability of this technique for predicting reproductive events. During the progression of this thesis, a recent study from Schlenker et al. (2021) used a similar method to remotely predict spawning behaviours of another large pelagic fish, Mahi-Mahi (*Coryphaena hippurus*) from acceleration data collected via pop-up satellite archival tags (PSATs). Spawning behaviours were characterised using and ensemble of classification algorithms, including Random Forest models that were used in Chapter 2 of this study, finding that spawning predominantly occurred at night-time. This further highlights the complications for ground-truthing reproductive behaviours of large pelagic fish that can occur during times of low-light levels. While accelerometer loggers from Chapter 2 were able to record swimming depth, and infer location within acoustic arrays via implanted acoustic transmitters, PSATs used be Schlenker et al. (2021) were able to divulge fine-scale responses to additional parameters recorded through tags such as temperature, light levels, and geographical data to make remote predictions about more detailed environmental conditions during predicted spawning. This timely study further highlights the demand for dependable techniques that can identify fine-scale reproductive behaviours of highly mobile pelagic fish, and demonstrates the capacity for acceleration metrics to be paired with surrounding geographical and environmental data to uncover important timing and areas of pelagic fish spawning in nature.

Outcomes from this thesis provide valuable information about the spawning behaviours of kingfish in southern Australia, specifically within the Neptune Islands and Coffin Bay areas. Identifying spawning behaviours is not only beneficial from a behavioural ecology perspective, but provides information to strategize fisheries management towards protecting vulnerable stocks during such aggregations (Domeier 2012). While genetic research has focused on revealing population structure of kingfish in Australia and New Zealand (Patterson & Swearer 2008, Miller et al. 2011), this thesis provided the first behavioural evidence of kingfish spawning in southern Australia. Both the Neptune Islands (Ron and Valarie Taylor Marine Park) and Coffin Bay (Thorny Passage Marine Park) regions where kingfish spawning was predicted through RF models in this study, were incorporated in the South Australian Marine Parks zoning plan implemented in 2014 (National Parks and Wildlife Service 2020). In particular, the Thorny Passage Marine Park includes allocated sanctuary zones (i.e., no-take areas) to assist in protecting suspected spawning aggregations of kingfish (DEW 2018), in addition to hosting an important nursery area for other coastal teleost species (e.g., whiting *Sillago* spp., pink snapper *Chrysophrys auratus*, flathead *Platycephalus* spp.). However, prior to findings from this thesis, descriptions of kingfish spawning in these areas were only anecdotal, based on visual descriptions of fish aggregating, flashing their sides, and pursuing burst swimming behaviours (Landscape South Australia 2016, Environment SA News 2018). Chapter 2 provided empirical evidence that kingfish are likely spawning in Coffin Bay, which was supported by high levels of activity in areas of the system where sanctuary zones were implemented (i.e., Kellidie Bay, Chapter 5, DEW 2018), particularly around new moons when large tidal cycles may be being utilised for egg and larvae dispersal. These results further support the ongoing protection of areas within Coffin Bay to allow successful spawning behaviours to occur during the seasonal aggregation. Although sample size was small with observations of spawning from five individuals only, the record of spawning behaviour from all three tagged fish in Coffin Bay suggest that such behaviour might be frequent during the spring – summer aggregation. The implementation of spatial management strategies to protect spawning individuals, particularly for transient and mobile species, is a major challenge facing fisheries conservation (Domeier 2012, Grüss et al. 2014). Although when implemented effectively, spatial protection of these aggregations can increase spawning-stock biomass and minimise disruption of spawning behaviours to maximise recruitment success of commonly angled and targeted species (Domeier 2012). Paired with information of timing and geographic location of movements around these aggregations (Chapter 5), these findings show that accelerometers paired with machine learning are a forthcoming option to identify the enigmatic reproductive behaviours of highly mobile species such as kingfish, and can contribute to advising and supporting efficacy of spatial management efforts to protect spawning aggregations and ensure viable populations continue.

While there are clear benefits to the application of accelerometers to predict naturally-occurring spawning behaviours, there were some limitations to the implementation of this method. Since kingfish in this study were targeted to be reproductively active, individuals were of relatively large body size (> 91 cm TL). However, the additional drag and obstruction from the logger packages (Jepsen et al. 2005) could disrupt the occurrence of desired behaviours of smaller-bodied individuals/species, and should be considered in future studies that use large biologging devices to characterise and identify naturally-occurring behaviours like spawning. This is particularly relevant in the marine environment where logger packages require additional equipment for recovery (i.e., non-compressible foam, satellite/radio transmitters, corrodible links), and largely limits the application of logger packages to large-bodied animals (e.g., > ~1 m in length: billfishes, tuna, sharks). Constraints of battery-life and storage systems in marine accelerometers restrict the temporal and geographic extent of deployments, with most products limited to deployments of a few days or week(s) (Broell et al. 2012), meaning that the timing of deployments with spawning events can be difficult to achieve. Alternatively, loggers can be programmed to reduce sampling frequencies to prolong battery life and storage, but this might affect the ability to record and identify complex behaviours like spawning and courtship if measurements are recorded too infrequently (Tsuda et al. 2006, Yasuda et al. 2013, Sakaji et al. 2018). Alternatively, threshold-based recording devices can prolong duration of deployments by only recording when movement exceed a particular threshold (Nishiumi et al. 2018), but this requires some knowledge of expected thresholds for desired behaviours. Effects of accelerometer sampling frequency on the behavioural classification performance of machine learning algorithms has been studied in juvenile lemon sharks (i.e., burst, chafe, headshake, rest, swimming behaviours; Hounslow et al. 2019), with 5 Hz deemed appropriate for classifying broad behaviour classes of sharks of similar size to kingfish. However, given the erratic movements during burst behaviours of large pelagic fish (i.e., spawning, feeding), it is probable that a higher resolution sampling rate, such as 50 Hz used in Chapter 2, is required for distinguishing between burst events. With current methodologies, logger packages (and PSATs such as those used by Schlenker et al. 2021) deployed in the wild also need to be physically recovered to obtain acceleration data. If deployed for too long, tagged individuals may swim large distances away from capture location, leading to increased effort and difficulty to relocate and collect the package. As a result, some background into the spatial and temporal occurrence of desired behaviours should be known prior to deploying accelerometers in order to maximise detection probability over short temporal scales. The difficulty ground-truthing kinematic measurements with visual behaviours is another limitation facing accelerometer studies (Rast et al. 2020). Movements of captive animals in tanks can be limited (e.g., due to shallow depth and small tank) and so recorded activities may therefore differ from natural behaviour, or behaviours that occur in nature may not be observed in captivity (Herborn et al. 2010, Rast et al. 2020). Additionally, some large pelagic fish are challenging to keep in captivity to ground-truth behavioural classes. Studies may pair accelerometers with animal-borne cameras to visually confirm naturally-occurring events to further substantiate predictions of spawning aggregations for some of these taxa (e.g., Marshall 1998, Marshall et al. 2007, Watanabe et al. 2008b), but this generates even greater limitations due to the typically short for battery life and high storage requirements for video images. The size of the tagging packages with video loggers included would also be greater than the accelerometer packages used in this thesis, making it only applicable to very large fishes, sharks, and marine mammals without causing detrimental effects from additional drag or obstruction.

6.3. Implications for wildlife tourism to consider mobile non-target pelagic species

The feasibility and success of wildlife tourism operations around the globe ultimately depend on predictable and reliable encounters with wildlife. The implementation of food-based provisoning is therefore often required to attract target-species and increase the consistency of encounters (Newsome & Rodger 2008, Knight 2009). While some industries have regulations in place to prohibit direct feeding of targeted animals (Laroche et al. 2007, Newsome & Rodger 2008, Meyer et al. 2021b), this thesis identified that behavioural (Chapter 3) and physiological effects (Chapter 4) of using food-based attractants can extend to non-target species, which are exceptionally underrepresented in the scientific literature (Trave et al. 2017, Meyer et al. 2020). Kingfish occurred closer to food-based operators and spent longer at the islands each day compared to days with acoustic-attractant only or when no operators were present (Chapter 3). On days that food-based operators frequented the islands, kingfish were more active during tourism operations and as a result spent more energy due to indirect feeding practices (Chapter 4). Additionally, even on days when no operators were at the Neptune Islands, kingfish activity was higher than any other installation in southern Australia (Chapter 5). While near year-round residency is common in sub-tropical to warm temperate areas of Australia (i.e., New South Wales; Brodie 2016, Brookhouse et al. 2016), the thermal climate at the Neptune Islands Group is largely outside the thermal boundaries described for optimal kingfish larval growth and survival (>21 – 26.5°C; Abbink et al. 2012) and reproductive output (>20°C; Gillanders et al. 1999). However, kingfish were persistent throughout the year at the Neptune Islands, despite only 6% of days at the Neptune Islands being above 20°C. Although kingfish in the wild may be more adaptable and resilient to cold climates than captive stocks, current insights into aggregations of kingfish in temperate Australian climates of similar oceanographic condition to the Neptune Islands have revealed strong seasonal trends in residency, with individuals completely leaving these areas during the cold winter months (e.g., Coffin Bay [Chapter 5], Port Augusta [T Clarke pers. obs.], Lady Julia Percy Island *Deen Maar* [J Rizzari pers. obs.]). This thesis found that year-round residency at the Neptune Islands may be reflective of an 'ecological trap' (Schlaepfer et al. 2002), where indirect feeding from cage-diving operations is suppressing environmental cues that would otherwise drive movements away from the islands during winter months when thermal conditions restrict physiological processes (i.e., metabolism, growth, reproduction). Since the inception of commercial cage-diving tourism in South Australia in the early 2000s, the number of operating days has continued to rise (from ~124 days/year 2000 – 2006 to ~265 days 2008 – now; Bruce & Bradford 2013). While these findings highlight the potential for wildlife tourism to impact large pelagic fish behaviour and movements over fine- (i.e., daily) and potentially extended (i.e., year-round residency) temporal-scales, weekly residency and space use were not influenced by the number of operating days (Chapter 3) and some individuals still undertook long-range movements away from the islands (Chapter 5). Without an understanding into the detailed residency and movements of similarly-sized kingfish prior to the inception of cage-diving tourism, or at comparable temperate offshore island groups, it is difficult to interpret if high residency at the Neptune Islands throughout the year was attributed to long-term effects from cage-diving tourism, or rather represent typical movements of large individuals in southern Australia.

As mobile animals that often rely upon vertical and horizontal migrations for foraging, reproduction, and following of preferable oceanographic conditions (e.g., Galuardi et al. 2010, Jansen & Gislason 2011, Richardson et al. 2016), large pelagic fishes are particularly vulnerable to behavioural shifts due to supplemental feeding from wildlife tourism. Studies into the concept of ecological traps (Schlaepfer et al. 2002) in marine wildlife tourism has gained traction (Semeniuk & Rothley 2008, Pini-Fitzsimmons et al. 2018). However, implications for large pelagic fish are largely understudied compared to large, focal species (e.g., sharks and rays), but remains an important consideration. Modifications to pelagic habitats such as through drifting fish aggregating devices (FADs) are suggested to create ecological traps by modifying the environment that these fish reside, and have major effects on behaviour and movements of pelagic fish (e.g., mahi-mahi *Coryphaena hippurus* , rainbow runner *Elagatis bipinnulata*, wahoo *Acanthocybium solandri*, tunas *Thunnus* spp., etc.) by altering natural movements to feeding or spawning areas (Marsac et al. 2000, Dagorn et al. 2010). Whilst kingfish at the Neptune Islands were in good physiological condition (Chapter 4), and some individuals were observed undertaking large-scale movements away from the islands (Chapter 5), health and fitness of individuals might instead be affected by disrupting ecologically-important behaviours and migrations due to increased dependence on the food-based attractant as a food source (Marsac et al. 2000, Dagorn et al. 2010). Although the potentially negative effects of wildlife tourism may be geographically-limited, these effects can accumulate with other anthropogenic pressures that effect movements and behaviours of pelagic fishes, e.g., habitat alterations (Marsac et al. 2000, Andersson 2011), direct (overfishing) and indirect (i.e. prey availability) pressures from fisheries (Block et al. 1998, Heino & Godø 2002, Golet et al. 2007), and changing climate conditions (Robinson et al. 2015, Champion et al. 2018, Petrik et al. 2020). Findings from Chapters 3 and 4 highlight those large pelagic fishes should be considered when developing and implementing management strategies for food-based tourism operations, and emphasise an additional aspect to consider when accounting for anthropogenic effects on movements and behaviours. Baseline studies of residency and movements, paired with energetic budgets and physiological status of both focal and non-focal species prior to implementation of food-based tourism operations could be used to provide more detailed insights into implications of provisioning on movement and behavioural ecology of mobile species.

In spite of near year-round residency and behavioural changes exhibited by kingfish in response to cage-diving operators using food-based attractant (Chapters 3 and 4), kingfish at the Neptune Islands were in relatively good condition (Chapter 4), comparable to areas of suitable habitat from the Australian east coast (Champion et al. 2020a). Additionally, three individuals were predicted to undertake reproductive behaviours soon after being tagged at the Neptune Islands (Chapter 2). Findings of this thesis suggest that feeding on bait and chum from food-based provisioning operators may be required to compensate for increased energy expenditure during cage-diving operations reflected by the increased activity demonstrated in Chapter 4 (Barnett et al. 2016, Brunnschweiler et al. 2018, Huveneers et al. 2018). While bioelectrical impedance measurements did not detect a negative effect on body condition, a more sensitive assessment of oxygen consumption and metabolic processes could be estimated by estimating energy expenditure and compare the activity budget of yellowtail kingfish when operators are present *vs*. absent. Brodie et al. (2016) developed a bioenergetics model for free-ranging kingfish under natural conditions based on estimates of oxygen consumption rates in response to swim speed under varying conditions. This offers an opportunity for future research to quantify the metabolic cost of if the increased activity at the Neptune Islands, and highlight if activity partitioning towards interaction with vessels is overcompensating for energetic requirements (i.e., growth, metabolism, reproduction, waste). Additionally, information of the calorific value and quantities of bait and chum (i.e., *Thunnus maccoyii* gills, guts) consumed by kingfish could be used to substantiate if food-attractant being consumed is sufficient to compensate for shifts in energetic budgets linked to the increased activity.

Although findings from this thesis indicated that cage-diving tourism can disrupt natural behaviours and energetics, well-managed tourism and cooperation with policymakers can have potential benefits for effected targeted and non-focal species (Ballantyne et al. 2009, Apps et al. 2018, Meyer et al. 2021a). Like the Neptune Islands, marine wildlife tourism often occurs in marine protected areas globally (e.g., New Zealand [Okakari Point]; Cole 1994, Mediterranean [Ustica Island]; Milazzo et al. 2005, Australia; Lord Howe Island Marine Park, Great Barrier Reef Marine Park, GBRMP 2005, Brookhouse et al. 2013, Brazil [Abrolhos Bank]; Paula et al. 2018, Hawaii [Molokini Shoal]; Philips et al. 2019) and offers a non-lethal alternative form of wildlife use. Increased residency and space use within these areas therefore enhances the level of protection for highly targeted species like kingfish, and additionally contributes to supplementary compliance in these areas (Read et al. 2011, Campbell et al. 2012, Arias & Sutton 2013).

6.4 Physiological responses of pelagic ectotherms in a variable and changing environment

Behavioural and energetic responses of species are sensitive to changes in the environment (Wilson et al. 2006, Del Raye & Weng 2015, Huveneers et al. 2018), yet there remains a scarcity of quantitative evaluations using data collected in the field. My thesis showed that acoustic tags can be used to identify changes in the activity status of a large pelagic fish due to anthropogenic (Chapter 4) and natural (Chapter 5) changes in the environment. These findings highlight the sensitivity of kingfish activity to abiotic factors (e.g., temperature, hour of the day, moon, and tide input), which consequently reflects the rate at which individuals expend energy and in turn, the long-term energetic strategies that influence the fitness and survival of individuals and populations (Brown et al. 2004, Fossette et al. 2012). Previous applications of acoustic telemetry have been used to enhance fishery management by inferring movements and residency of species in reproductive grounds (Pecl et al. 2006, Espinoza et al. 2015) and occurrence overlap with fishing pressures (Melnychuk et al. 2017), but these methods offer little information about the effects of surrounding environments on the energetic expenditure of animals during the course of their movements. Findings from this thesis show that acoustic tracking can build on these studies by inferring energetic expenditure under different conditions, advancing our understanding of how environmental conditions influence the physiology of large pelagic fish in temperate and sub-tropic environments.

Prior to this study, understanding of kingfish ecology in southern Australia predominantly relied upon mark-recapture (Gillanders et al. 2001, Hutson et al. 2007, Hobday & Campbell 2009), or habitat-modelling approaches based on catch data from fisheries and recreational tagging programs (Brodie et al. 2015, Champion et al. 2018, Champion et al. 2020b). Whilst some studies have advanced these insights to identify activity between recaptures by quantifying survival of angled individuals (Roberts et al. 2011), responses contaminant exposure (Taylor et al. 2018), habitat suitability (Champion et al. 2020b), efficacy of acoustic arrays to detect fine-scale movements (Udyawer et al. 2018), and energetic budgets in coastal *vs*. estuary environments (Chapter 3 from Brodie 2016), these studies were all situated on the eastern coast of Australia only, and studied fish that were substantially smaller (450 – 890 mm TL) compared to South Australian fish from this thesis (800 – 1,510 mm). These larger individuals are prone to more extensive movements and are thus exposed to more variable environmental conditions (Gillanders et al. 1999, Hutson et al. 2007). My findings build on the understanding of large, reproductively mature kingfish ecology in southern Australia and reveal environmental parameters that influence the activity of kingfish from warm, sub-tropical areas (~25°C, Coffs Harbour) to cool temperate regions (~13°C Neptune Islands, Coffin Bay). Kingfish energetic expenditure (inferred through activity) was sensitive to changes in environmental conditions across the south-east Australian distribution, which mediate metabolic processes and have consequential implications for physiological processes (Wilson et al. 2006, Gleiss et al. 2009, Watanabe et al. 2019).

Sea surface temperature was the greatest environmental driver of kingfish activity, emphasising the temperature-dependence of ectothermic species linked with the facilitation of important behaviours and metabolic processes (Payne et al. 2016). In Australia, temperate and sub-tropical oceans are warming (Bohaty & Zachos 2003, Duran et al. 2020), leading to tropicalisation of marine communities through poleward shifts in the distributions and movements of sub-tropical and temperate species (Johnson et al. 2011, Cheung et al. 2012, Pecl et al. 2019). Kingfish are an example of such range extensions, with distributions extending poleward from south-eastern Australia facilitated by changes to sea surface temperature and eddy kinetic energy (Champion et al. 2018). Habitat suitability due to temperature has previously been linked to the physiological condition of kingfish measured through BIA, with condition of individuals peaking at ~21 – 22°C (Champion et al. 2018) which corresponds with optimal growth and physiological responses in captive environments (Abbink et al. 2012). As marine climates continue to warm, kingfish habitats in south-eastern Australia may increase beyond productive temperatures, and expose individuals to conditions beyond optimal thermal tolerances (Payne et al. 2016, Payne & Smith 2017), or lead to fish expending more energy in areas that are otherwise required for less energetically-costly behaviours. Alternatively, cold climates such as the Neptune Islands may warm and become preferable habitats that support growth and reproduction. Activity of kingfish was also strongly influenced by bathymetry, with individuals most active in shallower environments. Although kingfish often occupy deeper waters and topographic structures near continental-shelfs (Hobday & Campbell 2009), shallower coastal habitats where individuals were most active provide an environment that is used by coastal-pelagic fish for transport, controlling larval dispersion, and foraging strategies (Bakun & Parrish 1982, Watanabe et al. 2019), behaviours which may be reflected through heightened energetic expense in these areas. While the extensive and dynamic movements of mobile pelagic fish pose difficulties for spatial management strategies (White et al. 2017, Richardson et al. 2018), my findings show that energetic responses of animals to surrounding conditions can subsequently highlight spatial areas that are ecologically important for large pelagic fish and could be targeted by management tactics where required. These findings offer an opportunity for dynamic ocean management strategies which are applicable to rapid changes in space and time in response to near real-time data (Lewison et al. 2015, Maxwell et al. 2015).

Large pelagic fishes are often highly mobile, capable of extensive movements across continental-scales and influenced by biological and environmental cues that are associated with resource needs (Block et al. 2011, Espinoza et al. 2016, Huveneers et al. 2021b). Findings from this thesis highlighted that although kingfish spent up to 80% of time at the Neptune Islands Group (Chapter 3) and daily behaviours were influenced by cage-diving operations (Chapters 3 and 4), some individuals were still detected undertaking large-scale movements up to ~1,800 km across the south-eastern coast of Australia. The vast distributions and tendency of large-bodied species to cover extensive distances can lead to difficulties when studying effects of environmental conditions on the fine-scale behaviours of animals, and subsequently complicate management and conservation efforts (Heupel et al. 2015). In more recent years, acoustic tracking arrays have increased in number and extent of locations through facilitated collaborative systems that are capable of tracking mobile marine animals across large geographic scales (i.e., continental-wide). Extensive tracking networks combining receiver arrays have been employed in North America (Pacific Ocean Shelf Tracking – POST; Welch et al. 2002, Ocean Tracking Network (OTN) in Canada; Jackson 2011, Integrated Tracking of Aquatic Animals in the Gulf of Mexico - iTag; Currier et al. 2015, Kirkpatrick et al. 2016, Whoriskey & Hindell 2016, Florida Atlantic Coast Telemetry - FACT; Griffin et al. 2018), South Africa (Acoustic Tracking Array Platform – ATAP; Cowley et al. 2017), and Europe (Permanent Belgian Acoustic Receiver Network; Reubens et al. 2019, European Tracking Network; van der Knaap et al. 2021). The Integrated Marine Observing System (IMOS) Animal Tracking Facility is a collaborative acoustic tracking network in Australia, which was used in this study (Chapter 5). The network integrates a series of continental-wide receiver arrays owned by IMOS, in cooperation with independent installations owned by individual research groups, with all detections uploaded and publicly accessible via the Australian Ocean Data Network (AODN) and IMOS Animal Tracking Database (https://animaltracking.aodn.org.au/; Hoenner et al. 2018). The database hosts > 920 active acoustic receivers, and over 102.8 million detections from ~9,600 individuals of 150 species across Australia, and has proven to be valuable to study large-scale movements and residency of a range of species (Heupel et al. 2015, Brodie et al. 2018) and distinguish human impacts on behaviours (e.g., COVID-19 pandemic; Huveneers et al. 2021a). My thesis expands on previous application of traditional telemetry techniques, which has mainly been used to quantify environmental drivers of horizontal and vertical movements, and highlights that such networks provide an opportunity to identify details of activity, and energy expenditure of species across a continental-scale, via acoustic tags equipped with accelerometer sensors. While conventional accelerometer loggers can be used to examine fine-resolution characteristics of behaviour classes over narrow time-series, my findings show that traditional telemetry methods equipped with lower-resolution sampling acceleration sensors deliver an opportunity to identify energetic partitioning of species over extended temporal and spatial scales. This was the first study to employ a new process (via the recently developed R package 'IMOSTrack') to extract environmental parameters for each animal activity measurement from the Australian Ocean Data Network Portal based on timing and geographic location of detections collected via the IMOS Animal Tracking Database. I highlight the effectiveness of this approach to streamline the accessibility of stored environmental data corresponding to individual detections, without requiring additional parameter sensors that can increase tag size and reduce record frequency of other sensors (i.e., activity).

6.5 Management implications

While kingfish stocks are considered to be sustainable in both Western and Eastern Australian jurisdictions (Hughes & Stewart 2020), rising threats from anthropogenic pressures imply that proactive measures to maintain and preserve natural populations should be considered. Despite extensive movements (Chapter 5; Gillanders et al. 2001, Hutson et al. 2007) and genetic connection (Miller et al. 2011, Symonds et al. 2014) in south-eastern Australia, management regulations of kingfish vary between state jurisdictions (Table 6.1). Recreational size limits (45 – 65 cm) and boat possession limits (2 [QLD] – 10 [Tas]; Table 6.1) are variable between states within eastern Australia, in addition to highly variable recreational catch estimates (3 – 199 t, Table 6.1). Commercial kingfish catch in Australia is not managed by catch limits or fishing effort (https://www.afma.gov.au/fisheries-services/catch-limits), but rather state-to-state restrictions of permitted gear types and accessibility. These commercial restrictions also vary, from just limited entry (i.e., limited licences, SA) to size limits, spatial closures, vessel restrictions and licensing limits (VIC, NSW, QLD). Kingfish in south-eastern Australia could be exposed to varying degrees of management and pressure from fisheries, including in areas significant for apportioning of energetic budgets. Future dynamic management considerations for large pelagic fishes such as kingfish should consider the extent of movements and their activity in response to environments throughout their distribution rather than varying levels of protection which could undermine one another (Cabral et al. 2010).

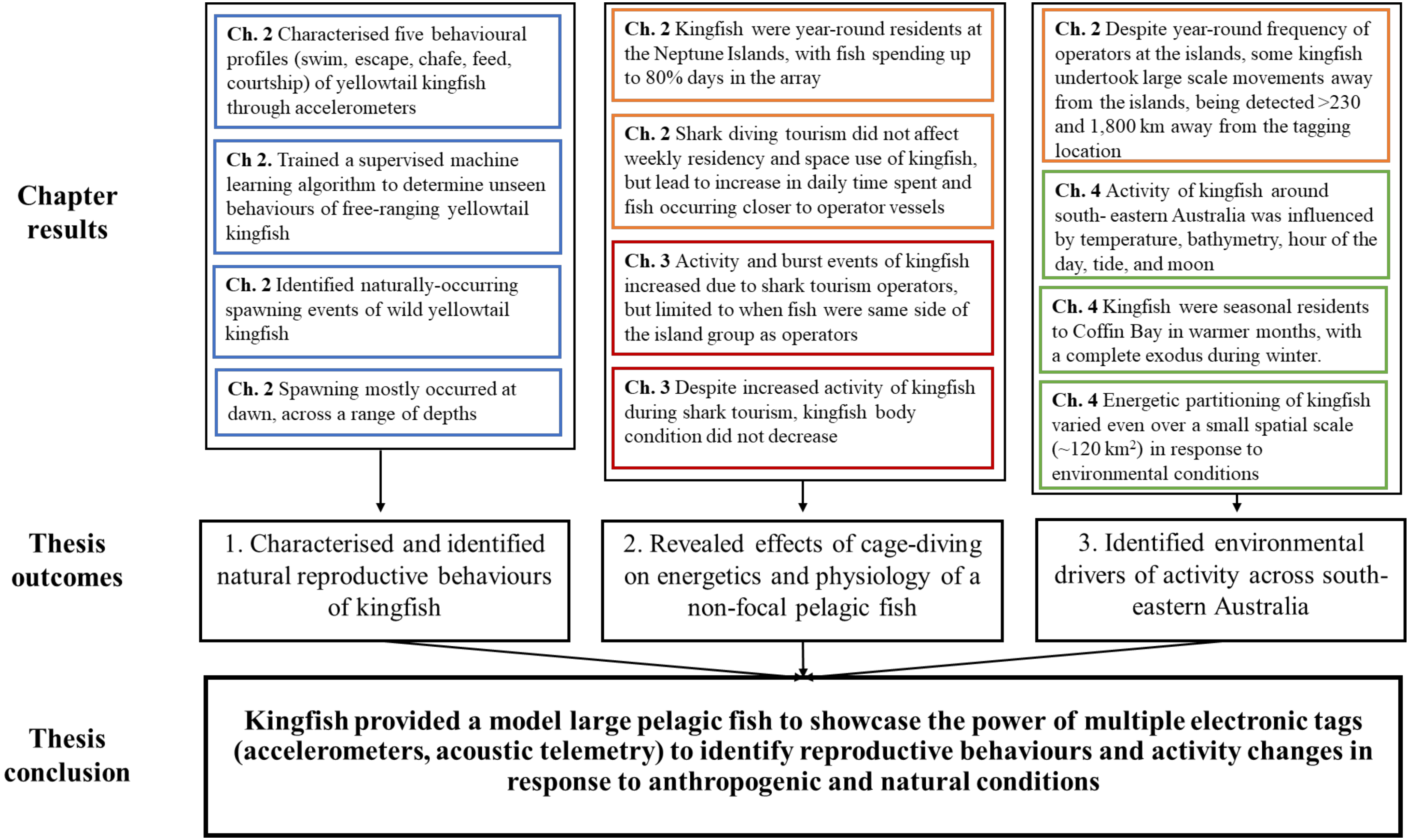
Table 6.1. Yellowtail kingfish (*Seriola lalandi*) recreational and commercial management methods in different state jurisdictions of Australia.

Genetic stock	State	Recreational limits (min size, possession limit, catch estimate)	Commercial management methods, catch estimate
Eastern Australia	[1,2]Queensland	60 cm, 2, 9t (2013/14)	Limited entry, size limits, spatial closures, vessel restrictions, 4.97t
	[3]New South Wales	65 cm, 5, 129t (2017/18)	Limited entry, size limits, spatial closures, vessel restrictions, 75.62t
	[4]South Australia	60 cm, 3, 199t (2013/14)	Limited entry, 1.82t
	[5]Victoria	60 cm, 5	Gear restrictions, licenses, limited entry, spatial closures
	[6]Tasmania	45 cm, 10, 3t (2017/18)	Size limits, trip limits
Western Australia	[7]Western Australia	60 cm, 3, 7 t (2017/18)	Limited entry, size limits, spatial closures, vessel restrictions, 2.89t

Table references: 1 https://www.frdc.com.au/, 2 https://www.qld.gov.au/, 3 https://www.dpi.nsw.gov.au/, 4 https://www.pir.sa.gov.au/, 5 https://vfa.vic.gov.au/, 6 https://www.tas.gov.au/, 7 http://rules.fish.wa.gov.au/

6.5 Conclusions

This thesis used kingfish as a model pelagic species to reveal the power of multiple animal biologging and tracking tools (i.e., accelerometers, acoustic telemetry) to understand important behaviours and environmental divers of large pelagic fish activity and movement (Figure 6.1). These findings provide a new insight into reproductive behaviours and movements of kingfish in southern Australia, but also showcased techniques that can be adapted to other areas or species and contribute to understanding activity budgets of large pelagic fish and the effects of wildlife tourism. Ultimately, employing adaptable approaches to detect behavioural change will be vital to ensuring biological shifts are identified and addressed in rapidly changing pelagic environments.



Chapter results

Ch. 2 Characterised five behavioural profiles (swim, escape, chafe, feed, courtship) of yellowtail kingfish through accelerometers

Ch 2. Trained a supervised machine learning algorithm to determine unseen behaviours of free-ranging yellowtail kingfish

Ch. 2 Identified naturally-occurring spawning events of wild yellowtail kingfish

Ch. 2 Spawning mostly occurred at dawn, across a range of depths

Ch. 2 Kingfish were year-round residents at the Neptune Islands, with fish spending up to 80% days in the array

Ch. 2 Shark diving tourism did not affect weekly residency and space use of kingfish, but lead to increase in daily time spent and fish occurring closer to operator vessels

Ch. 3 Activity and burst events of kingfish increased due to shark tourism operators, but limited to when fish were same side of the island group as operators

Ch. 3 Despite increased activity of kingfish during shark tourism, kingfish body condition did not decrease

Ch. 2 Despite year-round frequency of operators at the islands, some kingfish undertook large scale movements away from the islands, being detected >230 and 1,800 km away from the tagging location

Ch. 4 Activity of kingfish around south- eastern Australia was influenced by temperature, bathymetry, hour of the day, tide, and moon

Ch. 4 Kingfish were seasonal residents to Coffin Bay in warmer months, with a complete exodus during winter.

Ch. 4 Energetic partitioning of kingfish varied even over a small spatial scale (~120 km^2) in response to environmental conditions

Thesis outcomes

1. Characterised and identified natural reproductive behaviours of kingfish

2. Revealed effects of cage-diving on energetics and physiology of a non-focal pelagic fish

3. Identified environmental drivers of activity across south-eastern Australia

Thesis conclusion

Kingfish provided a model large pelagic fish to showcase the power of multiple electronic tags (accelerometers, acoustic telemetry) to identify reproductive behaviours and activity changes in response to anthropogenic and natural conditions

Figure 6.1. Graphical representation of overall thesis, summarising chapter results, thesis outcomes, and thesis conclusion.

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APPENDIX

Table S1. Mean weekly residency index (RI) and activity space (BBKUD-50) of yellowtail kingfish with varying number of operating days.

Operating Days/Week	***N* (RI)**	**Mean Residency (RI)**	***N* (BBKUD-50)**	**Mean Activity Space (BBKUD-50)**
0	68	0.554 ± 0.03	43	0.309 ± 0.02
1	9	0.476 ± 0.09	3	0.308 ± 0.01
2	16	0.527 ± 0.06	12	0.298 ± 0.04
3	86	0.488 ± 0.03	52	0.335 ± 0.03
4	103	0.559 ± 0.03	69	0.306 ± 0.01
5	167	0.599 ± 0.02	126	0.316 ± 0.01
6	222	0.652 ± 0.02	190	0.339 ± 0.01
7	38	0.650 ± 0.05	32	0.340 ± 0.02

Table S2. Estimated operator type coefficients (*β*) and their standard errors (SE), *t*-values of factors included in the top-ranked model (indicated for each variable) for models testing weekly a) residency, b) activity space, and daily c) time spent and d) distance to nearest operator. Significant values are shown in bold.

Level	*β*	SE	DF	t-value	p-value
a) Weekly residency					
Detection index ~ 1 (intercept only)					
(Intercept)	**0.538**	**0.024**	**659**	**22.51**	**0**
b) Weekly activity space					
BBKUD ~ 1 (intercept only)					
(Intercept)	**0.319**	**0.013**	**497**	**25.37**	**0**
c) Daily time spent					
*Time ~ Operator Type * Temperature*					
(Intercept, No operator)	3.52	3.43	1.03		
Temp	0.53	0.19	2.76		
Acoustic	2.09	1.19	1.75		
One Food-based	0.36	0.97	0.37		
One Food-based+Acoustic	1.76	0.96	1.84		
Two Food-based	2.14	1.07	2.01		
All Operators	1.13	1.19	0.96		
d) Daily distance to operators					
*Distance ~ Operator Type * Temperature*					
(Intercept, Acoustic)	9.36058	5.67636	1.64905		
Temperature	0.58513	0.31962	1.83073		
All Operators	-5.1859	2.0385	-2.544		
One Food-based	-3.6767	2.07696	-1.7703		
One Food-based+Acoustic	-4.9138	2.06822	-2.3759		
Two Food-based	-6.2586	1.99824	-3.1321		

Table S3. Estimated deterrent level coefficients (*β*) and their standard errors (SE), and t-values in the top-ranked model for the effect of operator type on activity of kingfish at the Neptune Islands.

Level	β	SE	t-value
Intercept; No operators	-1.28169	0.038596	-33.208
Temperature	0.074709	0.00091	82.138
Acoustic	0.012189	0.006227	1.958
One Food-based	0.101046	0.002681	37.694
One Food-based+Acoustic	0.056696	0.003555	15.947
Two Food-based	0.124784	0.003459	36.074
All Operators	0.13487	0.003254	41.454

Table S4. Estimated deterrent level coefficients (*β*) and their standard errors (SE), and t-values in the top-ranked model for the effect of interactions between provisioning, side of the island, and Before/After Control/Impact on activity of kingfish at the Neptune Islands.

Level	β	SE	t-value
Intercept	-1.26213	0.047922	-26.337
Before	0.06256	0.006825	9.166
During	0.040497	0.006235	6.496
No food	-0.00034	0.009329	-0.037
Same	0.091919	0.007128	12.895
temp	0.07195	0.00096	74.966
Before:No food	-0.03708	0.010886	-3.406
During:No food	-0.04402	0.009946	-4.426
Before:Same	-0.09837	0.008652	-11.37
During:Same	0.037928	0.007869	4.82
No food:Same	0.0082	0.041067	0.2
Before:No food:Same	-0.09052	0.043155	-2.098
During:No food:Same	-0.14284	0.042815	-3.336

Table S5. Summary of receiver stations within acoustic arrays for kingfish detections collected through the Integrated Marine Observing System Animal Tracking Database.

Project name	Sampling year(s)	Installation	Station Name	Latitude	Longitude	Detections
Paul Butcher Kingfish	2009	Sydney (coastal)	Magic Point	-33.956	151.265	18
			Manly	-33.826	151.298	4
		Sydney Harbour	Dobroyd Head	-33.814	151.275	304
			Spit Bridge	-33.803	151.246	50
			Bantry Bay	-33.785	151.230	395
			Quakers Hat	-33.812	151.235	7,206
			Shark Bay	-33.847	151.264	15,059
			Shark Island	-33.858	151.259	55
			Clarke Island	-33.863	151.242	4
			SIMS	-33.839	151.259	238
			Taylors Bay	-33.850	151.250	840
			Western Wedding Cake	-33.840	151.264	14,225
			Sow and Pigs	-33.836	151.270	262
			Clifton Gardens	-33.842	151.255	123
			Mann Point	-33.843	151.186	1,290
			Sugarloaf	-33.794	151.225	250
			Castle Cove	-33.785	151.220	253
			Clontarf	-33.808	151.249	45
			Castlecrag	-33.802	151.231	2,639
			Green Channel Buoy No. 6	-33.828	151.272	11,876
NSW DPI Coastal and Estuarine Fish Tracking (CEFT)	2013	Coffs Harbour	SIMP 5 - Sth Sol Manta Arch	-30.203	153.381	2,105

	SIMP 6 - Sth Sol Boulder Wall	-30.202	153.301	4,428
	SIMP 7 - Sth Sol Buccanans Wall	-30.207	153.503	1,096
	SIMP 7 - Sth Sol Buchanans Wall	-30.207	153.265	1,091
Sydney (coastal)	Between Bondi And South Head (Sth)	-33.873	151.287	33
	BL 2	-33.900	151.295	2
	BL 4	-33.908	151.309	455
	CTBAR NewHeadland	-33.798	151.296	1
	CTBAR NewNorth	-33.799	151.295	1
	CTBAR NewWest	-33.799	151.294	1
	Dunbar South	-33.851	151.291	583
	FAD Botanywide	-33.995	151.446	10
	Long Reef	-33.738	151.329	3,090
	North Head	-33.826	151.300	117
	Offshore Artificial Reef Sydney	-33.847	151.300	332
	SG 4	-33.826	151.298	106
	Sydney Mooring 140m	-34.000	151.450	2
Sydney Harbour	Balmoral Bay	-33.823	151.256	7
	Bantry Bay	-33.785	151.230	15,814
	Black Channel Buoy - Entrance	-33.831	151.274	25

			Castle Cove	-33.785	151.220	10,710
			Castlecrag	-33.802	151.231	3,860
			Chowder Bay	-33.839	151.257	1,280
			Cobbler's Beach	-33.823	151.264	1,040
			Quaker's Hat	-33.812	151.235	1,719
			Red Channel Buoy - Entrance	-33.831	151.277	167
			Spit Bridge	-33.803	151.246	95
			Sugarloaf Bay	-33.794	151.225	1,024
			Western Wedding Cake	-33.840	151.264	1
Kingfish in South Australia	2018-2021	South Neptune	South Neptune	-35.326	136.116	351
		North Neptune Islands	ST01	-35.210	136.028	2,357
			ST02	-35.211	136.032	6,949
			ST03	-35.208	136.026	5,918
			ST04	-35.205	136.017	4,193
			ST05	-35.206	136.022	2,018
			ST06	-35.213	136.046	1,140
			ST07	-35.214	136.044	2,348
			ST08	-35.211	136.033	4,586
			ST09	-35.213	136.028	3,561
			ST10	-35.211	136.025	7,136
			ST11	-35.206	136.014	3,579
			ST12	-35.209	136.022	10,015
			ST13	-35.212	136.031	6,483
			ST14	-35.209	136.023	3,039
			ST15	-35.211	136.026	11,122

2019-2021	Coffin Bay Array	CB01	-34.594	135.457	1187
		CB02	-34.605	135.472	187
		CB03	-34.617	135.475	166
		CB04	-34.607	135.497	61
		CB05	-34.603	135.484	27
		CB06	-34.609	135.504	27
		CB07	-34.614	135.503	19
		CB08	-34.612	135.452	848
		CB09	-34.552	135.427	18497
		CB10	-34.595	135.415	1672
		CB11	-34.566	135.438	538
		CB12	-34.597	135.427	413
		CB13	-34.549	135.435	701
		CB14	-34.541	135.418	1945
		CB15	-34.633	135.406	105
		CB16	-34.618	135.397	478
		CB17	-34.612	135.400	441
		CB18	-34.605	135.402	593
		CB19	-34.600	135.362	210
		CB20	-34.590	135.382	1196
		CB21	-34.590	135.374	190
		CB22	-34.589	135.367	54
		CB23	-34.572	135.365	244
		CB24	-34.565	135.347	147
		CB25	-34.546	135.315	3093
		CB26	-34.542	135.361	217
		CB27	-34.521	135.371	67

	CB28	-34.522	135.362	48
Total	**93**			**212,497**

Table S6. Average environmental parameters from south-eastern Australian receiver arrays used for Generalised Additive Mixed Model.

Factor	Installation	Average	n	SE
SST	Coffin Bay	16.1	33371	0.013
	Coffs Harbour	23.4	8720	0.016
	North Neptune	17.0	73660	0.006
	South Neptune	17.9	351	0.026
	Sydney (coastal)	20.5	4755	0.030
	Sydney Harbour	20.9	90853	0.005
	Total	**18.9**	**211710**	**0.006**
Bathy	Coffin Bay	-5.5	33371	0.009
	Coffs Harbour	-20.8	8720	0.082
	North Neptune	-15.0	73660	0.014
	South Neptune	-14.0	351	0
	Sydney (coastal)	-15.4	4755	0.158
	Sydney Harbour	-13.5	90853	0.042
	Total	**-13.1**	**211710**	**0.021**
dist2land	Coffin Bay	1.1	33371	0.002
	Coffs Harbour	9.0	8720	0
	North Neptune	26.0	73660	0
	South Neptune	31.0	351	0
	Sydney (coastal)	1.0	4755	0
	Sydney Harbour	1.0	90853	0
	Total	**10.1**	**211710**	**0.026**
tide	Coffin Bay	0.555	33371	0.001
	Coffs Harbour	1.101	8720	0.004
	North Neptune	0.020	73660	0.001
	South Neptune	-0.003	351	0.012
	Sydney (coastal)	1.016	4755	0.007

	Sydney Harbour	0.369	90853	0.002
	Total	**0.321**	**211710**	**0.001**
moon	Coffin Bay	0.447	33371	0.002
	Coffs Harbour	0.410	8720	0.003
	North Neptune	0.480	73660	0.001
	South Neptune	0.839	351	0.009
	Sydney (coastal)	0.521	4755	0.005
	Sydney Harbour	0.275	90853	0.001
	Total	**0.385**	**211710**	**0.001**

Table S7. Estimated factor coefficients (β) and their standard errors (SE), t-values, and approximate significance (p-values) of factors included in the top-ranked model for activity drivers south-eastern Australia. Smooth and random terms showing df (estimated degrees of freedom), F (Fisher-Snedecor distribution, continuous probability distribution) and p-values (approximate significance, significant values are shown in bold).

Terms	Factor	β	SE	t value	p-value
Fixed	**Intercept (depth)**	**-2.72**	**0.491**	**-5.519**	**>0.01**
	latitude	**0.09**	**0.014**	**6.524**	**>0.01**
	SST	**0.03**	**0.0004**	**61.051**	**>0.01**
	bathy	**-0.001**	**0.0001**	**-12.102**	**>0.01**
	tide	**-0.013**	**0.002**	**-7.934**	**>0.01**
	moon	**-0.01**	**0.002**	**-6.195**	**>0.01**
		df	**F**	**p-value**	
Smooth	**hour**	**20.27**	**21069.7**	**>0.01**	
Random	**transmitter**	**57.19**	**598.8**	**>0.01**	
	year	4.25	19763.3	0.04	

Table S8. Estimated factor coefficients (β) and their standard errors (SE), t-values of factors included in the top-ranked model for activity drivers in different areas of Coffin Bay (indicated for each variable). Significant interactions are shown in bold.

Terms	Factor	β	SE	t value	p-value
Fixed	**Intercept (Brothers)**	**-1.16**	**0.22**	**-5.2**	**>0.01**
	Dutton	**-1.11**	**0.13**	**-8.5**	**< 2e-16**
	Kellidie	**-1.08**	**0.32**	**-3.4**	**>0.01**
	Long Beach	**0.33**	**0.16**	**2.0**	**0.044**
	Mouth	-0.12	0.21	-0.6	0.558
	Moon	**0.14**	**0.04**	**3.8**	**>0.01**
	Temperature	**0.05**	**0.01**	**7.7**	**>0.01**
	Tide	-0.10	0.07	-1.4	0.155
	Dutton*Moon	**-0.20**	**0.04**	**-4.9**	**>0.01**
	Kellidie*Moon	**-0.25**	**0.08**	**-3.0**	**>0.01**
	Long Beach*Moon	-0.05	0.05	-1.1	0.283
	Mouth*Moon	**-0.20**	**0.05**	**-4.1**	**>0.01**
	AreaDutton*Temperature	**0.05**	**0.01**	**7.9**	**>0.01**
	Kellidie*Temperature	**0.08**	**0.02**	**4.2**	**>0.01**
	Long Beach*Temperature	-0.01	0.01	-1.6	0.110
	Mouth*Temperature	0.02	0.01	1.7	0.084
	Dutton*Tide.height	0.14	0.07	1.9	0.059
	Kellidie*Tide.height	-0.09	0.11	-0.8	0.407
	Long Beach*Tide.height	-0.04	0.09	-0.5	0.642
	Mouth*Tide.height	-0.17	0.09	-1.8	0.068
Smooth	**Hour*Brothers**	**6.56**	**22**	**10.7**	**>0.01**
	Hour*Dutton	**14.39**	**22**	**62.5**	**>0.01**
	Hour*Kellidie	**9.68**	**22**	**4.1**	**>0.01**
	Hour*Long Beach	**10.06**	**22**	**14.0**	**>0.01**
	Hour*Mouth	**15.65**	**22**	**4.9**	**>0.01**
Random	**Transmitter**	**4.98**	**5**	**638.8**	**>0.01**
	Week number	**1.00**	**1**	**1327.1**	**>0.01**

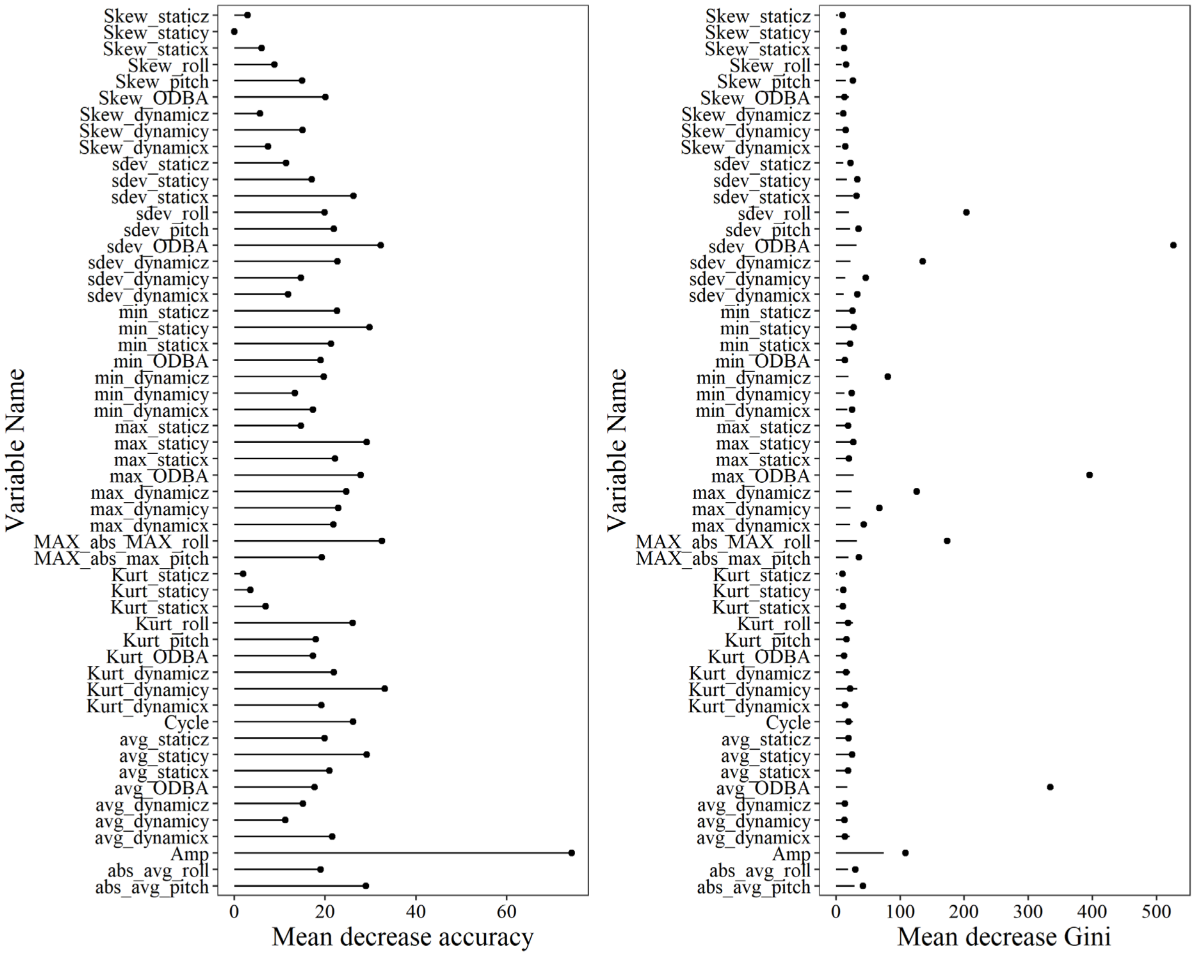


Figure S1. Variable importance plots for predictor variables. Mean decrease in accuracy shows how model performance decreases if a predictor variable is removed from the model, and mean decrease in Gini Index shows the importance of a predictor variable based on Gini Impurity Index for the calculation of splits in trees.

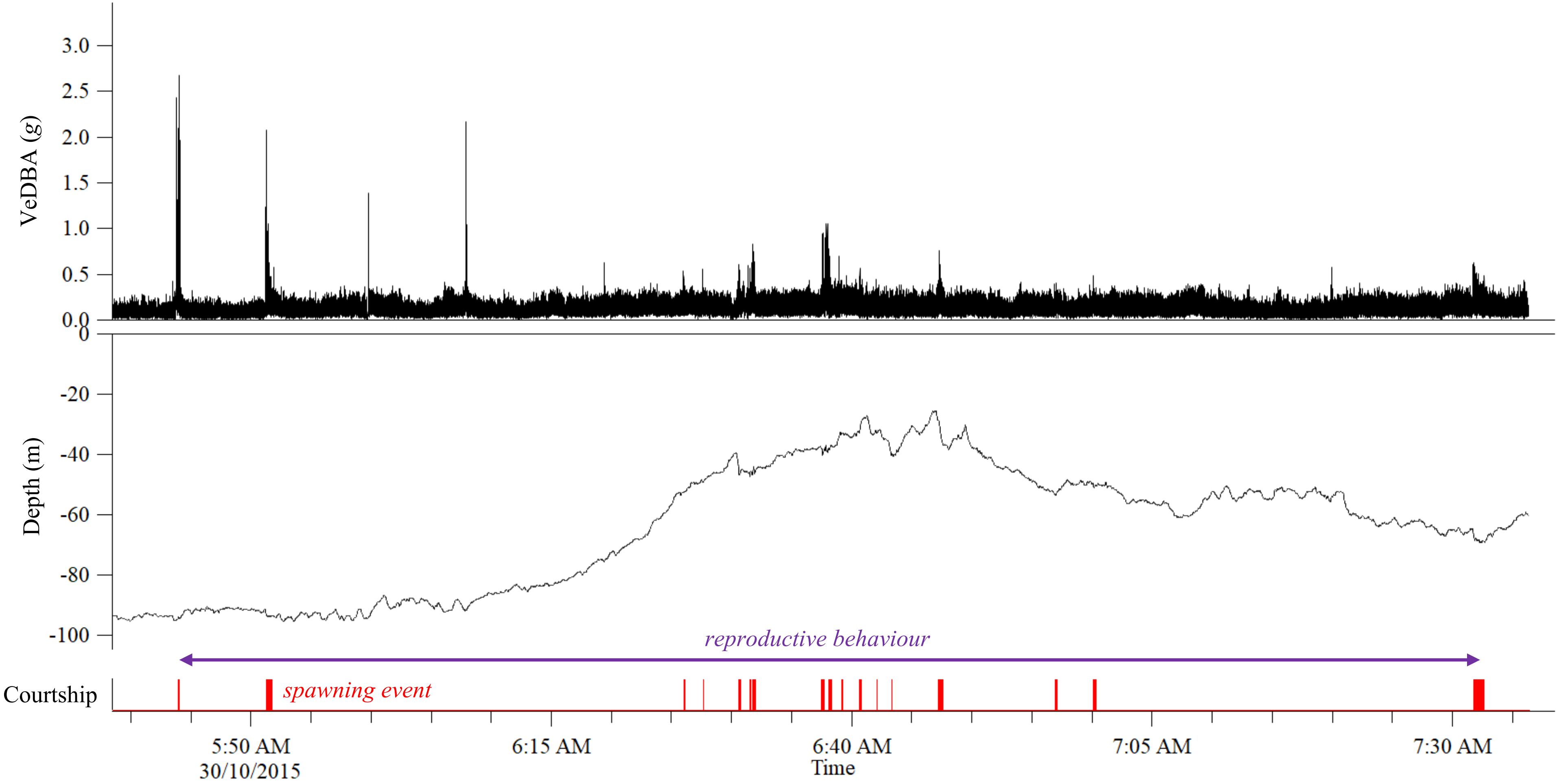
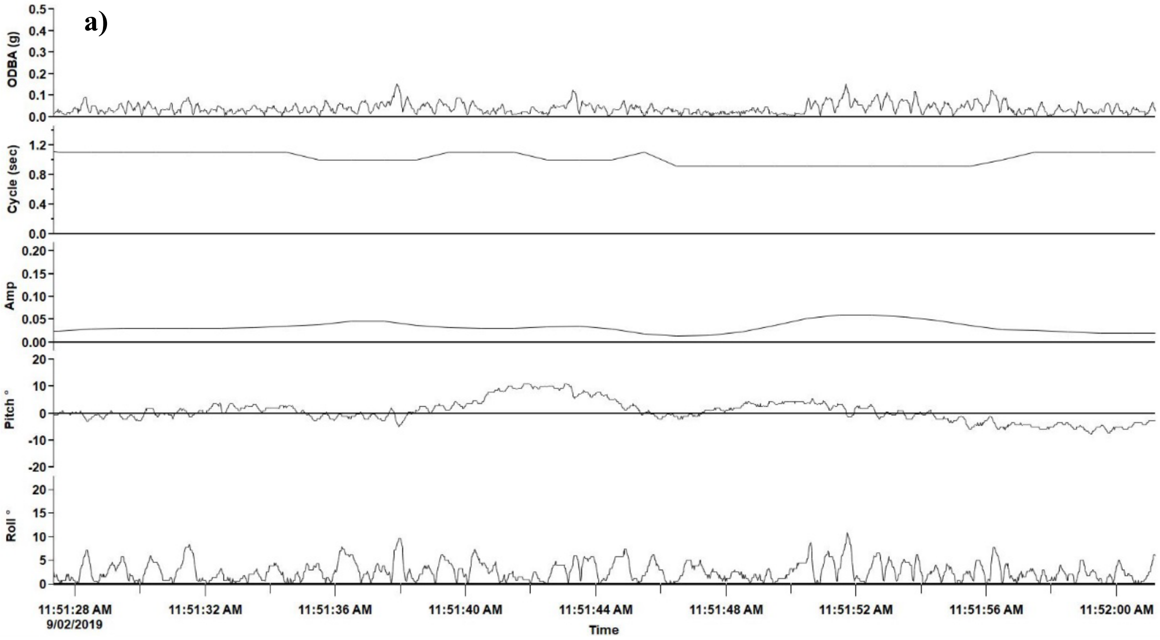


Figure S2. Example of spawning events (n = 16, red markers) and reproductive behaviours (n = 1, purple arrow) as predicted from RF model applied on free-ranging Kingfish.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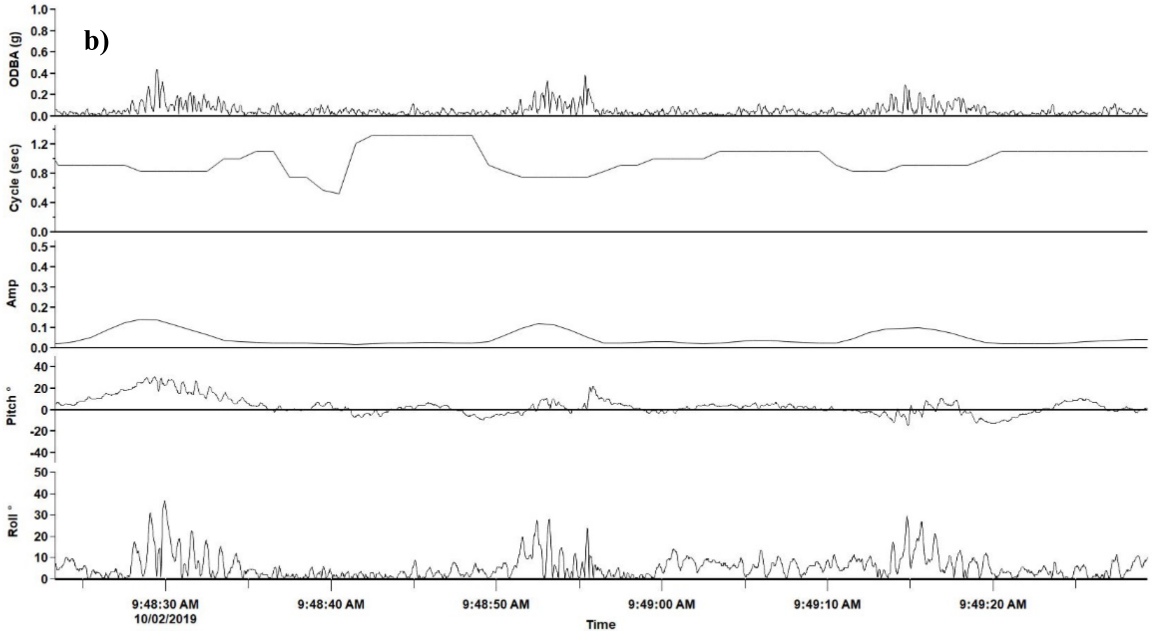
ODBA (g)
Cycle (sec)
Amp
Pitch °
Roll °
11:51:28 AM
9/02/2019
11:51:32 AM
11:51:36 AM
11:51:40 AM
11:51:44 AM
11:51:48 AM
11:51:52 AM
11:51:56 AM
11:52:00 AM
Time


b)
ODBA (g)
Cycle (sec)
Amp
Pitch °
Roll °
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10/02/2019
9:48:40 AM
9:48:50 AM
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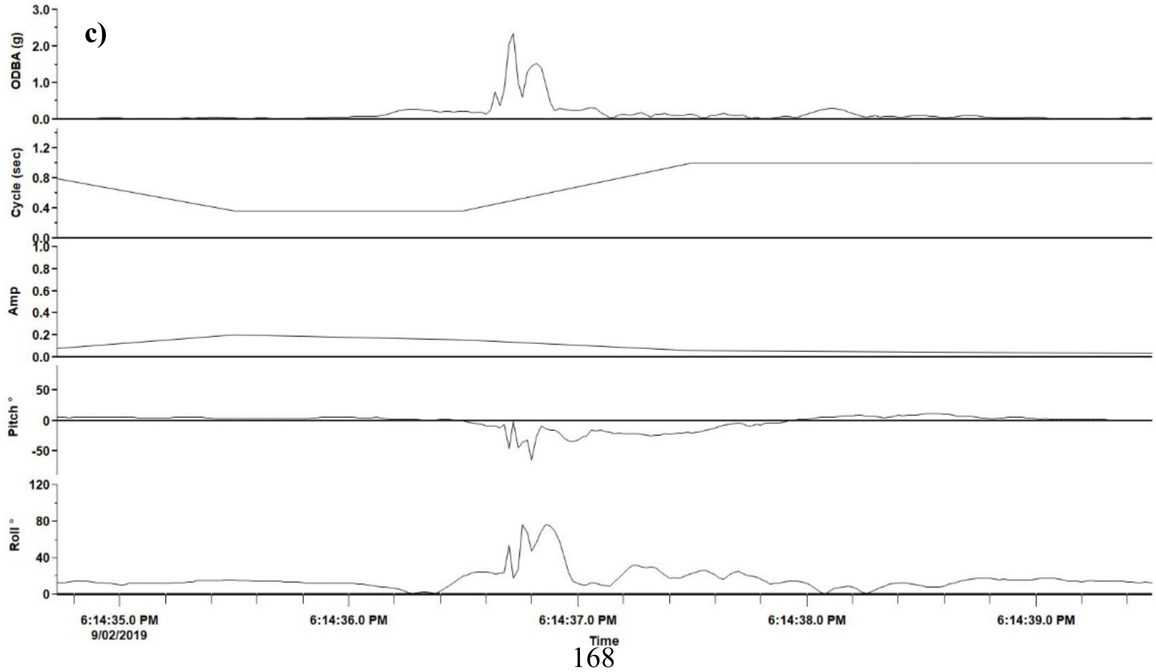
9:49:10 AM
9:49:20 AM
Time


c)
ODBA (g)
Cycle (sec)
Amp
Pitch °
Roll °
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9/02/2019
6:14:36.0 PM
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6:14:39.0 PM
Time

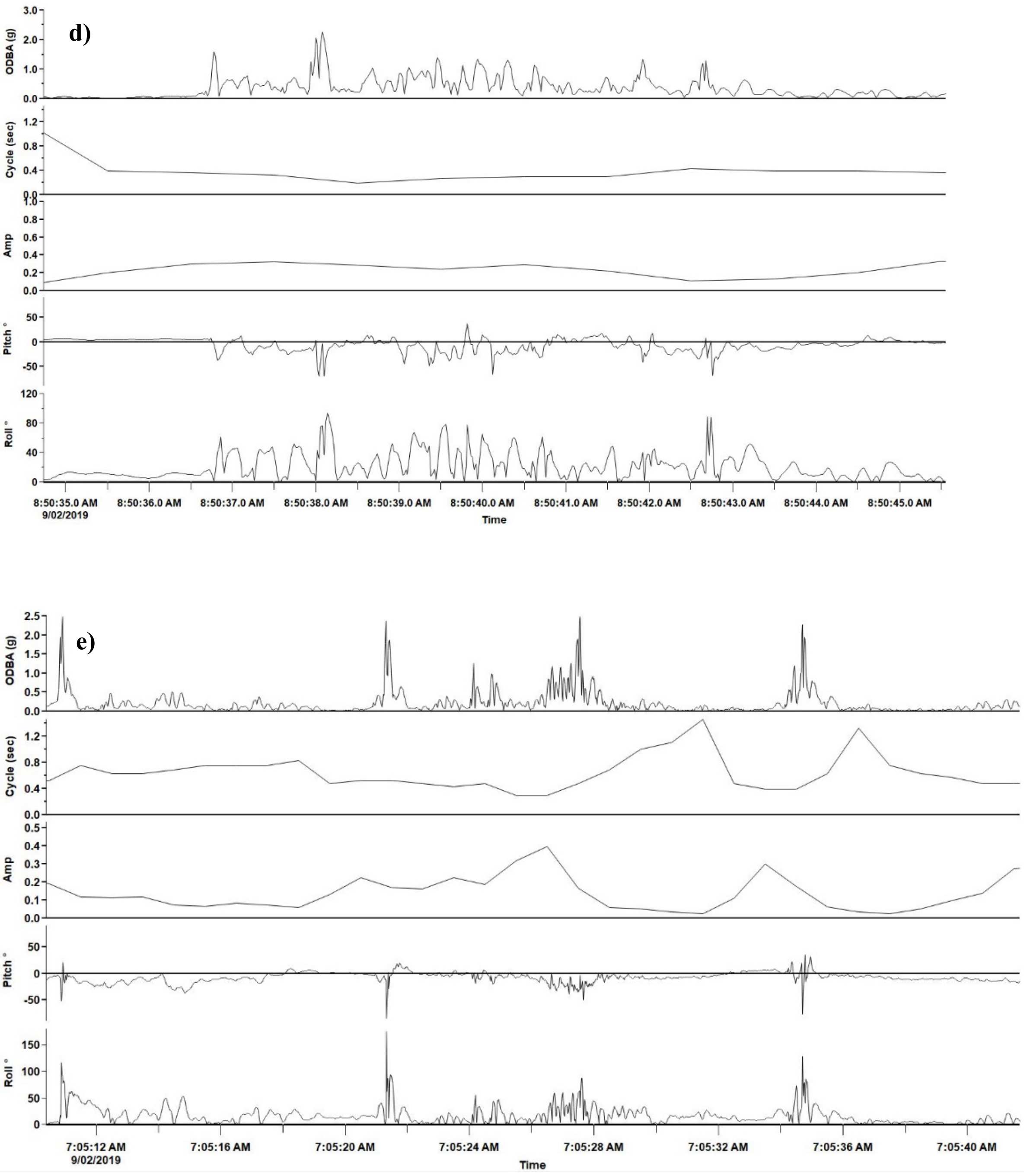


Figure S3. Acceleration signatures for a) swim, b) escape, c) chafe, d) feed, and e) courtship behavioural classes from captive Yellowtail Kingfish recorded via accelerometer loggers.

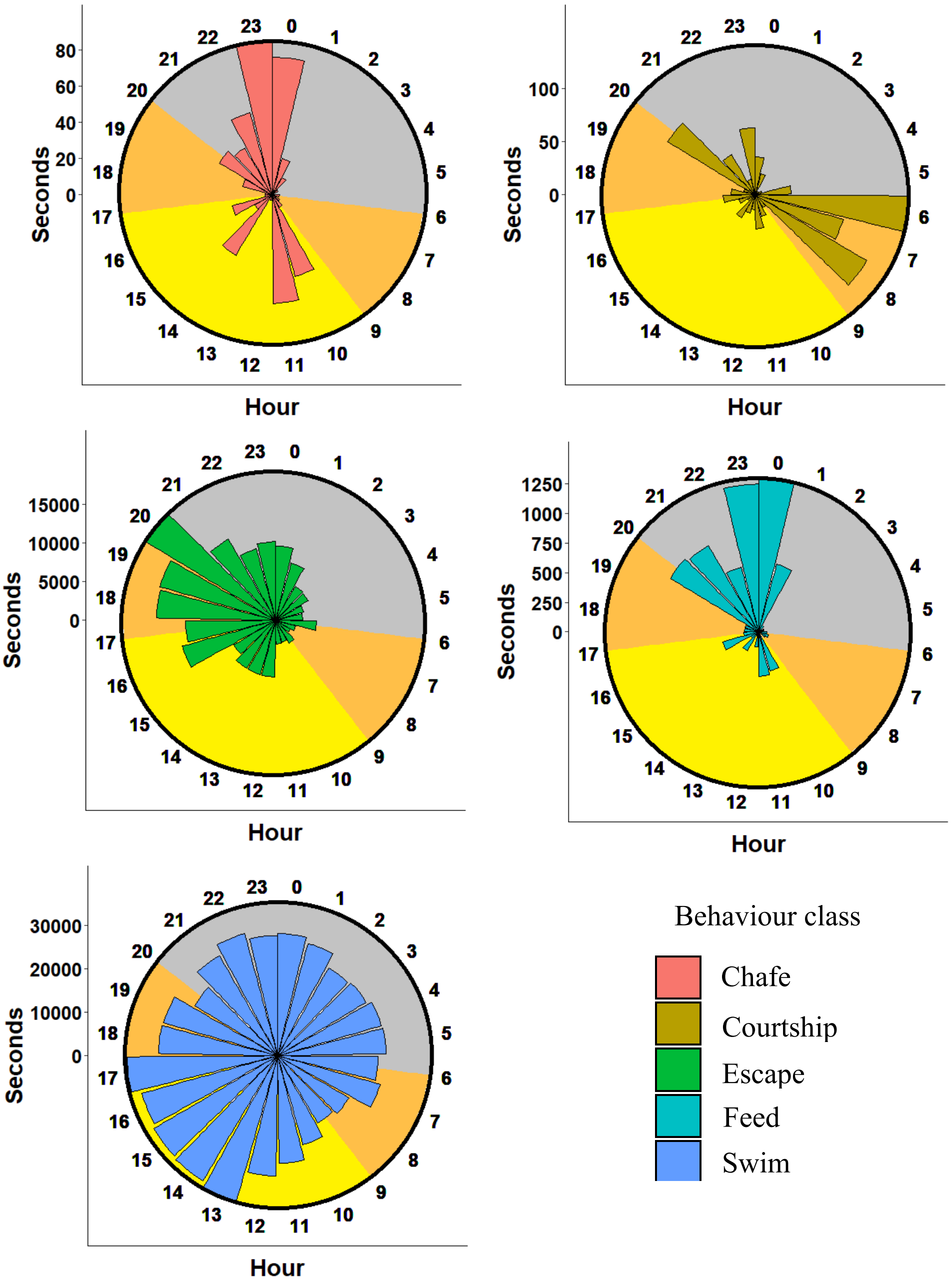


Figure S4. Number of 1 second increments predicted from free-ranging Yellowtail Kingfish at each hour of the day. Time of day is indicated by dawn (orange, 0600 – 0900), dusk (orange, 1700 – 2000), day (yellow) and night (grey).

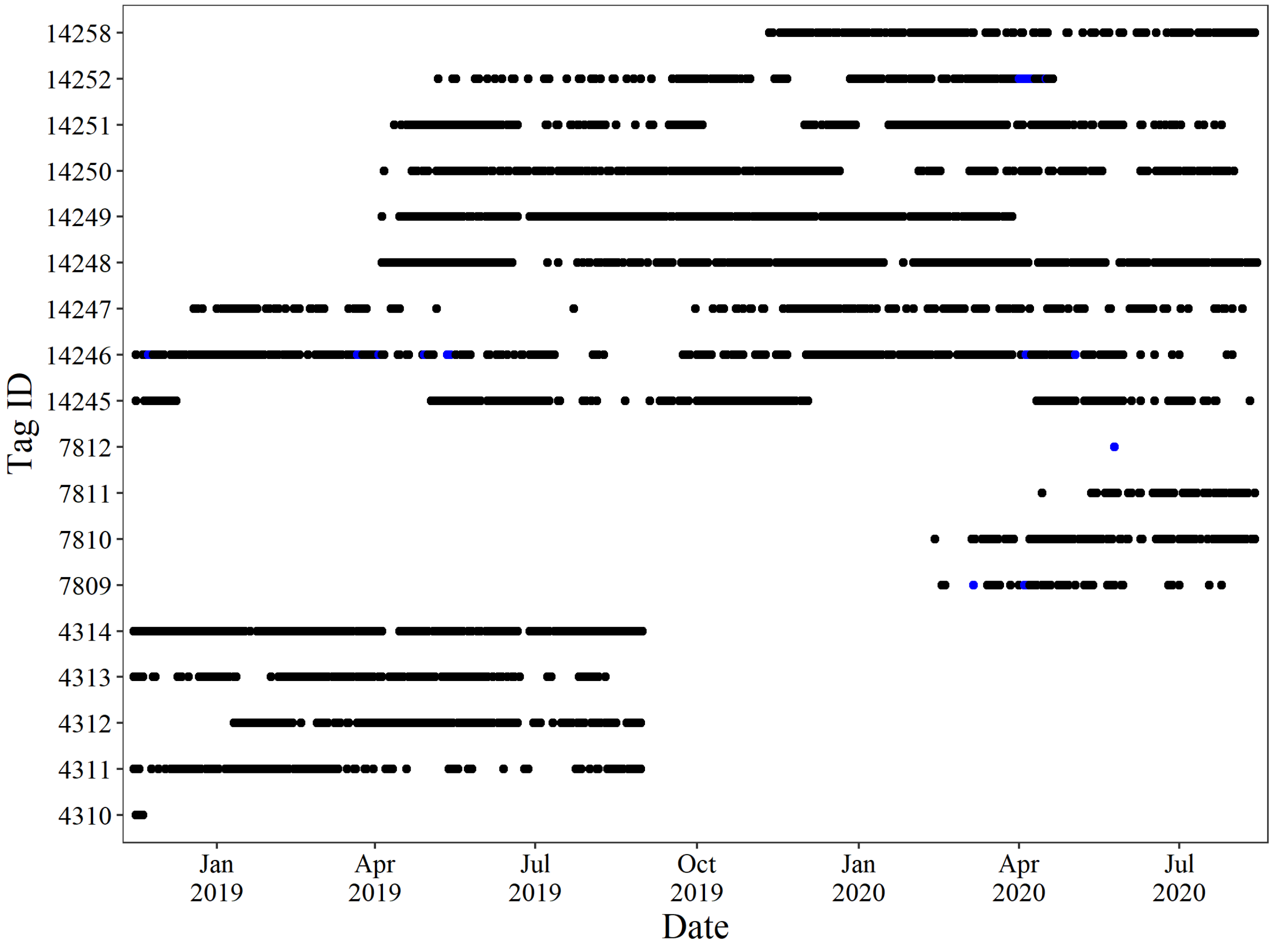
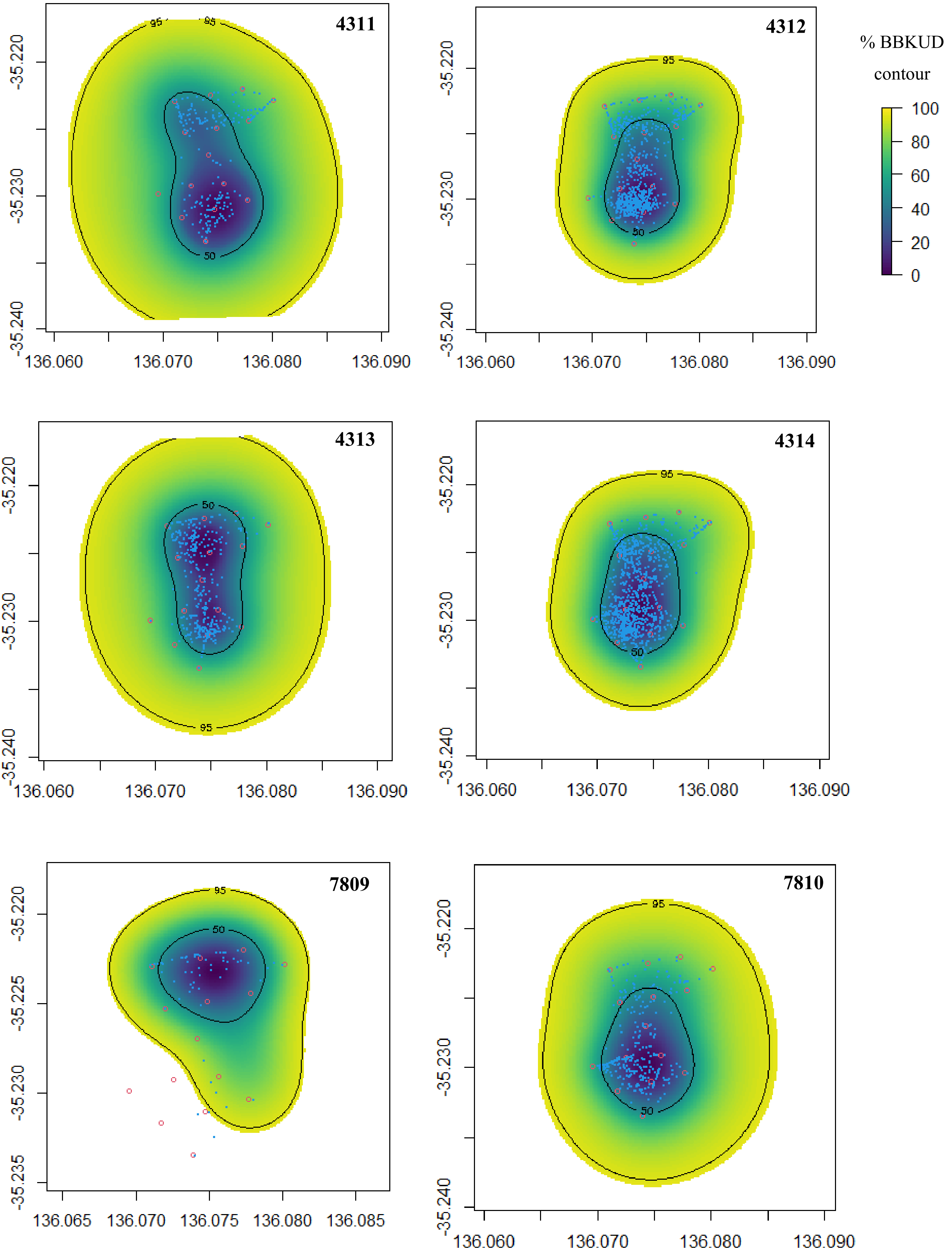
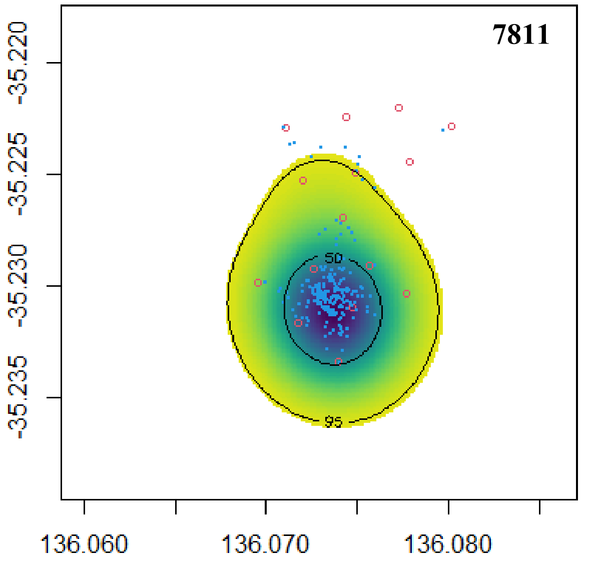


Figure S5. Abacus plot showing residency of 18 acoustically tagged kingfish at north (black) and south (blue) Neptune Islands between August 2018-20.


4311
4312
4313
4314
7809
7810
% BBKUD
contour
100
80
60
40
20
0
95
50
-35.220
-35.225
-35.230
-35.235
-35.240
136.060
136.065
136.070
136.075
136.080
136.085
136.090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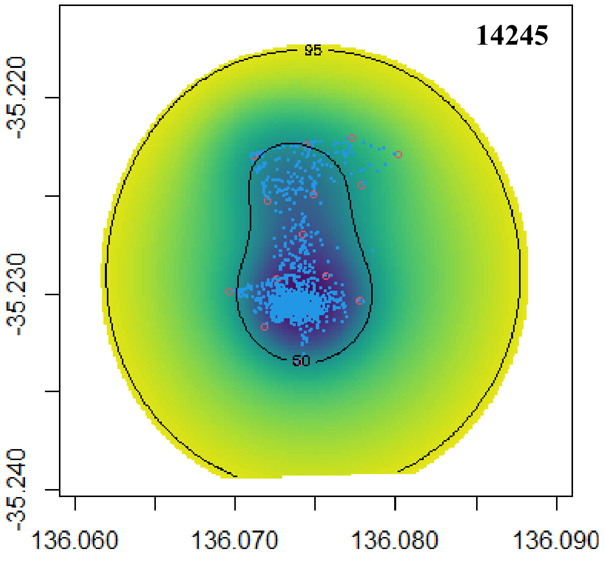
-35.230
-35.235
136.060
136.070
136.080
50
95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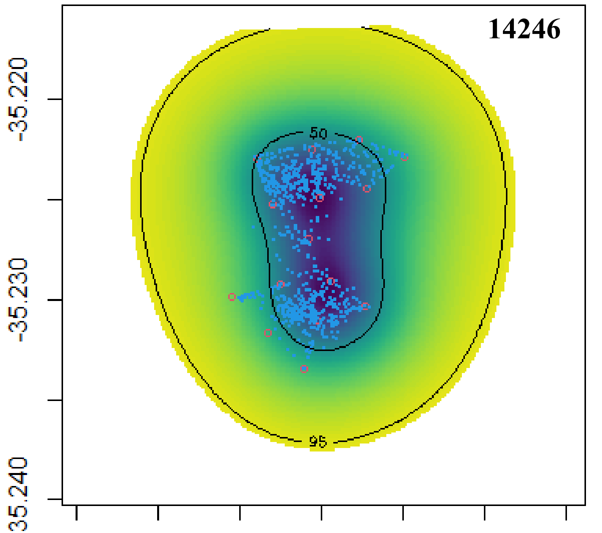
-35.240
136.060
136.070
136.080
136.090
95
50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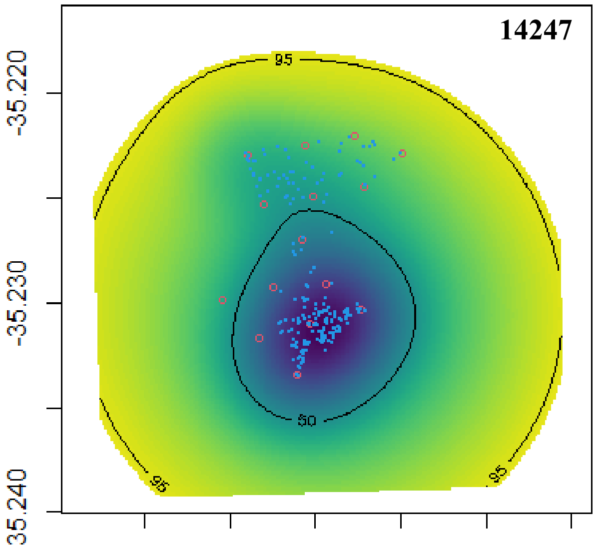
-35.240
136.060
136.070
136.080
136.090
50
95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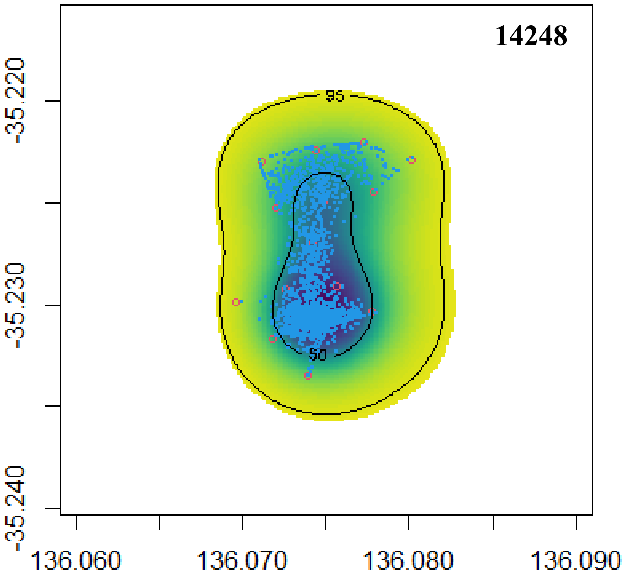
-35.230
-35.240
136.065
136.075
136.085
95
50
95
95


14248
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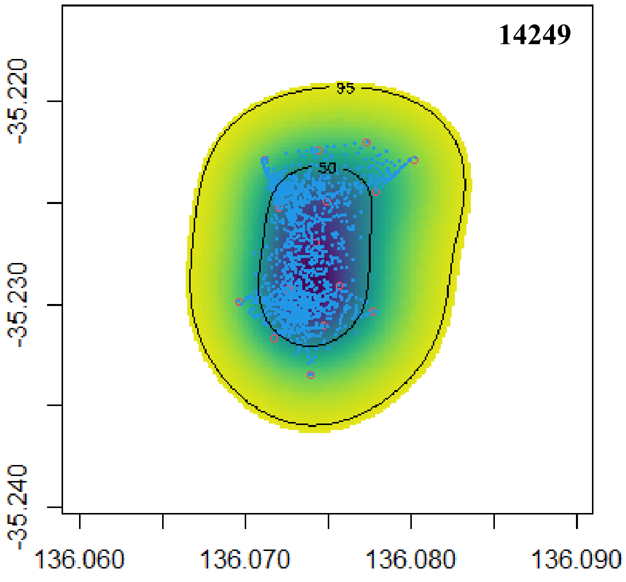
95
50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-35.240
136.060
136.070
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136.090
95
50

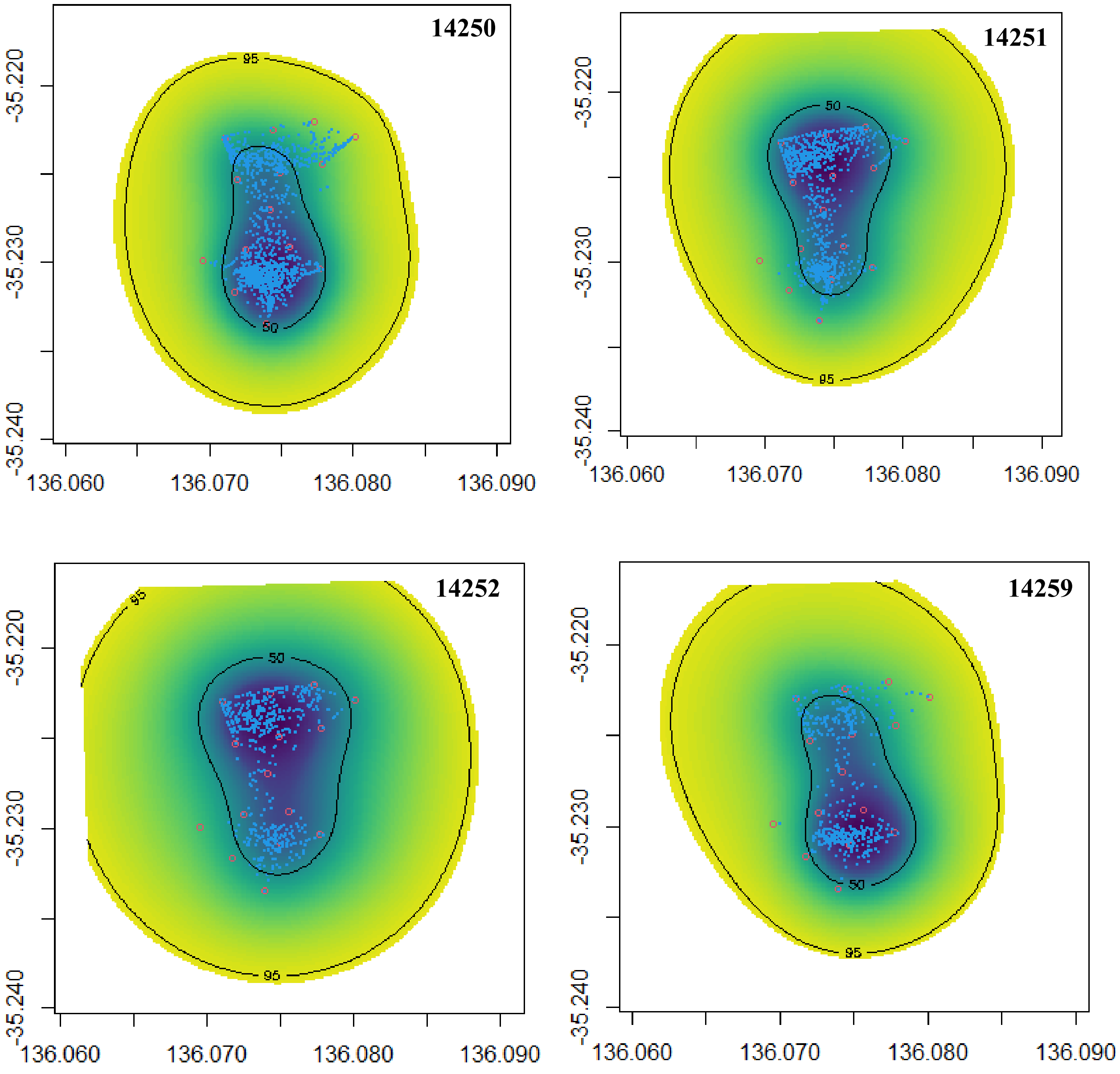

Figure S6. Overall activity space (BBKUD 50- and 95% contours) of yellowtail kingfish at the Neptune Islands. Estimates of 60-minute centre of activities are shown in blue. Location of VR2W acoustic receivers are shown in red.

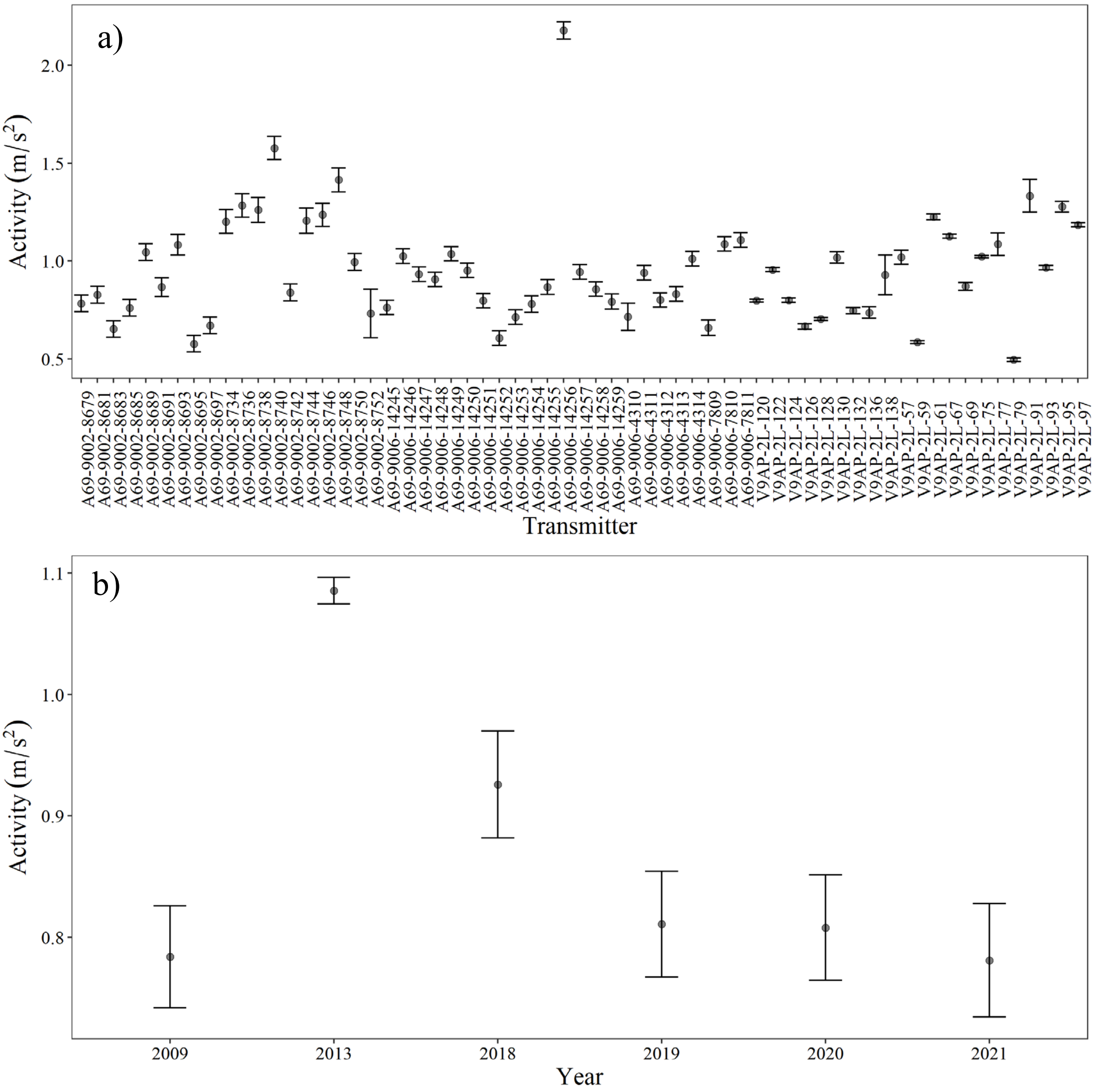

Figure S7. Estimated marginal means (predicted values ± SE) of kingfish activity for random effects; a) Transmitter ID and b) Year in Generalised Additive Mixed Model for activity in south-eastern Australia.