Beyond Jaws: exploring the unseen influence of white shark cage-diving on silver trevally (*Pseudocaranx georgianus*)


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By

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CONTENTS

THESIS SUMMARY

Wildlife tourism often uses food-based attractants to aggregate focal species, unintentionally attracting and feeding non-focal species, the impact of which is poorly understood. In South Australia's Neptune Islands Group Marine Park, bait and berley (southern bluefin tuna *Thunnus maccoyii*) is used to entice white sharks (*Carcharodon carcharias*) to cage-diving vessels, inadvertently attracting silver trevally (*Pseudocaranx georgianus*). These silver trevally form large aggregations around cage-diving vessels as they consume the bait and berley, often impeding tourists' views of the focal white sharks. The impacts of the white shark tourism industry on the spatiotemporal distribution and behaviour of silver trevally, and potential flow-on effects on their physiological processes (i.e., growth, reproduction, healing) is unknown. This study aimed to comprehensively assess how the aggregatory behaviour and feeding of bait and berley may affect silver trevally movements, abundance, growth, and physiological condition.

Due to impacts on the spatiotemporal distribution and activity of similar non-focal species, I first monitored the movements, distribution, and activity of 25 silver trevally in response to cage-diving operators using a fine-scale acoustic telemetry array (Chapter 2). The number of days silver trevally were present per week and the number of hours per day at the Neptune Islands increased by 32% and 20%, respectively, when operators were present. However, a seasonal exodus by 76% of individuals triggered by low water temperature suggested that silver trevally are not permanent residents of the Neptune Islands, and still undergo natural movements away from this near-continuous source of food. Cage-diving tourism also reduced the core space use of silver trevally, aggregating them at the surface (< 5 m depth), close to food-based operators. Despite changes in space use and residency, overall activity did not substantially increase when operators were present, despite frequently observed bursts of acceleration. The near-continuous feeding on bait and berley, large amount of time spent at the Neptune Islands, and the lack of increased activity might result in an energy surplus in silver trevally and affect growth, reproduction, and physiology.

With an understanding of the spatiotemporal distribution and activity of the silver trevally (Chapter 2), the size of the affected population remained unknown. Therefore, I developed and tested novel mark-resight methods (Chapter 3), using the most precise method to quantify and assess trends in the population size of silver trevally occupying the Neptune Islands (Chapter 4). I tagged 700 silver trevally with conventional identification tags, undertook monthly surveys over two years, and used the acoustically tagged silver trevally from Chapter 2 to estimate resighting probability to improve the precision of modelled population size. I estimated up to ~4000 silver trevally at the Neptune Islands, with the population size decreasing with temperature, aligning with the seasonal exodus observed in Chapter 2. However, the number of silver trevally was not affected by the intensity of cage-diving operations.

I then tested the physiological effects of silver trevally exposure to bait and berley using age-at-length, bioelectrical impedance, and fatty acid analysis (Chapter 5). The silver trevally at North Neptune Islands that are frequently exposed to bait and berley were larger than silver trevally of the same age from locations with similar habitats, but without supplemental feeding from cage-diving operations. This was supported by the higher levels of Eicosapentaenoic and Oleic acid in silver trevally from North Neptune Islands. Eicosapentaenoic and Oleic acid, which are known to be high in the bait and berley used, are also known to be important for multiple physiological functions and to increase the overall growth performance, welfare, and condition of teleosts. However, mortality rate and body condition were similar across locations, indicating that while silver trevally may grow faster, consumption of bait and berley may not lead to negative effects on the health or fitness of silver trevally.

This is the first study to assess the ecology of silver trevally in temperate southern Australia, and how it is influenced by wildlife tourism, providing a baseline for impacts of supplemental feeding on a non-focal species. I found effects on the movement, behaviours, and growth of silver trevally, but broader impacts on their health and physiology were undetected. Importantly, despite the effects described here, exodus from the Neptune Islands during cold periods, and the effect of temperature on population size, indicates that silver trevally are still undergoing natural movements and behaviours triggered by thermal cues. Overall, my study comprehensively assesses the ecology of silver trevally through a multidisciplinary approach, showing that small and non-focal species can be affected by provisioning, despite under representation in management frameworks and investigative studies.

DECLARATION

I certify that this thesis:

1. does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university

2. and the research within will not be submitted for any other future degree or diploma without the permission of Flinders University; and

3. to the best of my knowledge and belief, does not contain any material previously published or written by another person except where due reference is made in the text.

Signed

Date 21/12/2023

AUTHOR CONTRIBUTIONS, PERMITS AND FUNDING

The following outline the author contributions and acknowledgments for each chapter:

Chapter 2

The conception and design, as well as the acquisition of field data, involved the efforts of **J Dennis**, L Meyer, T Clarke, and C Huveneers. **J Dennis** was responsible for analysing and interpreting the research data. H Pederson made substantial contributions to the design of the research and played a key role in the analysis and interpretation of the research data. All authors actively participated in revising drafts of this chapter.

I want to express my gratitude to the operators involved in white shark cage-diving industry: Rodney Fox Shark Expeditions, Calypso Star Charters, and Adventure Bay Charters. Special thanks go to the dedicated staff and crew who supported and facilitated my field work. Additionally, appreciation goes out to the members of the Southern Shark Ecology Group and other volunteers from Flinders University for their assistance in sampling silver trevally and maintaining acoustic receiver arrays.

Chapter 3

The conception and design, as well as the acquisition of field data, involved the efforts of **J Dennis**, L Meyer, and C Huveneers. **J Dennis** was responsible for analysing and interpreting the research data. C Dudgeon made substantial contributions to the design of the research and played a key role in the analysis and interpretation of the research data. All authors actively participated in revising drafts of this chapter.

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Dennis JD, Meyer L, Dudgeon C, Huveneers C 2021. Assessing the effect of non-lethal consumptive activities on a non-focal species, presented at World Fisheries Congress (oral presentation).

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Dennis JD, Meyer L, Dudgeon C, Huveneers C 2020. Assessing the effects of cage-diving activities on a non-focal species, presented at the Australian Society for Fish Biology Conference (oral presentation).

Dennis JD, Meyer L, Huveneers C 2019. Collateral provisioning: effects of cage-diving on silver trevally (*Pseudocaranx georgianus*), presented at Flinders University Higher Degree of Research Conference (oral presentation).

Dennis JD, Meyer L, Huveneers C 2019. Collateral provisioning: effects of cage-diving on silver trevally (*Pseudocaranx georgianus*), presented at the Department of Environment and Water (oral presentation).

OTHER PAPERS OR CONTRIBUTIONS

Huveneers C, Clarke T, **Dennis JD**, Matley J, Meyer L, Roberts C 2023. Ecologic and economic assessment of the impact of COVID lockdowns and travel restrictions on the white shark cage-diving industry. (**In preparation**)

Niella Y, Meyer L, Clarke T, **Dennis JD**, Pederson H, Huveneers C 2024. Effects of wildlife tourism on white shark associative behaviour. Animal Behaviour.

Clarke T, Whitmarsh S, Champion C, Pederson H, Meyer L, **Dennis JD**, Dwyer R, Huveneers C 2023. Influence of shark tourism on the activity and physiological condition of a non-focal pelagic fish. ICES Journal of Marine Science.

Davey J, Clarke T, Niella Y, **Dennis JD**, Huveneers C 2023. Seasonal variation in space use and residency of the southern eagle ray *Myliobatis tenuicaudatus* in a temperate ecosystem. Marine Ecology Progress Series, 705:77-94

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Dennis JD, Grammer G, Ward T, Smart J, Huveneers C 2021. Using otolith chronologies to identify extrinsic drivers of growth of 2 commercially targeted small pelagic fish species. Fishery Bulletin, 119: 135-148.

Whitmarsh SK, Amin DB, Costi JJ, **Dennis JD**, Huveneers C 2019. Effectiveness of novel fabrics to resist punctures and lacerations from white shark (*Carcharodon carcharias*): Implications to reduce injuries from shark bites. PLOS ONE 14.

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PREFACE

This thesis adopts a thesis by publication format, presenting a collection of peer-reviewed style articles as standalone contributions to the overall research theme. The structure may thus result in some repetition across chapters, a deliberate choice for clarity and completeness within each chapter. Readers are encouraged to recognize the deliberate thematic overlap, appreciating the connection of the research and the cumulative contributions across the thesis to advance the understanding of impacts from wildlife tourism on non-focal species.

CHAPTER 1

General Introduction

1.1 Fish in the Anthropocene

The current geological epoch, termed the Anthropocene is characterised by the dominance of human activities on the climate and environment (Bailey et al., 2022). Since the 1950s, human influence on the natural world has continued to increase as human populations rapidly increase and expand, altering natural processes, and introducing pollutants (Lewis and Maslin, 2015). The impacts of human influence is so pervasive that anthropogenic stressors have been observed in every ecosystem globally, i.e., terrestrial (Ellis, 2011, Hoffmann et al., 2019, Raboin and Elias, 2019); deep-sea and shallow seas (Parton et al., 2019, Wheeler et al., 2020, Alava et al., 2023); and freshwater (Søndergaard and Jeppesen, 2007, Proulx et al., 2019, Häder et al., 2020).

Fish play an active role in the maintenance and functioning of marine ecosystems, occupying almost every trophic level, from the small zooplanktivores to meso-predators and higher top-level predators (Holmlund and Hammer, 1999). Predator-prey interactions involving fish are prominent regulatory processes in aquatic ecosystems affecting the structure, resilience, and stability of food web dynamics and species diversity (Hiddink et al., 2008, Baum and Worm, 2009). Fish also facilitate connection between ecosystems through daily, seasonal, and annual migrations, transporting nutrients across habitats and ecosystems (Polis et al., 1997). For example, millions of pacific sardines (*Sardinops sagax*) undertake a spawning migration during the sardine run, whereby the concentrated abundance during these spawning aggregations attracts opportunistic predators such as gamefish, sharks, seabirds, and marine mammals (Teske et al., 2021). These events act as a source of energy that many species rely on to support physiological processes and behaviours (Metcalfe, 1986, McBride et al., 2015, Kaplan et al., 2019).

The increasing demand for seafood supports wild-caught fisheries and aquaculture industries, providing food for ~1 billion people and 17% of the global protein for human consumption (Pikitch et al., 2014). Fishes therefore play an essential role in food security, especially in developing countries (Henchion et al., 2017). Wild-caught fisheries and aquaculture industries are also economically important, supporting employment and income (Béné et al., 2016, Naylor et al., 2021, Boyd et al., 2022, FAO, 2022). In 2020, ~59 million workers were employed in wild fisheries and aquaculture, with a combined value of ~US$406 billion (wild fisheries US$141 billion; aquaculture US$265 billion) from production of 178 million tonnes (FAO, 2022). Direct economic values also do not consider the indirect economic value of wild fisheries and aquaculture (i.e., processing and transport industries, consumer marketing), estimated to be approximately three times the direct economic value (Lafferty et al., 2015). Several extractive (i.e., recreational fishing; Ditton et al., 2002) and non-extractive (i.e., snorkelling/scuba-diving; Mota and Frausto, 2014) industries also rely on fishes for personal fulfilment and cultural significance (Ignatius and Haapasaari, 2018), further providing social and economic benefits (Cooke et al., 2019, Pascoe et al., 2023). The broad and diverse importance of fishes, both ecologically and economically, highlights the significance of ensuring sustainable use, particularly as anthropogenic activities continues to increase, potentially impacting fish populations (Díaz et al., 2019, He and Silliman, 2019, Popper and Hawkins, 2019).

In a rapidly changing environment, the increasing overlap and interactions between humans and fish has led to pervasive changes to fish populations (Levin and Poe, 2017, He and Silliman, 2019, Duarte et al., 2021, Bennett et al., 2023). Global fisheries harvesting fish stocks has continued to rise at a rate that has resulted in ~35% of fish stocks categorised as overfished or unsustainable in 2019 (FAO, 2022). Such declines not only impact the exploited species, but can affect entire ecosystems through bottom-up or top-down processes (Shakouri et al., 2010, Duncan et al., 2019). Some extractive methods can also have additional indirect impacts through habitat destruction or modification, e.g., trawling (Jennings and Kaiser, 1998, Halpern et al., 2015, Collie et al., 2017). Non-extractive methods can also affect fish populations. Coastal urbanisation and industrialisation has led to increased reliance on coastlines and oceans for human habitation and infrastructure (i.e., ports; Semeniuk and Cresswell, 2018), and recreation (Defeo and Elliott, 2021). Human expansion has led to increased pollutants and contaminants (Nieukirk et al., 2004, Erbe and McPherson, 2017, Bernaldo de Quirós et al., 2019, Defeo and Elliott, 2021), the spread of diseases (Baskin, 2006, Bowley et al., 2021), introduction of invasive species (Bailey, 2015), and disruption of key behavioural and physiological processes (Haviland-Howell et al., 2007, Hildebrand, 2009, Erbe et al., 2019). Additionally, climate change is driving substantial and wide-spread changes to the marine environment, including raised ocean temperature (Johnson and Lyman, 2020), ocean acidification (Doney et al., 2020), oxygen dead-zones (Altieri and Diaz, 2019), eutrophication (Ngatia et al., 2019, Malone and Newton, 2020), and greater environmental variability (Righetti et al., 2019). Fish can respond to such environmental changes by adjusting their behaviours (e.g. shifting vertical or horizontal movements, residency). This can lead to physiological impacts (i.e. increase rates of oxygen uptake; Clarke and Johnston, 1999) or changes to acid-base regulation (Cattano et al., 2018, Bailey et al., 2022), which in turn can influence vital metabolic processes, resulting in changes to the energy available for overall fitness (Chabot et al. 2016; Pankhurst and Munday 2011).

Other human activities such as provisioning, i.e., the action of providing wildlife with a supplemental food source, is overlooked in comparison to extractive pressures such as fishing. Yet, instances of provisioning are increasing globally and can affect fish communities and ecosystems (i.e., altering community compositions, foraging behaviours, and species abundances; Wen et al., 2019, Shutt and Lees, 2021). Intentional feeding involves food resources being directly provided to wildlife to feed or attract species either for management (human-wildlife conflicts or species recovery; Jones et al., 1995, Martínez-Abraín and Oro, 2013), research (Huveneers et al., 2018b, Whitmarsh et al., 2019), or tourism-related purposes (Sengupta et al., 2021, Meyer et al., 2022). Such intentional feeding occurs globally, across ecosystems, with a range of focal taxa (Green and Higginbottom, 2000, Oro et al., 2013, Meyer et al., 2019, Araujo et al., 2020). Human-mediated provisioning can also be unintentional, whereby wildlife use human food sources such as crops or fisheries catch (i.e., depredation; Mitchell et al., 2018), food waste (i.e., aquaculture waste Felsing et al., 2005, Elvines et al., 2023), or industry discards (Depestele et al., 2019). For example, 9.13 million tonnes of annual fisheries catch was discarded as unwanted fish (i.e., high grading; Berg, 2019, Standal and Hersoug, 2023) and offal (Gilman et al., 2020, Viglia et al., 2022). Such practices has contributed to ~52 % of seabird species globally consuming marine fishing industry discards (Oro et al., 2013), constituting the primary food source in some populations and altering predator-prey interactions in others (Votier et al., 2004, Bicknell et al., 2013, Oro et al., 2013). Both unintentional and intentional provisioning increases the foraging success of species through a predictable and spatially- and temporally-consistent food resource, far greater than is possible from natural sources (Becker and Hall, 2014). With the multitude of possible stressors from a variety of anthropogenic sources, identifying and quantifying causative human impacts to develop appropriate mitigation and management strategies is a priority to account for, and remedy these impacts.

1.2 Wildlife tourism

Wildlife tourism is one of the fastest-growing sectors of the tourism industry, with millions of annual participants globally (Scheyvens, 1999, Wearing and Neil, 2009, Trave et al., 2017). Wildlife tourism a significant source of both direct and indirect income, providing an alternative to the extractive use of resources (i.e., hunting and fishing; Higginbottom and Tribe, 2004), and is an effective tool for sustainable development of economies while protecting biodiversity (Twining-Ward et al., 2018). Wildlife tourism represented ~8.25% of the global tourism gross domestic products in 2022 (7.6%; US$2 trillion; WTTC, 2023), had a value of US$165 billion in 2022, which is predicted to nearly double to US$300 billion in the next decade (Insight, 2022). Such economic benefits are driving the continued expansion and emergence of new operations targeting a diverse array of taxa (Patroni et al., 2018). Wildlife tourism has centred many of its core values on the promotion, sustainability, and conservation of the focal species (i.e., species targeted by the tourism operation), ensuring longevity of their industry. Such values have created both on-site (i.e., increased understanding or emotional responses to wildlife encounters) and offsite benefits (i.e., environmental awareness, philanthropic support; Higginbottom and Tribe, 2004, Apps et al., 2018), as well as psychological benefits (Muloin, 1998, Curtin and Kragh, 2014).

Wildlife tourism continues to increase in popularity, with operators using a range of practices to facilitate interactions between participants and species (Meyer et al., 2022). Practices to interact with wildlife can be simple, such as viewing naturally-occurring aggregations (Chapman and Jones, 2009), anticipating seasonal migratory routes (Sprogis and Waddell, 2022), or fenced nature reserves (Noack et al., 2019), allowing passive interactions between tourists and wildlife. However, many focal species are often naturally dispersed in low densities or have short residency periods as they undertake long-range movements or migrations. Controlling for predictability and close-proximity of encounters for tourists can therefore be challenging, placing pressure on operators to ensure customer satisfaction. In response, operators will often use olfactory (e.g., feeding; Meyer et al., 2019), visual and auditory attractants (attracting, e.g., decoys and bird calls; Vagabov and Eldarov, 2019), or habitat modifications (e.g., artificial light and reefs; Lima et al., 2019), collectively referred to as provisioning (Meyer et al., 2022), to generate consistent, predictable, and up-close encounters. In terrestrial environments direct animal feeding, feeding stations, intentional growth of grasses or nectar-rich shrubs, and providing water is common practice to aggregate wildlife for convenient and consistent viewing (Green and Higginbottom, 2000). For example, feeding stations are used to increase density of game species for hunters, with ~2.8 trillion tonnes of shelled corn provided to big game ungulates every year in the United States (Oro et al., 2013, Murray et al., 2016). Likewise in the marine environment the feeding of sharks and teleosts for tourism also occurs, e.g., whale sharks in the Philippines are provided 150–400 kg per day of sergestid shrimp to allow in-water tourists to observe feeding individuals (Barry et al., 2023), and aggregations of yellowtail kingfish (*Seriola lalandi*) among other coastal fishes are fed aquaculture pellets and bread by tourists at Lord Howe Island (Brookhouse et al., 2013). As the demand for close encounters and unique experiences with wildlife is propelled by the influences of social media (Bergman et al., 2022) and economic benefits (Huveneers et al., 2017a, Barnes et al., 2019, Healy et al., 2020), so will the occurrence of new wildlife tourism operations to meet this demand.

Exposure to provisioning can have a range of short- and long-term effects on the focal species of wildlife tourism operations (Orams, 2002, Higginbottom et al., 2003, Trave et al., 2017, Meyer et al., 2021). However, the extent of these effects is varied, with some negatively impacting the focal species (i.e., negative), while others can be beneficial (i.e., positive), or have negligible impacts (i.e., neutral). Observed effects include changes to daily residency (negative; Hansen et al., 2023), feeding behaviour (negative; Brookhouse et al., 2013), diel movement patterns (negative; Fitzpatrick et al., 2011), home ranges (negative; Senigaglia et al., 2022), residency (neutral to positive; Brunnschweiler and Barnett, 2013, Sengupta and Radhakrishna, 2018), abundance (neutral; Clarke et al., 2013), encounter rates (neutral to negative; Brunnschweiler et al., 2014), diet (negative; Hines, 2011), energy requirements (neutral to positive; Brunnschweiler et al., 2018), and metabolic rate (negative; Barnett et al., 2016, Barry et al., 2023). These examples highlight the spectrum of effects from negative to positive that can be caused by provisioning and that effects are highly species and site specific. While wildlife tourism management and regulations have traditionally focused on focal species effects from tourism (Meyer et al., 2021), there is a limited understanding of how provisioning practices affect other species within the ecosystem.

1.3 Non-focal impacts

Provisioning during wildlife tourism is focused on attracting focal species, although such practices also lead to the unintentional attraction and feeding of non-focal species (Donalty et al., 2003, Inslerman et al., 2006, Meyer et al., 2021). In some terrestrial situations, non-focal species have been observed to consume the majority of the food supplied (i.e., 98 % of food intended for game wildlife is consumed by non-game species such as rabbits and rodents; Donalty et al., 2003, Inslerman et al., 2006). Similarly, in the marine environment, wildlife tourism industries will typically select supplemental food that is similar to the natural prey items of focal species (Brunnschweiler et al., 2018, Barry et al., 2023), which are unlikely to represent the natural diets of the non-focal animals that are also attracted by, and consume, the food provided. Yet, in both marine and terrestrial environments, tourism management frameworks and polices that ensure the ecological sustainability of industries and conservation of focal species often do not account for the effects of these industries on non-focal species. Most studies examining the effects of wildlife tourism have largely been on focal species, with only 7% exploring non-focal species or ecosystem-wide effects (Trave et al., 2017, Meyer et al., 2020). Similar impacts to those observed in focal species have also been observed in non-focal species (Clarke et al. 2023, Vignon et al., 2010, Meyer et al., 2020), providing some of the only evidence of non-focal impacts. Due to the lack of studies examining non-focal impacts the need for further research has been highlighted in several studies and reviews (Gallagher et al., 2015, Trave et al., 2017, Gallagher and Huveneers, 2018, Patroni et al., 2018, Meyer et al., 2020, Meyer et al., 2021).

The impacts of provisioning from non-tourism-based industries on non-focal species can provide an insight into the potential effects of provisioning from tourism operations. In the terrestrial environment, about 85% of studies assessing behavioural responses of wildlife to supplementary (i.e., at risk populations) or diversionary feeding stations show some effects on non-focal species (Milner et al., 2014), with supplemental food sources increasing predation rates (Cooper and Ginnett, 2000, Hamilton et al., 2002) and in some cases poisoning non-focal species (i.e., containing species specific toxic compounds; Brown and Cooper, 2006). In the marine realm, wild fish often scavenge on waste material such as faecal matter and uneaten food pellets from open ocean aquaculture pens (Felsing et al., 2005) which also results in the organic enrichment of benthic habitats and flow on effects on benthic species (Elvines et al., 2023). Consumption of supplemental food sources has been detected in the fatty acid profiles of wild fishes, showcasing alterations to the diet and nutrition of these non-focal species, which can impact their physiology and behaviours (Fernandez-Jover et al., 2011, Uglem et al., 2014, Barrett et al., 2019), alter diets (Elvines et al., 2023, Takahata et al., 2023), and increase growth (Barrett et al., 2019) and energy stores (Uglem et al., 2014). Similar impacts on non-focal species have been observed from marine wildlife tourism operations that uses food-based attractant. For example, wildlife tourism can increase site fidelity and reduce space use of smooth stingray (Rizzari et al., 2017), alter fish behaviour and increase predation frequency (Milazzo et al., 2006), and increase the prevelance of parasite infestations of blacktip grouper *(Epinephelus fasciatus*; Vignon et al., 2010), none of which are the species targeted by the tourism industry.

The use of provisioning can result in an individuals' inability to adapt to the novel situation presented by the supplemental food source and to individuals being caught in an ecological trap. Human-driven change (i.e., through provisioning) can supress an individual's ability to assess a habitat's true quality, resulting in behaviours based on false or altered environmental cues which they believe will maximise their fitness (Battin, 2004). Without negative feedback to discourage or prevent detrimental behaviour or interaction, the positive reinforcement can lead to reduced survival (Schlaepfer et al., 2002, Norris et al., 2013), altered reproductive behaviours (Pelicice and Agostinho, 2008, Penteriani et al., 2018), physiological impacts (Huang et al., 2018, Krams et al., 2022), and decreased overall fitness (Corcoran et al., 2013, Hale and Swearer, 2016). Due to the maladaptive behaviours and habitat selection that can occur due to provisioning, animals can become dependent on the human-mediated food source or anthropogenic cues that provides positive reinforcement (Semeniuk, 2009). In wildlife tourism, ecological traps from supplemental feeding have previously been described at popular tourism sites (Semeniuk, 2009, Corcoran et al., 2013). At the Cayman Islands, Stingray City Sandbar receives ~1 million visitors per year, with tourists feeding squid to southern stingrays (*Dasyatis americana*; Corcoran et al., 2013), altering their diel behaviour patterns, reduced their activity space, and increased site fidelity to the feeding site. These changes and increased concentration of individuals within a small area led to increased physical contact between conspecifics, parasite loading, disease transmission, and physical injuries, altered blood chemistry, resulting in poorer body condition, and subsequently impacting fitness (Semeniuk et al., 2007, Semeniuk and Rothley, 2008, Semeniuk et al., 2009). While these changes in focal species can be mitigated through policy and management strategies, similar ecological traps can occur for non-focal species which are typically not considered in industry regulations.

1.4 Study site and white shark cage-diving

The Neptune Islands group in South Australia is an offshore temperate group of granite islands, 60–70 km southeast of Port Lincoln (Figure 1). The island group is comprised of the North Neptune and South Neptune Islands, that are ~12 km apart (Figure 1B) and are characterised by seagrass, sand, and macroalgae reef substrate. The islands host local and migratory sea birds (e.g., white breasted sea eagles *Haliaeetus leucogaster*, osprey *Pandion haliaetus*, cape barren goose *Cereopsis novaehollandiae*, shy albatross *Thalassarche cauta*), breeding colonies of Australian sea lions (*Neophoca cinerea*) and long-nosed fur seals (*Arctocephalus forsteri*), as well as diverse fish and elasmobranch communities (Whitmarsh, 2019). In 2012, these islands became part of the Neptune Islands Group (Ron and Valerie Taylor) Marine Park due to the range of ecologically important resident and transient species found at the Neptune Islands group, with the South Neptune Island group becoming a habitat protection zone and the North Neptune Island group becoming a sanctuary zone (Baker, 2004, DEW, 2016, DEWNR, 2012).

White shark cage-diving is a globally popular form of wildlife tourism, occurring in Australia, South Africa, United States, Canada, and New Zealand. The Neptune Islands Group Marine Park is home to the only location where white shark cage-diving tourism is permitted in Australia. Beginning in the late 1970s in Spencer Gulf (South Australia) and expanding to several location by the early 2000s, cage-diving activities were restricted to the Neptune Islands Group in 2002. Cage-diving is permitted at the North and South

Neptune Islands, but ~85% of tours occur at North Neptune Islands (J Dennis, unpublished data). Due to prevailing weather and ocean conditions, cage-diving operators typically anchor on the south-eastern side or northern side of the North Neptune Islands group (Figure 1C). From 2007, the industry expanded from two operators running tours on ~125 days year^{-1} (2000–2006) to three operators taking tourists to the Neptune Islands more than twice as much (~265 days year^{-1}; 2008–2011; Bruce and Bradford, 2013). This increase in cage-diving intensity altered the residency and spatiotemporal distribution of white sharks at the Neptune Islands (Bruce and Bradford, 2013, Huveneers et al., 2013). In response, the South Australian White Shark Tour Licensing Policy was developed and implemented by the South Australian Government in 2014, limiting the number of operators (3), operating days (12 per fortnight), and the daily quantity of food-based attractant used by operators (100 kg per food-based operator). Two cage-diving operators use a near-continuous plume of berley (minced southern bluefin tuna *Thunnus maccoyii*) and tethered baits (southern bluefin tuna gills and stomachs) to entice sharks into the field of view of tourists (Huveneers and Lloyd, 2017, Huveneers et al., 2017b, Meyer et al., 2020), while an additional third company used sound-based stimuli (music played through underwater speakers) to attract white sharks.

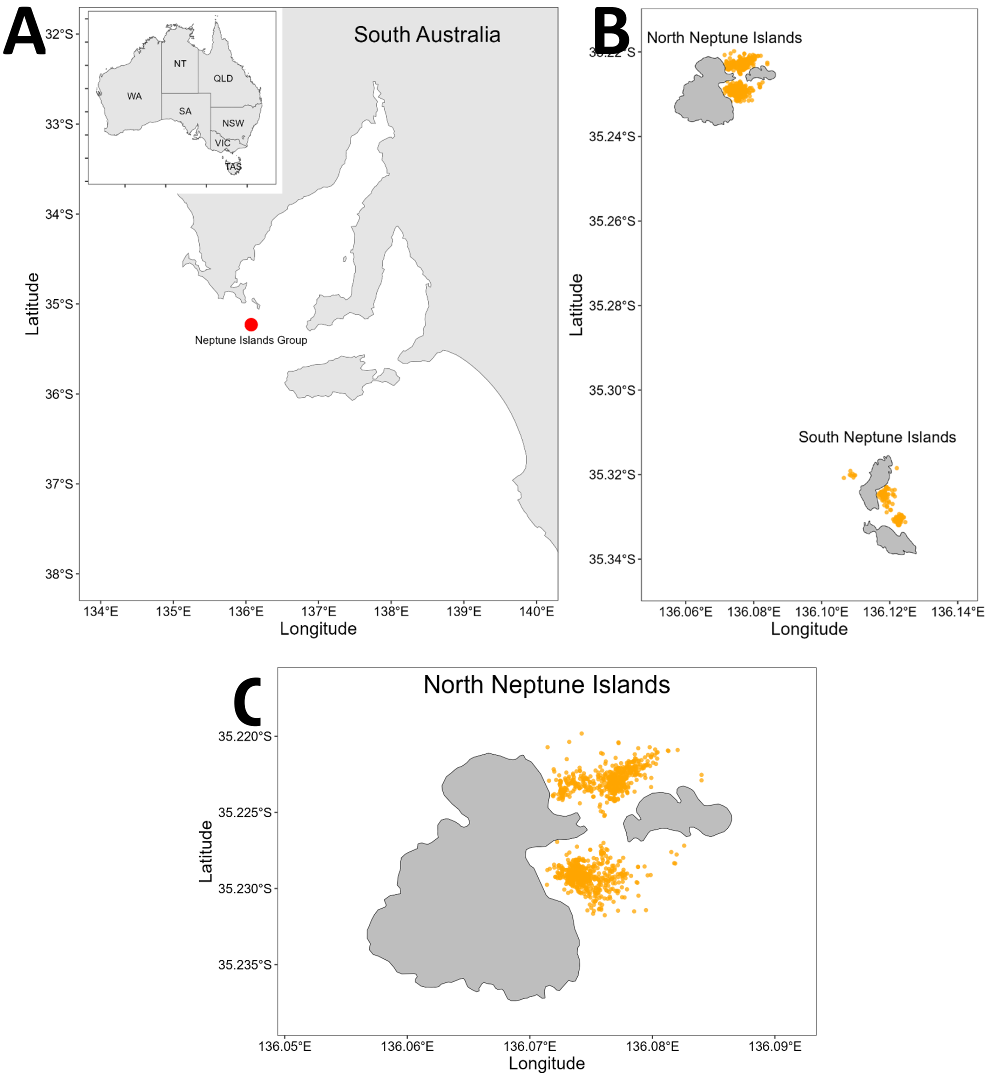


Figure 1. Locations of the **A.** Neptune Islands Group within South Australia, and locations of cage-diving operator anchorages at North (**B, C**) and South Neptune (**B**) Islands between August 2019–August 2022.

White sharks interacting with the cage-diving operators are not intentionally fed as the bait is retracted before sharks can consume it. While the berley particles are too small to be consumed by white sharks, several non-focal species have altered diets owing to the consumption of these berley particles and bait, including: coastal-pelagic fishes (silver trevally *Pseudocaranx georgianus,* yellowtail kingfish *Seriola lalandi*), reef fishes (horseshoe leatherjacket *Meuschenia hippocrepis*, bluethroat wrasse *Notolabrus tetricus,* magpie perch *Pseudogoniistius nigripes*), and rays (southern eagle ray *Myliobatis tenicaudatus*, smooth ray *Bathytoshia brevicaudata*; Meyer et al., 2020). Incidental feeding at the Neptune Islands has also been shown to influence the behaviour and residency of several of these non-focal species. Large pelagic yellowtail kingfish increased daily residency and activity and burst events while interacting with the cage-diving operators (Clarke et al., 2022, Clarke et al., 2023). Similarly, cage-diving increased site fidelity and altered the space use of smooth rays (Rizzari et al., 2017). An assessment of the dietary composition of several demersal and pelagic species also demonstrated diet alterations resulting from the bait and berley used by the cage-diving industry (Meyer et al., 2020).

At the Neptune Islands, silver trevally is the most frequently observed non-focal species, forming large aggregations around the cage-diving vessels, impeding tourists' views of white sharks (J. Dennis, A Fox, A Wright, pers. obs.; Supplementary material 1). The ensuing tourist dissatisfaction has led operators to state that silver trevally are “in plague proportion” and to propose a need for culling silver trevally at the Neptune islands. The bait and berley used by the cage-diving industry provide an unnaturally high protein- and calorie-rich food source to the non-focal silver trevally (Gomon et al., 2008). Consuming most of the bait and berley, silver trevally make quick bursts of acceleration towards fresh tethered baits when they are thrown in the water and appear to be constantly present around the cage-diving vessels (Supplementary material 2). However, it is unknown if these are the same individuals staying close to the vessels or that the silver trevally population is so large that schools of silver trevally are constantly present around the cages even if individuals remain next to the vessels for short periods. Reports from the industry suggest that the consumption of this bait and berley may be increasing the abundance of silver trevally at the Neptune Islands (A Fox, pers. obs.), while biochemical tracers and stomach content analysis show that the diet of silver trevally at the Neptune Islands shifted due to the consumption of bait and berley (Meyer et al., 2020). Similar non-focal carangids at the Neptune Islands Group which share the observed change in diet have displayed behavioural changes from interactions with the industry, leading to implications for their energy budgets and physiology (Clarke et al., 2022, Clarke et al., 2023). Previous studies suggest that in instances of increased activity, additional food intake might be required for these species to compensate for heightened energy expenditure from interacting with tourism operations (Barnett et al., 2016, Barry et al., 2023, Clarke et al., 2023). Considering the effects observed for focal and non-focal species interacting with wildlife tourism and provisioning, it is unknown whether effects from the industry on silver trevally extend beyond diet to their spatiotemporal distribution, behaviour, activity, and abundance. Combined with the previously documented dietary shift (Meyer et al., 2020), the energy budgets of silver trevally could become unbalanced, with flow-on effects for physiological processes (i.e., growth, reproduction, healing). Furthermore, positive reinforcement from provisioning has the potential to impede environmental cues that trigger natural movements and behaviours, leading to an ecological trap, further impacting the health and fitness of the silver trevally.

1.5 Silver trevally

Silver trevally is a schooling reef-associated benthopelagic carangid, occurring in temperate estuarine and near-shore waters (Gomon et al., 2008, French et al., 2013) from northern Perth (Western Australia) to northern Sydney (New South Wales), as well as Norfolk island and New Zealand in the Tasman Sea (Smith-Vaniz and Jelks, 2006, Gomon et al., 2008). Juveniles typically inhabit shallow reef in coastal regions, moving to deeper waters as they grow, with the oldest individuals residing in > 60 m depth (Rowling and Raines, 2000, Farmer et al., 2005). Silver trevally are often observed at 300–400 mm total length, but can grow up to ~900 mm, with individuals from Australia aged up to 18 years (Rowling and Raines, 2000). Silver trevally from New Zealand display significantly greater longevity and maximum sizes, with some individuals reaching over 45 years and up to ~1200 mm (Walsh et al., 2014). Reaching maturity between 2–4 years, spawning occurs over an extended period as they are serial batch spawners with indeterminate fecundity (Rowling and Raines, 2000, Gomon et al., 2008). Spawning occurs in southern and eastern Australia from early spring to summer in estuaries and coastal waters, although the exact period has been suggested to vary with latitude (Farmer et al., 2005). The diet of silver trevally changes ontogenetically, feeding on small benthic invertebrates and zooplankton as juveniles and transitioning to benthopelagic teleosts and small cephalopods when they attain a larger size (i.e., > 220 mm; French et al., 2012, French et al., 2013). Multiple movement types have been suggested for silver trevally within south-eastern Australia, with some individuals being relatively sedentary (i.e., recaptured at tagging locations; Fowler et al., 2018; home range < 1.3 km^2; Fairclough et al., 2011) or exhibiting strong homing behaviour (i.e., range of < 10 km; Fowler et al., 2018, and < 4 km; Taylor et al., 2018), while others undertake extensive migrations of over 500 km along the NSW coast in 17 days (Fowler et al., 2018).

The biological stock structure of silver trevally is currently uncertain, with varying species complexes across different regions and jurisdictions. Silver trevally is present in all jurisdictions except Queensland and Northern Territory (Smith-Vaniz and Jelks, 2006, Gomon et al., 2008). Stock status determination for the Commonwealth and all states is considered to be sustainable, except for New South Wales which is currently depleted due to the decline in commercial and recreational catches and biomass estimates, and impaired recruitment (Fowler et al., 2023). In South Australia, silver trevally are a tertiary species within the Marine Scalefish fishery, with a total catch of ~9 tonnes in 2021–2022 (Smart et al., 2023). While the commercial targeting of silver trevally in South Australia is limited compared to other states and fisheries (e.g. ~329 tonnes year-1 Australia-wide; Fowler et al., 2018), they are often targeted by recreational anglers

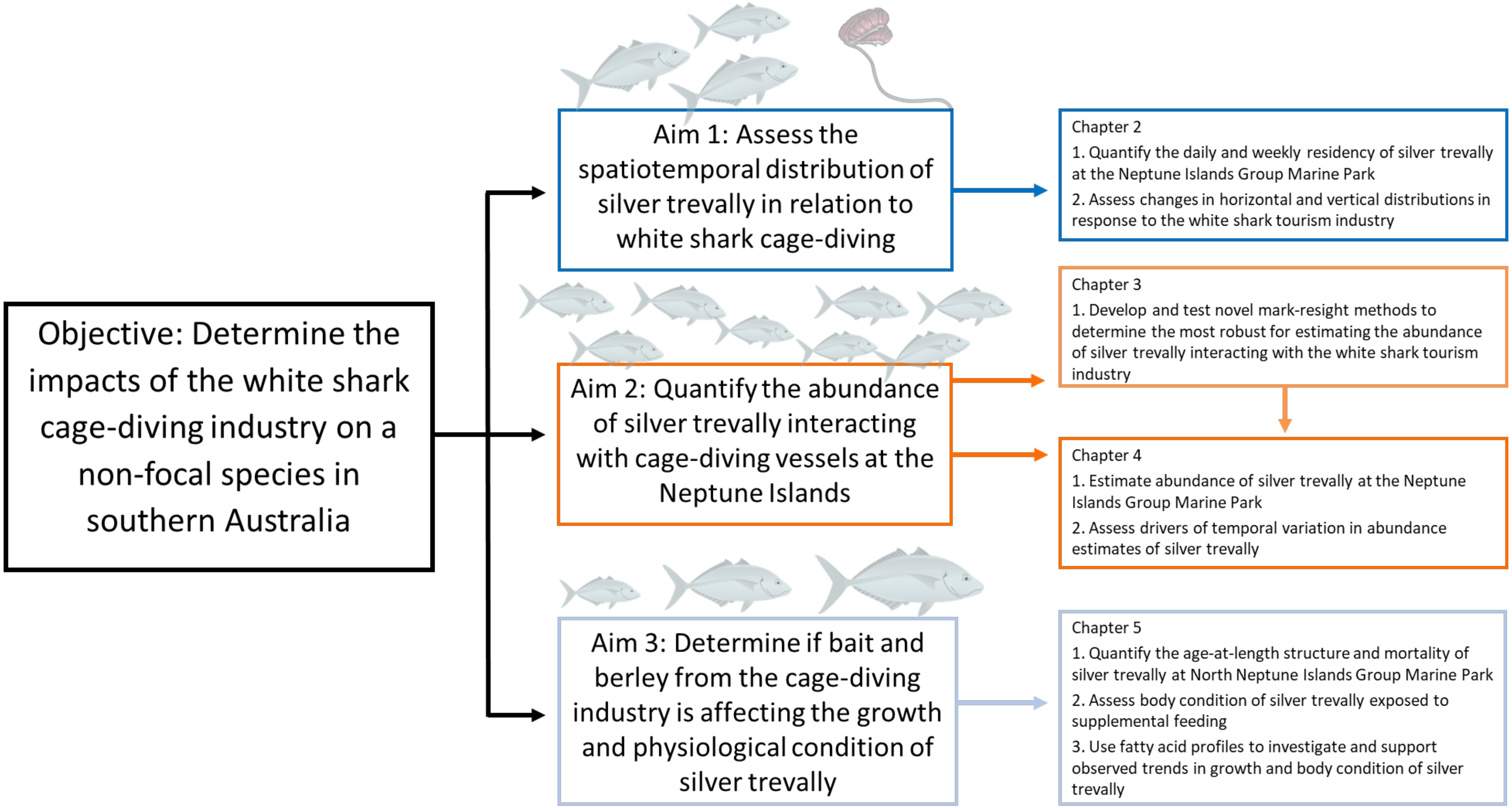
(33,228 individuals ± 12,878 standard error in 2021–2022; Beckmann et al., 2023). In light of the closures placed on snapper fishing in South Australia (Drew et al., 2022) and the strong fighting ability of silver trevally, recreational anglers in South Australia may increasingly target the species.

1.6 Research objectives

The main objective of this study was to determine the impact of the white shark cage-diving industry in South Australia on silver trevally, and assist managers make informed decisions regarding the management of the industry and its potential effects on non-focal species. This objective branches into three overarching aims to:

1) assess the spatiotemporal distribution of silver trevally in relation to white shark cage-diving;
2) quantify the abundance of silver trevally interacting with cage-diving vessels at the Neptune Islands; and
3) determine if bait and berley from the cage-diving industry is affecting the growth, and physiological condition of silver trevally

To address these aims, I have compiled four data chapters (excluding this introductory and general discussion, each with specific aims and goals which link to the overall objective of this study (Figure 2). Findings will provide important information about the interactions between non-focal species and supplemental feeding from wildlife tourism, supporting the need for management of tourism operations and anthropogenic activities to account for non-focal species when considering the ecological sustainability of a tourism industry.



Objective: Determine the impacts of the white shark cage-diving industry on a non-focal species in southern Australia

Aim 1: Assess the spatiotemporal distribution of silver trevally in relation to white shark cage-diving

Aim 2: Quantify the abundance of silver trevally interacting with cage-diving vessels at the Neptune Islands

Aim 3: Determine if bait and berley from the cage-diving industry is affecting the growth and physiological condition of silver trevally

Chapter 2

1. Quantify the daily and weekly residency of silver trevally at the Neptune Islands Group Marine Park
2. Assess changes in horizontal and vertical distributions in response to the white shark tourism industry

Chapter 3

1. Develop and test novel mark-resight methods to determine the most robust for estimating the abundance of silver trevally interacting with the white shark tourism industry

Chapter 4

1. Estimate abundance of silver trevally at the Neptune Islands Group Marine Park
2. Assess drivers of temporal variation in abundance estimates of silver trevally

Chapter 5

1. Quantify the age-at-length structure and mortality of silver trevally at North Neptune Islands Group Marine Park
2. Assess body condition of silver trevally exposed to supplemental feeding
3. Use fatty acid profiles to investigate and support observed trends in growth and body condition of silver trevally

Figure 2. Overall objective and aims of thesis with each chapter’s contribution to those aim.

1.7 Thesis structure

Chapter 1 provided a general introduction of the challenges fish face in the Anthropocene epoch, wildlife tourism, and impacts on non-focal species. I then introduced the potential implications of white shark cage-diving on the spatiotemporal distribution, behaviour, activity, and physiology of silver trevally. This chapter presents a brief introduction to the key topics included in the thesis, as more details are provided within the subsequent data chapters.

Chapter 2 examined the influence of white shark cage-diving on the spatiotemporal distribution and activity of silver trevally at the Neptune Islands. Silver trevally residency, space use, depth, and activity were assessed over 2.5 years using acoustic tracking, and compared during times that food-based operators were present and absent. This chapter aligns with aim 1 (Figure 2).

Chapter 3 developed and compared three new mark-resight/recapture methods to estimating the abundance of schooling pelagic fish. These findings relate to aim 2 (Figure 2) and was accepted in the *Journal of fish biology*.

Chapter 4 uses the best method developed and tested in Chapter 3 to estimate the abundance of silver trevally at the Neptune Islands Group Marine Park. Monthly resighting surveys were conducted for two years and used to estimate monthly abundance of silver trevally, comparing variations to environmental variables and cage-diving intensity. Findings from this chapter align with aim 2 (Figure 2).

Chapter 5 investigated the effects of supplemental feeding from white shark cage-diving tourism on the growth and physiological condition of silver trevally at North Neptune Islands across multiple years. Silver trevally growth, mortality, body condition, and fatty acid profiles were assessed to reveal if bait and berley consumption was affecting trevally physiology and fitness. This chapter aligns with aim 3 (Figure 2).

Chapter 6 synthesises results from Chapters 2–5 and discusses the major findings and inferences for the improved understanding of the impacts of wildlife tourism on a non-focal species in southern Australia. This highlights that small and non-focal species can be affected by provisioning, despite being underrepresented in management regulations and policies of wildlife tourism

CHAPTER 2

Feeding from wildlife tourism alters the residency and space-use, but not the activity of a non-focal schooling bentho-pelagic fish

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2.1 Abstract

Many wildlife tourism operations use food-based attractants to aggregate focal species within view of customers. While this can adversely affect the focal species, there is limited understanding of its effects on non-focal species which often also respond to the food-based attractant. At the Neptune Islands Group Marine Park, South Australia, bait and berley are used to entice white sharks (*Carcharodon carcharias*) towards cage-diving vessels, but silver trevally (*Pseudocaranx georgianus*) are also attracted and form large aggregations around these vessels. Silver trevally feed on the bait and berley which affects their diet, but it is unknown whether these effects extend to the movements (i.e., residency and spatiotemporal distribution) and energy budgets. I used a fine-scale acoustic telemetry array (Vemco Positioning System) to monitor the movement and activity of 25 silver trevally in response to white shark tourism. The presence of cage-diving operators increased weekly residency and daily amount of time spent at North Neptune Islands by 32% and 20%, respectively, while also reducing their core space by aggregating silver trevally at the surface (< 5 m depth), close to food-based operators. Despite observations of silver trevally bursting towards tethered baits, changes in activity was minimal. Even though observed behavioural shifts as a result of provisioning were observed, seasonal exodus by 76% of individuals triggered by thermal conditions indicates that silver trevally still undergo natural movements and behaviours. However, the supplemental nutrients from feeding on bait and berley and substantial amount of time spent at the Neptune Islands has the potential to alter the energy budgets of silver trevally. Findings from my study reveal the impacts that wildlife tourism can have on non-focal schooling pelagic fish, supporting the need for wildlife tourism management to account for the whole ecosystem when determining the ecological sustainability of a tourism industry.

2.2 Introduction

Animal movements are instrumental in numerous ecological processes, such as nutrients and energy transfer, predator-prey interactions, and population dynamics, and ultimately drives global productivity within and across ecosystems (Bowler and Benton, 2005, Parsons et al., 2013, Hussey et al., 2015). These movements can occur over a few metres or kilometres in highly resident species (Barnett et al., 2012, Carlisle et al., 2019, Rider et al., 2021), to thousands of kilometres as part of seasonal migrations between hemispheres (Robinson et al., 2010, Bauer and Hoye, 2014). Animals move for various reasons, including habitat suitability (Boyce et al., 2016), foraging needs (Moorcroft and Barnett, 2008, Staniland et al., 2018), predator avoidance (Heupel and Hueter, 2002), or reproductive opportunities (Lassis et al., 2022). Anthropogenic activities can also influence movements (Morales et al., 2010, Corradini et al., 2021, Huveneers et al., 2021), e.g., in response to climate change (Bowler and Benton, 2005, Champion et al., 2018a, Gervais et al., 2021), habitat fragmentation and modification (Marques et al., 2020), introduced species (Tabak et al., 2017), or industries such as wildlife tourism (Trave et al., 2017).

Energy budgets balance energy assimilated through food, with energy lost through metabolic process (growth, repair, reproduction) and activity (Soofiani and Hawkins, 1985). As animals do not have accesses to unlimited resources, energy budgets manage the balance and allocation of the finite available resources to the multitude of physical and physiological processes required by an individual. Given this delicate balance, even minor changes in behaviour (Barry et al., 2023), environmental conditions (Volkoff and Ronnestad, 2020), frequency and quantity of feeding events (Brookhouse et al., 2013, Barnett et al., 2016), competition (Neuenfeldt et al., 2020), and locomotion (Fitzpatrick et al., 2011) inherently impact the energy budget of individuals. For example, a reduction in nectar and flower availability increases the foraging time of broad-billed hummingbirds (*Cynathus latirostris*), resulting in higher energy expenditure (Shankar et al., 2019). With movement and site fidelity inherently linked to energy gain and metabolic rate, changes to movement and behaviour patterns can alter individual's overall health, fitness, and energy budgets (Lusseau, 2004, Williams et al., 2006, Fitzpatrick et al., 2011).

Wildlife tourism is one of the fastest-growing sectors of the tourism industry, with millions of annual participants (Scheyvens, 1999, Wearing and Neil, 2009, Trave et al., 2017) and an estimated value of US$135 billion in 2022, that is predicted to grow to US$219 billion by 2032 (Insight, 2022). However, many tourism operators use olfactory (e.g., food; Meyer et al., 2019), visual and auditory attractants (e.g., decoys and bird calls; Vagabov and Eldarov, 2019), or habitat modifications (e.g., artificial light and reefs; Lima et al., 2019), collectively referred to as provisioning (Meyer et al., 2022) to ensure consistent and predictable up-close encounters for tourists. White shark (*Carcharodon carcharias*) cage-diving is a popular form of wildlife tourism, occurring at five locations globally, including at the Neptune Islands Group Marine Park in South Australia. At the time of my study, three operators ran cage-diving trips at the Neptune Islands, using different stimuli to aggregate white sharks within the field of view of the tourists (Huveneers et al., 2017b, Meyer et al., 2020, Clarke et al., 2022). Two operators used a near-continuous berley plume consisting of minced southern bluefin tuna (*Thunnus maccoyii*, tuna hereafter) and tethered baits (tuna gills and stomachs; Bruce and Bradford, 2013), while a third operator used music played through underwater speakers as an auditory attractant (Huveneers et al., 2018a, Clarke et al., 2022). Intentionally feeding white sharks is prohibited by industry regulations (i.e., bait is retracted before sharks can consume it; DEW, 2016) and the berley particles are too small to be consumed by white sharks. However, several non-focal species consume these berley particles and feed on the bait, including coastal-pelagic fishes (silver trevally *Pseudocaranx georgianus,* yellowtail kingfish *Seriola lalandi*), reef fishes (horseshoe leatherjacket *Meuschenia hippocrepis*, bluethroat wrasse *Notolabrus tetricus,* magpie perch *Pseudogoniistius nigripes*), and rays (southern eagle ray *Myliobatis tenicaudatus*, smooth ray *Bathytoshia brevicaudata*; Meyer et al., 2020). Incidental feeding of non-focal species at the Neptune Islands influence the movements and activity of some of these non-focal species, e.g., increased time spent around the Neptune Islands during cage-diving operations by smooth rays (Rizzari et al., 2017) and yellowtail kingfish (Clarke et al., 2022). Regular exposure to provisioning affects focal and non-focal species, with previous studies documenting changes in habituation (Brookhouse et al., 2013), abundance (Kurita, 2014), behaviour (Hansen et al., 2023), movement and residency (Maljković and Côté, 2011, Sengupta and Radhakrishna, 2018, Senigaglia et al., 2022), diet (Hines, 2011), and energy budgets (Maréchal et al., 2016, Barry et al., 2023). With provisioning from tourism at the Neptune Islands already influencing mobile and large-bodied benthic (smooth ray) and pelagic (yellowtail kingfish) species (Rizzari et al., 2017, Clarke et al., 2022, Clarke et al., 2023), there have been increased concerns that the cage-diving industry might affect other non-focal species (A Fox and A Wright, pers. comm.).

At the Neptune Islands, silver trevally is the most frequently observed non-focal species, forming large schools around the cage-diving vessels and cages, impeding tourists' views of white sharks (Supplementary material 1; J Dennis, unpublished data). Trevally also make quick bursts of acceleration towards fresh tethered baits when they are thrown in the water (Supplementary material 2). While the cage-diving industry has changed the diet of silver trevally (Meyer et al. 2020), it is unknown whether effects from the industry extend beyond diet to the spatiotemporal distribution and behaviour of silver trevally. Furthermore, the potential increase of activity from frequent accelerations towards the bait, combined with the previously documented dietary shift (Meyer et al., 2020), could unbalance the energy budgets of silver trevally with potential flow-on effects for physiological processes (i.e., growth, reproduction, healing).

Here, I used acoustic tracking and a Vemco Positioning System (VPS) array over three consecutive years (2019–2022) to assess the spatiotemporal distribution and behaviour (activity and depth) of tagged silver trevally interacting with white shark cage-diving operations. I aimed to quantify the daily and weekly residency of silver trevally around cage-diving vessels and assess changes in horizontal and vertical distributions in response to white shark tourism. Specifically, I hypothesised that 1) interacting with the cage-diving industry increases the residency and time spent of silver trevally at the Neptune Islands and decreases their space use; 2) silver trevally occur shallower when vessels are present because the food is disbursed on the surface, and 3) activity increases when cage-diving operators are present due to bursts of swimming to feed on the berley and bait.

2.3 Methods

Receiver array

I deployed 15 VR2AR acoustic receivers (Innovasea [formerly known as Vemco], Nova Scotia, Canada, innovasea.com) at the Neptune Islands Group Marine Park (-35° 13' 48", 136° 4' 12") for a continuous 3-year period from August 2019 to August 2022 (serviced every 12 months; Figure 3A). I designed the array to enable fine-scale positioning of tagged individuals through a VPS (Espinoza et al., 2011, Orrell and Hussey, 2022). I tested the detection range of receivers prior to designing and deploying the VPS array, which showed an 80% detection probability at ~300 m, as such, I deployed receivers ~300 m apart to allow simultaneous detections of transmitters integrated within the VR2AR by nearby receivers. In this approach, the internal clock of each receiver was synchronised, allowing the fine-scale position of tagged fish to be calculated using the difference in time-of-arrival of acoustic detections by multiple receivers (Espinoza et al., 2011). Time synchronisation of the array was performed in the Fathom Position software (Innovasea, version 2.0.3). Bathymetry of receiver positioning ranged from 8–46 m, and receivers were deployed on mooring consisting of 16–18 mm anchor chain links (50–100 kg), a rope canister to enable retrieval of anchor chains upon receiver recovery, and a 30 cm diameter sub-surface buoy. Due to a lack of synchronisation between both sides of the Neptune Islands, positional error corrections were performed separately for each side of the Neptune Islands (northern side, southern side; Figure 3A). I used linear regressions constructed between the measured horizontal positional errors of the synchronisation transmitters within each VR2AR receiver (HPEm), with the corresponding values or error sensitivity (HPE), to obtain the equations representative of the fine-scale positional errors for each side of the Neptune Islands. These linear equations were then applied to the silver trevally HPEs values to calculate the HPE for each fine-scale position. Positions had higher accuracy on the southern side (minimum error = 0.74 m) than on the northern side (minimum error = 28.28 m). The difference in accuracy between the two sides is due to differences in the noise (biological and physical) at the Island group. To account for this, all silver trevally positions with HPE errors > 40 m (i.e., < 2.9% of all silver trevally positions) were excluded from the analyses. This filtering process ensures only accurate positions are used, preventing implications and limitations due to positional error or detection efficiency from affecting this study.

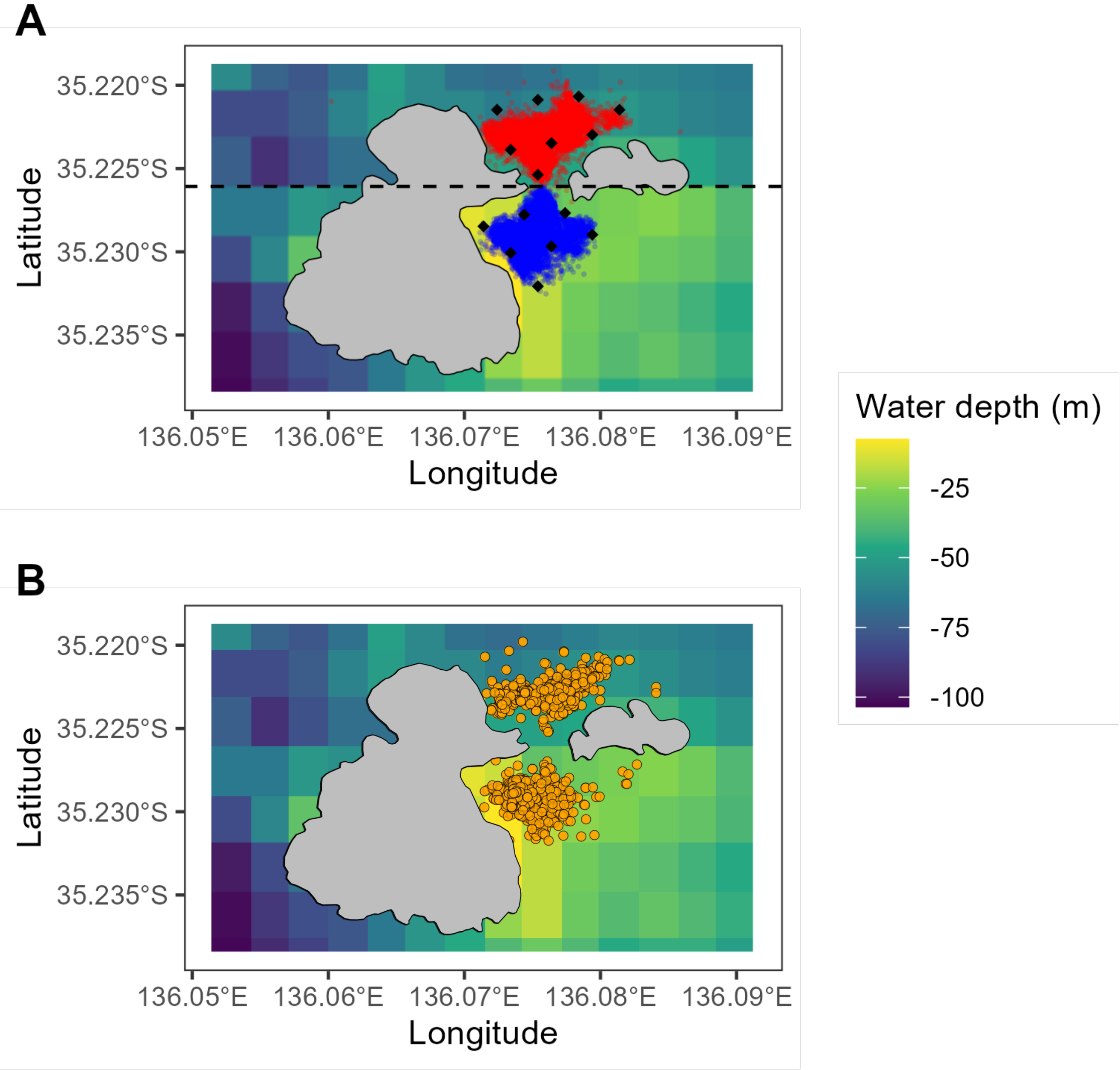

Figure 3. Map of the Neptune Islands Group in South Australia with (**A**) positions of 15 acoustic receivers (black diamonds) and VEMCO Positioning System (VPS) locations from 25 acoustically tagged silver trevally (*Pseudocaranx georgianus*) for the northern side (red circles), and southern side (blue circles), dashed line indicates northern and southern boundary; (**B**) positions of all white shark cage-diving operations for the duration of the study (orange circles).

Acoustic tagging

I surgically implanted acoustic transmitters (V9AP, Innovasea, Nova Scotia, Canada) into the peritoneal cavity of 25 silver trevally (15 in October 2019 [397 days battery life]; 10 in January 2021 [564 days battery life]; increase in battery life was due to new circuit board design using the same programming). I caught silver trevally via hook and line and anaesthetised using AQUI-S Aquatic Anaesthetic (15 mg/L, AQUI-S, New Zealand). I made a 20–30 mm incision on the ventral side of the peritoneal cavity, inserted the transmitter, and closed the incision using 2–3 absorbable running sutures (Monosyn 2-0/3-0, B. Braun). I implanted a conventional external tag into the dorsal musculature to identify acoustically tagged fish if recaptured. After tagging, I placed silver trevally in a recovery tank for 10–20 minutes before release. Acoustic tags were equipped with acceleration and pressure sensors (Supplementary material 3).

Data analysis

I recorded the daily positions of white shark cage-diving vessels and the duration of their operations through an industry-designed 'cage-diving mobile application (Figure 3B; Nazimi et al., 2018). The recorded data included anchoring location (latitude and longitude), time bait and berleying or sound attraction commenced and ceased, and operator type (food-based or sound-based attractant). Due to the irregular schedules of the operators, each day can have differing combinations of operator presence. Thus, I categorised each day into one of six *operator types*: no operators, all operators, one food-based, two food-based, sound-based only, or one food-based + sound-based. Additionally, I calculated operating days as the number of days at least one operator was present (i.e., one day for 1–3 operators present) within that week (i.e., 0–7 *operating days*) based on iso-week (Monday to Sunday) using the 'isoweek()' function from the `lubridate` package (version 1.9.0; Spinu et al., 2018) in R (R Core Team 2016). Finally, I categorised each day according to whether operators were present or absent (*operator presence*: operator days, non-operator days).

I conducted all analyses in the R statistical environment (version 4.2.1; R Core Team 2016) using the `VTrack` package (version 2.1.0; Campbell et al., 2012) with the Animal Tracking Toolbox extension (Udyawer et al., 2018). I investigated the responses of silver trevally to cage-diving operations using the following response variables: time spent in the array, weekly residency, distance between silver trevally and operators, volume of space use, depth, and activity. I estimated the amount of time spent (minutes) in the array (*daily residency*) for each individual by calculating the time between the first and last detections for each day detected. I calculated weekly residency as the proportion of days detected within an iso-week using the 'detectionSummary' function in `VTrack`. I investigated the volume of space used (m^3) by silver trevally at the Neptune Islands by calculating monthly three-dimensional kernel utilisation distribution core space (50%-3DKUD) and extent of space (95%-3DKUD) and estimating the overlap of space use (50%-3DKUD and 95%-3DKUD) between operator days and non-operator days (percentage overlap, i.e., more overlap = similar areas of space-use). Approximate positions of silver trevally within the Neptune Islands array were estimated through 60-min centres of activity (COAs; Simpfendorfer et al., 2002) using the 'COA' function in `VTrack` which were then used with the ‘vol3d()’ function in `KUD3D` (version 0.1.0; Udyawer et al., 2018), and code adapted from Simpfendorfer et al. (2012) and Cooper et al. (2014) to calculate monthly 3DKUDs and overlap.

For each silver trevally position estimated via the VPS, I calculated the *distance* in meters between silver trevally and the closest cage-diving operators using the 'distHarversine' function in `geosphere` (Hijmans et al., 2017). Distance between silver trevally and operators could not be calculated on non-operator days. I instead estimated dummy operator positions based on the normal distribution of the monthly mean latitude and longitude of existent operator positions, with a standard deviation of 0.0015 degrees (150 m; based on mean variation in anchorage positions)to add random variation to the dummy positions. I assigned *depth* to VPS position estimates with an activity value based on the closest detections with a pressure sensor value occurring within twenty minutes of the VPS position estimate.

Statistical models

I used Generalised Additive Mixed Models (GAMMs) to test the effects of white shark cage-diving on all response variables (Table 1). All GAMMs were created using the 'gam' function in the `mgcv` package (version 1.8-40; Wood and Wood, 2015). I included individual fish (*tagID*) and week since start of the study as a random effect in all models to account for the lack of independence within individuals and temporal autocorrelation, respectively. Prior to modelling, I examined temperature and month data for correlation using the ‘cor.test’ function in the `mgcv` package. These variables were highly correlated ($p \geq 0.05$; $r > 0.6$). I therefore excluded temperature from subsequent models and kept *month* as a cyclic variable. I selected the most appropriate statistical family and transformation through visual inspection of model residuals and distribution of the response variable. I selected the most parsimonious model using the Akaike Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson, 2004), using the 'dredge' function in the `MuMIn` package (version 1.46.0; Barton, 2019). I assess model likelihood using the bias-corrected relative weight of evidence for each model, AIC_c weight, where the smaller the weight, the lower the probability the model was `true’ (Burnham and Anderson, 2004). I used the contributions of the fixed effects (marginal $R^2$) and the fixed and random effects (conditional $R^2$) using the ‘r.sqauredGLMM’ function in package `MuMIn` (version 1.46.0; Barton, 2019) to explain the variance of the response variable when added to the model (Nakagawa and Schielzeth, 2013).

I used 8 GAMMs to assess the effects of cage-diving on silver trevally and test if residency, space use (horizontal and vertical), and behaviour were affected by cage-diving tourism (Table 1 & Table 2). I first tested whether the number and type of operators (i.e., *operator type*), and the intensity of cage-diving (i.e., *operating days*) affected how much time silver trevally spent at the Neptune Islands daily and weekly. This analysis revealed that silver trevally were not affected by the sound-based operator (see Results), which was further supported by *in-situ* observations where silver trevally were not seen around the sound-based operator. As a result, days when the sound-based operator was the only vessel present were combined with days when all operators were absent (no operator day; revised *operator type:* no operators, one food-based, two food-based) for all further analysis. Distance from operator values were square-root transformed prior to analysis. I then investigated silver trevally space use by assessing whether 3D space use (core 50%-3DKUD and extent 95%-3DKUD; m^3) was affected by *operator presence* (Table 2). Volumetric space values (50% and 95%) were square-root transformed prior to analysis. Additionally, *t* tests ($\alpha = 0.05$) were conducted to examine whether the mean proportion of overlap between operator days and non-operator days, for both 50%-3DKUD and 95%-3DKUD, varied from that expected if there were no pattern in proportions of overlap (i.e., mean proportion = 0.5; Udyawer et al., 2015). Proportional overlap values were arcsine-transformed prior to analysis.

I then assessed the effects of cage-diving on silver trevally depth (meters, m), testing if depth was affected by the *operator type*, *distance* between silver trevally and operator, and *hour* (Table 2). Depth values were square-root transformed prior to analysis. Finally, I investigated if silver trevally behaviour, i.e., activity, was affected by cage-diving operators. I tested whether activity was influenced by the number and *operator type*, *depth*, *distance* between silver trevally and operators, and *Hour* (Table 2). Activity values were log-transformed prior to analysis. My final GAMM assessed changes in silver trevally activity following the cessation of operations by examining activity across consecutive non-operator days (Table 2). Days when operators were present were assigned as day zero, with each consecutive non-operator day adding to the zero baseline before resetting to zero on the next operator day. Activity values were square-root transformed prior to analysis.

Table 1. Factors included in Generalised Additive Mixed Models (GAMMs) testing the effects of white shark cage-diving on the spatiotemporal distribution and behaviour of silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group, South Australia.

Factor	Factor type	Description
Time spent	Response variable	Time (minutes) between the first and last detections for each tagged individual for each day detected
Distance	Response variable/ Fixed effect	Distance (m) between silver trevally and the closest cage-diving operators
Weekly residency	Response variable	Detection index as a proportion of days detected within an iso-week. Value ranges from 0 to 1. 0 = not detected; 1 = detected every day
50%-3DKUD	Response variable	50% contour of three-dimensional kernel utilisation distributions (core space; m^3)
95%-3DKUD	Response variable	95% contour of three-dimensional kernel utilisation distributions (extent of space; m^3)
Depth	Response variable/ Fixed effect	Depth (m) of tagged fish from acoustic tag pressure sensor
Activity	Response variable	Activity (m/s^2) from acoustic tag three-dimensional acceleration sensors
Operator type	Fixed effect	Combination of operator types: no operators, all operators, one food-based, two food-based, acoustic only, one food-based + acoustic (used in time spent and weekly residency GAMMs)
Revised Operator type	Fixed effect	Combination of operator types: no operators, one food-based, two food-based (used in all analysis except time spent and weekly residency)
Operator presence	Fixed effect	Operator presence or absence at the Neptune Islands Group. Any operator present = Operator day, all operators absent = Non-operator day
Month	Cyclic	Month of the year (January – December)
TagID	Random effect	Individual tag ID for acoustically tagged silver trevally. The factor was included to account for the lack of independence within individuals
Week number	Random effect	Week number since start of the study. The factor was included to account for temporal autocorrelation
Month number	Random effect	Month number since start of the study. The factor was included to account for temporal autocorrelation
Operating days	Fixed effect	Number of operating days within a week. Value ranges from 0 to 7. 0 = all operators absent the whole week; 7 = at least one operator present every day of the week
Hour	Cyclic	Hour of the day the tagged individual was detected
Days since operator	Fixed effect	Number of consecutive non-operators days

Table 2. List of Generalised Additive Mixed Models (GAMMs) testing the effects of white shark cage-diving on the spatiotemporal distribution and behaviour of silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group, South Australia.

Response variable	Full model
Time spent	Operator type + $\text{Month}_{\text{cyclic}}$ + Tag ID_{rand} + Week $\text{number}_{\text{rand}}$
Weekly residency	Operating days + $\text{Month}_{\text{cyclic}}$ + Tag ID_{rand} + Week $\text{number}_{\text{rand}}$
Distance	Operator type*Hour + $\text{Month}_{\text{cyclic}}$ + Tag ID_{rand} + Week $\text{number}_{\text{rand}}$
50%-3DKUD	Operator presence + $\text{Month}_{\text{cyclic}}$ + Tag ID_{rand} + Month $\text{number}_{\text{rand}}$
95%-3DKUD	Operator presence + $\text{Month}_{\text{cyclic}}$ + Tag ID_{rand} + Month $\text{number}_{\text{rand}}$
Depth	Operator type*Distance + $\text{Hour}_{\text{cyclic}}$ + $\text{Month}_{\text{cyclic}}$ + Tag ID_{rand} + Week $\text{number}_{\text{rand}}$
Activity	Operator type*Distance + Operator type*Hour + Depth + $\text{Month}_{\text{cyclic}}$ + Tag ID_{rand} + Week $\text{number}_{\text{rand}}$
Activity	Days since operator + Tag ID_{rand} + Week $\text{number}_{\text{rand}}$

2.4 Results

I recorded the movements of 25 silver trevally at the Neptune Islands between November 2019 and August 2022 (978 days; Figure 4 & Figure 5). Trevally were detected across all 15 receivers deployed, from which I collected 542,014 detections (mean per silver trevally ± standard error: 21,680 ± 16,379). Individuals used both sides of the islands, with more detections recorded on the southern receivers (320,367; 60%) compared to the northern receivers (221,648; 40%). Mean residency over the 3-year period was 0.8 ± 0.01 SE (range: 0.17–1; proportion). Residency was lowest in winter (July 0.47 ± 0.04 and August 0.49 ± 0.08) and highest in summer (February 0.97 ± 0.01). From the detections, I estimated 25,070 VPS positions (1,003 ± 150 positions per silver trevally) and 70,985 COA positions (2,839 ± 410 positions per silver trevally). Estimated VPS and COA positions from both sides of the island were combined for all subsequent analysis. Cage-diving operators were present at the Neptune Islands on 657 of the 978 days of the study (67%), most commonly present for 5 (43 weeks) and 6 (43 weeks) days within a week, representing 58% of the study period (Figure 5 & Figure 6). Operating days were highest in summer (January 6.08 ± 0.14) and lowest in winter (August 2.36 ± 0.33; Figure 5 & Figure 6).

Time spent (daily residency)

The mean number of detections day^{-1} was 84 ± 4, with a mean time spent day^{-1} of 565 minutes ± 16. The top-ranked model ($w\text{AIC}_c = 0.5$; $R_c = 0.28$) included *operator type* and *month* (Table 3; Supplementary table 1) with *month* having the greatest influence on the time silver trevally spent within the array at the Neptune Islands (20.2%; Figure 6). The second-best model also had an $w\text{AIC}_c$ of 0.5 and included the same factors and *week*, but the variance explained was not improved. Time spent within the array each day was highest in January–March (summer and autumn; predicted time spent = 515 – 598 minutes), after which it decreased to the lowest residency in August (winter; 229 minutes). Time that silver trevally spent at the Neptune Islands array increased again in September–October (spring; 289 – 459 minutes predicted, Figure 6). *Operator type* also influenced daily time spent but had a smaller effect than *month* (3.6 vs. 20.2%; Table 3; Supplementary table 1; Figure 7). Time spent was highest when at least one food-based operator was present (~500 minutes predicted) compared to days when no operators or when only the sound-based operator was present (~415 minutes predicted, Figure 7). The random variable (*tagID*) also influenced the daily time spent by silver trevally in the Neptune Islands array, accounting for 4.4% of the model variation (Supplementary table 1).

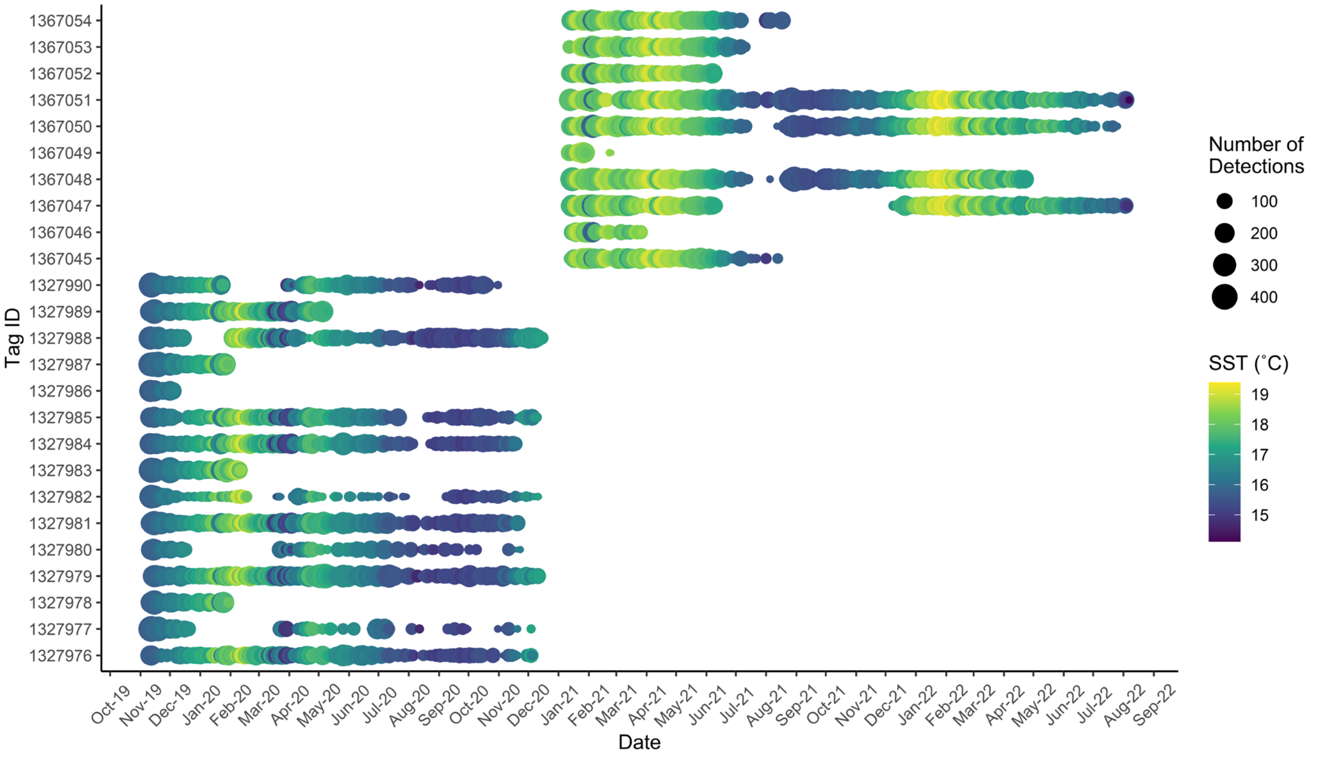

Figure 4. Abacus plot for 25 silver trevally (*Pseudocaranx georgianus;* 15 tagged in October 2019, 397 days battery life; 10 in January 2021, 564 days battery life) from the Neptune Islands, South Australia between November 2019 and August 2022. Size of point shows number of detections; Colour of point indicates sea surface temperature.

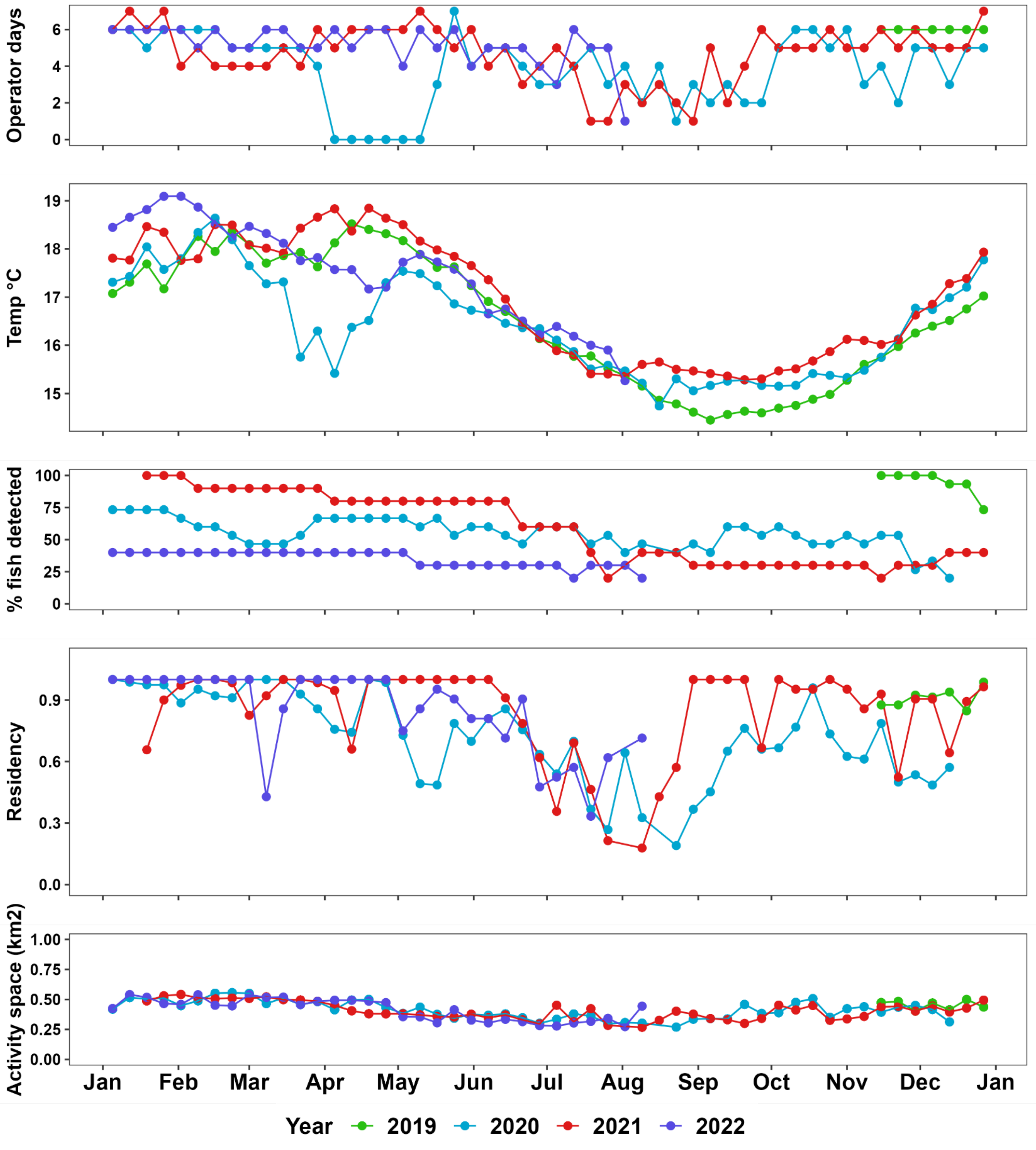

Figure 5. Weekly summary plot for silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group and for white shark cage-diving operators. Temperature was recorded and averaged across array of 15 acoustic receivers. Percentage of fish detected reflects proportion of tagged individuals at liberty. Residency indicates weekly detection index and activity space indicates 50% Brownian Bridges KUDs.

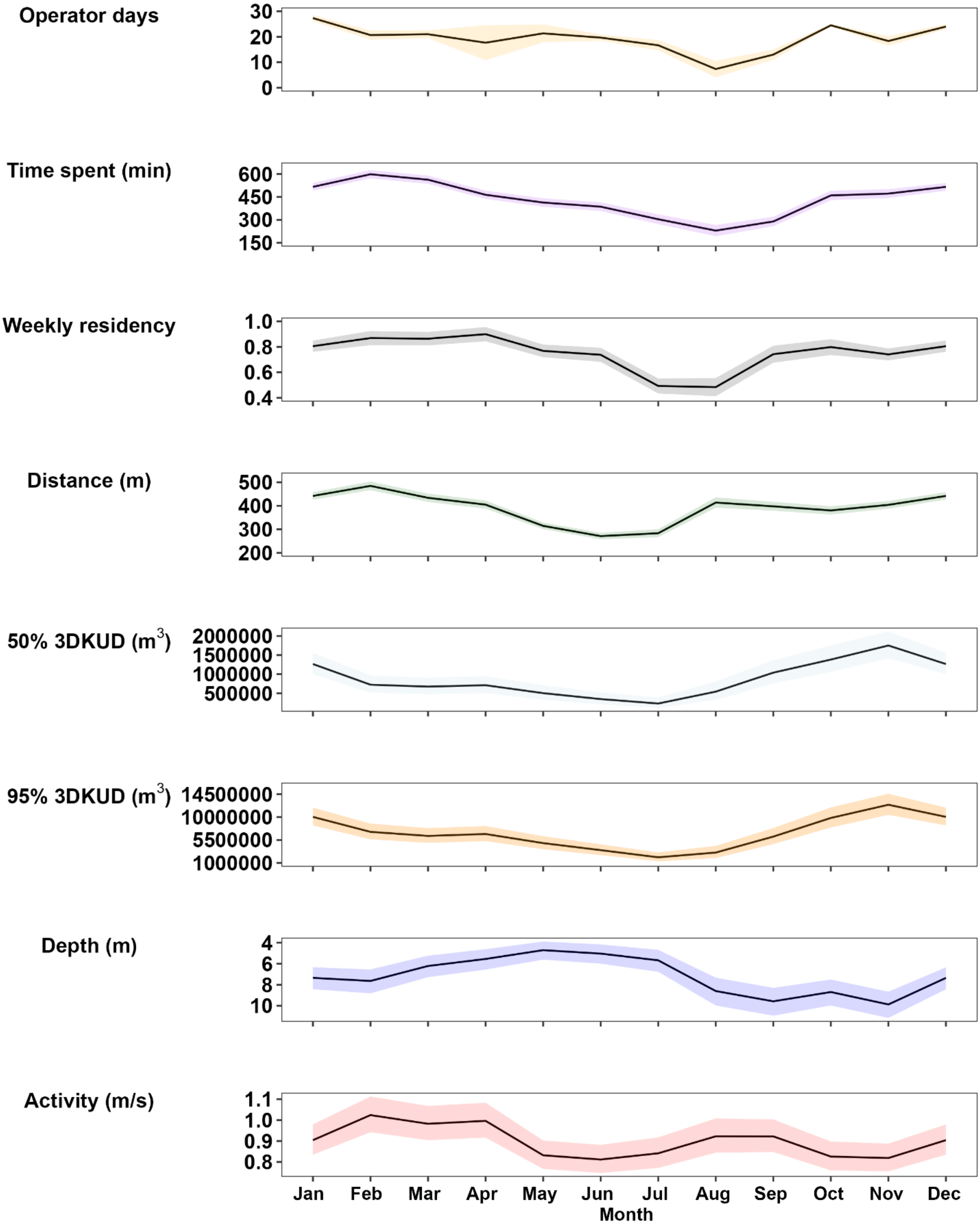

Figure 6. Number operator days by white shark cage-diving operators and predicted time spent (minutes), weekly residency (detection index), distance (m), depth (m), activity (m/s; separate models) of silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands for factor month. Shaded ribbons indicate 95% confidence intervals.

Table 3. Summary of models testing the effects of white shark cage-diving on the spatiotemporal distribution and behaviour of silver trevally (*Pseudocaranx georgianus*). df, degrees of freedom; AIC$_c$, Akaike's information criterion corrected for small sample size; LL, log-likelihood; ΔAIC$_c$, difference in AIC$_c$ between the current and the top-ranked model; *w*AIC$_c$, model probability; variance explained by R$_m$, marginal (fixed effects) R^2; R$_c$, conditional (fixed and random effects) R^2. Top-ranked model indicated in **bold**. Only the top 4 ranked models are presented for table clarity.

Model	df	AIC$_c$	ΔAIC$_c$	*w*AIC$_c$	LL	R$_m$	R$_c$
a) Time spent							
~ Operator type + Month$_{cyclic}$ + 1|TagID	**38**	**72684.65**	**0.00**	**0.50**	**-36303.33**	**0.04**	**0.28**
~ Operator type + Month$_{cyclic}$ + 1|TagID + 1|Week number	38	72684.67	0.02	0.50	-36303.33	0.04	0.28
~ Month$_{cyclic}$ + 1|TagID	33	72939.40	254.75	0.00	-36435.62	0.00	0.25
~ Month$_{cyclic}$ + 1|TagID + 1|Week number	33	72939.42	254.77	0.00	-36435.62	0.00	0.25
b) Weekly Residency (Detection index)							
~ Operating days + Month$_{cyclic}$ + 1|TagID + 1|Week number	**14**	**-108.99**	**0.00**	**1.00**	**68.91**	**0.03**	**0.32**
~ Operating days + Month$_{cyclic}$ + 1|TagID	13	-91.30	17.69	0.00	59.05	0.03	0.32
~ Operating days + Month$_{cyclic}$	12	-86.30	22.69	0.00	55.40	0.01	0.30
~ Operating days + Month$_{cyclic}$ + 1|Week number	12	-86.30	22.69	0.00	55.40	0.01	0.30
c) Distance to operators							
~ Operator type + Hour + (Hour*Type) + Month$_{cyclic}$ + 1|TagID + 1|Week number	**77**	**175544.80**	**0.00**	**1.00**	**-87694.42**	**0.12**	**0.18**
~ Operator type + Hour + (Hour*Type) + Month$_{cyclic}$ + 1|TagID	77	175563.80	19.01	0.00	-87704.43	0.12	0.18
~ Operator type + Hour + (Hour*Type) + Month$_{cyclic}$ + 1|Week number	56	175759.60	214.79	0.00	-87822.84	0.11	0.17
~ Operator type + Hour + (Hour*Type) + Month$_{cyclic}$	55	175785.50	240.77	0.00	-87836.91	0.11	0.17
d) Core space use (3DKUD-50 volume)							
~ Operator presence + Month$_{cyclic}$ + 1|ID + 1|Month number	**26**	**5559.83**	**0.00**	**0.62**	**-2751.50**	**0.11**	**0.47**
~ Operator presence + Month$_{cyclic}$ + 1|TagID	24	5560.82	0.99	0.38	-2754.04	0.11	0.47
~ Operator presence + Month$_{cyclic}$	10	5574.15	14.31	0.00	-2776.24	0.11	0.43
~ Operator presence + Month$_{cyclic}$ + 1|Month number	10	5574.16	14.32	0.00	-2776.24	0.11	0.43
e) Extent of space use (3DKUD-95 volume)							
~ Operator presence + Month$_{cyclic}$ + 1|TagID + 1|Month number	**29**	**6120.83**	**0.00**	**0.92**	**-3028.81**	**0.09**	**0.54**
~ Operator presence + Month$_{cyclic}$ + 1|TagID	28	6125.78	4.95	0.08	-3032.52	0.09	0.53
~ Operator presence + Month$_{cyclic}$	10	6165.09	44.25	0.00	-3071.99	0.09	0.47
~ Operator presence + Month$_{cyclic}$ + 1|Month number	10	6165.09	44.26	0.00	-3071.99	0.09	0.47
f) Depth							
~ Distance + Operator type + (Distance*Type) + Hour$_{cyclic}$ + Month$_{cyclic}$ + 1|TagID + 1|Weeknumber	**48**	**22055.24**	**0.00**	**1.00**	**-10978.79**	**0.03**	**0.31**
~ Distance + Operator type + (Distance*Type) + Hour$_{cyclic}$ + Month$_{cyclic}$ + 1|TagID	47	22071.23	15.99	0.00	-10987.95	0.03	0.31
~ Distance + Operator type + (Distance*Type) + Month$_{cyclic}$ + 1|TagID + 1|Weeknumber	41	22079.05	23.81	0.00	-10998.17	0.02	0.30
~ Distance + Operator type + (Distance*Type) + Month$_{cyclic}$ + 1|TagID	40	22091.95	36.72	0.00	-11005.75	0.02	0.30
g) Activity							
~ Depth + Distance + Hour + Month$_{cyclic}$ + Operator type + (Distance*Type) + (Hour*Type) + 1|TagID + 1|Weeknumber	**82**	**29494.64**	**0.00**	**0.95**	**-14663.98**	**0.06**	**0.17**
~ Depth + Distance + Hour + Month$_{cyclic}$ + Operator type + (Distance*Type) + (Hour*Type) + 1|TagID	82	29500.57	5.93	0.05	-14667.74	0.06	0.17
~ Depth + Distance + Hour + Month$_{cyclic}$ + Operator type + (Distance*Type) + 1|TagID + 1|Weeknumber	54	29527.83	33.19	0.00	-14708.76	0.05	0.17
~ Depth + Distance + Hour + Month$_{cyclic}$ + Operator type + (Distance*Type) + 1|TagID	54	29532.47	37.83	0.00	-14711.89	0.05	0.17
h) Days since last operator (Activity)							
~ Days since operator + 1|TagID	**44**	**33243.23**	**0.00**	**0.50**	**-16576.76**	**0.01**	**0.06**
~ Days since operator + 1|TagID + 1|Week number	44	33243.25	0.02	0.50	-16576.75	0.01	0.06
~ 1|TagID + 1|Week number	26	34139.53	896.30	0.00	-17042.79	0.00	0.05
~ 1|TagID	25	34144.51	901.28	0.00	-17046.42	0.00	0.05

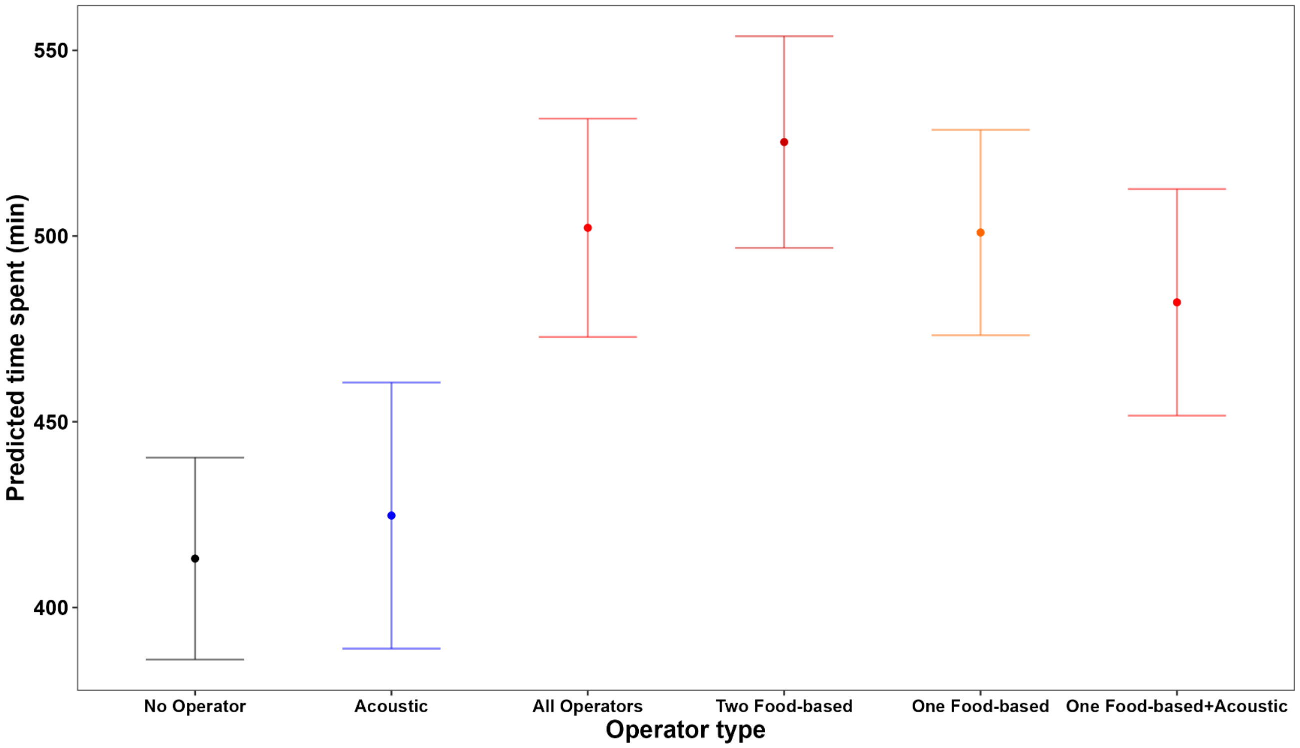

Figure 7. Predicted daily time spent (estimated marginal means from Generalised Additive Mixed Model) for silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands by operator type. Error bars indicate 95% confidence intervals.

Weekly residency

Mean weekly residency at the Neptune Islands was 0.81 ± 0.02 (measured values). The top-ranked model ($w\text{AIC}_c = 1$) included *month* and *operating days* within a week (Table 3; Supplementary table 1). *Month* had the greatest influence on the weekly residency of silver trevally within the array at the Neptune Islands (25.5% model variance explained; Table 3; Supplementary table 1; Figure 6). Weekly residency was highest in summer and autumn (January–April; predicted weekly residency = 0.8 – 0.9) and September–December (spring and summer; 0.75 – 0.85), decreasing in winter (July–August; ~0.5 predicted; Figure 6). *Operating days* also influenced silver trevally weekly residency but had a smaller effect than *month* (2.5% vs 25.5%; Table 3; Supplementary table 1; Figure 8). *Operating days* had a positive relationship with weekly residency, showing a consistent increase in weekly residency as the number of operator days increased (from 0.62 with 0 days of operators, to 0.82 with 7 days, Figure 8). Individual variation also influenced the weekly residency of silver trevally at the Neptune islands, with *tagID* explaining 2.9% of the model variation (Supplementary table 1).

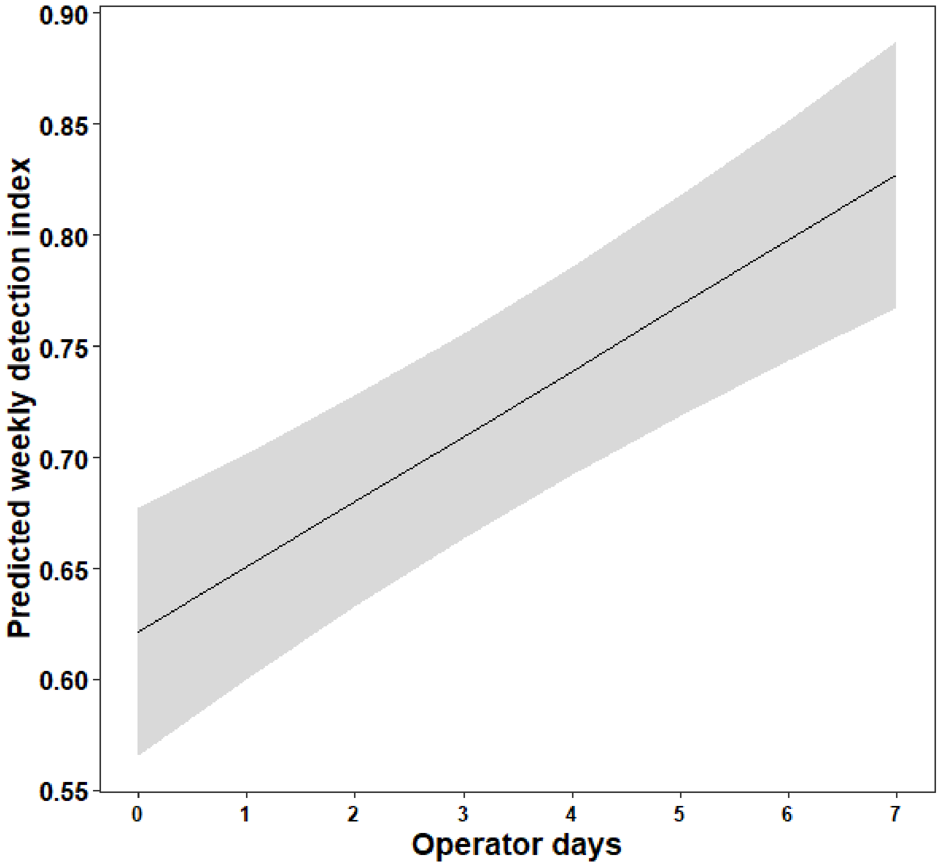

Figure 8. Predicted weekly residency (detection index) from Generalised Additive Mixed Models for silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group for the number of operator days within a week. Shaded ribbon indicates 95% confidence intervals.

Distance (All days; VPS)

The mean distance between silver trevally and food-based operators was 371 m ± 7 and was influenced by *month* and the interaction between *operator type* and *hour* ($w\text{AIC}_c$ = 1, Table 3; Supplementary table 1). The interaction between *operator type* and *hour* had the largest effect (i.e., 12.8% of model variance). The dummy distance when vessels were absent was consistent throughout the day around ~300 m and higher than the distance between silver trevally and vessels on days when operators were present. In contrast, distance when operators were present was more variable with small variations throughout the day (<200 m) and a rapid increase up to ~500 m after 17:00 (Figure 9). *Month* also influenced distance to the vessels but had a smaller effect than the *operator type* and *hour* interaction (5.3% vs 12.8%; Table 3; Figure 6; Supplementary table 1). Trevally were furthest from the operators in summer and autumn (December–March; ~475 m), after which it decreased to the closest distance in winter (June–July; ~275 m), prior to increasing again in winter and spring (August–October; ~400 m; Figure 6) Random model effects also influenced the distance of silver trevally to the operators, though the effect was small with *tagID* explaining <1% of the model variation.

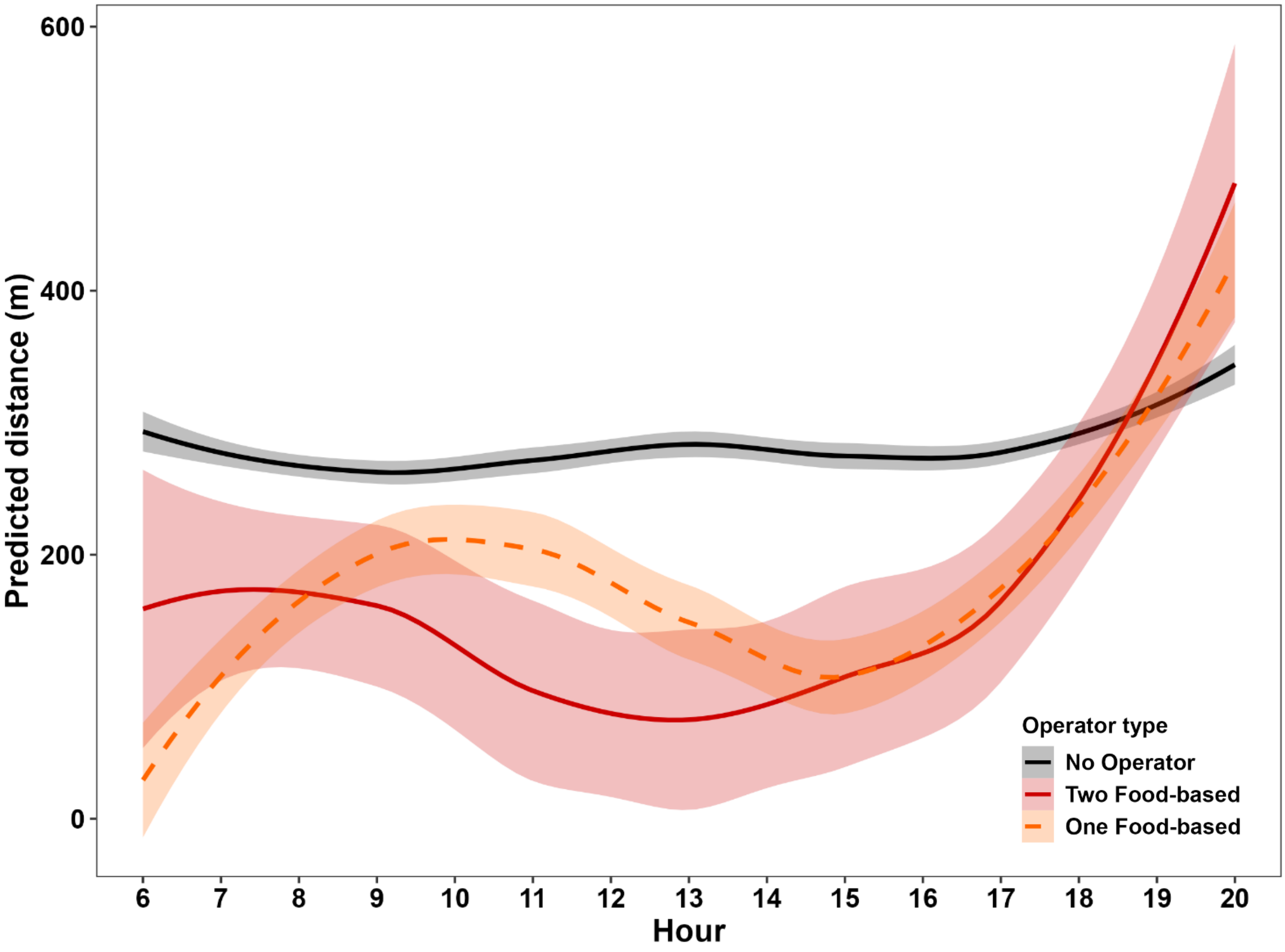

Figure 9. Predicted distance to nearest operator vessel (m) from Generalised Additive Mixed Models for silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group for the interaction between hour and operator type. Shaded ribbons indicate 95% confidence intervals.

3D-KUD

The mean volumetric space use was 1,163,686 m^3 ± 68,904 (3DKUD-50, core) and 8,191,458 m^3 ± 391,807 (3DKUD-95, extent; measured values), with both influenced by *month* and *operator presence* ($w\mathrm{AIC}_c = 0.62$ and 0.92 for 3DKUD-50 and 3DKUD-95, respectively; Table 3; Supplementary table 1). *Month* had the greatest influence on the volumetric space use of silver trevally (34.3% and 38.8% for 3DKUD-50 and 3DKUD-95, respectively; Supplementary table 1; Figure 6). Volumetric space use was highest in spring and summer (November–December), after which it decreased to the lowest volume in winter (June–August; Figure 6). *Operator presence* also influenced space use but had a smaller effect than *month* (11% vs 45% for 3DKUD-50 and 9% vs 48% for 3DKUD-95; Supplementary table 1; Figure 10A, B). For both 3DKUD-50 and 3DKUD-95, silver trevally occupied more space on non-operator days than operator days (Figure 10A, B). Random model effects also influenced the space use of silver trevally, with *tagID* explaining 2.2% and 3.9% of the model variation for 3DKUD-50 and 3DKUD-95, respectively (Supplementary table 1).

The core area, i.e., 3DKUD-50, used by silver trevally on operator days versus non-operator days overlapped by ~30% (Figure 10C) and was significantly different to a random pattern (t-test, $t_1 = -7.32$, $p < 0.001$), indicating that silver trevally use different core areas on operator days and non-operator days. In contrast, extent, i.e., 3DKUD-95, of area used by silver trevally on operator days versus non-operator days overlapped extensively (~70%; Figure 10C) and was significantly different to a random pattern (t-test, $t_1 = 13.69$, $p < 0.001$), indicating that silver trevally have a similar extent on operator days and non-operator days.

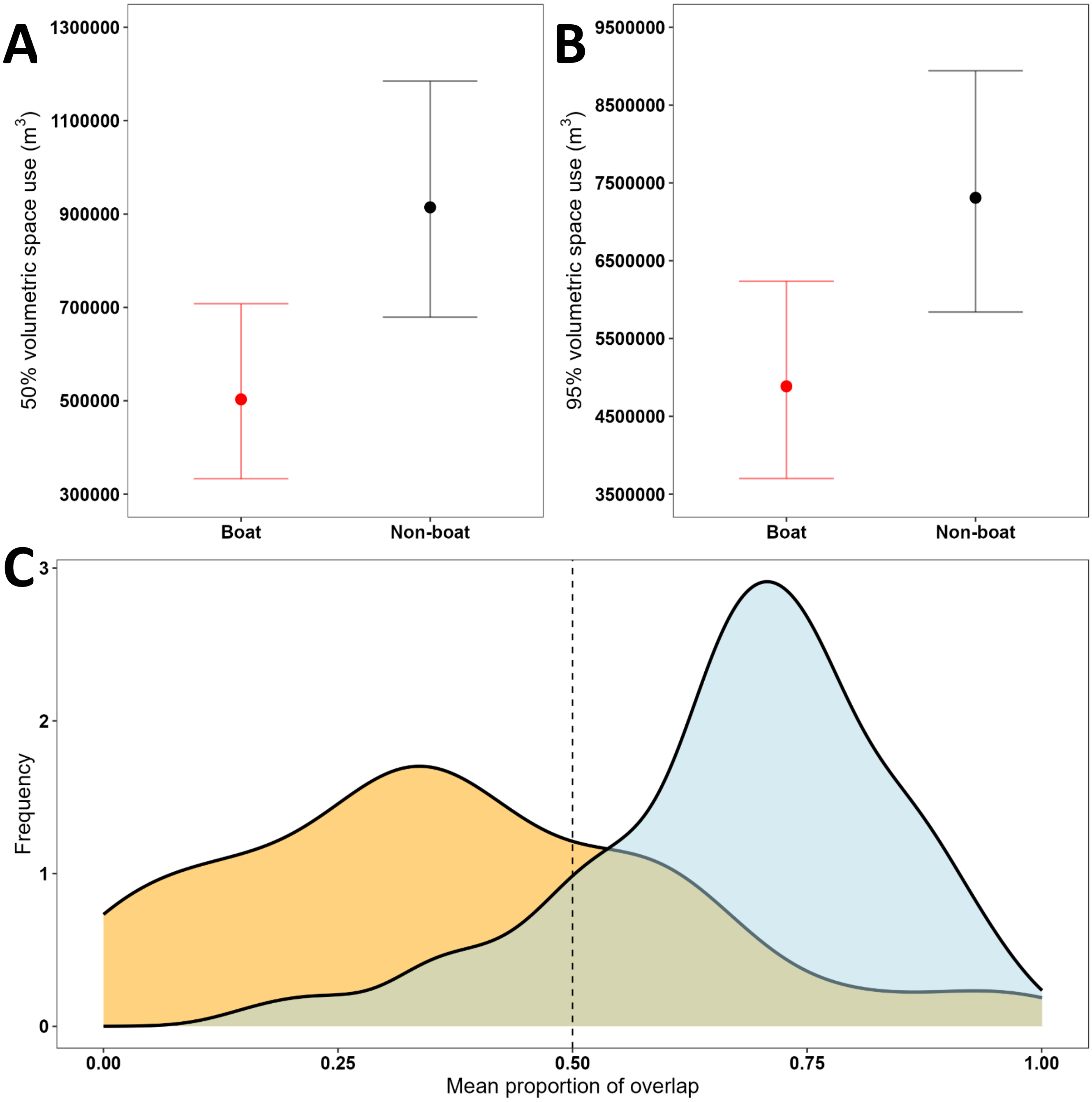

Figure 10. Differences in the use of **A**. 50% and **B**. 95% volumetric space on boat days and non-boat days by silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group. Error bars indicate 95% confidence intervals. **C.** Mean overlap between boat days and non-boat days for 50% (orange) and 95% (light blue) volumetric space.

Depth (All days; VPS)

Mean silver trevally depth at the Neptune Islands was 7.8 m ± 0.6 m (measured values). The top-ranked model ($w\mathrm{AIC}_c = 1$) included *month*, *hour*, and an interaction between *operator type* and *distance* (Table 3; Supplementary table 1). *Month* had the greatest influence on the depth of silver trevally within the array at the Neptune Islands (5.5%; Table 3; Supplementary table 1; Figure 6). Trevally were closest to the surface in autumn – winter (March–July; <5 m), after which they resided deeper in winter–spring (~10 m; August–November), prior to residing close to the surface again in summer (December; Figure 6). The interaction between *distance* and *operator type* also had an influence on depth but had a smaller effect than month (2.9% vs 5.5%; Table 3; Supplementary table 1; Figure 11). Trevally were closer to the surface when food-based operators were present (i.e., < 5 m) than on non-operator days within 300 m of the operators. Depth gradually increased to below that of no operator days as distance increased, but silver trevally remained in the upper 10 m of the water column (Figure 11). Days without operators showed a consistent depth of ~5 m irrespective of distance (Figure 11). *Hour* also influenced depth that silver trevally but had a small effect (0.2% of variance explained; Supplementary table 1). Random model effects also influenced the depth of silver trevally, with *tagID* explaining 28% of the model variation.

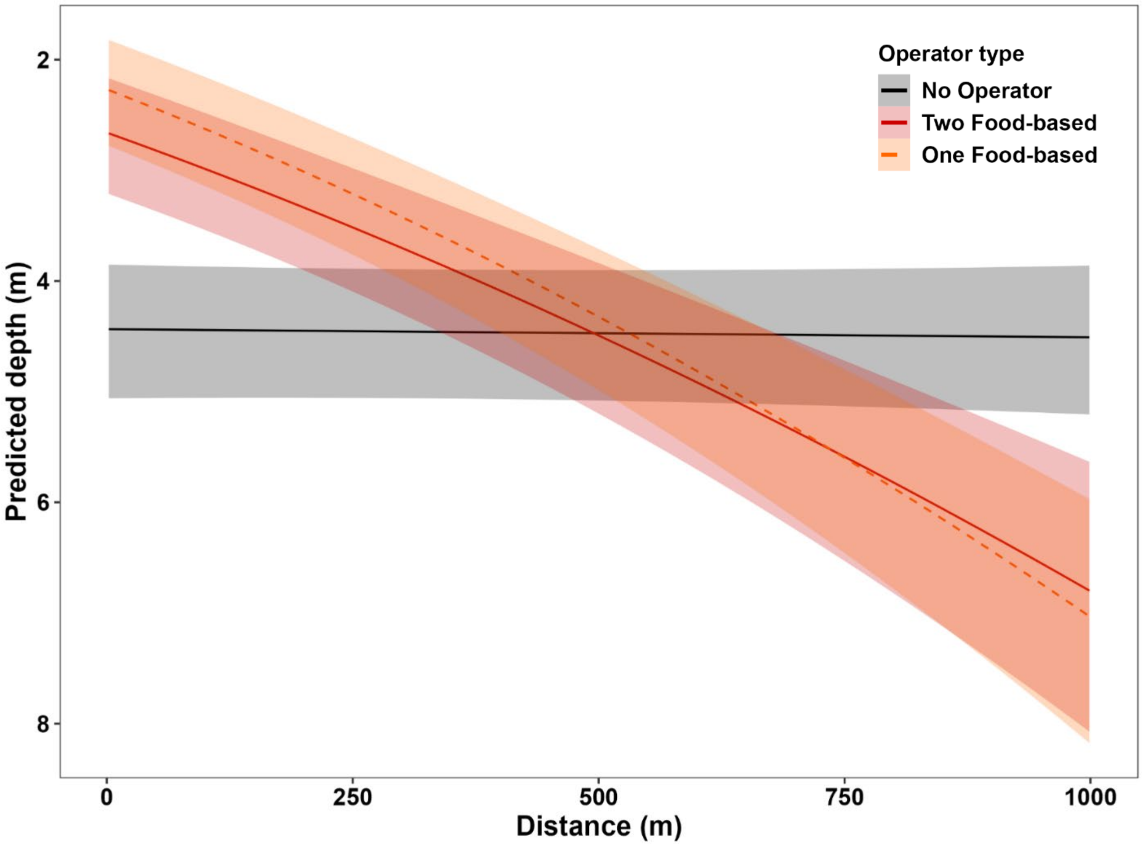

Figure 11. Predicted depth (m) from Generalised Additive Mixed Models for silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group for the interaction between distance and operator type. Shaded ribbons indicate 95% confidence intervals.

Activity (All days; VPS)

Mean activity was 1.2 ms^{-1} ± 0.05 (measured values), with the top-ranked model (wAIC$_c$ = 0.96) including *depth*, *month*, the interactions between *distance* and *operator type*, and between *hour* and *operator type* (Table 3; Supplementary table 1). *Depth* had the greatest influence on silver trevally activity (8.4% model variation explained; Table 3; Figure 12A; Supplementary table 1), with activity lowest when silver trevally were closer to the surface, and increased with depth (0.7 ms^{-1} at 0 m vs. 1.37 ms^{-1} at 38 m depth, Figure 12A). *Month* also influenced silver trevally activity, but had a smaller effect than *depth* (3.4% vs 8.4% respectively; Table 3; Figure 6; Supplementary table 1). Activity was highest in summer – autumn (January–April; 0.99 – 1.02 ms^{-1} predicted), after which it decreased to two low activity periods in autumn–winter (May–July; 0.81 – 0.84 ms^{-1} predicted) and spring (October–November; ~0.82 ms^{-1} predicted), with a small increase in activity in winter and spring (August and September; ~0.92 ms^{-1} predicted, Figure 6). The interaction between *hour* and *operator type* explained 1.6% of the model variation. Activity was higher from ~9:00 to ~16:00 across all operator types, and highest when one or two food-based operators were present with a higher peak of activity of up to 1.14 ms^{-1} (Figure 12B). The interaction between *distance* and *operator type* also influenced silver trevally activity, but had a smaller effect than the interaction between *hour* and *operator type* (0.86% vs 1.6%; Table 3; Supplementary table 1; Figure 12C). On days when food-based operators were present, silver trevally activity was highest close to the operators (~0.82 ms^{-1} at 0 m from vessels compared to ~0.6 ms^{-1} at 1,000 m), with activity slightly higher when two food-based operators were present compared to days when only one operator was present. In contrast, activity slightly increased with distance when operators were absent (0.79 ms^{-1} at 0 m from dummy vessel positions to 0.85 ms^{-1} at 1,000 m, Figure 12C). Random model effects also influenced the activity of silver trevally, with *tagID* explaining 9% of the model variation.

Days since last boat day

The number of consecutive non-operator days following a day of operation ranged from 1 to a period of 19 days during a COVID-19 closure (mean ± standard error: 1 day ± 0.07; Figure 13A). The top-ranked model (wAIC$_c$ = 0.5, Table 3) included *days since last boat*, but only explained 0.7% of the model variance (Table 3; Supplementary table 1). The second-best model also had an wAIC$_c$ of 0.5 and included the same factors and *week*, but the variance explained was not improved. Activity declined from 0 days to 5 days of no vessels, after which it returned to the day 0 baseline, followed by another decrease to 18 days, similar to that of 5 days (Figure 13B). The random variable (*tagID*) also influenced the activity of silver trevally and explained 5.1% of the model variation (Supplementary table 1).

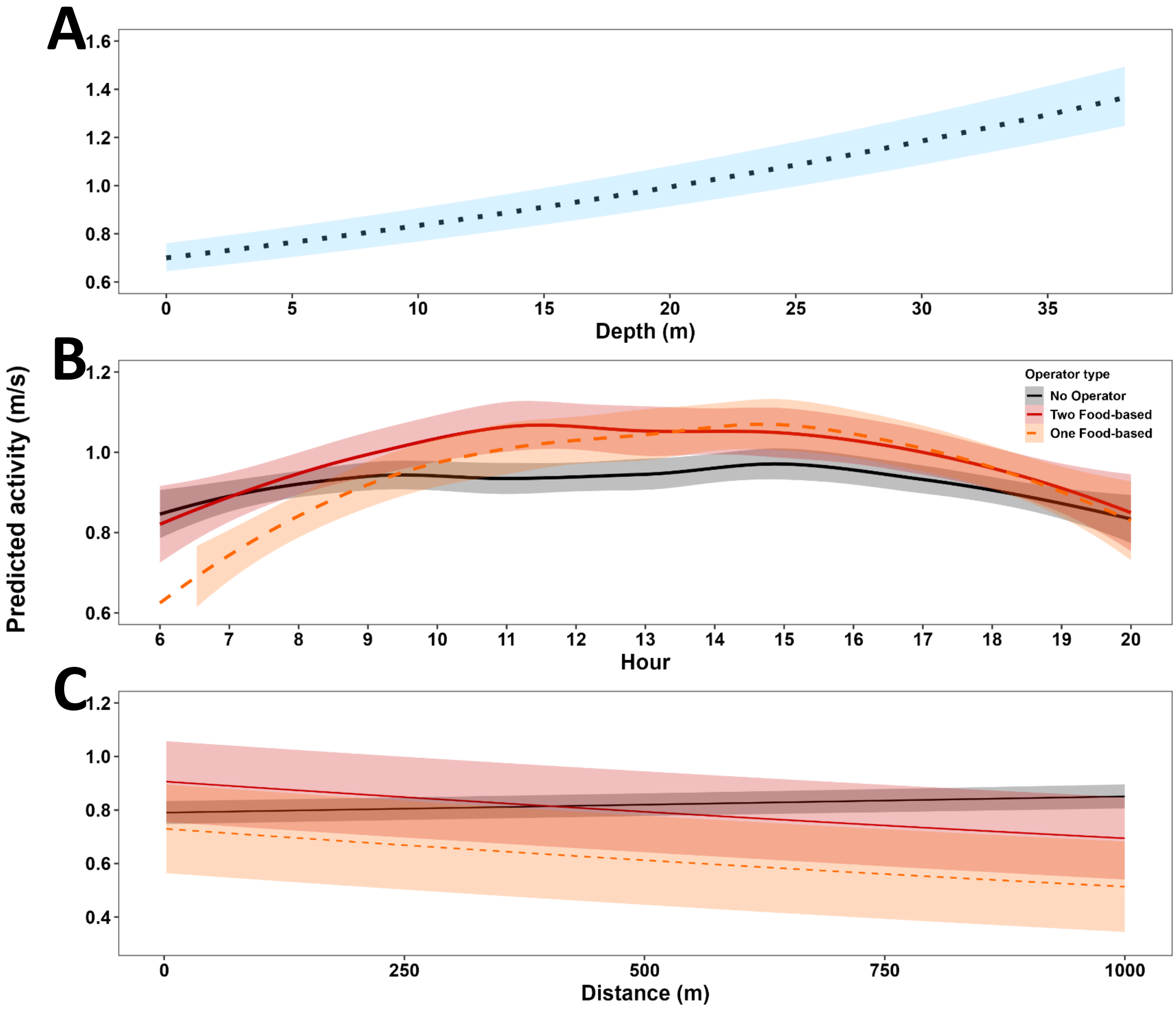

Figure 12. Predicted activity (ms^{-1}) from Generalised Additive Mixed Models for silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group for **A**. depth (m), R^2 = 8.4 % **B.** the interaction between hour and operator type, R^2 = 1.65%, and **C.** the interaction between distance and operator type, R^2 = 0.86%. Shaded ribbons indicate 95% confidence intervals.

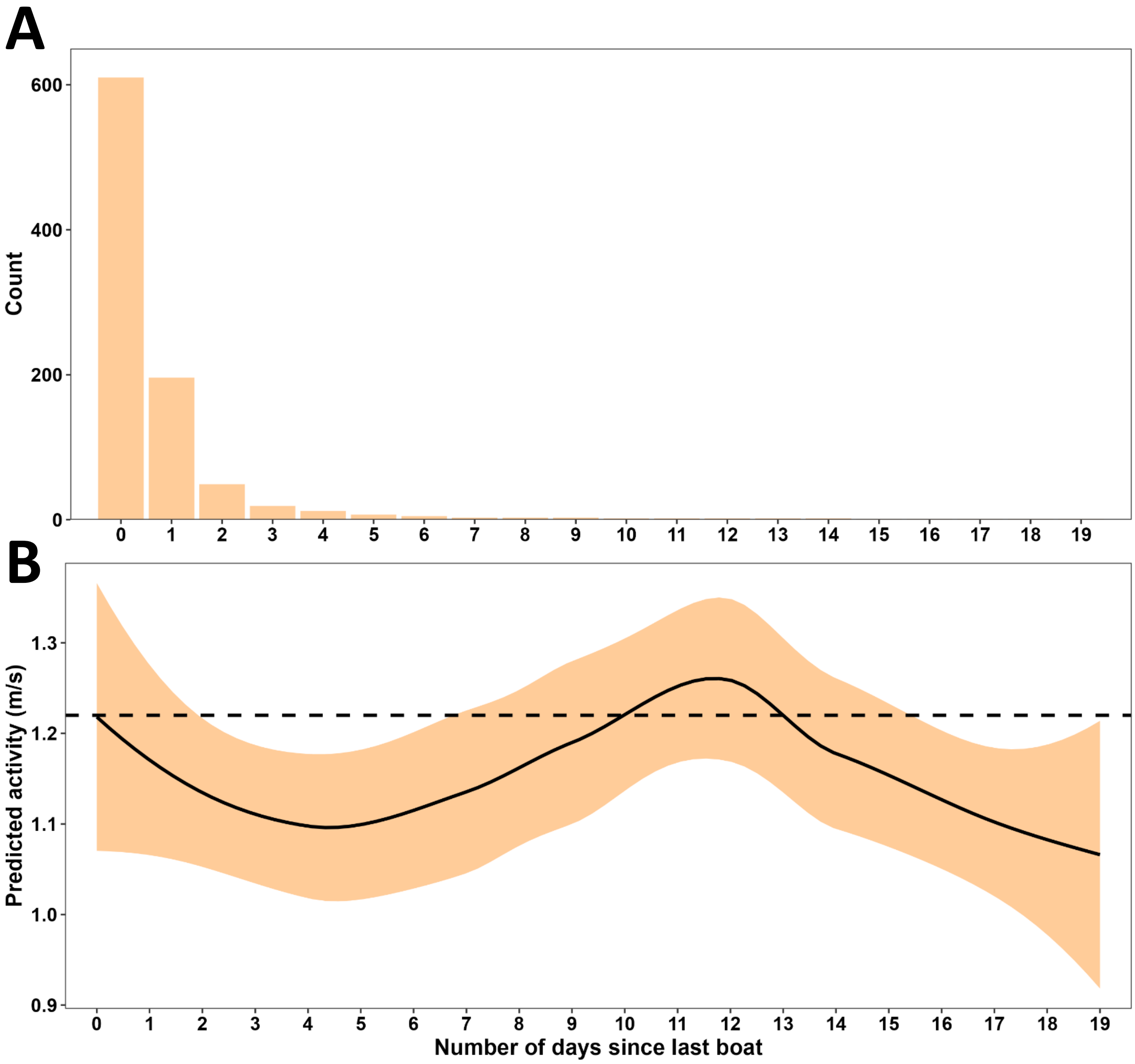

Figure 13. A. Count of number of days at the Neptune Islands Group for number of days since last boat **B.** Predicted activity (ms^{-1}) from Generalised Additive Mixed Models for silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group for number of days since last boat. Shaded ribbons indicate 95% confidence intervals, dashed line indicates predicted activity for 0 days since last boat.

2.5 Discussion

This study quantified the residency, space-use, and activity or silver trevally at a white shark cage-diving tourism site, revealing the impacts that wildlife tourism has on non-focal schooling pelagic fish (Figure 14). Cage-diving operations increased weekly residency and daily amount of time spent at the Neptune Islands, and changed the distribution of silver trevally, aggregating individuals at the surface (< 5 m depth) close to food-based operators, leading to a reduction of their core space use. These findings support my first two hypotheses, mirroring increases in residency and reductions in space use and distribution seen by non-focal species responding to provisioning. However, I did not detect the strong activity increase expected to occur from the observed swimming bursts to feed on bait and berley, as operator type alone did not significantly increase silver trevally activity (Figure 14), thus refuting the third hypothesis. These findings highlight the complexity in possible responses to wildlife tourism, and that changes in distribution might not necessarily lead to increased energy expenditure. I discuss the potential physiological and energy implications resulting from silver trevally feeding on the bait and berley, while their activity is minimally affected.

While silver trevally residency is high throughout the year, it is substantially increased by the cage-diving industry. Similar changes in residency at similar tourism sites have often been observed and has been linked to associative learning. The ability to link the location of an event or stimulus with time is known as time-place learning (Biebach et al., 1991, Schatz et al., 1999), and the frequent, regular, and predictable availability of the food during tourism operations or recreational activities can lead animals to predict when food will be available and show anticipatory behaviours (e.g. lemon sharks, Heinrich et al., 2021; short-tail stingrays, Pini-Fitzsimmons et al., 2018; and bottlenose dolphins, Jensen et al., 2013). However, time-place learning is unlikely to be occurring in silver trevally at the Neptune Islands, as the sporadic and variable non-operator days and the fluctuating operator arrival and departure times do not form a predictable pattern, thus prevent silver trevally from learning what days and what times food will be available. In addition, there are no permanent moorings at the Neptune Islands, so anchoring locations change daily, and thus silver trevally are unable to associate a specific location with easily-accessible food, other than the general areas of the Neptune Islands. Instead, silver trevally have likely learnt that easily accessible food is frequently available at the Neptune Islands, and have thus increased their residency in the area and respond to the food stimulus once disbursed by the operators (Heinrich et al., 2021). While silver trevally may have learnt to associate the presence of vessels with food, the lack of silver trevally and reduced amount of time spent around the sound-based operator suggests that silver trevally respond to the olfactory stimulus (i.e., bait and berley) rather than the mere presence of vessels.

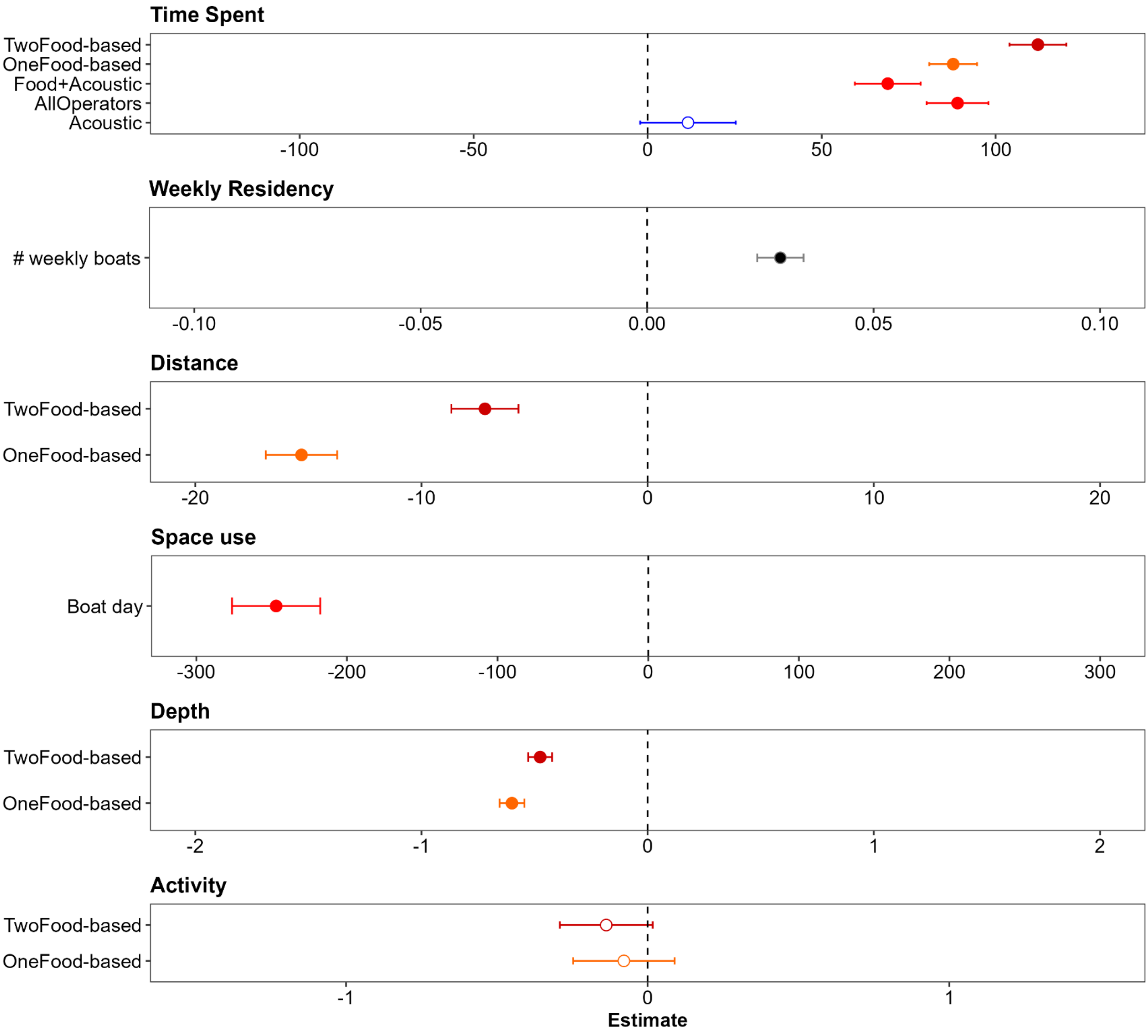

Figure 14. Estimated effect size coefficients (β; ± standard error) from Generalised Additive Mixed Models for silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands with operator variables in the top ranked model. Dashed line at zero indicates no boat/0 days. Red/orange indicates food-based operations, blue indicates acoustic operations. Solid fill p = 0; Hollow = non-significant.

Operators have used bait and berley at the Neptune Islands on at least 10 days per fortnight since ~2007. As silver trevally are seen feeding near-constantly on the bait and berley, resulting in substantial shifts in diet and nutrition (Meyer et al., 2020), they can meet their energy requirements from the food provided by the cage-diving industry (Drew and McKeon, 2019, Wen et al., 2019, Clarke et al., 2023). This could lead to silver trevally getting caught in an ecological trap (Semeniuk and Rothley, 2008, Semeniuk, 2009, Hale and Swearer, 2016), which occurs when positive reinforcement is muting natural environmental cues that trigger ecologically important behaviours and movements (Battin, 2004). Ecological traps created through wildlife tourism has been described at similar provisioning tourism site, where southern stingrays (*Hypanus americana*) in the Cayman Islands inverted natural diel activity patterns, and increased overlap in activity spaces, both of which had associated fitness costs (Corcoran et al., 2013). Trevally have been known to undertake large-scale migrations, with some exhibiting movements of over 500 km in 17 days, highlighting the potential mobility of the species (Rowling and Raines, 2000, Fowler et al., 2018). Here, I observed seasonal shifts, where the decrease in water temperature during the winter months at the Neptune Islands (i.e., June–August), in conjunction with the lower number of operating days observed during these months, may be triggering most of the silver trevally to leave the array. Some individuals did remain at the Neptune Islands during the seasonal exodus of up to 7 months when water temperature dropped below 16°C. Large migrations would explain the extended time away from the Neptune Islands. Interestingly, an uncharacteristic drop in temperature occurred in March–May of 2020 with water temperatures reaching that typical of July–August (~15°C vs. an average April temperature of ~18°C). This drop in temperature coincided with the departure of some transient and semi-transient individuals during these months, supporting that periodic reduction in residency are likely driven by temperature. This period also coincided with the longest break without operators for 13 years due to the COVID-19 travel restrictions, during which, silver trevally activity peaked after ~12 days without operators which may reflect silver trevally returning to natural behaviours and foraging (Huveneers et al. 2023, unpublished). While silver trevally movement, daily residency, and activity is influenced by cage-diving tourism while they occur at the Neptune Islands, 76% of individuals were still undertaking movements away from the islands triggered by thermal cues. Effects from ongoing exposure to provisional feeding is therefore not substantial enough to mask natural movements away from the area in cooler months (although 14% of individuals remained year-round), negating any impacts of an ecological trap. Instead, behavioural effects are likely limited to times when silver trevally and operators occur at the Neptune Islands, but also highlights the potential reliance of bait and berley as a food source when operators are present.

The small overlap of silver trevally core space between operator and non-operator days suggests that silver trevally occupy different areas of the Neptune Islands when cage-diving is occurring. This may result in fish occupying less suitable habitats during cage-diving operations. Anchoring locations of operators is predominantly based on prevailing winds and sea conditions, and most often occurs over shallow exposed sandy bottom. While these areas provide comfort and stability for cage-diving operations, they provide less natural structure and refuge for silver trevally, exposing silver trevally to increased predation risk compared to their natural rocky reef habitat (Forrester and Steele, 2004, Fairclough et al., 2011). In addition, a higher frequency of bursting events associated with chasing baits and berley can deplete anaerobic energy stores and cause lactate build-up (Payne et al., 2011), reducing manoeuvring capability needed to escape predators. As such, the change in habitat in combination with reduced anaerobic energy stores can increase the predation risk of silver trevally during cage-diving operations (Matyjasiak et al., 2023).

The large population of silver trevally at the Neptune Islands forms dense schools around the cage-diving vessels, which is supported by the small space use on berleying days, the low proportion of space use overlap between operator and non-operator days and is also observed by the tourists and operators. Schooling behaviours in teleosts has many benefits including reduced predation risk and antipredator functions (Magurran, 1990), increased foraging opportunities and success (Keenleyside, 1955), reduced hydrodynamic effects to increase swimming efficiency (Pitcher, 1993), and increased reproductive success when forming spawning aggregations (Keenleyside, 1955, Guerra et al., 2020). Despite the benefits of schooling behaviours, these dense aggregations can also increase intra-specific competition (Semeniuk and Rothley, 2008), disease (Behringer et al., 2020), injuries (Anders et al., 2019), and parasite loading (Brookhouse et al., 2013). Schools of silver trevally and yellowtail kingfish fed bread and pellets by tourists at Lord Howe Island displayed signs of increased aggression, altered foraging behaviours, microbial and parasitic infections, stomach ulcers, and skin lesions (Brookhouse et al., 2013). The similarities in species and feeding between the Neptune Islands and Lord Howe Island highlights the potential detrimental impacts of white shark tourism and associated use of berley and bait on silver trevally, especially considering that substantially more food is used at the Neptune Islands (up to 200 kg day^{-1}) than at Lord Howe Island (~10 kg day^{-1}), that feeding occurs more frequently (up to 12 days fortnight^{-1} vs. primarily summer months and during holiday periods), and the extreme size and density of silver trevally schools at the Neptune Islands (mean relative abundance per replicate: Lord Howe no-take zones ~8 vs. ~25 North Neptune islands; Meyer et al., 2020, Rees et al., 2021).

Trevally spend extended amounts of time densely aggregating in close proximity to the cage-diving vessels, which raises questions about the potential impacts of the concentrated waste output within a marine protected area (i.e., Neptune Islands Group Marine Park). Additionally, any bait and berley that not consumed by silver trevally and other non-focal species may reach the seabed below. Negative impacts from high nutrient loading has been observed in association with aquaculture operations, where organic and inorganic waste from finfish aquaculture can alter water quality, physio-chemical properties and microflora biodiversity of sediments, and increase algae growth and blooms through eutrophication (Buschmann et al., 2009). However, the potential impacts from increased nutrient loading is likely dependent on the fish concentration and amount of food introduced in the ecosystem. For example, the

South Australian southern bluefin tuna industry uses ~750 kg of sardines (*Sardinops sagax*) per day and cage (Svane and Barnett, 2008), with stocking densities of 5–10 kg m^{-3} (Ellis and Kiessling, 2016). Estimates of the biomass of silver trevally at the Neptune Islands is unknown but is likely to be smaller than those of standard aquaculture industries, and at a location with higher rates of water circulation. Future work should estimate the size of the Neptune Islands silver trevally population, and quantity of additional nutrients being introduced in the ecosystem to assess its potential impacts.

I hypothesised that silver trevally would be more active around cage-diving operators due to observations of silver trevally frequently having bursts of speed towards the bait when thrown in the water (J Dennis, pers. obs.; Supplementary material 2), and previous studies at the Neptune Islands showing that the activity of yellowtail kingfish increased by 18% during food-based operations (Clarke et al., 2023). Here the presence of food-based operators affected activity but did so minimally with the interactions between *operator type* and both *hour* and *distance* only explaining a very small percentage of the model variance (1.6% and 0.9% respectively). For example, while activity decreases with distance to vessels as would be expected if silver trevally activity increased around cage-diving vessels, the 95% confidence interval is large and activity in proximity to the cage-diving vessels is similar to activity when vessels were absent. This lack of cage-diving effect might be due to silver trevally, in between the bursts of speed towards the bait, milling into the current behind cage-diving vessels while they consume the near-continuous plume of berley (J Dennis, pers. obs.; Supplementary material 2). While I found no change in overall activity, it is possible that the rapid, short-duration bursting events are either too short (2–3 s) or infrequent to be detected by the acoustic transmitters (sampling rate 15 seconds every 270–330 seconds with a 3:1 activity depth transmission ratio). Even if this was the case, it indicates that these bursts are not frequent or long enough to lead to an overall increase in the activity of silver trevally. This presents an avenue for future work to assess the daily energy expenditure of silver trevally at the Neptune islands, confirming effects on energy expenditure associated with the lack of increase in activity.

Wildlife tourism can alter energy budgets by impacting activity and/or feeding of focal and non-focal species in terrestrial (i.e., leopards Panthera pardus; Ngoprasert et al., 2017; medium–large terrestrial mammals; Ouboter et al., 2021), and marine ecosystems (bottlenose dolphins *Tursiops truncatus*; Kassamali-Fox et al., 2020), including at the Neptune Islands (i.e., white sharks; Huveneers et al., 2018a). These studies suggested that in instances of increased activity, additional food intake might be required for these species to compensate for heightened energy expenditure resulting from interacting with tourism operations. However, the activity of silver trevally is only minimally affected by tourism, yet they consume particles of bait and berley near continuously, which is accentuated by the large number of days operators are at the Neptune Islands. The calorie content of tuna offal used for white shark tourism bait and berley (9.28 kj/g ± 0.63 SE; J Dennis, unpublished data) is substantially higher than that of natural prey items for silver trevally (e.g., cephalopod 3.3 kj/g; crustaceans 3.93 kj/g; J Dennis, unpublished data), which could result in a surplus of energy available for reproductive or somatic growth. Energy allocation typically reverts to reproductive growth from somatic growth in preparation for and during periods of spawning for teleosts, but will also be stored as fat prior (McBride et al., 2015). It would, therefore, be expected that the silver trevally at the Neptune Islands would not only be larger due to energy allocated to growth, but also have a higher proportion of fat stored. Future work should estimate somatic growth and physiological condition of silver trevally, in particular, length-at-age structures, body condition, and diet (Chapter 5), to assess the potential influence of this suspected energy surplus.

2.6 Conclusion

When examining influences of wildlife tourism operations, most studies and impact assessments focus on the large and charismatic focal species. This study identified impacts on silver trevally, a non-focal species which are often overlooked by traditional tourism management strategies (Meyer et al., 2022). This study identified effects of white shark tourism on the residency and space-use of silver trevally, while also highlighting potential implications for their health, energy budgets, and growth. Importantly, despite the effects described here, exodus from the Neptune Islands during cold periods occur for most individuals, indicating that silver trevally are still undergoing natural movements and behaviours triggered by thermal cues. Future research should focus on estimating the abundance of silver trevally at the Neptune Islands to quantify if the density of the population is contributing to nutrient loads, determine the health and growth implications from an associated surplus in energy and concentrated aggregations around cage-diving vessels. Findings from this study contribute to the limited but growing knowledge about the impacts of wildlife tourism on non-focal species, which is important for wildlife tourism management to account for the whole ecosystem when determining the ecological sustainability of a tourism industry.

CHAPTER 3

One fish, two fish, three fish, more: novel resighting method produces precise and cost-effective estimates of abundance


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"This is the pre-peer reviewed version of the following article: Dennis, J. D., Meyer, L., Dudgeon, C. L., & Huveneers, C. (2024). One fish, two fish, three fish, more: novel resighting method produces precise and cost-effective estimates of abundance. Journal of Fish Biology, 1–11, which has been published in final form at https://doi.org/10.1111/jfb.15902. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions."

3.1 Abstract

Estimates of abundance are essential to manage and conserve marine species. Numerous methods are available to determine population size, but suitability of methods for schooling fishes and the associated precision can vary depending on the species and system. Here, I developed and compared three mark-recapture/resight methods to assess the most robust method to estimate the abundance of silver trevally (*Pseudocaranx georgianus*). While the recapture rate was similar across the methods, the *Swim pass* method (resighting) recorded the largest number of individuals (mean ± standard error: 211 ± 14.9) and had the lowest coefficient of variation (CV; 4.5–12%) compared to *360-video* (resighting; 45 ± 2.1 individuals surveyed; 14.8–22.2% CV) and *Large-scale capture* methods (recapture; 30 ± 3.8 individuals surveyed; 17.3–26.5% CV). The inclusion of individual ID into the abundance estimator models for the *Large-scale capture* did not change the abundance estimates and showed similar resolution between the models (CVs: 18.2–26.7%). I showed that the *Swim pass* method is logistically easy to implement and generates precise estimates of silver trevally abundance. This new method provides a low-cost, time-efficient resighting method that can be adapted to suit similar aggregating pelagic species interacting with wildlife tourism operations, enabling researchers to rapidly estimate the abundance of species that have been previously difficult to count.

3.2 Introduction

Species abundance is a fundamental measure in ecology and is essential to manage and conserve populations and associated ecosystems (Sollmann et al., 2013). As a result, numerous methods have been developed to estimate abundance reliably and accurately across a wide range of spatial scales (Bradshaw et al., 2007, Lindegren et al., 2013). These methods include distance-sampling-based approaches (i.e., line transects; Hedley and Buckland, 2004), genetic approaches (e.g., close-kin genetics; Bravington et al., 2016), or capture-mark-recapture/resight (hereafter mark-recapture/resight) surveys (Jolly, 1965, White and Burnham, 1999). Mark-recapture/resight surveys are relatively popular due to their ability to produce robust estimates of abundance and other population demographics (i.e., apparent survival and transition probabilities; McClintock and White, 2009, McClintock et al., 2009a, McClintock et al., 2009b). Mark-recapture/resight surveys involve capturing and marking individuals, releasing them, and then recapturing or resighting them (Jolly, 1965, White and Burnham, 1999). Animal marking techniques vary extensively and include internal transmitters (i.e., acoustic telemetry; Dudgeon et al., 2015) or external tags, collars and bands, clipping and branding methods (Seber and Schofield, 2019), natural markings (Lee et al., 2014, Dudgeon et al., 2015), or genetic markers (Pfaller et al., 2019). The high versatility and flexibility in marking and recapture or resight methods have resulted in mark-recapture/resight approaches being widely applicable for a range of species in terrestrial (Judge et al., 2017), aerial (Lindberg, 2012), freshwater (Moe et al., 2020), and marine environments (Ward-Paige et al., 2010). These methods can also be used for populations with an unknown number of marked individuals, when multiple surveys are possible with or without replacement (i.e., an individual can be sighted more than once or can only be sighted once), or when the population is demographically open (i.e., open to births, deaths, emigration, and immigration; McClintock and White, 2009, McClintock et al., 2009a, McClintock et al., 2009b). As such, mark-recapture/resight methods provide a flexible framework for assessing population size and dynamics. However, low capture and recapture probabilities and the inability of some mark-recapture/resight models to handle heterogeneity in detection probability can also affect the abundance and other demographic parameters estimated (McClintock and White, 2009, McClintock et al., 2009a, McClintock et al., 2009b, Sollmann et al., 2013). Considering the potential for biased method to lead to over or underestimation of abundance, or to provide relative abundances only rather than true abundances (Dettloff, 2023), it is essential to select the most appropriate method based on the biology and ecology of the species and the logistics at the study site.

At the Neptune Islands Group Marine Park in South Australia, bait and berley (minced southern bluefin tuna, *Thunnus maccoyii*) are used by the cage-diving industry to attract white sharks (*Carcharodon carcharias)*. This process incidentally attracts large aggregations of schooling fish, silver trevally *Pseudocaranx georgianus* (Huveneers et al., 2013) and anecdotal reports from the cage-diving industry suggest that the abundance of silver trevally is increasing to the point of obscuring viewing of the target animals and affecting customer satisfaction (A Fox & A Wright, pers. comm.). A study on the foraging ecology of silver trevally also showed a shift in silver trevally diet due to resource subsidy from the berley/chum used by the tourism industry (Meyer et al., 2020). Understanding the impacts of the cage-diving industry and whether the number of silver trevally at the Neptune Islands is increasing requires the ability to quantify and monitor the silver trevally population. However, quantifying abundance is logistically difficult due to the large numbers of silver trevally aggregating and their schooling nature (Meyer et al., 2022). Previous efforts to estimate abundance based on mark-recapture methods were not successful with no recaptures using standard fishing methods (i.e., rod and line), despite sighting of tagged individuals at the time of the surveys (J Dennis, pers. obs.). Given the difficulties in getting recaptures using standard methods, I developed and compared three novel mark-resight/recapture methods to determine the most robust method for estimating the abundance of silver trevally interacting with cage-diving vessels. Specifically, I compare precision in abundance estimates among two resighting methods and one recapture method. I discuss the benefits and disadvantages of each approach and the applicability of the most robust method for estimating abundance for similar systems. I propose that the best-performing method has future applications for estimating the abundance of schooling pelagic fishes with high abundance and density.

3.3 Methods

Tagging

I caught 350 silver trevally at the North Neptune Islands Group Marine Park, South Australia (-35° 13' 48", 136° 4' 12"), using hook-and-line and tagged individuals with plastic T-bar anchor tags (hallprint, South Australia) between the 15th–21st of October 2019. I inserted tags in the muscle below the first dorsal fin, capturing, releasing, and resighting silver trevally onboard the tourism boats at the cage-diving sites within a small area of ~0.5 km^2.

Recapture/resight protocol

Previous methods attempting to recapture silver trevally at the Neptune Islands Group have been unsuccessful due to the high-density schooling nature (J Dennis, pers. obs.). Therefore, new approaches were required due to the lack of appropriate methods. I designed three mark-recapture/resight methods that were tested monthly over five months (October–February) to determine the optimum method to estimate silver trevally abundance. During the 5-month study period, three surveys of each method were undertaken within three consecutive days each month. Each survey was considered a different replicate (i.e., one replicate per method per day). The *360-video* and S*wim pass* are new resighting methods I developed, and the *Large-scale capture* is a new recapture method based on a traditional dip-net fishing technique.

360-video

I developed this method to enable a 360-degree view to be observable within a single frame to maximise the number of individual fish counted. The *360-video* method used four GoPro Hero7 cameras (wide angle, resolution 1080p, acquisition 60 frames per second) mounted on each side of a square wooden board, facing out (Figure 15A). The opening angle of each camera underwater was ~94° resulting in a 360° field of view across the four cameras. I deployed the *360-video* setup from the stern of the cage-diving vessel at ~1 m depth for a soak time of 5 minutes, i.e., one replicate. I released approximately 500 g of berley in the water above the camera during the deployment every ~1.5 minutes. I synchronised all four videos from each replicate using the moment the *360-video* entered the water, joining videos together to allow simultaneous viewing (i.e., 360° field of view) using xilisoft video converter (http://www.xilisoft.com). For each 5-minute video replicate, I performed counts at each consecutive minute increment (± 10 seconds of each minute, five counts total) using VLC media player (https://www.videolan.org), recording the maximum number (MaxN) of tagged and untagged individual fish presenting their left side in a single frame. I excluded fish showing the right side as I was unable to confirm whether or not the individual was tagged. I calculated the mean number of tagged and untagged individuals across the five 1-minute MaxN counts.

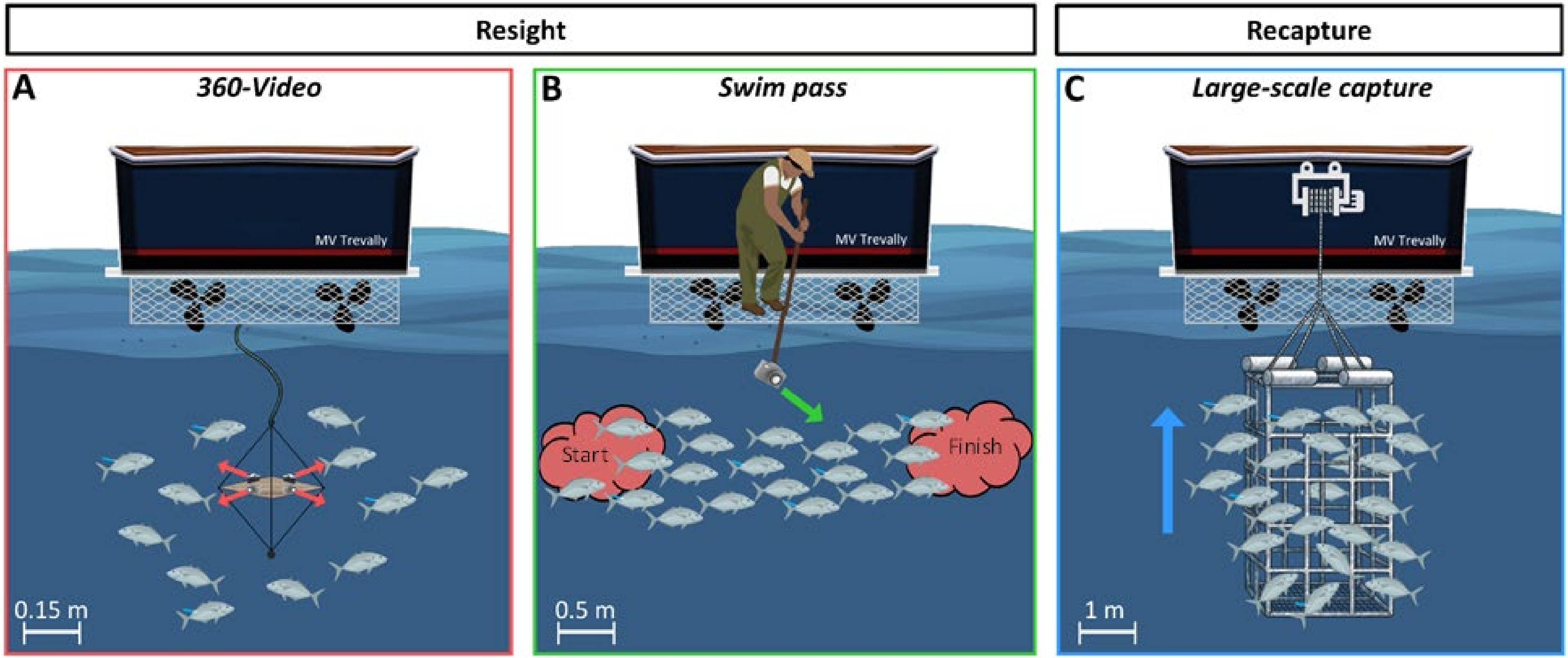

Figure 15. Mark-resight and recapture methods. A: 360-Video comprised four GoPro Hero7 cameras mounted on each side of a square wooden board, facing out, deployed from the stern of a vessel to visually sight tagged and untagged individuals (silver trevally *Pseudocaranx georgianus*). B: Swim pass method wherein fish are aggregated at ”start” with berley and then prompted to swim to ”finish” with additional berley, resulting in individuals showing the tagged side to a single camera lowered from a vessel as they swim from start to finish. C: Large-scale capture where fish are aggregated into the submerged cage before it is lifted, capturing fish within the cage, where they are counted by hand, recording fish ID number if tagged, and then released. Mesh covering the sides of the cage not depicted here. Note the scale bar refers to methods (360-video apparatus, silver trevally swim distance, cage). Fish, cage gaps, and boats are not to scale (silver trevally size range 300–600mm). While not indicated, berley is used in all three methods.

Swim pass

I developed the *Swim pass* to survey large numbers of fish while avoiding multiple counts of the same individual during each sampling period. I aggregated the Trevally on the port side of the anchored shark cage-diving vessel within the study area by releasing approximately 500 g of berley. When ~90% of the visible silver trevally were aggregated on the port side, I threw ~1 kg of berley to the opposite side (starboard), prompting silver trevally to swim across the vessel's stern, exposing their left side to the viewer. I positioned a GoPro Hero7 (wide angle, resolution 1080p, 60 frames per second) mounted on the end of a pole at ~1 m depth to record the left side of the silver trevally as they swam between the two aggregation points (Figure 15B). Filming continued until silver trevally ceased swimming towards the starboard side of the vessel (< 1 minute), preventing any fish from being double-counted. I later viewed the footage at 0.25 speed, recording the total number of tagged and untagged individuals as they swam through the screen for the length of the video (Supplementary material 4). The individual was not recorded if the left dorsal region was not visible (e.g., obscured by another fish). Each *Swim pass* was considered a different replicate.

Large-scale capture

During daily shark cage-diving operations, silver trevally can be incidentally caught in the cage (approx. dimensions 1.85 m x 1.85 m x 2 m) when lifted out of the water. This method was extended as a new recapture method to use the shark-cage as a large dip net (Figure 15C). Prior to the survey, I closed all gaps in the cage using a diamond mesh, preventing any silver trevally to escape, regardless of their size (mesh not shown in Figure 15C). I submerged the shark-cage below the surface and used ~1.5 kg berley to aggregate silver trevally around and above the cage. Once an aggregation of silver trevally formed on top of the cage, I lifted the cage from the water, capturing a large number of silver trevally in a single event. The shark-cage remained semi-submerged, allowing silver trevally to continue swimming while I entered the cage to catch silver trevally by hand, count them, and, if tagged, record the fish ID number before releasing all fish. A rigid cage prevented the sides from collapsing when lifted, preventing overcrowding, stress, or injuries to the silver trevally. Each cage submersion was considered a different replicate.

Data analysis

Comparison of methods for detecting fish

I tested differences in the total (tagged and untagged) number of individuals sighted or recaptured (hereafter all referred to as sighted) between methods using generalised linear models (GLM) with a Poisson distribution and log-link function. I tested the difference in the recapture rate (percentage of tagged silver trevally) between methods using GLM with a negative binomial distribution based on a visual examination of residuals and distributions. For the model testing the number of tagged individuals sighted against the capture method, I included the total fish observed as an offset variable to account for differences in the total number of individuals sighted per replicate and method. I included the month to test for temporal variation as sampling occurred over consecutive months (5 months). The models included month and method as categorical fixed effects, with relative support for each model tested using the Akaike's Information Criterion (AIC) corrected for small sample sizes (AIC_c; Burnham and Anderson, 2002) through the dredge function in the package `MuMln` (Barton, 2019). All analyses were performed in R v.3.5.0 (R Core Team 2016).

Mark-recapture/resight abundance analysis for different methods

For each mark-recapture/resight method, I used a robust design approach to estimate silver trevally abundance across sampling periods. I used five primary sampling intervals (months), with a minimum of three secondary sampling periods within each primary sampling interval (except for *Large-scale capture* in December, which only had two secondary sampling periods). I repeated sampling in case of a failed survey (i.e., camera failure), but only one replicate was used for each secondary sampling period. Encounter histories of individual fish was not possible from the *360-video* and *Swim pass* methods because tag ID number could not be read on the video footage. As such, I constructed artificial encounter histories, consisting of counts of tagged and untagged individuals instead of encounter histories for each tagged fish (McClintock et al., 2009b). For the *Large-scale capture* method, I also constructed artificial encounter histories to allow for comparison between methods (*Large-scale capture* without ID). I used the artificial encounter histories of each method (including Large-scale capture without ID; McClintock et al., 2009b) to generate mixed log-normal estimator (LNE) models. I constructed the LNE models holding recapture probability as constant over time, *p*(.), to assist with model convergence, and time-variant for abundance *N*(t) to vary with sampling periods. Additionally, as heterogeneity models do not apply when tag IDs are unknown, I fixed heterogeneity of capture probability (σ) at 0 in the LNE model (σ = 0; McClintock et al., 2009b). I implemented the LNE models using the unidentified marks logit-normal mark resight option fitted with the logit link function within the model in Program MARK version 9.0 (White and Burnham, 1999). I also used the Poisson log-normal estimator (PNE) model to estimate population abundance from the *Large-scale capture* with the inclusion of individual ID as the model can incorporate this information (Large-scale capture with ID; McClintock and White, 2009, McClintock et al., 2009a, McClintock et al., 2014). I constructed the PNE model allowing for time variation across sampling periods for the intercept for mean resighting rate α(t), individual heterogeneity of capture probability σ(t), and the number of unmarked individuals *U (t; McClintock and White, 2009)*. I implemented the PNE model using a robust design option fit with the log link function in Program MARK version 9.0 (White and Burnham 1999). Finally, I calculated the coefficient of variation (CV) for all population abundance estimates to facilitate the comparison of variation among methods.

Model assumptions

Sampling must be classified as with or without replacement as it dictates which estimator can be used. If sampling is without replacement, each individual can only be seen once during each sampling occasion. For sampling with replacement, each individual can be sighted more than once. As each method I used was designed to only allow the resighting of an individual once during each secondary sampling survey, sampling is considered to be without replacement.

The inability to account for individual heterogeneity in the *360-video* and *swim pass* methods may result in underestimates of abundance. However, this does not affect the aim of my study, i.e. to compare three new methods, as all three methods are similarly affected by heterogeneity in capture probability (Veech et al., 2016). It was also assumed that all individuals have the same probability of recapture/resight, regardless of size, sex, or other demographics. As none of the methods used is biased towards a specific size range or other demographics, they have the same probability of sighting/capture. As such, I am confident that this assumption is satisfied. Heterogeneity in capture probability should be estimated in future studies to improve the accuracy of my methods.

Marks were individually identifiable for the *Large-scale capture* method, which satisfies the assumptions of the PNE model. Under a closed population model scenario for both the LNE and PNE, the population is assumed to be closed to births, deaths, immigration, and emigration within primary sampling intervals. In this scenario, all 350 marked silver trevally are available for resighting. As the present study lasted for only five months, births and deaths are expected to be minimal considering that the lifespan of silver trevally is up to 25 years (Rowling and Raines, 2000). During the study period, fifteen silver trevally were internally tagged with acoustic transmitters at the Neptune Islands Group Marine Park, providing overlapping data from an acoustic array of 15 receivers (3.5 km^2; Chapter 2). The weekly residency (detection index) of the acoustically-tagged silver trevally during the study period was 0.9–1 (Chapter 2), confirming high site fidelity at the Neptune Islands. Even if some individuals were moving in and out of the study area within or among primary sampling period there is unlikely to be a net change, and it does not affect my ability to compare precision across the three methods. It also enables estimates of the super population associated with the study area (McClintock and White, 2012) and provides reliable population estimates at the beginning of the study period (Alonso et al., 2015).

3.4 Results

Comparison of methods for detecting fish

For the total number of silver trevally sighted per survey, the full model including the interaction between month and method was the most parsimonious (AIC$_c$ weight = 1; Table 4). There were no differences in the number of silver trevally sighted between the *360-video* and the *Large-scale capture* methods, which both sighted a small number of silver trevally (mean ± standard error: 45 ± 2.1 and 30 ± 3.8 respectively; P = 0.64; β_{method} = 0.06 [baseline: *360-video*]; Table 5a). The number of fish caught through the *Large-scale capture* surveys was also the most variable (Figure 16A). The *Swim pass* method recorded the highest number of individuals per survey (211 ± 14.9) with a greater difference to the *360-video* (β_{method} 1.88) than the *Large-scale capture* (Figure 16A; Table 5a). The method type explained the most variation in the model. Although the number of silver trevally sighted also varied across months, the model effect size (i.e., coefficient) across methods was much greater than across months (largest β_{method} 1.88 vs. β_{month} 0.55 respectively; Table 5a). The interaction between month and method was also in the most parsimonious model but accounted for the smallest effect size ($\beta_{\text{month*method}}$ -0.81 vs *Swim pass* β_{method} 1.88; Table 5a).

For the recapture rate (percentage of tagged silver trevally), the full model including the interaction between month (October–February) and method (*360-video, Swim pass, Large-scale capture*) was also the most parsimonious (AIC_c weight = 1; Table 4b). Across the three methods, the number of tagged individuals sighted ranged from 0 to 65 per survey, with the mean recapture rate varying significantly by method and month ($P < 0.001$; Figure 16B; Table 5b). Within the method factor showed the largest coefficients β_{method} 0.5–2.4; Table 5b, with the *Swim pass* method producing the highest coefficient (β_{method} 2.44 [baseline: *360-video]*; Table 5b), while the other two methods were more similar (β_{method} = 0.54; Table 5b). Month (β_{month} 0.22–0.79; Table 5b) and the interaction between method and month ($\beta_{\text{month*method}}$ -0.93 – -0.01; Table 5b) was also in the top ranked model, but had smaller coefficients than method (i.e., β_{method} 0.5–2.4; Table 5b). The recapture rate obtained by the *Large-scale capture* was more variable than the other two methods, increasing in November and December, and decreasing in February, while it stayed relatively stable for the other two methods (Figure 16B).

Table 4. Model selection table for Generalised Linear Models (GLMs) of (a) the total number of individuals (silver trevally, *Pseudocaranx georgianus*) sighted and (b) the recapture rate (percentage of tagged individuals) at the Neptune Islands Group, South Australia, from three recapture/resight methods across five primary sampling intervals (months). df = degrees of freedom, AIC_c = Akaike's Information Criterion corrected for small sample size, ΔAIC_c = difference in AIC_c between current and top model, AIC_cWt = AIC_c Weight, LL = log-likelihood. The top-ranked model is highlighted in **bold**

Variable	Model	Df	AIC_c	ΔAIC_c	AIC_cW_t	LL
(a) Total observations	Null	1	7099.9	5304.05	0	-3548.90
	Month	5	7012.4	5216.55	0	-3500.76
	Method	3	1875.8	79.99	0	-934.74
	Month + Method	7	1845.3	49.48	0	-914.83
	Month + Method + Month*Method	**15**	**1795.8**	**0**	**1**	**-878.97**
	Model	Df	AIC_c	ΔAIC_c	AIC_cW_t	LL
(b) Recapture rate	Null	2	75373.6	12883.78	0	-37684.71
	Month	6	74753.2	12263.40	0	37370.00
	Method	4	64284.0	1794.24	0	-32137.74
	Month + Method	8	62991.4	501.62	0	-31486.65
	Month + Method + Month*Method	**16**	**62489.8**	**0**	**1**	**-31224.37**

Table 5. Generalised Linear Models (GLMs) estimated coefficients (β), standard errors (SE), z-values, and the individual coefficient Type 1 error estimate (P) for each variable and factor included in the top-ranked models (~Month + Method + Month*Method) for (a) the total number of individuals (silver trevally, *Pseudocaranx georgianus*) sighted and (b) the recapture rate (percentage of tagged individuals) at the Neptune Islands Group, South Australia, from three recapture/resight methods across five primary sampling intervals (months). **Bold** values indicate significant values (<0.05).

Variable	Factor	β	SE	z-value	*P*
(a) Total observations	**Intercept**	**3.53**	**0.08**	**45.98**	**<0.001**
	Swim pass	**1.88**	**0.08**	**22.46**	**<0.001**
	Large-scale capture	0.06	0.12	0.47	0.64
	November	**0.21**	**0.10**	**2.09**	**0.03**
	December	0.15	0.11	1.36	0.17
	January	**0.37**	**0.10**	**3.83**	**<0.001**
	February	**0.55**	**0.10**	**5.48**	**<0.001**
	Swim pass: November	-0.19	0.11	-1.77	0.07
	Large-scale capture: November	**-0.77**	**0.18**	**-4.35**	**<0.001**
	Swim pass: December	**-0.32**	**0.12**	**-2.69**	**<0.001**
	Large-scale capture: December	**-0.66**	**0.19**	**-3.43**	**<0.001**
	Swim pass: January	**-0.42**	**0.11**	**-4.01**	**<0.001**
	Large-scale capture: January	-0.28	0.15	-1.85	0.06
	Swim pass: February	**-0.60**	**0.11**	**-5.46**	**<0.001**
	Large-scale capture: February	**-0.81**	**0.18**	**-4.59**	**<0.001**

	Factor	β	SE	z-value	*P*
(b) Recapture rate	**Intercept**	**1.18**	**0.05**	**24.84**	**<0.001**
	Swim pass	**2.44**	**0.05**	**50.28**	**<0.001**
	Large-scale capture	**0.54**	**0.07**	**8.01**	**<0.001**
	November	**0.22**	**0.06**	**3.64**	**<0.001**
	December	**0.39**	**0.06**	**6.12**	**<0.001**
	January	**0.60**	**0.06**	**10.93**	**<0.001**
	February	**0.79**	**0.06**	**14.01**	**<0.001**
	Swim pass: November	-0.06	0.06	-1.01	0.31
	Large-scale capture: November	-0.01	0.09	-0.08	0.94
	Swim pass: December	**-0.64**	**0.06**	**-9.83**	**<0.001**
	Large-scale capture: December	**-0.25**	**0.10**	**-2.46**	**0.01**
	Swim pass: January	**-0.71**	**0.06**	**-12.38**	**<0.001**
	Large-scale capture: January	**-0.50**	**0.08**	**-6.11**	**<0.001**
	Swim pass: February	**-0.93**	**0.06**	**-15.98**	**<0.001**
	Large-scale capture: February	**-0.85**	**0.09**	**-9.14**	**<0.001**

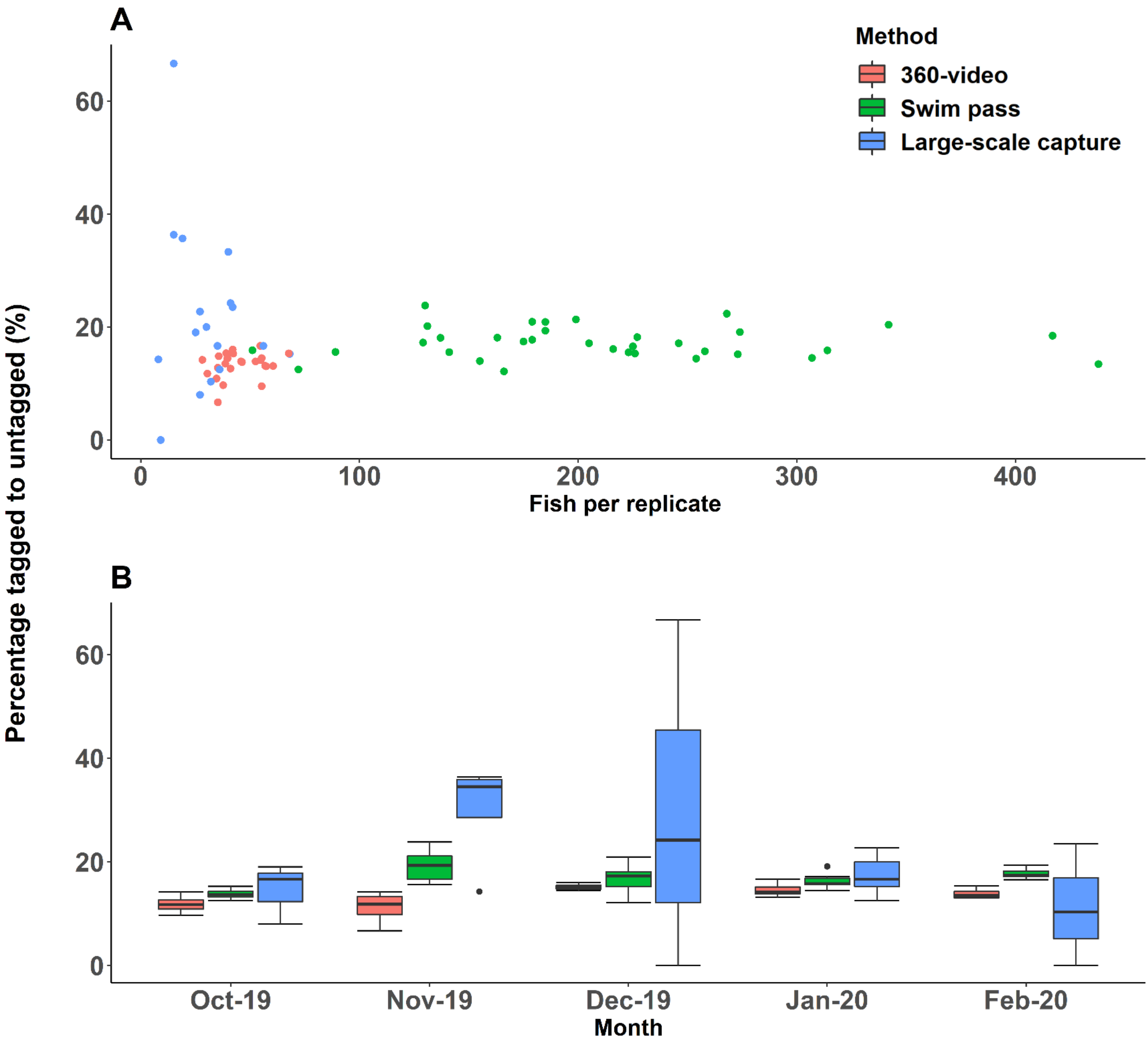

Figure 16. A: Recapture rate (percentage of tagged fish) and number of silver trevally (*Pseudocaranx georgianus)* observed per replicate for three recapture/resight methods (*360-video* [red], *Swim pass* [green], *Large-scale capture* [blue]), and **B**: Mean recapture rate across primary sampling intervals (months) for each recapture/resight method

Mark-recapture/resight abundance analysis for different methods

For all methods using the mixed log-normal estimator (LNE), the models had the structure p(.), σ =0 N(t), with the remaining models failing to converge. When using the PNE for the *Large-scale capture*, the model had the structure α (t) σ (t) U(t), with the remaining models failing to converge. The abundance estimates varied considerably across methods but had similar trends to the mean recapture rates (Table 6; Figure 17). Abundance estimates from the *360-video* were the largest, with the biggest variation around values. Estimates from the *Large-scale capture* were the lowest regardless of whether or not individual ID was included in the model. The *Swim pass* method had the smallest CV (4.5–12%) compared to the *360-video* (14.8–22.2%) and *Large-scale capture* (LNE method; 17.3–26.5%; Table 7; Figure 17). Inclusion of individual ID into the *Large-scale capture* abundance estimator (PNE model) resulted in similar abundance and CV estimates (18.2–26.7%) to the *Large-scale capture* LNE model (Table 7; Figure 17).

Table 6. Summary of three recapture/resight methods (360-video, Swim pass, Large-scale capture) across primary sampling periods (months).

Method	Method type	Count type	Individual ID	Berley used (kg)	Secondary periods within primary periods				
					Oct	Nov	Dec	Jan	Feb
360-video	Resight	MaxN	No	1.5	3	3	3	4	3
Swim pass	Resight	Point count	No	1.5	3	5	5	4	3
Large-scale capture	Recapture	Point count	Yes	1.5	3	3	2	3	4

Table 7. Coefficient of variation (%) for population estimates from three recapture/resight methods (360-video, Swim pass, Large-scale capture, Large-scale capture [with ID] across primary sampling intervals (months).

	Sampling month				
Method	October	November	December	January	February
360-video	22.17	18.44	19.64	14.75	17.21
Swim pass	11.96	4.49	5.67	6.59	6.96
Large-scale capture	24.68	19.16	22.39	17.32	26.46
Large-scale capture (with ID)	24.89	21.19	24.69	18.24	26.69

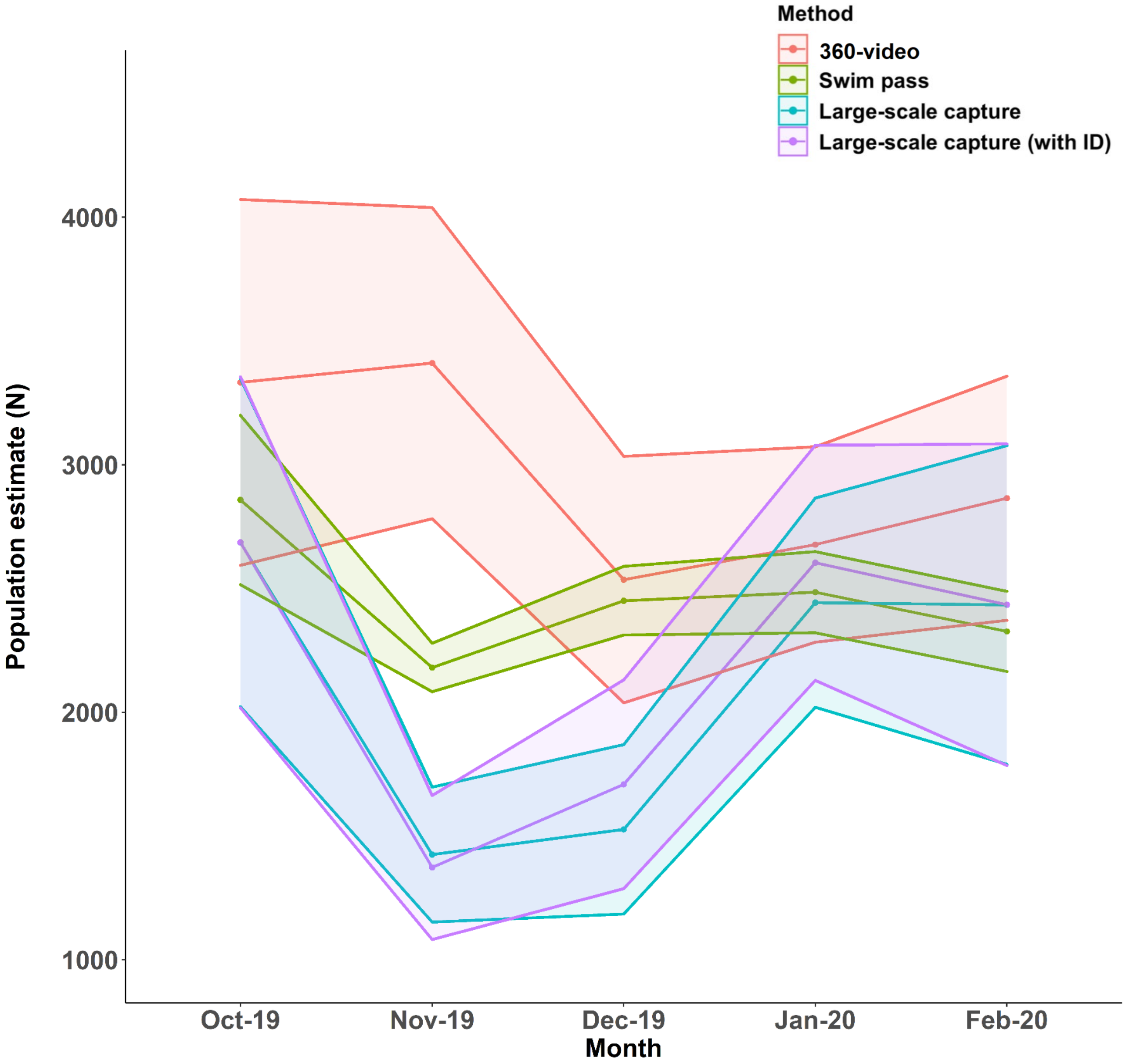

Figure 17. Population estimates for silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group, South Australia, from three recapture/resight methods (*360-video* [red], *Swim pass* [green], *Large-scale capture* [blue], *Large-scale capture [with ID*; purple]) across primary sampling intervals (months). Shaded error bars indicate standard error. All estimates were produced from the mixed log-normal estimator, except for *Large-scale capture* (with ID) estimates which were produced from the Poisson log-normal estimator incorporating individually marked individuals.

3.5 Discussion

My study developed and tested three novel mark-recapture/resight methods to determine the most effective method for estimating the abundance of a pelagic schooling fish. The *Swim pass* method recorded the largest number of fish per replicate and provided abundance estimates with the smallest CV. This method was also the easiest to implement as it could be undertaken rapidly and did not require extensive time to process videos (~5 minutes per video vs. ~60 minutes for the *360-video*). Further, the remaining methods involved additional practical limitations, both in the field (i.e., heavy machinery requirements, extensive cage preparation) and during analysis (i.e., video processing and manipulation), and had higher variance than the *Swim pass*. Finally, including individual ID in the mark-recapture models did not reduce standard error or CV because tagged fish were not recaptured multiple times, resulting in similar precision and abundance estimates to the *Large-scale capture* model without individual ID.

When selecting a method to determine the number of individuals within a population, it is important to use a method suitable for the population or species of interest and that will provide the most accurate and precise abundance and demographic parameter estimates (McClintock and White, 2012). The inability to survey a sufficient number of individuals can reduce the precision of the resulting estimates and lead to over or underestimates of abundance (McClintock and White, 2012). Here, I found that the low number of individuals surveyed by the *360-video* and *Large-scale capture* methods resulted in the abundance estimates being sensitive to small variations in the proportion of resighted/recaptured individuals. This likely explains the discrepancy in abundance estimates across methods in November where the small number of individuals surveyed by the *360-video* (45 ± 2.1) and *Large-scale capture* (30 ± 3.8) affected the accuracy of the estimates. In contrast, the *Swim pass* method surveys the largest number of fish (>200 individuals per survey; five-fold larger than the other methods) and has a higher resilience to small changes in the number of resighted individuals. This also contributed to this method having the lowest CV (4.5–12% vs. *360-video* 14.8–22.2% and *Large-scale capture* 17.3–26.5%).

Incorporating multiple data types into mark-recapture/resight models can alleviate some of the biases and challenges estimating the abundance of aquatic species. For example, the integration of acoustic telemetry can help accounting for variation in heterogeneity of capture probability (Bird et al., 2014, Dudgeon et al., 2015). Typically, inclusion of multiple data types will reduce the CVs of estimates, e.g., studies integrating spatial or age data obtained CV of 12.2–12.7% (Dudgeon et al., 2015) or 1.68–3.49% (Challenger et al., 2019) respectively, compared to studies that do not integrate multiple data types, e.g., CV of ~22% (Reisinger and Karczmarski, 2010, Sorrell et al., 2019). However, CVs produced here by the *Swim pass* are similar to values obtained in the previous studies that integrated multiple data sources, highlighting the high precision of this method which only utilises a single data type.

The inclusion of individual identification can provide flexibility and additional information in estimator models (McClintock and White, 2012). The inclusion of such information can account for different forms of overdispersion, e.g., individual detection probability heterogeneity (McClintock and White, 2012) or resighting rate heterogeneity (McClintock et al., 2009a), reducing the underestimation of abundance and overestimation of precision (McClintock et al., 2009a, McClintock et al., 2009b). Here, I was able to model *Large-scale capture surveys* with and without the inclusion of individual ID (LNE and PNE) but found no difference in the parameter estimates or CV. Despite the ability to include individual IDs in the analysis of *Large-scale capture* data, the low precision is likely a result of the inherent low number of fish surveyed during the *Large-scale capture* surveys (30 ± 3.8 SE), reducing the likelihood of recapturing individuals on multiple surveys. No individuals were recaptured on more than two occasions after initial marking. This low likelihood of recapturing individuals decreases the value of including ID in the estimator models and consequently does not improve precision. The inclusion of ID into the *Large-scale capture* survey could, therefore, increase precision if the overall number of individuals surveyed was increased (McClintock and White, 2012). Increasing the overall number surveyed could be achieved by using a larger custom-designed cage instead of the standard cage used by the white shark cage-diving industry, with the optimum cage size requiring additional testing to be estimated.

Inherent biases leading to the assumption of equal capture probability being violated (Abadi et al., 2013), e.g., trap happiness or net avoidance, can affect the accuracy and bias population estimates (Haxton and Friday, 2019, Wacker et al., 2021). My study uses bait and berley to aggregate silver trevally, potentially biasing my abundance estimates towards individuals that are more likely to respond to food-based attractant. It may also lead my estimates to represent the number of silver trevally around cage-diving vessels rather than the whole population of silver trevally at the Neptune Islands. However, I was specifically interested in the number of silver trevally interacting with cage-diving vessels and setting up an approach which will enable us to monitor changes in this population over time. Further, there should be no bias towards any method based on the use of food to attract silver trevally because bait and berley were used for all methods.

When estimating fish abundance, the following should be considered for method selection: cost, reproducibility, disturbance of the target species, and efficiency (McClintock and White, 2012). While the *360-video* was fast in the field, non-invasive, and relatively cost-effective, there was considerable investment in time for processing and analysing the videos, which needed to be converted, synched, and spliced (>60 minutes per video). While 360-cameras are now available, removing the need to use four separate cameras and subsequent video manipulation, fish counts from the *360-video* took substantially longer than the *Swim pass* method regardless of video footage manipulation (i.e., 360-cameras do not reduce the time required for fish counts, it only reduced video manipulation). Automated fish detection could be used to decrease fish count time from the *360-video* (and *Swim pass; (Ditria et al., 2020, Connolly* *et al., 2023)*). However, the training and construction of required deep learning models comes at a financial cost which may still exceed the cost of processing single-view footage manually (Connolly et al., 2023). In addition, tag sightability was low as silver trevally were not always oriented with their tagged side facing the camera, precluding some individuals from the count. While the *Large-scale capture* did not require video analysis, setting up the cage to catch silver trevally was time intensive. The *Large-scale capture* method is also more invasive than the other two methods, requiring recapturing fish at each sampling period instead of resighting fish. As the precision of the abundance estimates was not improved by the ability to identify individuals due to multiple recaptures being rare, the additional disturbance of the *Large-scale capture* method is not justified. The *Swim pass* method was the easiest to implement as it was rapid, only used a single camera, and did not require extensive video processing time. Furthermore, due to the orientation of the silver trevally during surveys, tag sightability was better than during *360-video* as the tagged side was always visible to the camera.

3.6 Conclusions

Implementing the best method to obtain precise abundance estimates is essential to effectively manage and conserve marine species. After testing three different methods for testing abundance of silver trevally around cage-diving I had a clear leader: the *Swim pass* method. This method captured the most animals per replication and showed the highest precision, including when compared against an approach that reduced individual heterogeneity through the inclusion of individual ID. Furthermore, the *Swim pass* method provides a low-cost, time-efficient resighting method that enables researchers to rapidly estimate the abundance of aggregating pelagic species. The applicability of this method extends beyond pelagic fishes interacting with wildlife tourism to other species and situations, such as schooling fish around aggregating devices (FADs; Dagorn et al., 2010) or anthropogenic structures (i.e., oil platforms, pipelines, wind farms; Meyer-Gutbrod et al., 2020), or to estimate stock size in aquaculture pens (Callier et al., 2018).

CHAPTER 4

Abundance of silver trevally (*Pseudocaranx georgianus*) exposed to a resource pulse from wildlife tourism

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4.1 Abstract

Supplemental feeding provides a spatiotemporally predictable and consistent food source for wildlife, which can affect their abundance and behaviour. At the Neptune Islands Group Marine Park in South Australia, bait and berley are used to entice white sharks (*Carcharodon carcharias*) towards cage-diving vessels. Silver trevally (*Pseudocaranx georgianus*) are also attracted, and feed on this supplemental food source, which affects their diet and movements (i.e., residency and spatiotemporal distribution; Chapter 2). The silver trevally form large aggregations around vessels with operators suggesting a subsequent increase in their abundance. I used five different mark-resight estimator models based on conventional tagging (n = 700) with improved parameterisation of resighting probability from acoustic tracking (n = 25) and a VEMCO Positioning System to estimate the abundance of silver trevally at a white shark tourism site. I estimated that the population of silver trevally reaches ~4,000 individuals, with abundance decreasing during periods of low water temperature, rather than in months with less cage-diving activity. This suggests that the supplemental feeding is not muting environmental cues or suppressing natural behaviours. Findings from this study provide abundance estimates for a non-focal population exposed to supplemental feeding from wildlife tourism, highlighting the large number of silver trevally interacting with cage-diving vessels. This supports the need for wildlife tourism management to account for non-focal species when considering the attractant used to ensure the industry's ecological sustainability.

4.2 Introduction

Estimates of abundance, density, and other demographic parameters are vital in population ecology, wildlife management, and conservation (Sollmann et al., 2013). Trends of such estimates can be used as indicators of population status, from which the recovery of at-risk populations (Haxton and Friday, 2019), harvestable biomass in fisheries (Hart et al., 2019), or responses to anthropogenic effects can be inferred (Clementi et al., 2021). The impacts of altering the size of a population can also extend beyond the impacted species to influence the supporting ecosystem (Hixon et al., 2002, Sollmann et al., 2013). As such, it is important to understand the processes that regulate and drive spatiotemporal changes in the abundance and density of populations.

Given unlimited resources, a population can theoretically grow exponentially (Allen and Hightower, 2010). However, abundance is regulated through density-dependent processes, preventing the population from exceeding its carrying capacity (Koons et al., 2015). Competition for resources (inter- and intraspecific; Meakin and Qin, 2020), particularly food availability, is one of the main factors underlying density-dependent processes (Post et al., 1999, Koons et al., 2015, Malpass et al., 2017, Cox and Gaston, 2018). In the marine environment, food availability is susceptible to substantial fluctuations based on environmental and climatic changes (Cury and Shannon, 2004), inter- and intraspecific competition (Gaston et al., 2009), and anthropogenic pressures (Cury and Shannon, 2004, Gaston et al., 2009, Barbraud et al., 2018). For example, upwelling events in the California Current ecosystem increase phytoplankton and zooplankton production, increasing anchovy (*Engraulis* spp.) biomass (Rykaczewski and Checkley, 2008). Contrary to this, extractive pressures such as fishing can decrease food availability by removing key prey species and reducing predator abundance (Collie et al., 2017, Barbraud et al., 2018). Fluctuations in food availability can occur over varying timescales, from decadal-scale shifts in the abundance of sardine (*Sardinops* spp.) and anchovy (Cury and Shannon, 2004), to seasonal availability in Pacific anadromous salmonids (*Oncorhynchus* spp.) during spawning migrations (Naughton et al., 2011). Due to the dynamic nature of food availability, marine consumers must adapt to fluxing food webs and recourse availablity to capitalise on favourable conditions, maintain their population size, or regulate it accordingly.

Natural pulses in resources typically occur across different temporal (i.e., daily; Bollens et al., 2011; seasonally; Beltran et al., 2021) and spatial scales (Yang et al., 2008), with no guarantee that the food source will be abundant or consistent (Becker and Hall, 2014). In contrast, anthropogenic activities intentionally and unintentionally supplying supplemental feed can create a spatially and temporally predictable resource pulse, with a consistency exceeding natural sources (Becker and Hall, 2014). Unintentional feeding involves wildlife using human food sources such as crops, food waste, or industry discards (Depestele et al., 2019). For example, 10.8 % of the global 84.6 million tonnes mean annual fishing catches was discarded as unwanted fish and offal (Gilman et al., 2020). Such food sources have contributed to ~52 % of seabird species globally consuming marine fishing industry discards (Oro et al., 2013), with the waste constituting the main food item in some populations and rates of discards altering predator-prey interactions in others (Votier et al., 2004, Bicknell et al., 2013, Oro et al., 2013). Provisioning can also be intentional, where supplemental feed are directly provided to wildlife to feed or attract species either for management (human-wildlife conflicts or species recovery; Jones et al., 1995, Martínez-Abraín and Oro, 2013), research (Huveneers et al., 2018b, Whitmarsh et al., 2019), or tourism-related purposes (Sengupta et al., 2021, Meyer et al., 2022). Both unintentional and intentional provisioning increase the foraging success of species through the consistent and predictable resource pulse, which can drive increases in abundance (Becker and Hall, 2014).

Supplemental feeding during wildlife tourism provides an abundant and predictable near-continuous food source (Oro et al., 2013, Sengupta et al., 2021). Due to the often-unpredictable occurrence, high dispersal, low densities, and short residency periods of wild animals, operators use food-based attractants to aggregate and attract species within view of tourists (Meyer et al., 2021). Use of such attractants can affect the abundance and behaviour of species interacting with tourism operations (Trave et al., 2017), e.g., increased relative abundance of silky sharks (*Carcharhinus falciformis*) at baiting stations (Clarke et al., 2013), increased encounter rates and abundance of bull sharks (*C. leucas*) at a dive site (Brunnschweiler et al., 2014), and behavioural change of sand mullet (*Myxus elongatus*), silver drummer (*Kyphosus sydneyanus*), yellowtail kingfish (*Seriola lalandi*), and silver trevally (*Pseudocaranx georgianus*) anticipating feeding from tourists (Brookhouse et al., 2013). Assessing populations to determine the presence of such impacts requires historical data, long-term monitoring, or the establishment of an initial estimate for the population to monitor and detect future change (Claassens and Harasti, 2020). At the Neptune Islands Group Marine Park (South Australia), two operators use a near-continuous berley plume of minced southern bluefin tuna (*Thunnus maccoyii*) and tethered baits (southern bluefin tuna gills and stomachs; Bruce and Bradford, 2013) to entice and aggregate white sharks within the field of view of the cage-diving tourists (Huveneers et al., 2017b, Meyer et al., 2020, Clarke et al., 2022). The intentional feeding of white sharks is prohibited by industry regulations (DEW 2016) and the berley particles are too small to be consumed by white sharks. However, large aggregations of highly resident silver trevally consume most of the bait and berley used by the operators (J Dennis, unpublished data). Reports from the industry suggest that the consumption of this food may be causing an increase in the abundance of silver trevally at the Neptune Islands (A Fox, pers. obs.). Due to the abundant food source available and its potential effects on density-dependent processes, the supplemental food may be decreasing resource related mortality, increasing the carrying capacity of the Neptune Islands, and subsequently support an increase in abundance. However, due to the lack of abundance estimates for the silver trevally prior to the use of bait and berley, or a comparable population within a marine protected area not exposed to supplemental feeding, this suspected increase cannot be confirmed. Given the potential negative impact on the health of silver trevally at the Neptune Islands (e.g., microbial and parasitic infections, stomach ulcers, skin lesions; Brookhouse et al., 2013) if the supplemental feeding is inflating the population, establishing an initial abundance estimate will allow future monitoring to determine change in silver trevally abundance and implement management strategies, if needed. While I am unable to assess long-term changes in abundance with changes in operator presence, I am able to explore short-term fluctuations throughout the year with fluctuations in cage-diving intensity, and how this influences silver trevally abundance.

Here, I use five different mark-resight estimator models based on conventional tagging with improved parameterisation of resighting probability from acoustic tracking and a VEMCO Positioning System (VPS) over two consecutive years (January 2020–January 2022) to estimate the abundance of silver trevally at the Neptune Islands Group Marine Park, South Australia. I aimed to estimate monthly abundance of silver trevally in a marine park exposed to a consistent resource pulse and assess drivers of variation over time. Specifically, I hypothesise that the abundance of silver trevally will be influenced by cage-diving intensity.

4.3 Methods

Conventional tagging (ID)

I caught silver trevally using hook-and-line at the North Neptune Islands Group Marine Park, South Australia (-35° 13' 48", 136° 4' 12"; hereafter Neptune Islands; ~12 km from South Neptune Island). I tagged individuals with plastic T-bar anchor tags (Hallprint Fish Tags, South Australia, hallprint.com) between the 15th–21st of October 2019 and between the 9th–29th of January 2021. I inserted tags in the muscle below the first dorsal fin, capturing, releasing, and resighting silver trevally onboard the tourism boats at the cage-diving sites within a small area of ~0.5 km^2.

Mark-resight protocol

I conducted mark-resight surveys monthly from January 2020 to November 2021. Mark-resight surveys were previously developed to survey large numbers of silver trevally while avoiding multiple counts of the same individual during each sampling period (swim pass survey; Chapter 3; Figure 18). I aggregated silver trevally on the port side of the stern of the anchored cage-diving vessel by releasing approximately 500 g of berley. When ~90% of the visible silver trevally were aggregated on the port side, I threw ~1 kg of berley to the opposite side (starboard), prompting silver trevally to swim across the vessel's stern, exposing their tagged side to the viewer. I positioned a GoPro Hero7 (wide angle, resolution 1080p, 60 frames per second) mounted on the end of a pole at ~1 m depth to record the tagged side of the silver trevally as they swam between the two aggregation points (Chapter 3). Filming continued until silver trevally ceased swimming towards the starboard side of the vessel (< 1 minute), preventing any fish from being double counted (Supplementary material 4). I later viewed the footage at 0.25 speed, counting the total number of tagged and untagged individuals as they swam through the screen for the length of the video. I did not record the individual if the tagged dorsal region was not visible (e.g., obscured by another fish). Each survey was considered a different replicate.

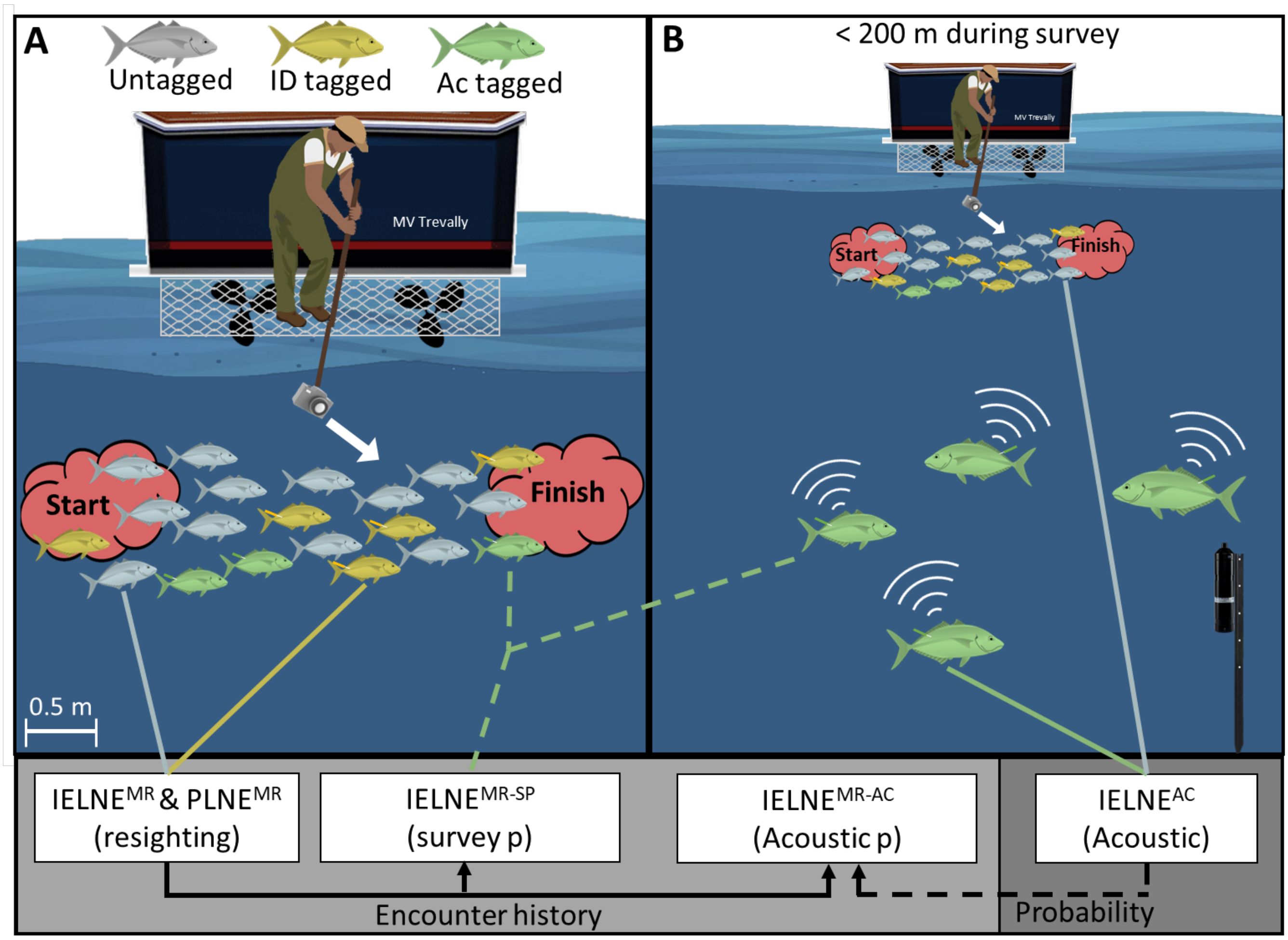

Figure 18. Mark-resight model input data from resighting surveys and acoustic detections for different models (acronyms and supporting information available in table 8): IELNE^{MR} & PLNE^{MR}: ID tagged individuals and untagged individuals during surveys. IELNE^{AC}: Acoustically detected individuals within 200 m during surveys, and unmarked silver trevally during surveys. IELNE$^{MR\text{-}AC}$: IELNE^{MR} model with MCMC simulations using resighting probability from IELNE^{AC} model estimates. IELNE$^{MR\text{-}SP}$: IELNE^{MR} model with MCMC simulations using resighting probability from detected acoustic fish and sighted acoustic fish during surveys. A. Resighting survey wherein fish are aggregated at starting point with berley and then prompted to swim to finish point with additional berley, promoting individuals to show tagged side to single camera lowered from a vessel. B. Acoustically tagged silver trevally within 200 m of the vessel during the resighting survey conducted in A. Solid lines indicates number of individuals of that fish type (i.e., untagged, marked, detected). Dashed line indicates resighting probability from model estimates (acoustic mode estimates) or derived from surveys (acoustically tagged sighted / detected). Grey silver trevally = untagged; Yellow silver trevally = ID tagged; Green silver trevally = Acoustically tagged.

Receiver array

I deployed 15 VR2AR acoustic receivers (Innovasea, Nova Scotia, Canada) at the Neptune Islands Group Marine Park for a continuous 3-year period from August 2019 to August 2022 (serviced every 12 months; Figure 19A). I designed the array to enable fine-scale positioning of tagged individuals through a VPS (Espinoza et al., 2011, Orrell and Hussey, 2022). I deployed receivers at a distance of ~300 m which as shown by range testing would detect ~80% of transmissions, allowing simultaneous detections of transmitters integrated within the VR2AR by nearby receivers. In this approach, the internal clock of each receiver was synchronised, allowing the fine-scale position of tagged fish to be calculated using the difference in time-of-arrival of acoustic detections by multiple receivers (Espinoza et al., 2011). Time synchronisation of the array was performed in the Fathom Position software (Innovasea, version 2.0.3). Receiver depth ranged from 8–46 m, and receivers were deployed on mooring consisting of 16–18 mm anchor chain links (50–100 kg), a rope canister to enable retrieval of anchor chains upon receiver recovery, and a 30-cm diameter sub-surface buoy. Due to a lack of synchronisation between both sides of the Neptune Islands, I performed positional error corrections separately for each side of North Neptune Islands (northern side, southern side; Figure 19B). I used linear regressions constructed between the measured horizontal positional errors of the synchronisation transmitters within each VR2AR receiver (HPEm), with the corresponding values or error sensitivity (HPE), to obtain the equations representative of the fine-scale positional errors for each side of the Neptune Islands. I then applied these linear equations to the silver trevally HPE values to calculate the HPE for each fine-scale position. Positions had higher accuracy on the southern side (minimum error = 0.74 m) than on the northern side (minimum error = 28.28 m). All silver trevally positions with HPE errors > 40 m (i.e. < 2.9% of all silver trevally positions) were excluded from the analyses.

Acoustic tagging

I surgically implanted acoustic transmitters (V9AP, Innovasea, Nova Scotia, Canada) into the peritoneal cavity of silver trevally. I caught silver trevally via hook-and-line and anaesthetised using AQUI-S Aquatic Anaesthetic (15 mg/L, AQUI-S, New Zealand). I made a 20–30 mm incision on the ventral side of the peritoneal cavity, inserted the transmitter, and closed the incision using 2–3 absorbable running sutures (Monosyn 2-0/3-0, B. Braun). I implanted a conventional external spaghetti tag into the dorsal musculature to visually identify acoustically tagged fish during resighting surveys (i.e., double tagged and a different colour to non-acoustically tagged fish). After tagging, I placed silver trevally in a recovery tank filled with a fresh supply of aerated seawater for 10–20 minutes before release.

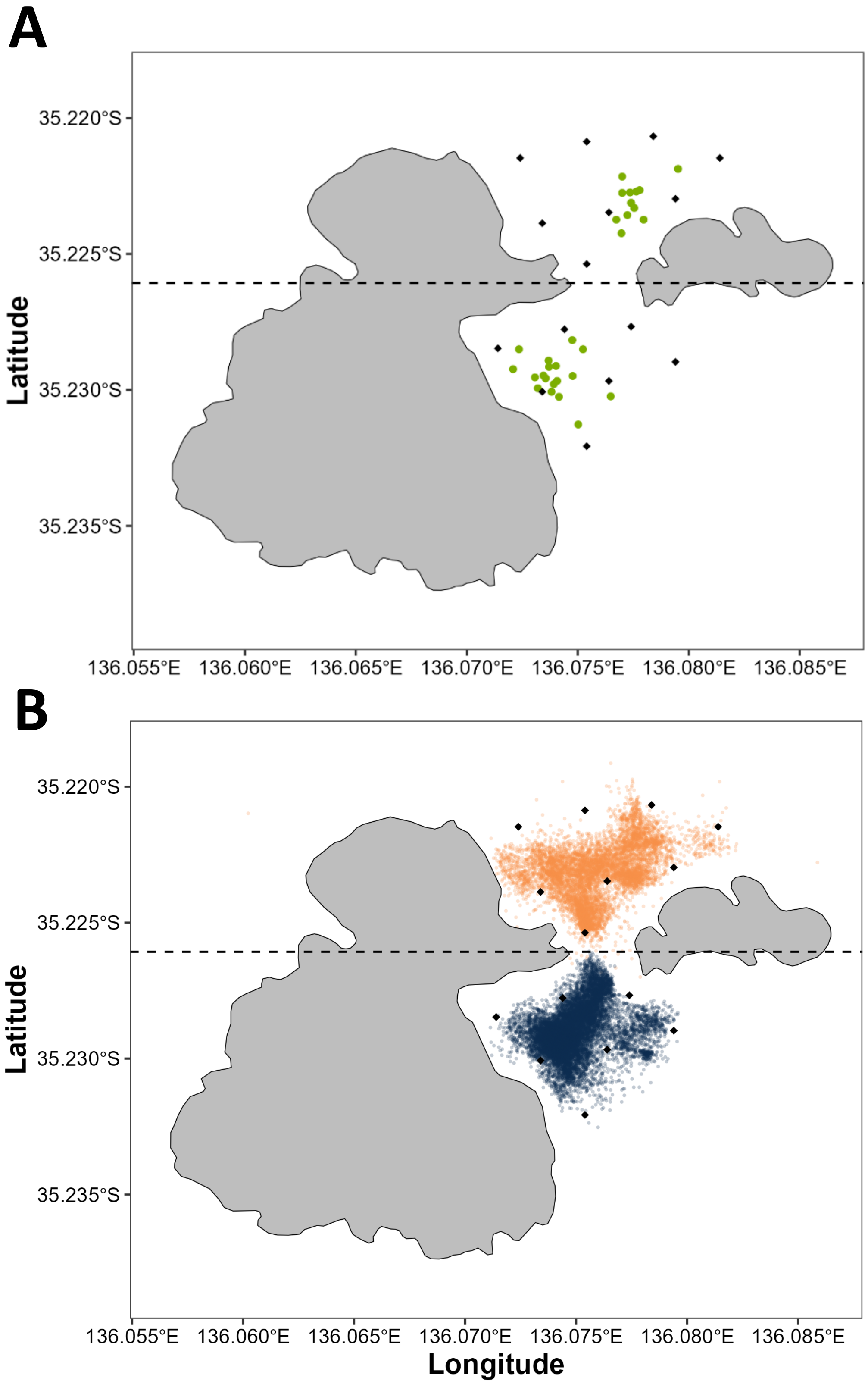

Figure 19. Map of the Neptune Islands Group Marine Park in South Australia with (**A**) positions of 15 acoustic receivers (black diamonds) and positions of all white shark cage-diving operations during mark-resight surveys (green circles); (**B**) VEMCO Positioning System (VPS) locations from 25 acoustically tagged silver trevally (*Pseudocaranx georgianus*) for the northern side (orange circles), and southern side (blue circles), dashed line indicates northern and southern boundary.

Model construction for mark-resight data

I implemented all models using the `RMark` package version 3.0.0 (Laake, 2013) in the R statistical environment (version 4.2.1; R Core Team 2016) to interface with Program MARK version 9.0 (White and Burnham, 1999). I performed mark-resight analysis on the data from the resighting surveys using a robust design approach to estimate silver trevally abundance across sampling periods (McClintock and White, 2012). I defined primary sampling intervals as months (January 2020–November 2021, n = 20), with secondary sampling periods as days within each primary sampling interval (2–6 surveys per month, n = 85). I repeated sampling in case of a failed survey (i.e., camera failure), but only one replicate was used for each secondary sampling period. Encounter histories of individual fish were not possible for surveys as tag ID number could not be read on the video footage. As such, I constructed artificial encounter histories, consisting of counts of ID tagged and untagged individuals instead of encounter histories for each tagged fish (Figure 18; Mcclintock et al., 2009). I used the artificial encounter histories to generate immigration-emigration log-normal estimator (IELNE) models (denoted as IELNE^{MR}; Table 8) and poisson log-normal estimator (PLNE) models (denoted as PLNE^{MR}; Table 8), allowing to compare which model provided the most precise abundance estimates.

Table 8. Mark-resight model input data from resighting surveys and acoustic detections for different models: IELNE^{AC}: Acoustically detected individuals within 200 m during surveys, and unmarked silver trevally during surveys. IELNE^{MR} & PLNE^{MR}: ID tagged individuals and untagged individuals during surveys. IELNE$^{MR\text{-}AC}$: IELNE^{MR} model with MCMC simulations using resighting probability from IELNE^{AC} model estimates. IELNE$^{MR\text{-}SP}$: IELNE^{MR} model with MCMC simulations using resighting probability from detected acoustic fish and sighted acoustic fish during surveys**.**

Models	Estimator	Marked	Unmarked	MCMC simulations	Resighting probability
IELNE^{MR}	Immigration-Emigration logit-normal	ID tagged	Untagged during surveys	No	Model estimates
IELNE^{AC}	Immigration-Emigration logit-normal	Acoustic detections	Untagged during surveys	No	Model estimates
IELNE$^{MR\text{-}SP}$	Immigration-Emigration logit-normal	ID tagged	Untagged during surveys	Yes	Estimated from detected acoustic fish and sighted acoustic fish during surveys
IELNE$^{MR\text{-}AC}$	Immigration-Emigration logit-normal	ID tagged	Untagged during surveys	Yes	Estimates calculated from IELNE^{AC} model
PLNE^{MR}	Unidentified marks Poisson log-normal	ID tagged	Untagged during surveys	No	Model estimates

The IELNE^{MR} models estimate two abundance types, the mean population size (N^{-}_{j}), and the super-population size (N^{*}_{j}) during primary sampling interval j. The population size refers to the mean number of silver trevally within the receiver array at the Neptune Islands during each primary sampling period. The super-population size refers to the silver trevally using both the area within the receiver array and the waters surrounding the Neptune Islands. The receivers at South Neptune Islands (~12 km south of North Neptune Islands) detected only one silver trevally tagged at North Neptunes for a single day over the study period, highlighting the lack of mixing between North and South Neptune Islands (Chapter 2), and thus indicates that the super-population resides around North Neptune Island. The IELNE^{MR} also estimates mean re-sighting probability of secondary occasion i during primary interval j (p_{ij}), the difference (α_{ij}) between the population size for secondary sampling occasion i of primary sampling period j and the mean population size for primary sampling period j (i.e., $\alpha_{ij} = N_{ij} - N^{-}_{j}$), and individual heterogeneity (σ^2_j) in resighting probability during primary sampling period j. I constructed IELNE^{MR} models allowing α to fluctuate through primary sampling periods (session dependent), as constant through time ([.]; i.e., does not change over sampling periods), or fixed at 0 (i.e., not estimated by model). I allowed p to fluctuate through primary sampling periods (session dependent) or as constant through time (.). I allowed N^{-} and N^{*} to fluctuate through primary sampling periods (session dependent). Additionally, as heterogeneity models do not apply when tag IDs are unknown, I fixed heterogeneity of capture probability (σ) at 0 ($\sigma = 0$; McClintock et al., 2009b).

The PLNE^{MR} models estimates the total population size (N_j) during primary occasion j. This estimate represents the total number of unmarked individuals in the population (U_j) and the number of marked individuals in the population (n_j) during primary sampling occasion j (i.e., $N_j = U_j + n_j$). The PLNE^{MR} also estimates the overall mean resighting rate (α_j) for primary occasion j, apparent survival between primary intervals (φ), individual heterogeneity (σ^2_j), and the probability of transitioning from an unobservable state at $j + 1$ (γ''). I constructed PLNE^{MR} models allowing α, γ'', and φ to fluctuate through primary sampling periods (session dependent) or as constant through time (.). I allowed U to fluctuate through primary sampling periods (session dependent). Finally, I fixed heterogeneity of capture probability (σ) at 0 ($\sigma = 0$; McClintock et al., 2009b).

I implemented the IELNE^{MR} and PLNE^{ME} models using the unidentified marks Immigration-Emigration logit-normal mark resight option and the unidentified marks Poisson log-normal mark resight option respectively (White and Burnham, 1999, Laake, 2013). I based model selection on Akaike's Information Criterion for small sample sizes (AIC_c; Burnham and Anderson, 2004) and model likelihood using the bias-corrected relative weight of evidence for each model, AIC_c weight, where higher values provide more support to the model (Burnham and Anderson, 2004).

Model construction for acoustic data

A limitation of mark-resight methods is the inability to determine the number of marked individuals available for resighting on a given occasion, limiting the precision of these models. To overcome this I can use radio or acoustically tagged individuals to inform the location of marked individuals, thus determining if they are present to be resighted (McClintock and White, 2012). I incorporated estimates of silver trevally positions from the VPS array, with concurrent resighting surveys to consider if a fish is present (i.e., within 200 m of survey, artificially sighted), absent, or not available (Figure 18). This was used to improve the precision and reduce the potential bias of abundance estimates over standard mark-resight methods.

To integrate the fish positions, I calculated distance (m) during a survey between silver trevally positions and the vessel using the 'distHarversine' function in `geosphere` (Hijmans et al., 2017). I constructed encounter histories based on the VPS position estimates of acoustically tagged silver trevally during the resighting surveys, where individuals detected within 200 m of the vessel during a survey were considered "sighted" and assigned a '1'. If an individual was not within 200 m of the vessel during a survey but were detected at North Neptunes Islands, it was assigned a '0' indicating it was present but not available during surveys. Finally, if an individual was not detected within the array for greater than 24 hours, it was assigned '.' as they were absent and therefore not available for resighting during the survey (Figure 18; Table 8). For the purpose of integrating the silver trevally positions, the number of unmarked silver trevally was the number of non-acoustically tagged silver trevally including conventional ID-tagged silver trevally (Figure 18; Table 8). I considered the marked super-population as the total number of acoustically tagged silver trevally deployed during that sampling period. I used encounter histories from the acoustic data for immigration-emigration log-normal estimator (IELNE) models (denoted as IELNE^{AC}). I constructed IELNE^{AC} models allowing α and σ to fluctuate through primary sampling periods (session dependent), as constant through time (.), or fixed at 0. I allowed p to fluctuate through primary sampling periods (session dependent), or as constant through time (.). I allowed N^{-} and N^{*} to fluctuate through primary sampling periods (session dependent). I implemented the IELNE^{AC} models using the Immigration-Emigration logit-normal mark resight option (White and Burnham, 1999, Laake, 2013).

Model construction for integrated mark-resight data

Estimates of resighting probability from IELNE^{MR} models based on mark-resight data only was low ($p < 0.1$). Low recapture probabilities for abundance estimates have the ability to overestimate abundance, the effects of which have been reduced in previous studies through the incorporation of acoustic telemetry data and fishing data in combination with a Monte Carlo simulation procedure (Dudgeon et al., 2015). Thus, I used acoustic telemetry to calculate resighting probability and reduce uncertainty and bias in the IELNE^{MR} model in two ways: 1) I calculated resighting probability using the number of acoustically tagged silver trevally sighted during resighting surveys in relation to the number of acoustically tagged silver trevally detected within 200 m of the vessel during surveys (integrated model denoted as IELNE^{MR-SP}; Figure 18; Table 8; see *Model construction for acoustic data*); and 2) resighting probability was estimated by the IELNE^{AC} model (integrated model denoted as IELNE^{MR-AC}; Figure 18; Table 8). For both the IELNE^{MR-SP} and IELNE^{AC} seperatley, I then used the mean and standard error of these estimate to derive beta parameters from a distribution of 1000 samples (interval 0, 1). Resighting probability was then randomly drawn and used as a fixed parameter for the data and top ranked IELNE^{MR} model. This was repeated 1000 times to build posterior distributions and capture estimation uncertainty (Dudgeon et al., 2015). I implemented the simulation loops of the IELNE^{MR-SP} and IELNE^{MR-AC} models using the unidentified marks Immigration-Emigration logit-normal mark resight option (White and Burnham, 1999, Laake, 2013).

Model assumptions

The receiver array deployed at the Neptune Islands encompasses the area used by the cage-diving operators but does not encompass the entire area around the Islands or surrounding waters. Although the daily and weekly residency of silver trevally at the Neptune Islands indicates high site fidelity (mean ± standard error: time spent day^{-1} 565 minutes ± 16; weekly residency 0.81 ± 0.02; Chapter 2), silver trevally may be outside the detection range of the array while still residing at the Islands (Chapter 2). Additionally, the extent of their movements outside of the array remains unknown, potentially reducing the precision of the abundance estimates. Based on this, I selected the IELNE model and PLNE models as the framework does not require geographic closure (IELNE) or geographic closure is only required within sampling primary sampling intervals (PLNE; McClintock and White, 2012). Another assumption of this approach is that sampling must be without replacement, where each individual can only be seen once during each sampling occasion. The survey method was designed to meet this assumption with individual resighting's occurring only once during each secondary sampling survey (Chapter 3). An important assumption is the ability to account for individual heterogeneity, which is not possible in the IELNE^{MR} and PLNE^{MR} models, possibly leading to underestimates of abundance. To account for possible underestimates, the output from the IELNE^{MR} and PLNE^{MR} models were compared to the models which can account for individual heterogeneity (i.e., IELNE^{AC}), with lower estimates from standard mark-resight models indicating if underestimation has occurred. It was also assumed that all individuals have the same probability of resighting, regardless of size, sex, or other demographics. As the method used is not biased towards a specific size range or other demographics, all individuals have the same probability of sighting. As such, this assumption is satisfied. Marks may or may not be individually identifiable when using IELNE and PLNE, which satisfies the assumptions for both the IELNE^{MR} and PLNE^{MR} where tags are not individually identifiable, and for the IELNE^{AC} which classifies marked individuals based on acoustic detections. An important assumption of the IELNE and PLNE is that marks are not lost, as overestimates of abundance can occur if marks are lost but fish are still assumed to be avaliable for resighting. Acoustic tags were internally implanted in silver trevally which minimises tag loss and allows the presence or lack thereof to be monitored based on acoustic detections. To minimise the effects of tag shedding throughout this study, models were estimated separately for sampling years, with new individuals being tagged at the beginning of each sampling year. Births and deaths are also expected to be minimal considering that the lifespan of silver trevally is up to 25 years (Rowling and Raines 2000). This is supported by high survival estimates from CJS models from acoustic data during this study (> 0.93; J Dennis, unpublished data). The possibility of some tag loss could result in overestimates of abundance. To account for the known number of tags present, I used the proportion of acoustic tags detected within the array during the survey to adjust the number of known marks for the $\text{IELNE}^{\text{MR}}$and PLNE^{MR}.

Statistical models

I used Generalised Additive Mixed Models (GAMMs) in the R statistical environment (R Core Team 2016) to test the effects of white shark cage-diving and environmental variation on abundance estimates produced from IELNE^{MR}, IELNE^{AC}, $\text{IELNE}^{\text{MR-SP}}$, $\text{IELNE}^{\text{MR-AC}}$, and PLNE^{MR} models seperately (Table 8). All GAMMs were created using the ‘gam’ function in the `mgcv` package (version 1.8-40; Wood and Wood, 2015). I included month since start of the study as a random effect integer (1–23) in all models to account for temporal autocorrelation. I selected the most appropriate statistical family and transformation through visual inspection of model residuals and distribution of the response variable. IELNE^{AC} and PLNE^{MR} estimates were log transformed prior to analysis. I selected the most parsimonious model using the Akaike Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson, 2004), using the ‘dredge’ function in the `MuMIn` package (version 1.46.0; Barton, 2019). I used the contributions of the fixed effects (marginal R^2) and the fixed and random effects (conditional R^2) in the ‘r.squaredGLMM’ function in package `MuMIn` (version 1.46.0; Barton, 2019) to explain the variance of the response variable when added to the model (Nakagawa and Schielzeth, 2013).

Biomass estimates

I estimated silver trevally biomass at the Neptune Islands using abundance estimates from the IELNE^{MR} model and lengths from the randomly sampled conventional ID-tagged silver trevally (n = 700). I used lengths to estimate individual weight in a Bayesian length-weight relationship (Froese et al., 2014):

$$Weight = 10^{log10(a)+ b\, log10(length)}.$$

Where intercept *a* (0.01413) and slope *b* (2.96) are length-weight relationship parameter estimates for silver trevally (*Pseudocaranx georgianus*) sourced from Froese et al. (2014), and length is the total length of the individual in cm. I then randomly sampled the weight distribution of the 700-silver trevally for the number of silver trevally estimated for each primary sampling period (i.e., months) by the IELNE^{MR} model.

4.4 Results

Mark-resight

I tagged 700 silver trevally with conventional ID tags at the Neptune Islands: 350 in October 2019 and 350 in January 2021. I tagged silver trevally on opposing sides of the dorsal fin in the dorsal musculature and with different coloured tags between years to differentiate between tagging periods. I resighted silver trevally during monthly surveys (primary sampling periods) from January 2020 to November 2021, with 85 resighting surveys (secondary sampling periods; 2–6 survey per primary sampling period) conducted across 20 months. I resighted a cumulative total of 1,810 tagged silver trevally and 14,068 untagged silver trevally across all resighting surveys. The mean number of tagged silver trevally sighted per survey was 28 ± 1.2 (± standard error), with the highest number being 47 (13% available tags). I sighted 164 ± 6.1 untagged individuals per survey, with a maximum of 362 untagged silver trevally in a single survey.

Acoustic monitoring

I acoustically tagged 25 silver trevally at the Neptune Islands: 15 in October 2019 (397 days battery life) and 10 in January 2021 (564 days battery life). The longer battery life was due to new circuit board design. I obtained 392,094 silver trevally detections (16,337 ± 2,320; Figure 20) across all 15 receivers deployed. Mean monthly residency over the 2-year period was 0.69 ± 0.02 (range: 0.13–1). Residency was lowest in July and August (0.47 ± 0.04 and 0.49 ± 0.08 respectively) and highest in February (0.97 ± 0.01). I estimated 17,457 VPS positions (759 ± 135 positions; Figure 19B). During resighting surveys, I sighted a cumulative total of 120 acoustically tagged silver trevally, with 4,932 positions estimated within 200 m of cage-diving vessels.

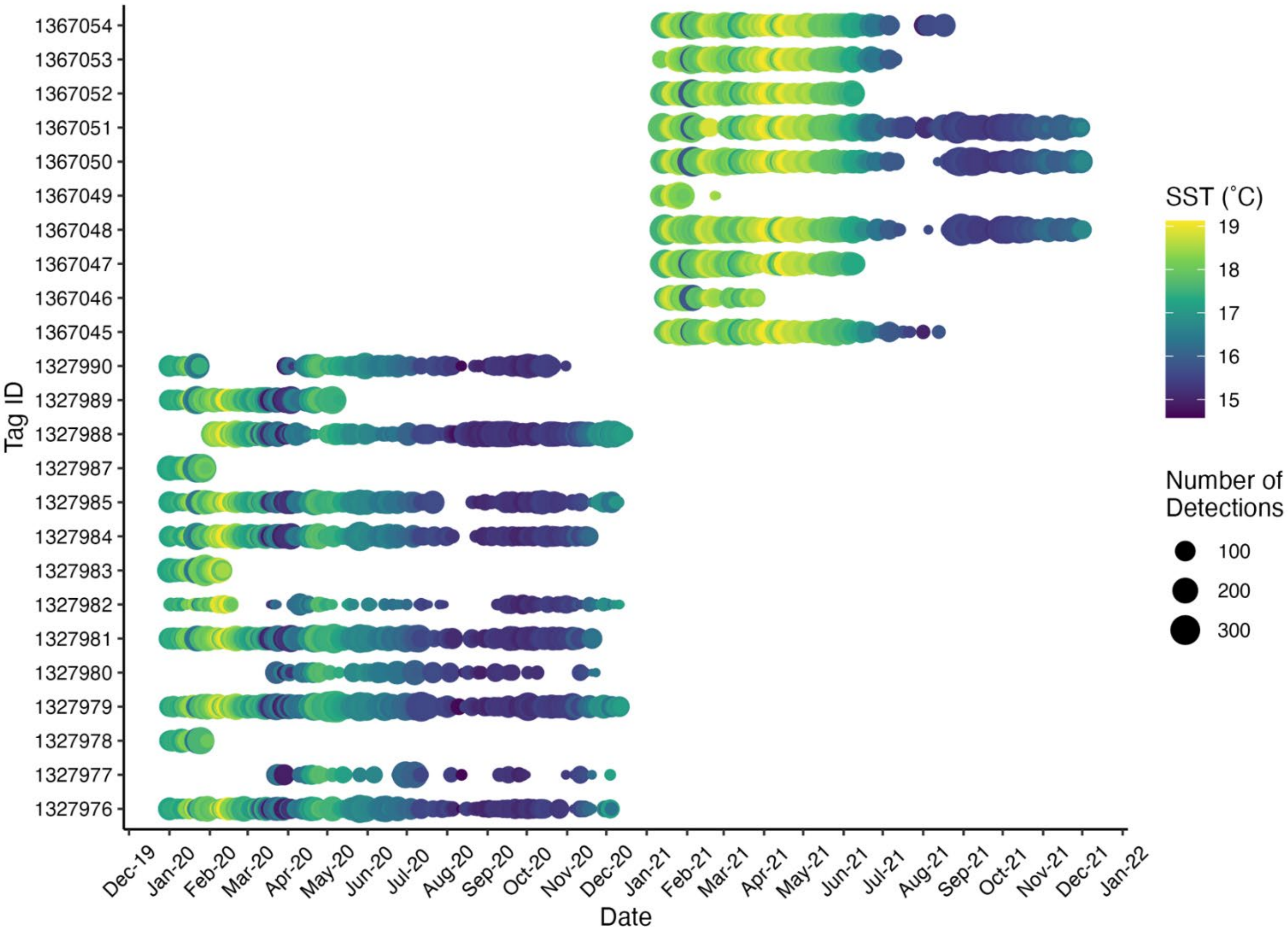

Figure 20. Abacus plot for 25 silver trevally (*Pseudocaranx georgianus;* 15 tagged in October 2019, 397 days battery life; 10 in January 2021, 564 days battery life) from the Neptune Islands Group Marine Park, South Australia between November 2019 and August 2022. Size of point shows number of detections; Colour of point indicates sea surface temperature.

Abundance modelling

For all parameters and all models, I estimated initial values from the simplest time-independent model to reduce convergence issues (White and Burnham, 1999). The most parsimonious model for the IELNE^{MR} had the model structure $p(.)$ σ (0) α (0) N^*(session) N^- (session) for both 2020 and 2021 (Supplementary table 2). Due to the top models containing α fixed at 0, estimates of the population size did not differ from the super-population size, thus only the mean population size was examined in all further analysis. The most parsimonious model for the PLNE^{MR} had the model structure $\varphi(.)$ σ (0) α (.) $\gamma''(.)$ U(session) for both 2020 and 2021 (Supplementary table 2). The most parsimonious model for the IELNE^{AC} had the model structure p(session) σ (.) α (session) N^*(session) N^- (session) for both 2020 and 2021 (Supplementary table 2).

The mean resighting probability estimates (*p*) for the IELNE^{MR} were low for 2020 (< 0.1) and very low for 2021 (< 0.04). Conversley, the resighting probabilities for the IELNE^{AC} were much higher than the IELNE^{MR} estimates of resighting probility for the same sampling occasions. For 2020, IELNE^{AC} resighting probabilities were approximetly twofold greater than IELNE^{MR} estimates ($p = 0.23 \pm 0.02$). For 2021, the IELNE^{AC} were approximetly tenfold greater than IELNE^{MR} estimates ($p = 0.43 \pm 0.04$).

Abundance estimates of silver trevally at the Neptune Islands were variable within and between years (Figure 21). Low number of *in-situ* silver trevally in August and September 2020 resulted in the inability to conduct resighting surveys. Number of silver trevally was also low in those months in 2021, resulting in the lowest abundance estimates. For 2020, The highest estimate was observed in April for the IELNE^{MR}, IELNE^{MR-SP}, IELNE^{MR-AC}, and PLNE^{MR} and in January for the IELNE^{AC} estimates. In 2021, the highest estimates were observed in Febuary and March for all five models. The abundance estimates from the IELNE^{MR} and PLNE^{MR} were consistently higher than the estimates from the IELNE^{AC}, except for January 2020 where estimates were similar. Estimates for IELNE^{MR}, PLNE^{MR} and IELNE^{MR-SP} were mostly similar throughout the study period, but IELNE^{MR-SP} was consistently lower than IELNE^{MR} in 2021.

The coefficient of variation (CV) for the abundance estimates from the IELNE^{AC} and PLNE^{MR} models had the highest variation for 2020 and 2021, respectively (Table 9). The lowest variation was observed for IELNE^{MR-AC} model for both 2020 and 2021 (Table 9). Coefficent of variance for models using Monte Carlo simulations with resighting probability estimates (IELNE^{MR-AC} and IELNE^{MR-SP} was lower in 2020 and 2021 compared to non-integrated models (IELNE^{MR} , IELNE^{AC} and PLNE^{MR}; Table 9).

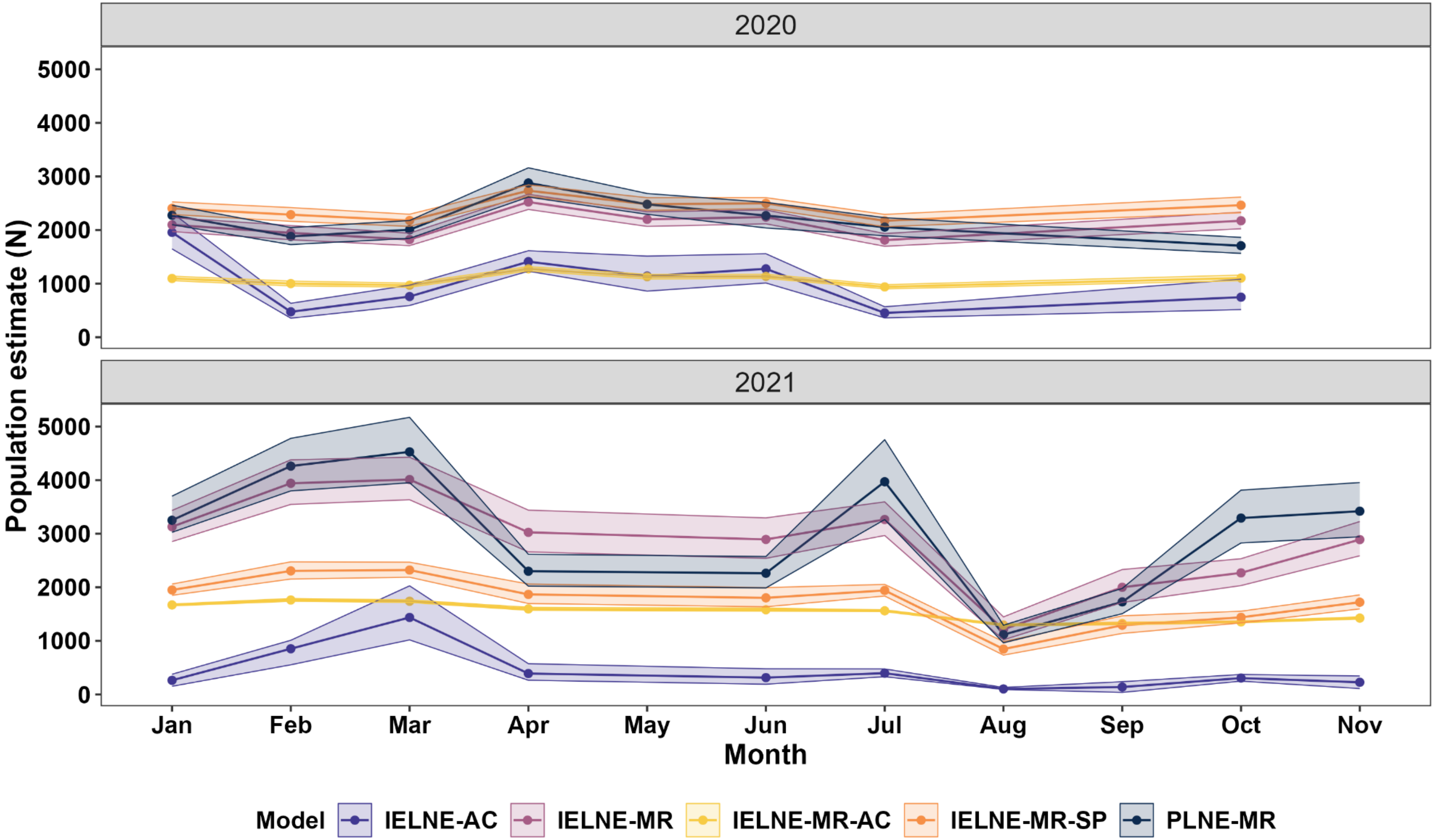

Figure 21. Abundance estimates for silver trevally (*Pseudocaranx georgianus*) from the Neptune Islands Group Marine Park, South Australia, for different mark-resight models: IELNE^{AC}: Acoustically detected individuals within 200 m during surveys, and unmarked silver trevally during surveys. IELNE^{MR} & PLNE^{MR}: ID tagged individuals and untagged individuals during surveys. IELNE^{MR-AC}: IELNE^{MR} model with MCMC simulations using resighting probability from IELNE^{AC} model estimates. IELNE^{MR-SP}: IELNE^{MR} model with MCMC simulations using resighting probability from detected acoustic fish and sighted acoustic fish during surveys. Shaded error bars indicate standard error.

Table 9. Mean abundance estimates with standard error and coefficient of variance (CV) for four mark-resight models for two sampling years (2020; 2021): $\mathrm{IELNE}^{\mathrm{MR}}$ and $\mathrm{PLNE}^{\mathrm{MR}}$: ID-tagged individuals and untagged individuals during surveys. $\mathrm{IELNE}^{\mathrm{AC}}$: Acoustic detections during surveys and untagged individuals during surveys. $\mathrm{IELNE}^{\mathrm{MR\text{-}AC}}$: $\mathrm{IELNE}^{\mathrm{MR}}$ model with MCMC simulations using resighting probability from $\mathrm{IELNE}^{\mathrm{AC}}$ model estimates. $\mathrm{IELNE}^{\mathrm{MR\text{-}SP}}$: $\mathrm{IELNE}^{\mathrm{MR}}$ model with MCMC simulations using resighting probability from detected acoustic fish and sighted acoustic fish during surveys.

Model	2020		2021	
	Mean abundance	CV	Mean abundance	CV
$\mathrm{IELNE}^{\mathrm{MR}}$	2102 ± 84	3.2	2864 ± 270	6.1
$\mathrm{IELNE}^{\mathrm{AC}}$	1027 ± 183	12.3	443 ± 128	6.5
$\mathrm{IELNE}^{\mathrm{MR\text{-}SP}}$	2403 ± 66	2.5	1749 ± 143	4.4
$\mathrm{IELNE}^{\mathrm{MR\text{-}AC}}$	1081 ± 38	2.0	1531 ± 54	2.2
$\mathrm{PLNE}^{\mathrm{MR}}$	2194 ± 130	4.04	3013 ± 356	7.1

Statistical modelling

The top-ranked GAMMS for $\mathrm{IELNE}^{\mathrm{MR}}$, $\mathrm{IELNE}^{\mathrm{MR\text{-}AC}}$, and $\mathrm{PLNE}^{\mathrm{MR}}$ ($w\mathrm{AIC}_c$ = 0.60, 0.61, and 0.23, respectively) included temperature (Table 10). Temperature had a positive linear relationship with abundance across both the $\mathrm{IELNE}^{\mathrm{MR}}$, $\mathrm{IELNE}^{\mathrm{MR\text{-}AC}}$ and $\mathrm{PLNE}^{\mathrm{MR}}$ models (Figure 22). Predicted abundance across the modelling approaches ranged 1,075–3,400 across a temperature range of 15.3–18.7°C (Figure 22). The lack of inclusion of operating days in any of the top-ranked models highlights the lack of influence of the cage-diving industry on the abundance of silver trevally throughout the year.

Table 10. Summary of models testing the effects of temperature and white shark cage-diving on abundance of silver trevally (*Pseudocaranx georgianus*). df, degrees of freedom; AIC_c , Akaike's information criterion corrected for small sample size; LL, log-likelihood; ΔAIC_c , difference in AIC_c between the current and the top-ranked model; $wAIC_c$, model probability; variance explained by R_m, marginal (fixed effects) R^2; R_c, conditional (fixed and random effects) R^2. Top-ranked model indicated in **bold**. Only the top 5 ranked models are presented for table clarity

Model	df	AIC_c	ΔAIC_c	$wAIC_c$	LL	R_m	R_2
$IELNE^{MR}$							
N ~ temperature + 1|month number	**3**	**286.73**	**0.00**	**0.60**	**-137.87**	**0.26**	**0.44**
N ~ temperature + operating days + 1|month number	4	289.03	2.30	0.19	-137.05	0.28	0.47
N ~ temperature	2	290.10	3.37	0.11	-141.20	0.26	0.26
N ~ temperature + operating days	3	292.71	5.98	0.03	-140.82	0.28	0.28
N ~ 1 (intercept only)	1	293.12	6.39	0.02	-144.16	0	0
$IELNE^{AC}$							
N ~ 1|month number	**2**	**37.86**	**0.00**	**0.66**	**-15.08**	**0**	**0.49**
N ~ temperature + 1|month number	3	40.66	2.81	0.16	-14.80	0.14	0.49
N ~ operating days + 1|month number	3	40.95	3.09	0.14	-14.94	0.13	0.48
N ~ temperature + operating days + 1|month number	4	44.03	6.17	0.03	-14.53	0.27	0.48
N ~ temperature	3	48.53	10.67	0.00	-20.41	0.14	0.14
$IELNE^{MR\text{-}SP}$							
N ~ 1|month number	**2**	**264.14**	**0.00**	**0.68**	**-128.21**	**0**	**0.55**
N ~ temperature + 1|month number	3	267.05	2.92	0.16	-127.99	0	0.55
N ~ operating days + 1|month number	3	267.38	3.25	0.13	-128.16	0	0.54
N ~ temperature + operating days + 1|month number	4	270.69	6.56	0.03	-127.86	0	0.54
N ~1 (intercept only)	2	277.49	13.35	0.00	-136.35	0	0
$IELNE^{MR\text{-}AC}$							
N ~ temperature + operating days + 1|month number	**4**	**236.92**	**0.00**	**0.61**	**-110.96**	**0.52**	**0.77**
N ~ temperature + 1|month number	3	237.82	0.90	0.39	-113.37	0.47	0.72
N ~ 1|month number	2	252.47	15.55	0.00	-122.40	0	0.25
N ~ operating days + 1|month number	3	255.69	18.77	0.00	-122.34	0.007	0.24
N ~ temperature	2	256.46	19.55	0.00	-124.37	0.14	0.14
$PLNE^{MR}$							
N ~ temperature	**2**	**18.453**	**0.000**	**0.237**	**-6.826**	**0.12**	**0.12**
N ~ 1|month number	2	18.453	0.000	0.237	-6.826	0	0
N ~ 1 (intercept only)	2	18.808	0.355	0.198	-5.547	0	0
N ~ temperature + 1|month number	3	19.558	1.106	0.136	-4.638	0.12	0.15
N ~ operating days	2	21.291	2.838	0.057	-6.788	0.003	0.003

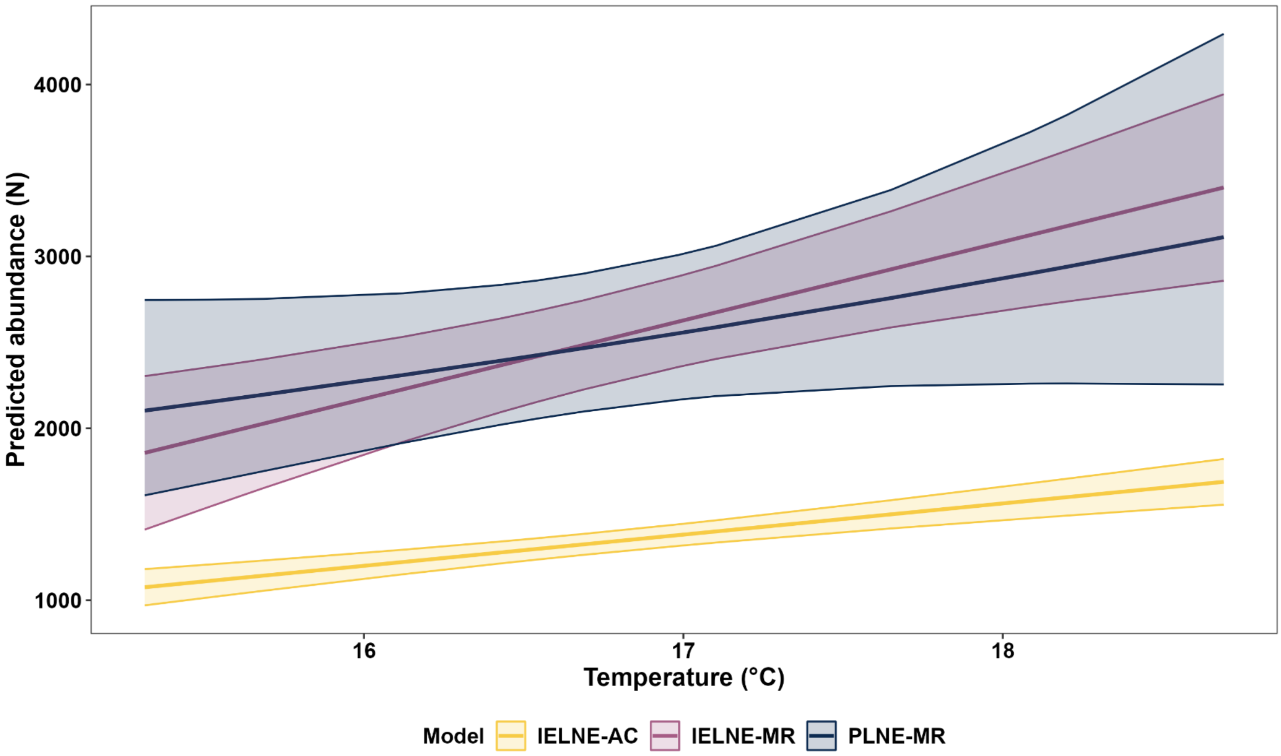

Figure 22. Predicted abundance from Generalised Additive Mixed Models (IELNE^{MR}, IELNE$^{MR\text{-}AC}$, and PLNE^{MR}) for silver trevally (*Pseudocaranx georgianus*) at the Neptune Islands Group Marine Park, South Australia, for temperature (°C). Shaded ribbons indicate 95% confidence intervals.

Biomass estimates

Estimated weights of the 700 randomly sampled silver trevally ranged 0.25–3.9 kg (1.25 ± 0.02 kg; Supplementary figure 1A) based on measured lengths ranging 26–69 cm (45 ± 0.25 cm; Supplementary figure 1B). Biomass estimates of the Neptune Islands silver trevally population varied across months (Figure 23). Biomass estimates for 2020 were lowest in July (2,240 kg) and highest in April (3,085 kg). Similarly for 2021, biomass was lowest in August (1,470 kg) and highest in March 2021 (4,923 kg).

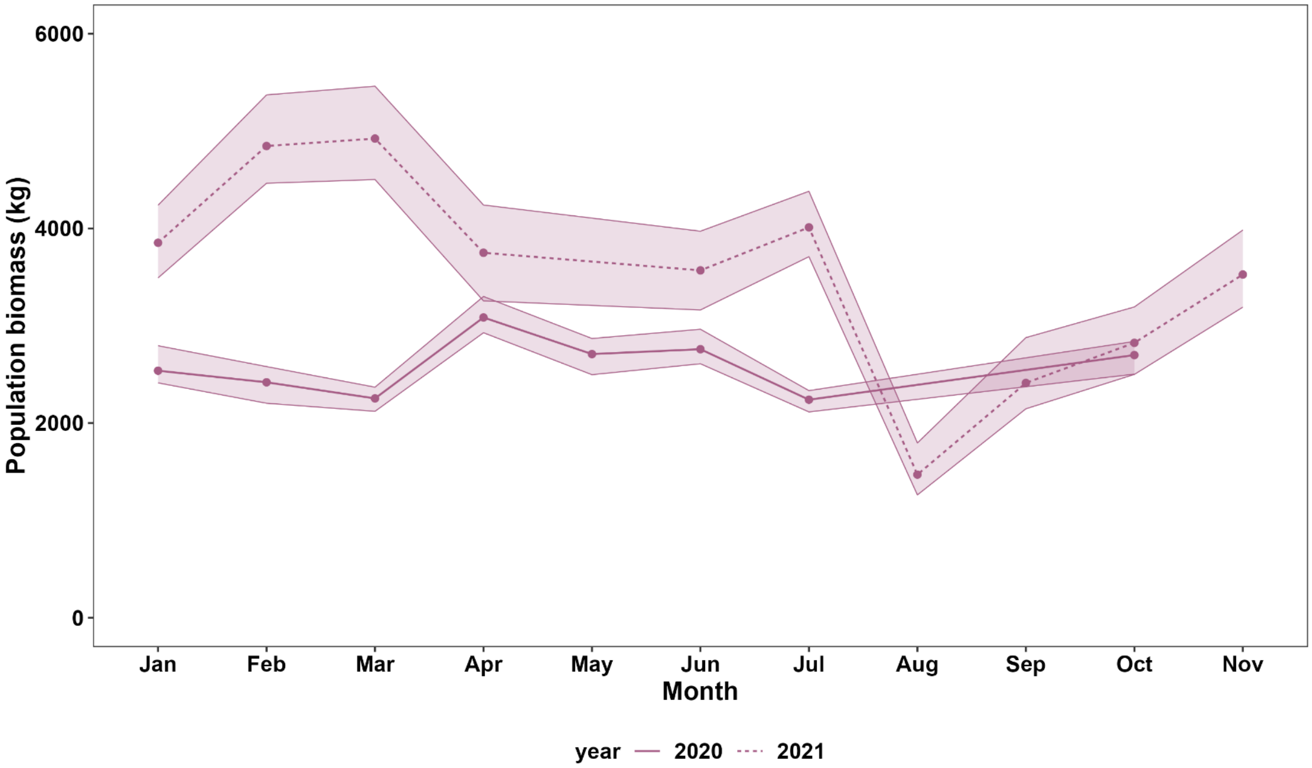

Figure 23. Estimated biomass for silver trevally (*Pseudocaranx georgianus*) from the Neptune Islands Group Marine Park, South Australia calculated from abundance estimates (IELNE^{MR}), and bayesian length-weight relationship (weight = $10^{\log10(0.0141)}$ + 2.96 * $\log_{10}$(length)) calculated for lengths of a randomly caught sample of 700 silver trevally. The weight distribution of the 700 silver trevally was then randomly sampled for the silver trevally abundance estimate for each primary sampling period (i.e., Months). Length-frequency distribution is assumed to be representative of the population. Solid line indicates 2020, dotted line indicates 2021.

4.5 Discussion

I integrated mark-resight modelling and acoustic tracking to quantify the abundance of a non-focal species with access to consistent supplemental food at a wildlife tourism site. The population size of silver trevally at North Neptune Islands is up to ~4,000 individuals, fluctuating between ~850 in winter and ~4,000 in summer. Population size was not affected by the monthly intensity of cage-diving tourism, but increased with temperature, highlighting the complexity in responses to supplemental feeding during wildlife tourism and refuting our hypothesis. Furthermore, this study provides initial population and biomass estimates of a semi-residential benthopelagic fish at an offshore temperate island group with supplemental provisioning.

Resources regulate populations through density-dependent processes, for example, limited resources increases mortality, naturally reducing population size (i.e., resource-related mortality; Zimmermann et al., 2018, Grossman and Simon, 2020, Rindorf et al., 2022). Conversely, an abundance of resources, such as the bait and berley provided by cage-diving operators, can increase reproductive output, accelerate growth, reduce size-at-maturity (McBride et al., 2015), and reduce mortality. Where supplemental feeding is persistent, it increases carrying capacity as seen in in terrestrial ungulates and birds (Schoech and Hahn, 2007, Schoech et al., 2008). Cage-diving tourism has provided an abundance of resources through supplemental feeding (up to 200 kg day^{-1}) for ~200 days year^{-1} since ~2007, likely decreasing resource related limitations and increasing the carrying capacity at the Neptune Islands. While it is not possible to compare the silver trevally population at the Neptune Islands to other areas or offshore islands as no other population estimates are available, the biomass of the silver trevally at the Neptune Islands (~1.5–5 tonnes) represents almost half of the total 2021/2022 commercial catch of silver trevally in South Australia (9 tonnes; Smart et al., 2023). The relatively large biomass and population size (~5 tonnes & ~4000 individuals) of silver trevally at the Neptune Islands compared to the total annual state catches suggests that the Neptune Islands hold an uncharacteristically large, and likely inflated population of silver trevally owing the persistent supplemental feeding from cage-diving operators.

Fluctuations in silver trevally numbers were driven by temperature, rather than cage-diving operations. Silver trevally abundance from the resighting surveys was consistently less in colder months (June–September), to the extent that I could not complete resighting surveys in August and September 2020 due to insufficient numbers of silver trevally, supporting the seasonal variation and low silver trevally abundance obtained from the models during those months. The low winter abundance is further supported by the acoustic telemetry data showing low residency at the Neptune Islands during the same colder months (Chapter 2). Importantly, while the population abundance may be inflated by the supplemental feeding, the lack of effect on monthly abundance from cage-diving operations highlights that current white shark tourism does not prevent natural movements away from the Neptune Islands. Such findings support the continued use of supplemental feeding for wildlife tourism; however, this is contingent on the natural fluctuations from abiotic influences remaining unmuted, as was observed for the silver trevally. Population estimates from this study can also be used to assess interannual shifts in silver trevally abundance and determine whether cage-diving is affecting the population of silver trevally in future years, potentially under different cage-diving management scenarios.

The supplemental feeding from cage-diving operators leads to silver trevally aggregating behind the cage-diving vessels within a ~0.06 km^2 area. With the potential for up to ~4,000 individuals being concentrated within such small area, the density of such aggregations could result in negative effects such as intra-specific competition (Semeniuk and Rothley, 2008), disease transmission (Behringer et al., 2020), physical injuries from impact with vessels and cage-diving equipment (Anders et al., 2019), and increased parasite loading (Brookhouse et al., 2013). For example, silver trevally and yellowtail kingfish aggregations fed bread and pellets by tourists at Lord Howe Island displayed signs of microbial and parasitic infections, stomach ulcers, skin lesions, and physical injury (Brookhouse et al., 2013). Such impacts have not yet been observed at the Neptune Islands (J Dennis, pers. obs.), despite the larger population and concentrations compared to Lord Howe Island (~4,000 versus up to 21 individuals day^{-1}, respecitvely; Brookhouse et al., 2013). This might be due to the water depth and flushing rates at the Neptune Islands being deeper than the site where feeding occurs at Lord Howe Island (25–30 m *versus* 1–2 m, respectively), providing a larger three-dimensional area for silver trevally to avoid direct contact with each other and the seabed, and facilitates flushing of eutrophic water with unhealthy bacteria from uneaten bread and waste. While silver trevally appear externally unharmed at the Neptune Islands, physiological impacts might still be present and should be examined.

Inflating and sustaining increased population size of predators can increase predatory pressures on prey species, extending undue top-down pressure on entire ecosystems, suppressing lower-level prey species particularly when food subsidies are exhausted (Koons et al., 2015, Hradsky et al., 2017, Lamarre et al., 2017, Malpass et al., 2017). Examples of this have been observed in terrestrial predators, with wolf (*Canis lupus*) populations increasing predatory pressure on alternate prey sources upon depletion of a pulsed food sources (Petroelje et al., 2019), and hyenas (*Crocuta crocuta*) depredating on live cattle when food subsidies were scarce (Yirga et al., 2012). At the Neptune Islands, the sustained large abundance of silver trevally could potentially increase predatory pressures on lower-level species when supplemental feeding is not available during operator absences or if the use of bait and berley was reduced through changes in policy and management (Schmidt and Hoi, 2002, Robb et al., 2008). Regardless of direct predation, the presence of large aggregations of predatory fish can alter prey behaviours and ecological processes through the landscape of fear effect (i.e., reduction in grazing time leading to increased abundance of primary producers; Lima, 1998, Freeman, 2006, Laundré et al., 2010). Monitoring of fish communities at the Neptune Islands and other offshore islands between 2015 and 2022 suggests that the broad fish assemblages at the Neptune Islands has not substantially changed (S Whitmarsh, unpublished data).

However, the quantity of bait and berley has also remained similar since 2011 and top-down effects may only become apparent if the supplemental feed is reduced or stopped altogether.

Similar to concerns surrounding the use of bait and berley at the Neptune Islands, one of the primary environmental impacts of open-cage finfish aquaculture is the discharge of solid wastes. Such waste includes uneaten feed and faecal material, causing localised organic enrichment of the seabed and eutrophication in the water column (Buschmann et al., 2009, Bannister et al., 2016, Elvines et al., 2023), leading to poor water quality (Price et al., 2015, Herath and Satoh, 2022), microflora biodiversity (Choi et al., 2022b, González-Gaya et al., 2022), and physio-chemical properties (i.e., sediment–water interactions; Hargrave et al., 1997, Farmaki et al., 2014), and increased algae growth (Findlay et al., 2009, Choi et al., 2022a). Such impacts mirror concerns about large silver trevally aggregations, supplemental feed, and subsequent discharge stemming from cage-diving operations (Chapter 2). Despite these concerns, the large silver trevally population may instead reduce the impacts of the bait and berley on the benthic environment and associated species through eco-moderation. Silver trevally are considered potential eco-moderators, limiting the effects of bait and berley on the diet of other non-focal species at the Neptune Islands by consuming the supplemental feeding at the surface before it reaches the seabed (Meyer et al., 2020). Eco-moderation has also been observed in some aquaculture settings, where non-focal species consume the uneaten feed and organic waste from the farmed finfish, limiting the impacts of excessive nutrient loading on the benthic environment (Felsing et al., 2005, Fernandez-Jover et al., 2011). The high mobility of silver trevally highlighted in Chapter 2 and the interannual variation in their residency combined with the high rates of water circulation at the offshore island might also contribute to minimising the impacts of nutrient loading from bait and berley. Fluctuations in silver trevally abundance and residency could influence the efficiency of impact moderation, particularly in winter when silver trevally numbers and residency are at their lowest (Chapter 2). However, this also coincides with the lowest operator intensity (i.e., ~10 operating days per month). Without assessing the benthic environment at the Neptune Islands for organic enrichment, it is unknown if the coinciding reduction in operations is sufficient to prevent impacts in the absence of silver trevally. As seen with whale falls, while temporary, play important roles in the nutrient cycling of deep-sea habitats (Smith et al., 2019), indicating that even temporary resource pulses can elicit big responses in benthic environments. Future work should assess the benthic habitats at the Neptune Islands throughout the year to determine concentrations of organic material in the sediment. Findings from assessments of organic enrichment would confirm the proposed lack of effect due to silver trevally eco-moderation, while also revealing changes throughout the year in response to cage-diving intensity.

Biases across the multitude of data types and models used for estimating abundance can lead to varying levels of over or underestimation of parameters (McClintock and White, 2009, McClintock et al., 2009b, Sollmann et al., 2013), mandating careful consideration of model selection (Dettloff, 2023). For example, biased resighting probabilities (e.g., from heterogeneity in resighting probabilities, sampling bias, loss of marks, trap shyness) reduce the precision and accuracy of population estimates, limiting the ability of models to detect trends in populations (Johnson et al., 2010). n 2020, mark-resight models with acoustic data integrated (IELNE$^{\text{MR-SP}}$) produced similar estimates and trends to the standard mark-resight models without the integrated acoustic data (IELNE$^{\text{MR}}$ and PLNE$^{\text{MR}}$). This similarity suggests either a lack of or consistent bias across these models. The two-standard mark-resight models (IELNE$^{\text{MR}}$ and PLNE$^{\text{MR}}$) also displayed similar trends and estimates in 2021, but models that used acoustic data (IELNE$^{\text{AC}}$, IELNE$^{\text{MR-SP}}$, IELNE$^{\text{MR-AC}}$) had lower abundance estimates. The lower number of acoustic tags deployed in 2021 (10 *versus* 15 in 2020) may have biased estimates from the models that used acoustic data (IELNE$^{\text{AC}}$, IELNE$^{\text{MR-SP}}$, IELNE$^{\text{MR-AC}}$) as there were insufficient tagged fish to capture the diversity of movement and residency patterns of silver trevally (see Chapter 2). Moreover, the reduced number of tagged individuals potentially increases the sensitivity of surveys to variations in the proportion of all marked individuals being sighted (Alexander et al., 1997, Hammond, 2009, McClintock and White, 2012, Murphy et al., 2019). Bias from low sample would likely lead to underestimates of abundance, as seen in 2021 with the models that used acoustic data (IELNE$^{\text{AC}}$, IELNE$^{\text{MR-SP}}$, IELNE$^{\text{MR-AC}}$). The extent of underestimation is highlighted by the similarity of the mean estimate for the IELNE$^{\text{AC}}$ model in 2021 (~443) and the maximum number of individuals sighted in a single resighting survey (402). In contrast, the standard mark-resight models (IELNE$^{\text{MR}}$ and PLNE$^{\text{MR}}$) produced consistent estimates between models and are based on a larger sample size of marked individuals which is consistent across years (i.e., 350 per year). Tagging identical numbers of individuals reduces differences between years, meaning variations in interannual estimates likely represent natural variations in the population rather than over- or underestimates. This is highlighted by the greater difference in mean estimates between sampling years for the acoustic model (IELNE$^{\text{AC}}$, ~56% decrease), compared to the standard mark-resight models (IELNE$^{\text{MR}}$ and PLNE$^{\text{MR}}$, ~26% increase). As such, these models present with fewer or less apparent biases compared to acoustic-based models and produced greater consistency between models and sampling years. Different forms of bias will always be present in population estimates (Tucker et al., 2019), with method or model selection based on that which contains the least. Thus, based on consideration of the models used here, the standard mark-resight models (i.e., visually sighted tags) present the lowest effects of bias and greatest consistency, likely representing the 'truest' abundance estimates.

4.6 Conclusions

Supplemental feeding provides both target and non-target species with increased resources, which can affect population abundance and individual behaviour. This study quantified the abundance of silver trevally at a wildlife tourism site with supplemental feeding, identifying intra-annual variation linked to environmental variability rather than impacts from cage-diving intensity. Notably, the intra-annual variations in population size linked to thermal cues indicate the bait and berley are not muting environmental cues or suppressing natural behaviours. Additionally, I provide the first population and biomass estimate of a semi-residential benthopelagic fish at an offshore temperate island group which was previously limited to anecdotal observations. Estimates of silver trevally abundance were produced from five different estimator models, highlighting how standard mark-resight modelling approaches can still present with less biases and greater precision than methods integrating multiple data types. Future research should continue to monitor the abundance of silver trevally at the Neptune Islands to determine if the overall population size is increasing over time, but also assess the benthic environment for organic enrichment to confirm the absence of impact. Findings from this study provide abundance estimates for a non-focal species exposed to supplemental feeding, highlighting the large number of silver trevally interacting with cage-diving vessels. Given the potential negative impacts of inflated abundance on both the affected population and associated environment, initial abundance estimates of non-focal species allows future monitoring to detect changes in the population through time. Using these initial estimates, management can implement strategies, if needed, to reduce impacts on non-focal species (i.e., reduce provisioning) or impacts resulting from increased abundance of non-focal species (i.e., reduce population size), ensuring the ecological sustainability of wildlife tourism industries.

CHAPTER 5

Impacts of supplemental feeding on the growth, body condition, and fatty acid profiles of silver trevally (*Pseudocaranx georgianus*)

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5.1 Abstract

Many wildlife tourism industries use supplemental food to attract focal species, but smaller, non-focal animals can also consume the food provided and be negatively impacted. At the Neptune Islands Group Marine Park, South Australia, bait and berley are used to entice white sharks (*Carcharodon carcharias*) close to cage-diving operators, but silver trevally (*Pseudocaranx georgianus*) are also attracted and form large aggregations around these vessels. Silver trevally feed on the bait and berley which affects their diet and movements (i.e., residency and spatiotemporal distribution), and could also impact their health and energy budgets. I assessed the growth (n = 604), body condition (n = 700), and diet (n = 46) of silver trevally at the Neptune Islands to determine whether the effects of supplemental feeding extend beyond diet and movements. Trevally at the cage-diving site were 15% and 46% larger than silver trevally from offshore and coastal locations, respectively. However, body condition (measured by bioelectrical impedance analysis) and mortality rate was similar across locations, suggesting that the surplus of energy from supplemental feeding is devoted to somatic growth. Higher levels of fatty acids (eicosapentaenoic acid and oleic acid) which facilitate growth were present in the diet of silver trevally from the Neptune Islands, likely contributing to the increased growth. My findings show that supplemental feeding can influence the growth of a non-focal pelagic fish, highlighting the importance of accounting for non-focal species in the management of supplemental feeding practices. Furthermore, I provide the first evidence of responses in the growth of a semi-resident benthopelagic fish at an offshore temperate island group exposed to supplemental feeding.

5.2 Introduction

Humans intentionally feed wildlife to aggregate animals for management and recreational purposes by providing food above and beyond naturally available resources (Murray et al., 2016). For example, supplemental feeding is widely used by managers (Dubois and Fraser, 2013) to support declining, depleted, or endangered populations that may be resource-limited (i.e., food supplementation; Ewen et al., 2015, Heard and Zimmerman, 2021) or divert wildlife away from unsuitable areas or reduce human wildlife interactions (i.e., diversion feeding; Conover and Conover, 2022). Supplemental feeding is also a popular means to increase the likelihood of encountering wildlife. For example, feeding stations can increase density of game species for hunters (i.e., ~2.8 trillion tonnes of shelled corn is provided to big game ungulates every year in the U.S; Oro et al., 2013, Murray et al., 2016), food is provided for wildlife watching (i.e., bird watching; Valentine and Birtles, 2004, Dayer et al., 2019), and in tourism to generate consistent, predictable, and up-close encounters with wildlife (Meyer et al., 2022). Feeding from these supplemental food sources can exceed the caloric intake required to meet daily requirements (Brunnschweiler et al., 2018), thus providing surplus energy leading to increased fat stores and accelerated growth (Silva et al., 2020). However, supplemental feeding can also have damaging impacts when the feed is of low nutritional value and disrupt foraging behaviours or the consumption of natural food sources. For example, the common practice of feeding ducks and other waterfowl with bread greatly impacts the individual's nutrition and body condition (Burt et al., 2021). Supplemental feeding can also facilitate behavioural impacts, including changes in movement and residency (Maljković and Côté, 2011, Brookhouse et al., 2013, Shlepr et al., 2021, Clarke et al., 2022, Senigaglia et al., 2022), predator-prey dynamics (Maynard et al., 2020), abundance and concentration of individuals leading to pathogen transmission (Becker and Hall, 2014, Becker et al., 2015), and risk of physical injury (Brookhouse et al., 2013).

The acquisition and use of energy is an underlying process that drives every component of a fish's life cycle from larvae to death, guided by the delicate balance of their energy requirements. Energy budgets balance the energy assimilated through food, with energy lost through metabolic processes (i.e., growth, cell repair, gamete development) and used across various activities (e.g., daily and large-scale migratory movements, courtship behaviours, predator avoidance, and parental care; Soofiani and Hawkins, 1985). Despite many processes requiring energy, it is a finite resource. As such, an individual's growth (Metcalfe, 1986), survival (Naidoo and Glassom, 2019), and fecundity (Marshall, 2007) are determined by the allocation of energy, with each component of the energetic budget having its own requirements at different temporal scales (Soofiani and Hawkins, 1985, Muller et al., 2019). For example, during early life, juvenile fish are exposed to high rates of size-related mortality, resulting in the prioritisation of energy allocation to growth to increase survival (Post and Parkinson, 2001, McBride et al., 2015). Once individuals approach the size of maturity, energy allocation shifts, with surplus energy devoted to reproductive growth (i.e., maturation, production of gametes) and behaviours (i.e., courtship, parental care, migration to spawning grounds), rather than somatic growth (Marshall, 2007). Such energy shifts can be observed during spawning periods of some marine fishes, whereby the high energy demand of reproductive processes results in a reduction of available energy for somatic growth and repair, with reduced energy acquisition causing a decline in the overall condition of individuals (Fordham and Trippel, 1999, McBride et al., 2015). Surplus energy not devoted to metabolism, reproductive processes, or somatic growth is allocated as storage (i.e., fat stores in the muscle, liver, or mesenteric fat; Moraes and de Almeida, 2020). Fat storage is vital to counteract fluctuations in food availability (i.e., seasonal or interannual cycles; Pérez-Jiménez et al., 2012), as fat is accumulated in times of high resource availability to increase survival during subsequent periods of resource scarcity (Post and Parkinson, 2001, Stallings et al., 2010). Therefore, individuals that maximise energy stores reduce their susceptibility to resource-related mortality and, as a result, maximise their fitness (Post and Parkinson, 2001, Willis and Hobday, 2008).

With the health of fish inherently linked to the input and output of energy, supplemental feeding has the potential to influence physiological functions of animals (Cowey and Sargent, 1972, Hardy and Kaushik, 2021). Many wildlife tourism industries use supplemental food similar to the natural prey items of focal species (Brunnschweiler et al., 2018, Barry et al., 2023), but such items are unlikely to represent the natural diets of smaller, non-focal animals that can also consume these provisional food sources. This change in diet has the potential to cause deficiencies in essential nutrients (i.e., fatty acids, amino acids, vitamins, minerals; Hardy and Kaushik, 2021), preventing optimal physiological functioning (Sawyer et al., 2016). For example, polyunsaturated fatty acids (PUFA) are particularly important fatty acids, playing a myriad of structural and functional roles, including being major components of the brain and nervous system, and are key regulators (metabolic and physiological) of growth, development, reproduction, and health (Chow, 2007). As such, all vertebrate species have a dietary requirement for certain PUFAs, whereby a dietary deficiency can result in stunted growth, limited reproductive success, disease, and death, making them essential components of fish nutrition (Sargent et al., 1995). With these PUFAS playing key roles in health and functioning of physiological processes, changes in diet through wildlife tourism could result in negative consequences for the impacted individuals.

At the Neptune Islands Group Marine Park (South Australia, Figure 24), two cage-diving operators use a near-continuous berley plume consisting of minced southern bluefin tuna (*Thunnus maccoyii*) and tethered baits (southern bluefin tuna gills and stomachs; Bruce and Bradford, 2013) to entice and aggregate white sharks within view of the cage-diving tourists (Huveneers et al., 2017b, Meyer et al., 2020, Clarke et al., 2022). Intentionally feeding white sharks is prohibited by industry regulations (DEW, 2016), and the berley particles are too small to be consumed by white sharks. However, large aggregations of highly resident silver trevally (*Pseudocaranx georgianus*) consume the bait and berley used by the operators (Chapter 2). Biochemical profiles and stomach content analysis show that the diet of silver trevally at the Neptune Islands shifted due to the consumption of bait and berley (Meyer et al., 2020). Additionally, silver trevally at North Neptune Islands (where most of the cage diving occurs, hereafter North Neptunes) use less space (m^3) and spend more time in close proximity to cage-diving operators across daily and weekly temporal scales, but activity (inferred via acceleration) was not affected (Chapter 2). Previous wildlife tourism studies suggested that in instances of increased activity, additional food intake might be required for these species to compensate for heightened energy expenditure resulting from interacting with tourism operations (Barnett et al., 2016, Barry et al., 2023, Clarke et al., 2023). However, with the activity of silver trevally not being affected by tourism and the near-continuous consumption of bait and berley, silver trevally may be susceptible to improved physiological condition and faster growth due to a surplus in available energy (Chapter 2).

Here, I investigated the effects of supplemental feeding from white shark cage-diving tourism on the growth, body condition, and fatty acid profiles of silver trevally at North Neptunes, South Australia, across multiple years (2016–2022). Specifically, I aimed to 1) assess the age-at-length structure and mortality of silver trevally at North Neptunes compared to control locations with similar coastal and offshore habitats, but without supplemental feeding; 2) measure changes in the body condition of silver trevally exposed to supplemental feeding; and 3) compare the fatty acid profiles of silver trevally at North Neptunes to the control locations to investigate if fatty acids associated with supplemental feeding can explain any changes in growth and body condition. Based on suggested surplus energy for the silver trevally and physiological effects observed in similar non-focal species, I hypothesised that 1) silver trevally at North Neptunes have a higher growth rate and grow to larger sizes at the same age as silver trevally from control locations; 2) body condition of silver trevally at North Neptunes is higher due to feeding on bait and berley; 3) shifts in diet from natural prey to bait and berley result in an increase in essential fatty acids that supports faster growth and improved body condition.

5.3 Methods

Study site and sample collection

I collected silver trevally from March 2016 through June 2022 at the Neptune Islands Group Marine Park (-35° 13' 48", 136° 4' 12", Figure 24) and at comparable control locations of similar depth and habitat but without cage-diving (Figure 24). I categorised locations into three habitat types: *North Neptunes*, *offshore* (silver trevally caught at offshore islands or reefs > 15 km from the mainland), and *coastal* (silver trevally caught < 15 km from the mainland, or within Gulf St Vincent or Spencer Gulf; Figure 24). I caught silver trevally via hook-and-line from research and cage-diving vessels or obtained silver trevally from recreational and commercial fishers. I recorded fork length (FL) and total length (TL) from each silver trevally, which I then used for growth (n = 604), body condition (n = 700), and fatty acid (n = 46) analyses.

Otolith preparation and increment analysis

I removed sagittal otoliths, rinsed them with water and air-dried them. I embedded otoliths in clear epoxy resin and thin-sectioned (~300 µm) them through the primordium (i.e., core) using a single-blade low-speed sectioning saw (IsoMet Low-speed precision cutter, Buehler, Illinois, USA). I mounted sections on glass slides, polished them using diamond sanding discs (15 microns, 600 mesh) and viewed them using a stereo microscope (2.5× magnification; Olympus SZX7, Olympus Corp., Tokyo, Japan) under both reflected and transmitted light. To ensure aging accuracy and count reproducibility, I trained the reader with a reference library containing 100 otoliths of known ages prior to aging otoliths. Age at capture of the fish caught for this study were within the age range for otoliths in the reference library. I double-blind aged all otoliths. A second trained reader aged a subset of the study samples to assess the precision of age estimates. Annual deposition of growth bands has been validated in silver trevally using bomb radiocarbon (Kalish and Johnston, 1997), marginal increment analysis (Farmer et al., 2005), and oxytetracycline (Rowling and Raines, 2000). These validations confirm that each growth increment, composed of a translucent zone and an opaque zone, represents one year of growth. I assigned a birthdate of January 1 based on the timing of spawning for silver trevally (spring–autumn; James, 1984). I followed protocols detailed in Walsh et al.

(2014), with zone counts converted to decimalised age based on the date of capture, nominal birth date, and date of increment formation (Panfili et al., 2002) for subsequent growth analysis.

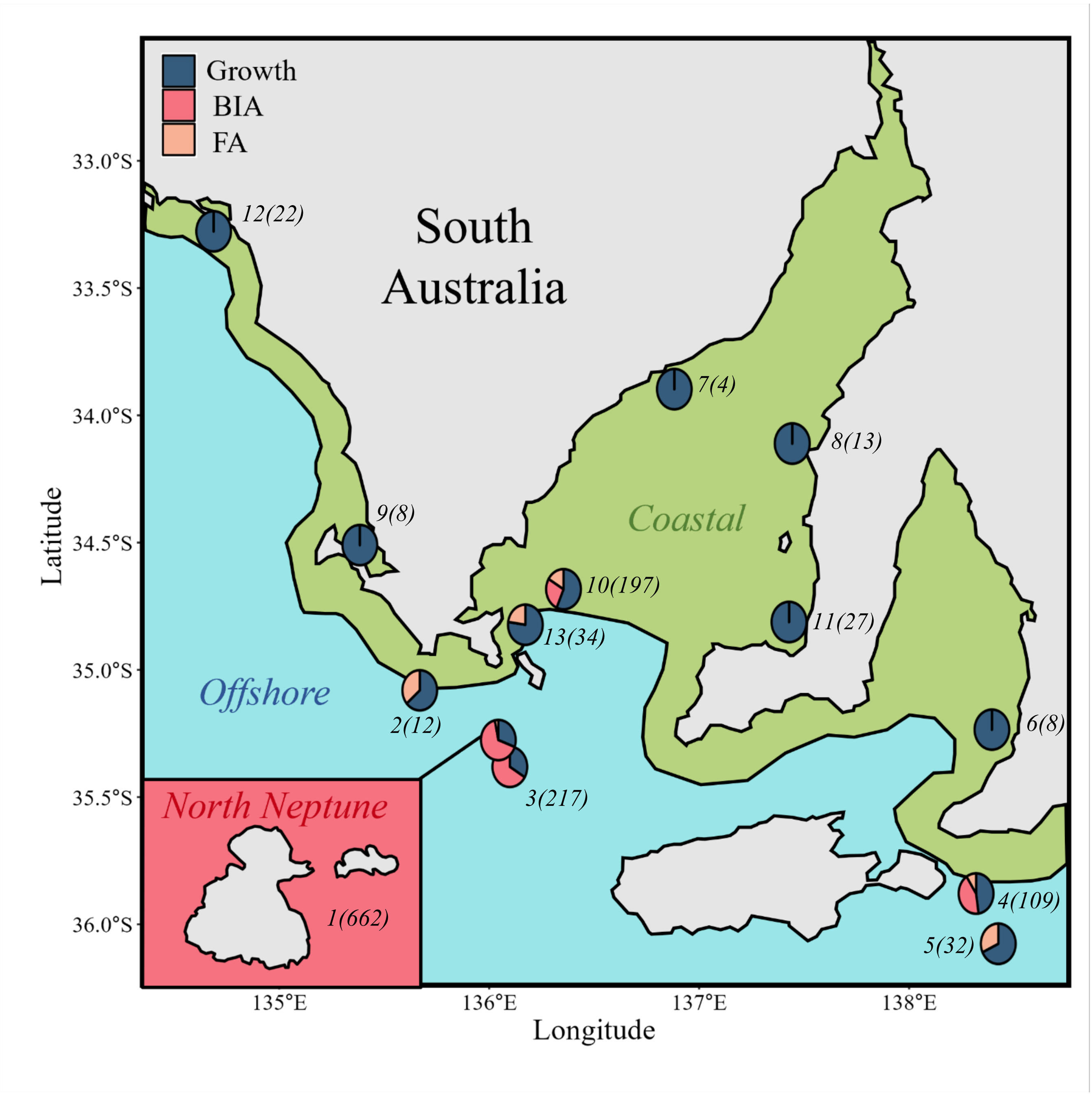


Figure 24. Map of silver trevally (*Pseudocaranx georgianus)* collected from different sampling locations in South Australia, and (inset), the Neptune Islands Group. Coloured regions indicate habitat types, North Neptunes (red), Offshore (blue), and Coastal (green). Icons indicate proportion of samples for different analysis types (Growth = length-at-age analysis, BIA = Bioelectrical Impedance Analysis, FA = Fatty acid analysis). Numbers indicate location ID; Parentheses indicate total number of samples for that location (n). 1 = North Neptune, 2 = Liguana, 3 = South Neptune, 4 = The Pages, 5 = Saunders Bank, 6 = Aldinga, 7 = Arno Bay, 8 = Cape Elizabeth, 9 = Coffin Bay, 10 = Dangerous Reef, 11 = Point Turton, 12 = Port Kenny, 13 = The Passage.

Growth analysis

I conducted all analyses in the R statistical environment (version 4.2.1; R Core Team 2016). I used a multi-model approach using the `AquaticLifeHistory` package (Smart et al., 2016), where estimates of growth parameters for all individuals from each sampling location were derived by fitting length-at-age data with the von Bertalanffy growth model (Von Bertalanffy, 1938, Beverton and Holt, 1957):

$$L_a = L_\infty - (L_\infty - L_0)e^{-ka},$$

the logistic growth model (Tsoularis and Wallace, 2002),

$$L_a = \left(L_\infty L_0 e^{ka}\right) / \left(L_\infty - L_0\left(e^{ka} - 1\right)\right),$$

and the Gompertz growth model (Tjørve and Tjørve, 2017),

$$L_a = L_0 e^{\left(log(L_\infty/L_0)(1 - e^{-ka})\right)},$$

where L_a is the length-at-age a, L_0 is the length-at-birth, *k* is the growth completion parameter, and L_∞ is the asymptotic length. The *k* parameter cannot be compared between models as it is unique to each (Smart and Grammer, 2021). I fixed length-at-birth (L_0) at 5 mm for all models based on the larval size of silver trevally (Syahailatua et al., 2011). I selected the most parsimonious growth model using the Akaike Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson, 2004) and the bias-corrected relative weight of evidence for each model, AIC_c weight, where the smaller the weight, the lower the probability the model was 'true' (Burnham and Anderson, 2004). I compared differences in growth between habitats using a likelihood-ratio chi-square test on data with age ranges truncated to the smallest maximum age between habitats (Ogle, 2018). I estimated total annual mortality (*A*) using regression method catch curve analysis of age data for each habitat type using the `FSA` package in the R statistical environment (Ogle, 2018). Selective sampling occurred during the collection of samples from North Neptune Islands to ensure overlapping sample size ranges as control locations, and thus, the age structure did not represent a random sample of catch for that population. I used an age-length-key constructed from the aged samples from North Neptune Island, assigning ages based on the measured lengths of a random catch of 700 silver trevally sampled as part of a mark-resight study concurrent with the present (Chapter 4), using the `FSA` package and following procedures outlined in Ogle (2018). I used the resulting age structure to produce mortality estimates for North Neptune Island (termed North Neptune unaged; Supplementary figure 2). I then compared differences in mortality estimates between habitats using an analysis of variance (ANOVA) test (Ogle, 2018).

Body condition analysis

I quantified body condition of silver trevally using Bioelectrical Impedance Analysis (BIA). I collected three replicate BIA measures along the dorsal musculature of silver trevally on a non-conductive measurement mat using the Seafood Analytics Certified Quality Reader (BIA tool; Certified Quality Foods, Inc., United States of America). I calculated the mean of replicate measurements for each silver trevally. I assessed for variation between replicate BIA measures to identify error values (i.e., insufficient contact between probes and silver trevally), with replicate measures > 2° deemed outliers and excluded prior to calculating the mean. Bioelectrical Impedance Analysis measures two paths of electrical current: resistance (R) and reactance (X_c). Resistance reflects extracellular material (i.e. fat), which is non-conductive and is indicated by higher measurements of R (Cox and Heintz, 2009, Cox et al., 2011). Reactance is a measure of the total volume of healthy cells, indicated by the ability of a substance to hold a charge (Hartman et al., 2015). I derived values of the electrical phase angle from measurements of R and X_c obtained using the BIA tool. Phase angle (degrees) is a measure of the angle between the R and X_c vector components of impedance, ranging from 0°to 90°:

$$\text{Phase angle } (°) = \left(\arctan\left(\frac{\mathrm{X}_c}{\mathrm{R}}\right)\right) \times \frac{180°}{\pi} \cdot$$

High phase angle represents good body condition (Willis and Hobday, 2008), and is a measure that has been used as a proxy to infer the body condition of teleosts (Willis and Hobday, 2008, Hartman et al., 2015, Champion et al., 2020, Clarke et al., 2023). I used Generalised Additive Mixed Models (GAMMs) to test the effect of bait and berley on the body condition of silver trevally, testing the effect of *habitat*, *Length* (fish total length), and *month* on the phase angle of silver trevally:

$$\text{Phase angle } (°) \sim \text{Habitat} + \text{Length}_{\text{smooth}} + \text{Month}_{\text{cyclic}}$$

Prior to modelling, I tested the correlation between water temperature recorded by acoustic receivers (Chapter 2) and month using the 'cor.test' function in the `mgcv` package (version 1.8-40; Wood and Wood, 2015). These variables were highly correlated ($p \geq 0.05$; $r > 0.6$), so I excluded temperature from subsequent models and kept *month* as a cyclic, random variable. I created models using the 'gam' function in the `mgcv` package. I selected the most appropriate statistical family and transformation through visual inspection of residuals and distribution of the response variable. I selected the most parsimonious model and used the contributions of the fixed effects (marginal R^2, R_m) and the fixed and random effects (conditional R^2, R_c) to explain the variance of the response variable when added to the model (Nakagawa and Schielzeth, 2013).

Fatty acid analysis

I measured the silver trevally and sampled the muscle from the dorsal musculature which was immediately frozen (−4°C), transported to the laboratory, and freeze-dried for subsequent fatty acid analysis. I weighed approximately 0.025 g of dried muscle per individual into 20 mL glass test tubes for fatty acid extraction by direct transmethylation (Parrish et al., 2015). I soaked tissue in 3 mL of 10:1:1 methanol:dichloromethane:hydrochloric acid solution at 80°C for two hours. After the two-hour solvent soak, I removed the samples from the heat and cooled to ambient temperature before the addition of 1 mL of milli-Q water and 1.8 mL of 2:1 hexane:dichloromethane solution, followed by vortex mixing and centrifuging at 2000 RPM for 5 minutes. I removed the upper layer containing the fatty acid methyl esters (FAMEs) which I removed and placed into 2 mL glass vials. I placed vials under nitrogen gas streams to evaporate the solvent, leaving pure FAMEs. I repeated the addition of 1.8 mL of hexane:dichloromethane solution and dehydration with nitrogen gas three times, maximizing the FAME retention. I suspended the FAMEs in 1 mL of dichloromethane for subsequent quantification and identification using Gas Chromatography Mass Spectrophotometry (GCMS) analysis with an Agilent Technologies 5975C Series GC/MSD (Agilent Technologies, Inc., USA) equipped with Triple-Axis HED-EM Detector, SGE Analytical Science (Ringwood, Victoria, Australia) BP21 capillary column (15 m length, 0.25 mm internal diameter, and 0.25 µm film thickness), Agilent 7683B Series Injector, and Agilent/HP 7683 automatic liquid sampler. I performed quality checks throughout the analysis with a blank sample containing 1 mL dichloromethane at the start of each run, plus an internal fatty acid standard (C4-C24) (Sigma-Aldrich, USA). I analysed the output, processing using MassHunter Qualitative Analysis software and the National Institute of Standards and Technology Institute (NIST; https://www.nist.gov) database of fatty acid compounds. I reported Individual fatty acid values as a percentage of the total fatty acids per sample analysed, and those contributing <0.1 % were removed from the dataset. I used Canonical analysis of principal coordinates (CAP) to visualise differences in fatty acid profiles between North Neptunes, coastal and offshore habitats. I quantitatively tested for differences between habitat types using PERMANOVAs, and contribution to variance using SIMPERs in PRIMER (version 7, with PERMANOVA+ add-on).

5.4 Results

Growth analysis

I aged a total of 604 silver trevally, 207 from North Neptunes, 233 from coastal locations, and 164 from offshore locations (Supplementary table 3), with the size of silver trevally ranging from 184–740 mm (mean ± standard error: North Neptunes 477 ± 7.7 mm; coastal 316 ± 3.4 mm; offshore 376 ± 7.5 mm; Figure 25A). Age range varied between habitat types, ranging from 2.42–16.42 years old for North Neptunes, 1.25–10.25 for coastal, and 2.5–16.92 for offshore (Figure 25B). The top-ranked models for each habitat type indicated that the von Bertalanffy growth model was the most parsimonious model (all location $w\text{AIC}_c = 1$), and thus was used for all subsequent estimates of growth parameters. Estimates of von Bertalanffy growth parameters for silver trevally at North Neptunes were significantly different to both coastal ($\chi^2 = 227.88$, $p < 0.001$; Figure 26) and offshore habitats ($\chi^2 = 80.48$, $p < 0.001$; Figure 26), but also between coastal and offshore habitats ($\chi^2 = 42.99$, $p < 0.001$; Figure 26). Trevally from North Neptunes had a similar growth rate to those from offshore habitats (Table 11) but has a higher asymptotic length than both the offshore and coastal fish (Table 11). Coastal silver trevally grew faster than both North Neptunes and offshore fish (Table 11) but had the smallest asymptotic length (Table 11). Separation in growth curves between North Neptunes and control locations began at approximately one years old for offshore silver trevally, and 2.5 years old for coastal silver trevally. Offshore silver trevally reached L_∞ at 16 years, with North Neptune silver trevally 75 mm larger at the same age. Similarly, coastal silver trevally reached L_∞ at 10 years, with silver trevally from North Neptune 216 mm larger at the same age (Figure 26). Finally, I estimated total annual mortality (*A)* for each of the habitat types, with no significant difference in mortality at North Neptune (34.99%) compared to offshore (39.16%; $F_1 = 2.3$, $p = 0.14$; Figure 27) and coastal (42.98%) habitats ($F_1 = 0.72$, $p = 0.4$; Figure 27).

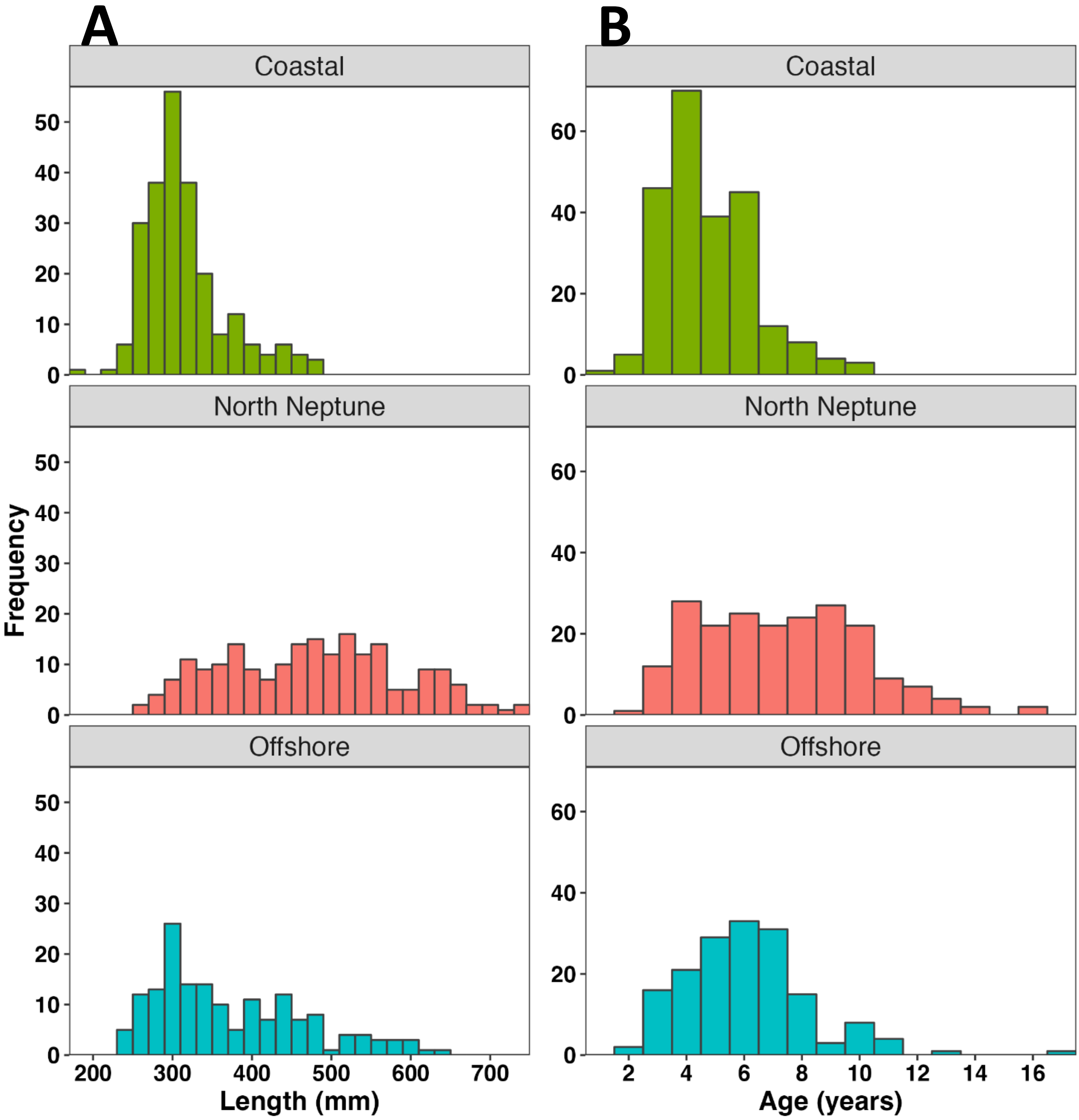


Figure 25. A: Size, and **B:** Age structures, for silver trevally (*Pseudocaranx georgianus)* sampled across different habitat types in South Australia. Coastal n = 233 (8 locations), North Neptune n = 207 (1 location), Offshore n = 164 (5 locations) Bin widths 25 mm and 1 year, respectively.

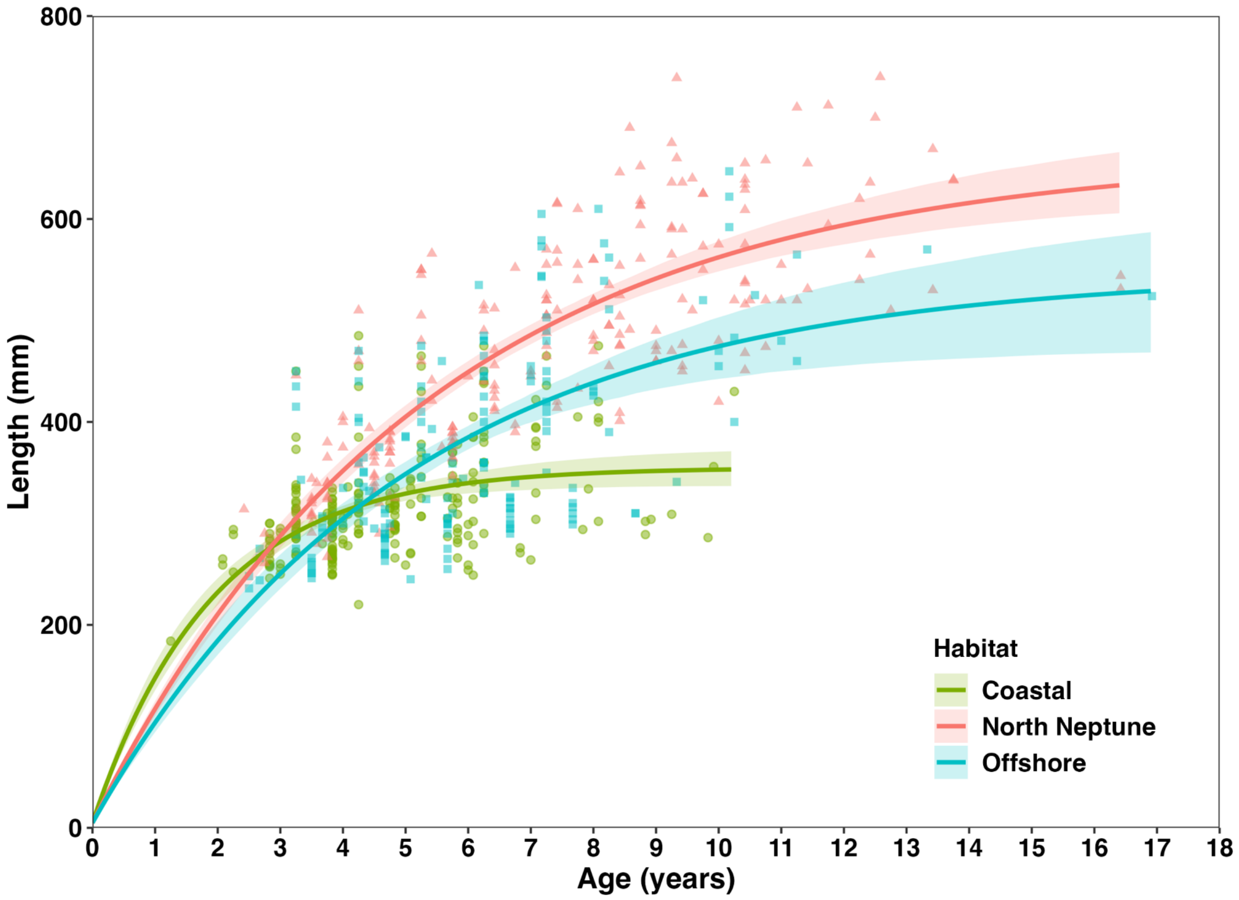


Figure 26. Von Bertalanffy growth curves for silver trevally (*Pseudocaranx georgianus*) for different habitat types from South Australia. Circle points and solid line indicate Coastal habitat; triangle points and short dash indicate North Neptune habitat type; square points and long dash indicate Offshore habitat. Coastal n = 233 (8 locations), North Neptune n = 207 (1 location), Offshore n = 164 (5 locations).

Table 11. Estimates of von Bertalanffy growth parameters for silver trevally (*Pseudocaranx georgianus*) collected from different habitat types in South Australia during 2016–2022. The parameters include the asymptotic length (L_∞) and the growth coefficient (k). SE indicates standard errors of the mean.

Habitat	$L_\infty \pm$ SE	k ± SE
North Neptunes	664.00 ± 16.44	0.19 ± 0.01
Offshore	547.04 ± 30.13	0.20 ± 0.02
Coastal	354.80 ± 6.65	0.52 ± 0.04

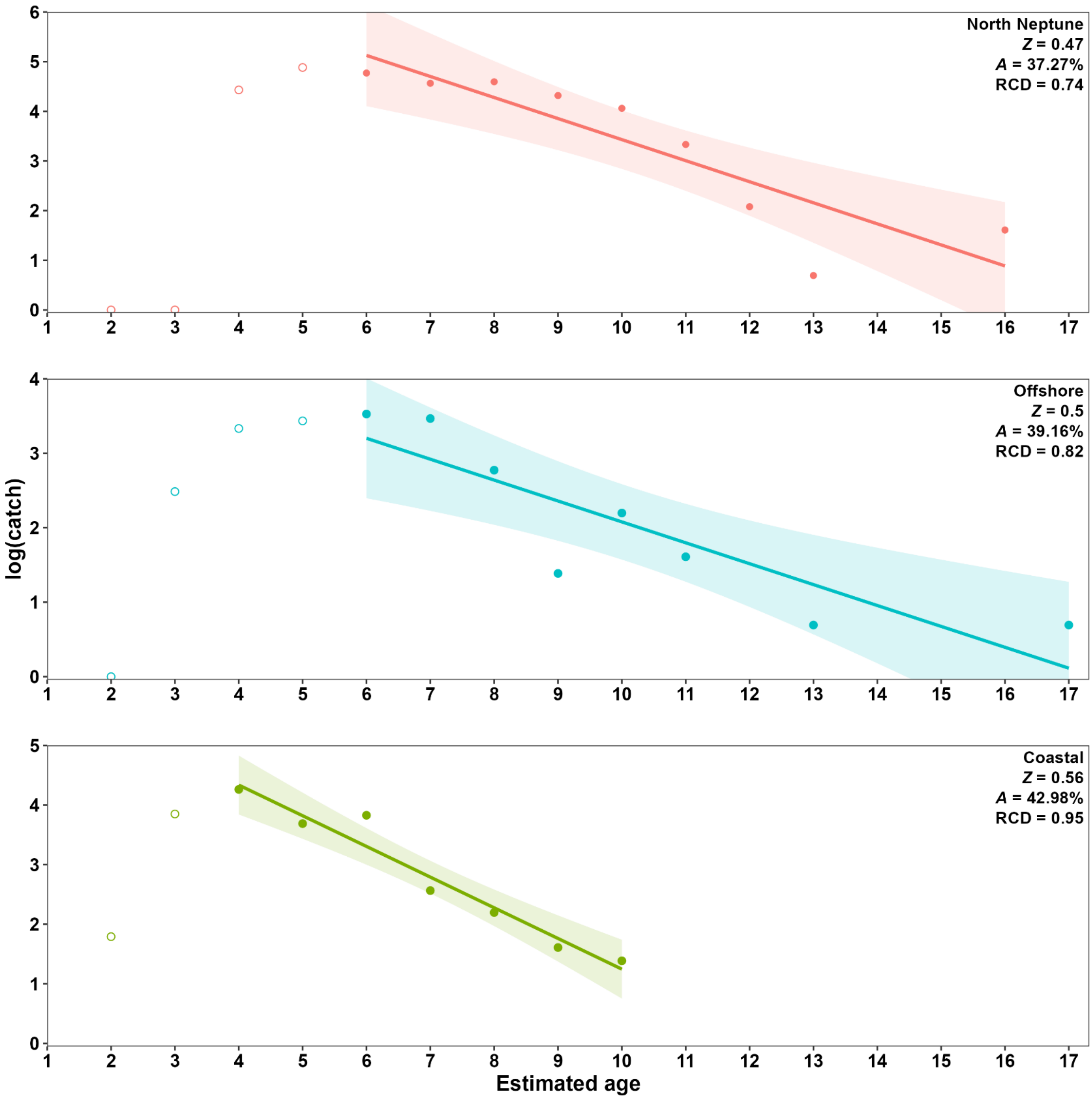


Figure 27. Catch-curves indicating mortality of silver trevally (*Pseudocaranx georgianus)* sampled from different habitat types from South Australia. Hollow points indicate estimated ages not used for mortality estimates. Solid points indicate estimated ages used for mortality estimates. Coastal n = 233 (8 locations), North Neptune n = 700 (1 location), Offshore n = 164 (5 locations).

Body condition

I measured body condition of 700 silver trevally, 449 at North Neptunes, 60 at coastal locations, and 191 at offshore locations (Figure 24). Body condition (phase angle) ranged from 15.73–34.56° (mean = 25.81 ± 0.11°; Figure 26) at North Neptunes, 13.42–28.28° at coastal locations (19.71 ± 0.42°; Figure 26), and 15.02–29.21° at offshore locations (23.27 ± 0.2°; Figure 26). Due to potential influence of fish length on body condition (Pratchett et al., 2023), I truncated data to the minimum size from North Neptunes (310 mm) and maximum size of offshore and coastal (525 mm) to compare body condition of fish within a similar size range. The top-ranked model ($w\text{AIC}_c = 0.44$) included *habitat*, *length*, and *month*, with these factors explaining 62% of the model variance (Table 12). *Length* and *month* had similar influence on the body condition of silver trevally (34% and 30%, respectively), with body condition increasing as size increased before reaching an asymptote of ~25° at ~425 mm (Figure 28A), and with body condition being highest in December and January, and lowest in June–August (Figure 28B). *Habitat* also influenced body condition but had a smaller effect than *length* and *month* (14% of model variance explained *versus* 34% and 30% respectively; Figure 28C). There was no significant difference in body condition of silver trevally between North Neptune and offshore habitats ($p = 0.78$, df = 1), but both were significantly higher than silver trevally from coastal habitats. ($p > 0.001$; Figure 28C).

Table 12. Summary of model testing the effect of bait and berley on the body condition of silver trevally (*Pseudocaranx georgianus*). df, degrees of freedom; AIC_c , Akaike's information criterion corrected for small sample size; LL, log-likelihood; ΔAIC_c , difference in AIC_c between the current and the top-ranked model; $w\text{AIC}_c$, model probability; variance explained by R_m, marginal (fixed effects) R^2; R_c, conditional (fixed and random effects) R^2. Top-ranked model indicated in **bold**. Only the top 5 ranked models are presented for table clarity.

Model	df	AIC_c	ΔAIC_c	AIC_cW_t	LL	R_m	R_c
Phase angle ~ Habitat + $\text{Length}_{\text{Smooth}}$ + $\text{Month}_{\text{Cyclic}}$	**14**	**2062.6**	**0**	**0.441**	**-1016.44**	**0.48**	**0.61**
Phase angle ~ Habitat + Habitat* $\text{Length}_{\text{Smooth}}$ + $\text{Month}_{\text{Cyclic}}$	18	2064.4	1.82	0.178	-1013.03	0.39	0.60
Phase angle ~ Habitat* $\text{Length}_{\text{Smooth}}$ + $\text{Month}_{\text{Cyclic}}$	16	2064.8	2.17	0.149	-1015.32	0.25	0.60
Phase angle ~ $\text{Length}_{\text{Smooth}}$ + Habitat* $\text{Length}_{\text{Smooth}}$ + $\text{Month}_{\text{Cyclic}}$	15	2065.2	2.60	0.12	-1016.6	0.25	0.59
Phase angle ~ Habitat + $\text{Length}_{\text{Smooth}}$ + Habitat* $\text{Length}_{\text{Smooth}}$ + $\text{Month}_{\text{Cyclic}}$	19	2065.7	3.06	0.095	-1012.86	0.39	0.60

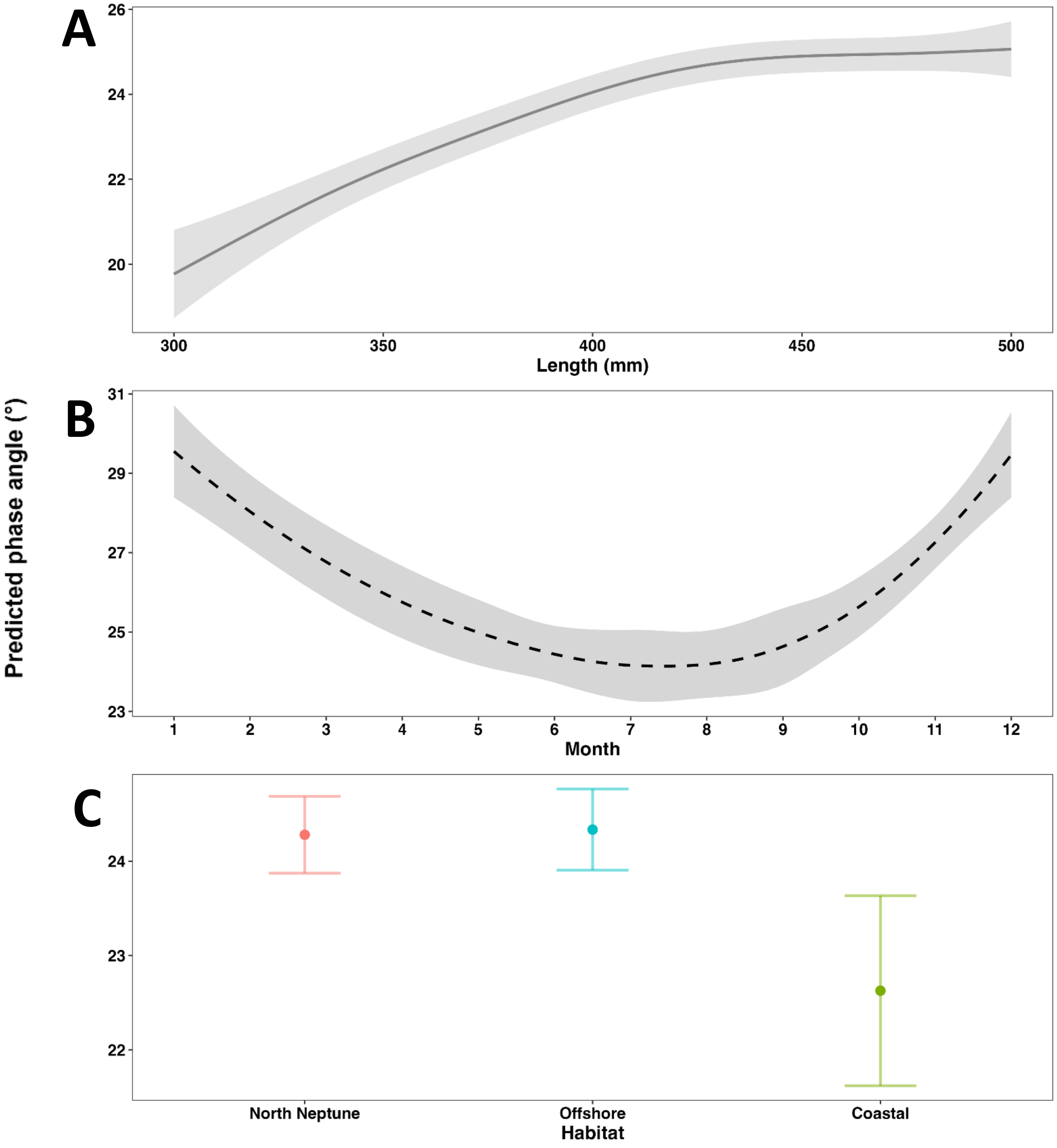


Figure 28. Predicted phase angle (marginal means) of silver trevally (*Pseudocaranx georgianus*) from South Australia showing effects of **A)** total length (mm), **B)** month, and **C**) habitat. Shaded error bars and error bars indicates 95% confidence intervals. Coastal n = 60 (1 location), North Neptune n = 449 (1 location), Offshore n = 191 (5 locations).

Fatty acids

I examined the muscle fatty acid profiles from 46 silver trevally captured from March 2016–June 2022 at North Neptunes (n = 7), coastal locations (n = 24), and offshore locations (n = 15). Due to the effect of season on fatty acid profiles (C Huveneers, unpublished data; Armstrong et al., 1994, de Souza et al., 2020), and the lack of samples overlapping for all *habitats* and seasons, I only used samples collected during spring as this was the season with the most samples in each habitat. There were significant differences among the fatty acid profiles of individuals with the formation of distinct clusters with specific profiles for *habitat* (MS = 987.17, $F_{2,34}$ = 13.8, p(perm) = 0.001; Figure 29). Average dissimilarity between North Neptunes–coastal (11.2%), and North Neptunes–offshore (9.85%), was higher, but comparable to the dissimilarity between coastal–offshore habitats (9.25%). Seven fatty acids were driving a cumulative dissimilarity of ~70% between habitats (Table 13; Figure 29). SIMPER analysis for *habitat* indicated North Neptunes silver trevally had higher levels of oleic acid (OLA; 18:1ω9; mono-unsaturated), eicosapentaenoic acid (EPA; 20:5ω3; poly-unsaturated), and palmitoleic acid (PAL; 16:1ω7; mono-unsaturated), and lower levels of arachidonic acid (ARA; 20:4ω6; poly-unsaturated), docosahexaenoic acid (DHA, 22:6ω3; poly-unsaturated), palmitic acid (16:0; saturated), and stearic acid (18:0; saturated) compared to coastal and offshore habitats (Table 13).

Table 13. SIMPER results for muscle fatty acid profiles of silver trevally (*Pseudocaranx georgianus*) from different habitats in South Australia. Results ordered by percentage contribution of fatty acid to dissimilarity. DHA = docosahexaenoic acid; OLA = oleic acid; PAL = palmitoleic acid; EPA = eicosapentaenoic acid; ARA = arachidonic acid.

Fatty acid	Av. Concentration	Av. Concentration	Av. Dissimilarity	Dissimilarity SD	Contribution %	Cumulative %
a) Offshore & Coastal (Av. Dissimilarity 9.25)	Offshore	Coastal				
22:6 ω 3cis (DHA; poly-unsaturated)	6.2	5.25	1.68	1.56	18.13	18.13
18:1 ω 9cis (OLA; mono-unsaturated)	2.64	3.18	1.17	1.31	12.6	30.72
14:0 (myristic acid; saturated)	1.1	1.6	1.03	1.23	11.14	41.86
16:1 ω 7cis (PAL; mono-unsaturated)	1	1.22	0.71	1.12	7.72	49.58
16:0 (palmitic acid; saturated)	4.98	5.26	0.69	1.14	7.47	57.05
20:5 ω 3cis (EPA; poly-unsaturated)	2.25	2.09	0.67	1.3	7.26	64.31
20:4 ω 6cis (ARA; poly-unsaturated)	1.89	2.06	0.64	1.29	6.94	71.26
b) Offshore & North Neptune (Av. Dissimilarity 9.85)	Offshore	North Neptune				
18:1 ω 9cis (OLA; mono-unsaturated)	2.64	3.53	1.62	1.68	16.46	16.46
14:0 (myristic acid; saturated)	1.1	1.71	1.14	1.4	11.57	28.04
18:0 (stearic acid; saturated)	3.88	3.26	1.08	3.09	10.93	38.97
16:1 ω 7cis (PAL; mono-unsaturated)	1	1.57	1.06	1.51	10.78	49.75
20:5 ω 3cis (EPA; poly-unsaturated)	2.25	2.66	0.89	1.3	9.05	58.8
22:6 ω 3cis (DHA; poly-unsaturated)	6.2	5.89	0.79	1.3	7.98	66.78
20:4 ω 6cis (ARA; poly-unsaturated)	1.89	1.55	0.75	1.66	7.63	74.4
c) Coastal & North Neptune (Av. Dissimilarity 11.24)	Coastal	North Neptune				
22:6 ω 3cis (DHA; poly-unsaturated)	5.25	5.89	1.33	1.32	11.85	11.85
18:0 (stearic acid; saturated)	3.98	3.26	1.24	1.88	11.06	22.91
18:1 ω 9cis (OLA; mono-unsaturated)	3.18	3.53	1.21	1.37	10.75	33.66
20:5 ω 3cis (EPA; poly-unsaturated)	2.09	2.66	1.14	1.38	10.17	43.83
16:0 (palmitic acid; saturated)	5.26	4.71	1.09	1.27	9.65	53.48
14:0 (myristic acid; saturated)	1.6	1.71	1.02	1.38	9.04	62.53
16:1 ω 7cis (PAL; mono-unsaturated)	1.22	1.57	0.98	1.42	8.75	71.28

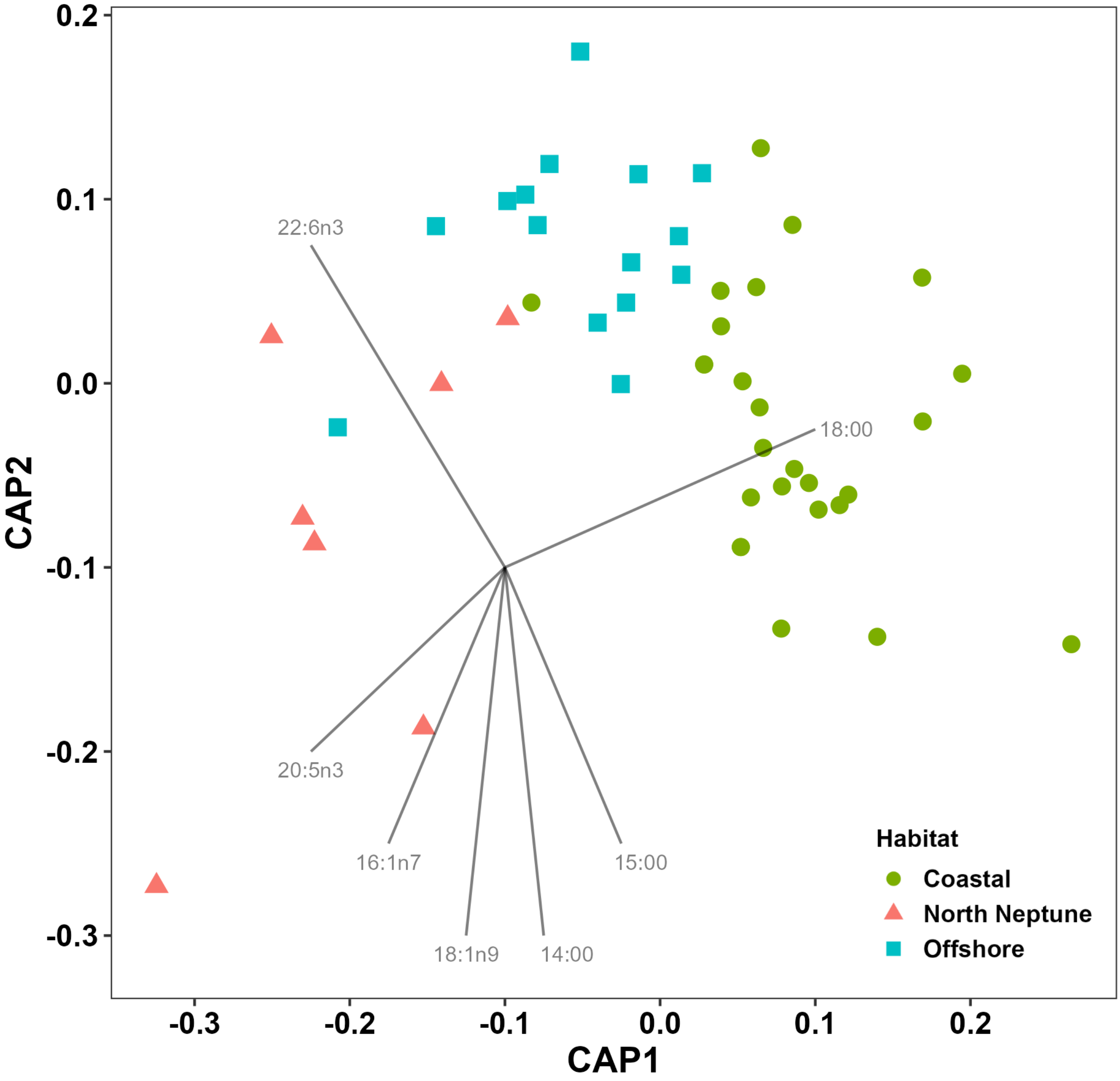


Figure 29. Canonical analysis of principal coordinates for muscle fatty acid samples collected during Spring from silver trevally (*Pseudocaranx georgianus)* from different habitat types in South Australia. Vector overlay indicates highest contributing fatty acids to the dissimilarity. All PUFAs displayed are cis bonded. Coastal n = 24 (1 location), North Neptune n = 7 (1 location), Offshore n = 15 (2 locations)

5.5 Discussion

This study enhances my understanding of the effects of supplemental feeding on the physiology and nutrition of a non-focal species and shows that wildlife tourism increases silver trevally growth and altered fatty acid profiles. However, despite increased growth and altered dietary indicators, I found that feeding from shark cage-diving tourism does not affect mortality or body condition. Based on the growth curves for different habitat types, trevally interacting with shark tourism grew to larger sizes at the same age than silver trevally from offshore or coastal habitats that are not exposed to supplemental feeding. Despite access to supplemental food, silver trevally from North Neptunes had comparable body condition to individuals from similar offshore habitats without supplemental food, suggesting that the surplus energy from consuming bait and berley is devoted to somatic growth rather than stored as excess fat. In addition, both trevally from North Neptunes and offshore habitats had greater body condition than trevally from coastal habitats. I also observed differences in essential fatty acid profiles between habitat types, with fish from North Neptunes having higher levels of OLA, EPA, and PAL, and lower levels of ARA, DHA, 16:0, and 18:0 compared to silver trevally from offshore and coastal habitats. Overall, these findings highlight that providing supplemental feed to non-focal species does not always lead to negative impacts on individuals and provides the first evidence of increases in growth of a non-focal species at a wildlife tourism site exposed to food-based provisioning.

Differences in growth rates and asymptotic lengths between North Neptunes and offshore and coastal habitats, suggests that resource availability is driving impacts on somatic growth. Animals typically respond to resource availability through changes in survival and somatic growth, whereby limited resources can increase mortality or result in slower growth (Zimmermann et al., 2018, Hale et al., 2020). Conversely, resource abundance, such as through the supplemental feeding at North Neptunes, may increase the rate at which fish grow. Most fish follow a biphasic growth relationship, growing rapidly as a juvenile, which subsequently decelerates as an adult (Von Bertalanffy, 1957, Skeeles and Clark, 2023). However, individuals with surplus energy (i.e., access to excess food through supplemental feeding), are not as limited by the energy requirements of reproduction at maturation, providing more energy for continued somatic growth (Skeeles and Clark, 2023). As silver trevally at North Neptunes have been exposed to supplemental feeding for up to 16 years (Bruce and Bradford, 2013), consumption of bait and berley likely provides surplus energy throughout their maturation, facilitating individuals to grow larger. In comparison, silver trevally in offshore locations had a similar growth rate, but smaller asymptotic size, likely following natural decelerations of growth due to reduced energy available during maturation (i.e., smaller individuals; Skeeles and Clark, 2023). Similarly, an overall reduction in food availability for silver trevally in coastal locations would drive the reduced asymptotic size compared to both offshore habitats and North Neptunes (Middleton et al., 2013, Doubleday et al., 2017, Messer et al., 2021). This finding is supported by the physiological concepts underpinning the von Bertalanffy growth function, where density-dependent growth mediated by food affects the asymptotic size, not the growth rate (Lorenzen and Enberg, 2002).

Body condition provides a measure of physiological status that has been used to infer habitat suitability for pelagic fishes (Champion et al., 2020, Clarke et al., 2023). The greater body condition and faster growth of silver trevally from offshore and North Neptunes habitats (also an offshore island) compared to coastal habitats suggests that offshore regions might be more suitable for silver trevally and provide greater resource availability. Trevally from offshore habitats and North Neptunes were sampled between the Bonney Coast and the eastern Great Australian Bight (Kämpf, 2010, Richardson et al., 2020) where sporadic wind-driven summer upwelling events (Lewis, 1981, Kämpf et al., 2004) support high levels of primary productivity (Ward et al., 2006, van Ruth et al., 2010) and high densities of small pelagic fishes (McLeay et al., 2003, Dennis et al., 2021). This region provides abundant food with essential nutrients for many species, including silver trevally (Goldsworthy et al., 2013). In contrast, coastal silver trevally were collected in the South Australian gulfs (i.e., Gulf St. Vincent and Spencer Gulf), which can be nutrient limited (Middleton et al., 2013, Doubleday et al., 2017, Messer et al., 2021), due to the lack of riverine input (Dimmlich et al., 2004) and salinity-driven density fronts restricting mixing (Messer et al., 2021). The low productivity within these gulfs likely limits food availability, which in turns impacts the body condition of coastal silver trevally. As fish are ectotherms, the temperature of a habitat is also a key component of habitat suitability (Clarke and Johnston, 1999). Fish have an optimum thermal range (Valenza-Troubat et al., 2022), outside of which metabolic costs increase (Sebens, 1987) and oxygen transport to tissues becomes limited (Ern et al., 2016), slowing overall kinematics (Parisi et al., 2020) and thus prey capture (Valenza-Troubat et al., 2022). This can, in turn, affect growth as shown by a study recording a 50% increase in somatic growth in silver trevally kept at 20°C compared to those kept at 13°C (Valenza-Troubat et al., 2022). The temperature range in the coastal habitats (12–25°C; Roberts et al., 2012, Roberts et al., 2019), is greater and more variable (i.e., due to influence from climatic conditions; Roberts et al., 2019) than in offshore regions (15–22 °C) which are generally more consistent (Dimmlich et al., 2004, Richardson et al., 2018). Consequently, coastal silver trevally might be outside their optimum temperature range for longer periods and are subject to larger thermal fluctuations compared to offshore silver trevally. The high and variable temperature within the gulfs likely increases physiological demand, explaining lower somatic growth compared to offshore silver trevally.

The accelerated growth at North Neptunes raises concerns of whether the increase in silver trevally somatic growth compromises other aspects of their physiology (i.e., less energy allocated to other physiological processes; Marshall, 2007, McBride et al., 2015). However, the similar body condition of silver trevally from North Neptunes and offshore habitats indicates that the energy allocated for increased growth is not occurring at the cost of their physiological condition. Studies examining field metabolic rate at tourism sites revealed greater energetic costs from interactions with operators, resulting in increased activity and metabolic rate compensating for consuming baits and/or berley (i.e., surplus energy compensates for increased energy expenditure, not toward increased physiological condition; Barnett et al., 2016, Clarke et al., 2023). However, silver trevally at North Neptunes did not increase activity around food-based operators, despite increased residency (daily and weekly), and occurring closer to the surface near to bait and berley (Chapter 2). Due to the extended exposure to supplemental food without additional energy expenditure, surplus energy was expected to lead to better body condition in the North Neptunes silver trevally. However, despite suspected surplus energy and observed increases in growth, energy from the bait and berley consumption did not lead to better condition, as the energy is likely allocated to somatic growth instead.

Trevally mortality was similar across all habitats. Yet, fish mortality is typically higher in coastal habitats than offshore regions because of increased fishing pressure due to accessibility for recreational and commercial fishing sectors (Johnson et al., 2015). However, South Australian recreational catches of silver trevally are similar between coastal and offshore regions (57% and 43%, respectively; Beckmann et al., 2023), reducing the expected discrepancy in fishing-related mortality between regions. Furthermore, most coastal and Neptune Islands silver trevally were caught within no-fishing sanctuary zones alleviating this source of mortality altogether. The lack of differences in mortality between silver trevally from offshore regions and the Neptune Islands suggests that, while supplemental feeding increase somatic growth, it does not affect mortality.

Immigration and emigration is a confounding factor of life-history parameters, whereby estimates (i.e., growth, mortality, condition, nutrition) can capture the effects of movements between regions (Ogle, 2018, Harry et al., 2022), leading to biased estimates being used for management purposes. While silver trevally at the Neptune Islands have high site fidelity, some individuals displayed transient behaviours, leaving the islands for extended periods (up to 7 months between detections; Chapter 2), even when provided with supplemental food. The spatial extent of this movement is however unknown, due to high mobility, silver trevally are capable of intermediate scales of movements (Fowler et al., 2018), indicating they may be residing in the offshore reefs surrounding the Neptune Islands, or could be undertaking large-scale migrations across geographic regions. Uncertainty in the population connectivity and post-settlement movements of silver trevally has contributed to broad fisheries management strategies (Smith-Vaniz and Jelks, 2006, Gomon et al., 2008). This uncertainty must be addressed to determine the extent of connectivity across regions and life-history stages, and if the cage-diving industry has the potential to interrupt important links and confound results here. Population genetic surveys have been conducted on similar carangids in the past (Miller et al., 2011), revealing stock structures and population stratification through genome-wide DNA markers (Alexander et al., 2009, Jombart and Ahmed, 2011). Furthermore, in conjunction with otolith chemistry (Gillanders, 2005, Elsdon et al., 2008, Reis-Santos et al., 2023), connectivity patterns at different life stages and between different areas (i.e., spawning and nursery areas, and adult habitats) can be quantified using natural chemical tags in otoliths and other hard parts (i.e., isotopes and trace elements; Gillanders et al., 2015, Tanner et al., 2016). Understanding the population structure and dynamics of silver trevally through this future work provides essential information for the management of populations at biologically relevant spatial scales (Gillanders, 2002, Reis-Santos et al., 2018, Reis-Santos et al., 2023). Furthermore, understanding the connectivity of silver trevally across habitats and their life history addresses any confounding effects of movements on estimates of growth, mortality, body condition, and nutrition here, while also revealing potential impacts from the cage-diving industry if connectivity is interrupted.

While silver trevally at North Neptunes consume the bait and berley provided by cage-diving operators (Meyer et al., 2020), silver trevally at non-tourism sites feed on a wide range of prey items such as cephalopods, benthic invertebrates, zooplankton, and small benthopelagic fish (J Dennis, unpublished data; French et al., 2013). Due to the importance of essential fatty acids in maintaining physiological functions (Turchini et al., 2022) and their limited ability to synthesise fatty acids *de novo* (Sargent et al., 1995), essential fatty acid deficiencies from poor diet can reduce fish growth, survival, and development (Tocher et al., 2008). Arachidonic acid (ARA) and Docosahexaenoic acid (DHA) are essential omega-6 and omega-3 fatty acids that play essential roles in different physiological processes, and were found in low levels in North Neptunes Trevally due to the low levels of DHA and ARA found in bait and berley (Meyer et al., 2020). The unaltered body condition of North Neptunes silver trevally suggests this lower level is physiologically inconsequential, as the importance of DHA and ARA in fish is highly species, life history stage, sex, and location-specific (Xu et al., 2022). Alternatively, the lack of available DHA and ARA may not hamper growth but instead prevent the expected increase in body condition in silver trevally at North Neptunes. While the southern bluefin tuna used as bait and berley by cage-diving operators at the Neptune Islands is low in ARA and DHA, it is rich in EPA and OLA, and is likely the source of higher EPA and OLA in North Neptunes silver trevally (Meyer et al. 2020). Eicosapentaenoic acid (EPA) is another essential omega-3 fatty acid and is highly abundant in marine ecosystems, originating from primary producers, which is then bioaccumulated and stored in higher trophic level species. Under natural conditions (i.e., when not fed bait and berley rich in EPA), silver trevally are not high trophic level species and contain low levels of EPA. EPA is important for multiple physiological functions including maintaining cellular membrane structure, immunity and inflammatory regulation, and metabolism modulation (Lutfi et al., 2023). Aquaculture fish fed diets formulated with high levels of EPA increase their growth, robustness, and condition (Tian et al., 2017, Lutfi et al., 2023). Similarly, the OLA found in high levels in North Neptunes silver trevally and in the bait and berley (Meyer et al. 2020) is a heavily catabolized fatty acid used for energy pertaining to growth and reproduction (Tocher, 2003). Controlled diet studies have shown OLA improves nutrient uptake without affecting growth, and mitigates negative impacts from excessively high-lipid diets (Martins et al., 2023). As such, the higher levels of EPA and OLA may nutritionally support the accelerated growth of silver trevally at

North Neptunes while maintaining the body condition of supplementally fed silver trevally to the same level as the offshore silver trevally feeding naturally.

5.6 Conclusions

Supplemental feeding at tourism sites can impact the physiology and diet of non-focal species consuming the attractant. This study identified the effects of a supplemental food source from white shark tourism on the growth, body condition, and diet of non-focal coastal fish, while also highlighting the suitability of offshore habitats throughout southern Australia. Despite supporting increases in growth, the supplemental feeding is not sufficient in volume, duration, or nutrition to concurrently increase body condition or decrease mortality. Importantly, higher levels of essential fatty acids that improve and support growth suggest that the bait and berley provided may be a nutritionally sufficient substitute for the natural diet of silver trevally, supporting accelerated growth. Future research should focus on understanding the connectivity across regions and life-history stages of silver trevally in southern Australia, to determine the population structure and dynamics throughout their life and across disparate coastal and offshore habitats; with a focus on if and how connectivity may be influenced by white shark tourism. Findings from this study contribute to the limited, but growing knowledge of the impacts of provisioning on non-focal species, highlighting the importance of accounting for non-focal species in the management of supplemental feeding (Meyer et al., 2021). Furthermore, I provide the first evidence of responses in the growth of a semi-resident benthopelagic fish at an offshore temperate island group exposed to supplemental feeding.

CHAPTER 6

General discussion

6.1 Thesis overview

Food-based attractants are often used in wildlife tourism to aggregate focal species, unintentionally attracting and in some cases feeding non-focal species. The impacts of such practices are poorly understood, with few studies exploring the topic (Trave et al., 2017, Meyer et al., 2021). Non-focal species can consume most of the food supplied (Donalty et al., 2003, Inslerman et al., 2006), but management strategies, policies, and research is focused on understanding and mitigating the impacts of provisioning on focal species. Yet, non-focal species are likely to be affected by wildlife tourism in different ways to focal animals.

Using a multidisciplinary approach, I investigated the impacts of wildlife tourism on the spatiotemporal distribution, activity, population abundance, growth, and physiology of silver trevally (*Pseudocaranx georgianus*) attracted by bait and berley (southern bluefin tuna *Thunnus maccoyii*) used by white shark (*Carcharodon carcharias*) cage-diving vessels. Specifically, this thesis shows changes to the space use and residency of silver trevally exposed to provisioning from wildlife tourism, with weekly (number of days silver trevally were present per week) and daily (number of hours per day at the Neptune Islands) residency increasing by 32% and 20%, respectively, when operators were present (Chapter 2). Cage-diving tourism also reduced the core space use of silver trevally, aggregating them close to food-based operators at the surface (< 5 m depth). Despite changes in space use and residency, and frequently observed bursts of acceleration, overall activity did not substantially increase when operators were present. Estimates of population size using novel mark-resight methods developed in this thesis (Chapter 3) revealed a population of up to ~4,000 silver trevally, with seasonal variations and abundance peaking in summer (Chapter 4). However, population size was not influenced by the monthly frequency of cage-diving operations. Notably, I also documented a seasonal exodus from the Neptune Islands by 76% of tagged individuals, triggered by low water temperature (Chapter 2), and seasonal variations in population size linked to temperature (Chapter 4), suggesting that silver trevally are not permanent residents at the Neptune Islands. The departure of silver trevally from this near-continuous food source suggests the bait and berley is not muting environmental cues or suppressing natural movements and behaviours. The silver trevally at North Neptune Islands that were frequently exposed to bait and berley were larger than silver trevally of the same age from offshore locations with similar habitats, but without supplemental feeding from cage-diving operations (Chapter 5). The accelerated growth is nutritionally supported by the higher levels of Eicosapentaenoic and Oleic acid in silver trevally from North Neptune Islands, as these fatty acids increase the overall growth performance, welfare, and condition of teleosts (Chapter 5). However, mortality rate and body condition was similar to control locations, indicating that while silver trevally may grow faster, the consumption of bait and berley does not change the survival, nor fitness of silver trevally (Chapter 5). My thesis is the first study to comprehensively assess the impacts of wildlife tourism on a non-focal species, providing a baseline for impacts of supplemental feeding on a non-focal species. Overall, my study used a multidisciplinary approach to show that small and non-focal species can be affected by provisioning, despite being often unaccounted for in management frameworks and studies assessing the impacts of wildlife tourism.

6.2 Ecological disruption: impacts on non-focal movement and behaviour

Environmental cues are important regulatory processes for animals, dictating when to reproduce (Juntti and Fernald, 2016), perform migratory behaviours (Winkler et al., 2014), or how they choose a suitable habitat (i.e., abundant resources, thermal optimum; Huijbers et al., 2012). Interruption of these environmental drivers is becoming more pervasive (i.e., through human-driven climate change; Altieri and Diaz, 2019; pollution; Olsén, 2010, Olivares-Rubio and Arce, 2023; habitat modifications; Dagorn et al., 2010, Dagorn et al., 2013, Johnson and Lyman, 2020), preventing ecologically important movements, and inadvertently trapping individuals in unsuitable areas with sub-optimal resources or outside their thermal ranges (Schlaepfer et al., 2002, Battin, 2004). Provisioning of wildlife has been shown to interrupt or prevent these important movements and migrations (i.e., for habitat selection; Boyce et al., 2016; foraging needs; Moorcroft and Barnett, 2008, Staniland et al., 2018; predator avoidance; Heupel and Hueter, 2002; or reproductive opportunities; Lassis et al., 2022). While this thesis shows that silver trevally exposed to provisioning were still undertaking movements away from the Neptune Islands (Chapters 2 & 4), the increasing residency with cage-diving operations suggests that cage-diving does affect movement patterns, and that higher intensity of cage-diving (e.g., greater number of days at the Neptune Islands) could lead to further disruptions to fine-scale movement, and potentially migrations. Silver trevally in other locations undertake large-scale migrations, with some exhibiting movements of over 500 km in 17 days, highlighting the mobility of the species (Rowling and Raines, 2000, Fowler et al., 2018). Such migrations would explain the extended time away from the Neptune Islands, which might be linked to pre-spawning behaviours as is suggested for silver trevally in other regions (Fowler et al., 2018). Spawning behaviours are key components of reproduction that drive a populations productivity and success (Tamario et al., 2019). As such, important reproductive behaviours could be hindered if responses to environmental cues were suppressed. Furthermore, the increased residency at the Neptune Islands longer than expected naturally could result in undue foraging pressure on prey species or expose silver trevally to temperatures outside their optimal thermal range. Temperature greatly affects the metabolic rate of teleosts (Clarke and Johnston, 1999), with individuals outside of their thermal range having higher energy expenditure (Sebens, 1987), restricted physiological processes (Neubauer and Andersen, 2019, Volkoff and Ronnestad, 2020), and reduced oxygen transport to tissues (Ern et al., 2016), prey capture and digestion (Valenza-Troubat et al., 2022), reproductive output (Pankhurst and Munday, 2011), and larval growth and survival (Moyano et al., 2017). Overall, my study showed that provisioning may interrupt ecologically important species-specific movements, preventing reproductive behaviours and trapping wildlife in unsuitable areas; highlighting the need for baseline studies of non-focal species to assess the natural behaviours and ecosystem services which may be interrupted. Effects from Interrupting ecologically important movements and behaviours can also reach beyond non-focal species and extend to the ecosystems they are connected to and are supported through these movements (Polis et al., 1997, Teske et al., 2021).

Humans ability to provide resources to wildlife at a consistency, quantity, or quality beyond what is naturally available can create desirable cues in unsuitable habitats, increasing the likelihood of species falling into an *ecological trap* (Schlaepfer et al., 2002, Becker and Hall, 2014). Combined with anthropogenic pressures (i.e., fisheries; Block et al., 1998, Heino and Godø, 2002; habitat degradation; Marsac et al., 2000, Andersson, 2011; and climate change; Champion et al., 2018b, Petrik et al., 2020, Robinson et al., 2015, Golet et al., 2007), impacted species can be faced with cumulative challenges. However, the opposite might occur at the Neptune Islands where provisioning and spatial management are cumulatively beneficial (i.e., marine parks; McClanahan and Mangi, 2000, Smallwood et al., 2011, Laffoley et al., 2019). Current conditions at the Neptune Islands Group Marine Park resemble more of an *ecological haven* than an *ecological trap* (Chapters 2 & 4; Schlaepfer et al., 2002, Battin, 2004). Indeed, silver trevally are not subject to anthropogenic pressures but are supplied with supplemental food which increases their growth and physiological maintenance instead (Chapter 5). These benefits, however, remain conditional on provisioning not preventing natural behaviours by muting responses to environmental cues, in which case the Neptune Islands would default back to an *ecological trap* (Battin, 2004). Leveraging the benefits of an *ecological haven* provides a unique conservation strategy to support at-risk populations. As feeding endangered or at-risk populations is already successfully used in terrestrial conservation (Heard and Zimmerman, 2021), combining supplemental feed programs with wildlife tourism operations provide an opportunity to promote and support non-focal species populations that may be otherwise at risk, while allowing operators to provide an improved experience for participants through provisioning of focal species

6.3 Physiological toll: non-focal provisioning and energy budgets

Increased energy expenditure can lead to negative health impacts, as individuals expend more energy than they assimilate, reducing the energy available for important processes such as growth (Metcalfe, 1986), body condition (Silva et al., 2020), reproductive output (i.e., fecundity; McBride et al., 2015), overall fitness (Pankhurst and Munday, 2011, Chabot et al., 2016), and ultimately survival (Naidoo and Glassom, 2019). This was not observed at the Neptune Islands, as silver trevally do not expend additional energy when interacting with cage-diving vessels (Chapter 2), but instead grow larger (Chapter 5). The increase in somatic growth can be attributed to an energy surplus, given silver trevally consume a food source with greater caloric value than natural prey items (9.28 kj/g ± 0.63 *versus* cephalopod 3.3 kj/g; crustacean 3.93 kj/g; J Dennis, unpublished data). Increases in activity from interactions with wildlife provisioning have been observed in both focal and non-focal species, whereby the increased energy expenditure can be compensated by consuming supplemental feed (Barnett et al., 2016, Brunnschweiler et al., 2018, Huveneers et al., 2018a, Barry et al., 2023, Clarke et al., 2023), mitigating negative fitness impacts associated with energy deficits. However, this is contingent on the food being accessible. This is particularly the case for other non-focal species which may increase energy expenditure in an attempt to consume seemingly available food, but are outcompeted and thus cannot recuperate energy losses. For example, while the silver trevally aggregate at the source of bait and berley, other species (i.e., leather jackets *Meuschenia hippocrepis*) may increase their movements in relation to the cage-diving vessels attempting to consume supplemental food (i.e., increased energy expenditure), but are subsequently outcompeted by the more mobile silver trevally. Thus, what is an *ecological haven* for some species may be an *ecological trap* for others. Findings from this thesis demonstrate that interactions with wildlife provisioning does not always result in increased energy expenditure and subsequent energy deficit, which would prevent important physiological processes, highlighting the complexity of responses to sources of provisioning. While findings produced here were conducted after long-term exposure of a single non-focal species to wildlife provisioning, assessing a species' field metabolic rate, energy requirements, and the caloric value of proposed provisioning prior to implementing operations will allow the proactive development of bioenergetic models (Boisclair and Leggett, 1989, Hansen et al., 1993). Predicting potential responses *a priori* allows modifications to proposed practices (i.e., sufficient caloric value to compensate for shifts in energy budgets) to mitigate potential negative impacts on species interacting with tourism.

Best practice for mitigating the impacts of provisioning is proactive management, performing detailed assessments of all species and environmental components prior to commencing the activity, preventing impacts from occurring from the onset. However, as many wildlife tourism industries are already well established and practices are often grandfathered in, in conjunction with impacts on non-focal species only recently gaining interest (Gallagher et al., 2015, Trave et al., 2017, Gallagher and Huveneers, 2018, Patroni et al., 2018, Meyer et al., 2020, Meyer et al., 2021), many species are likely already impacted or exposed to pressures from different forms of provisioning. With species potentially already dependent on provisioning as a food source (Marsac et al., 2000, Dagorn et al., 2010), reactive management practices can no longer simply remove the source of impact. Removal of the provisioning essentially eliminates a resource which a population might now rely on, resulting in significant resource-related mortality (Meakin and Qin, 2020), increased predation pressure on prey species (Koons et al., 2015, Malpass et al., 2017), or further physiological impacts than when provisioned. Similarly, associative learning with wildlife provisioning (Jensen et al., 2013, Pini-Fitzsimmons et al., 2018, Heinrich et al., 2021), can expose species to other anthropogenic pressures in the absence of provisioning (Block et al., 1998, Heino and Godø, 2002, Golet et al., 2007). For example, as silver trevally responded to olfactory stimulus (Chapter 2), exploitation of this response could make individuals susceptible to fishing-related pressures in the sudden absence of bait and berley or when they depart the Neptune Islands. Findings from this thesis highlight how assessments of impacts prior to changing or stopping provisioning practices can reveal potential change which can in fact worsen the effects on the individuals. The potential for future impacts under changing management presents opportunities for future work to examine potential effects on the wider ecosystem which were not examined here.

6.4 Nutritional ecology: exploring balanced diets and eco-moderation

A balanced diet of essential nutrients and energy (i.e., vitamins, minerals, proteins, lipids, carbohydrates; Lall and Tibbetts, 2009) is required to meet the physiological needs of growth, reproduction, and health, but also influences an individual's plasticity and adaptability to stressors (Lall and Tibbetts, 2009, Raubenheimer et al., 2009, Raubenheimer, 2011). Disruption of this balance by providing food with limited nutritional value results in macronutrient-imbalanced diets, restricting animals from achieving intake targets (Raubenheimer and Simpson, 2019) and limiting physiological processes (Simpson and Raubenheimer, 2012). Despite silver trevally exhibiting a change in diet (Chapter 5; Meyer et al., 2020), they were in good body condition, had increased growth (Chapter 5), and the population fluctuated naturally with no increases in mortality (Chapters 4 and 5). The nutritional value of the southern bluefin tuna used may be a superior substitute for the natural diet of silver trevally (i.e., cephalopods, benthic invertebrates, zooplankton, and small benthopelagic fish; J Dennis, unpublished data; French et al., 2013). While showing enrichment of some fatty acids pertaining to growth (Chapter 5), southern bluefin tuna provides the essential macro and micronutrients required for maintaining the health and fitness of silver trevally (Hardy and Kaushik, 2021). While silver trevally unintentionally benefited from the type of provisioning used, it demonstrates that consideration of non-focal species through well-managed tourism and cooperation with policymakers can benefit both the focal and other non-focal species that may be exposed to provisioning (Ballantyne et al., 2009, Apps et al., 2018, Meyer et al., 2021). For example, altering supplemental feed to represent the natural diets of non-focal species, as is implemented for focal species (Brunnschweiler et al., 2018, Barry et al., 2023), would maintain the natural balance of nutrients and energy for impacted individuals. Reducing quantities of provisioning in line with non-focal species would alleviate impacts from occurring from the onset. However, when considering reductions in provisioning, prior assessments of energy use are required to ensure species are not dependent on provisioning as an energy source (Barnett et al., 2016, Brunnschweiler et al., 2018, Huveneers et al., 2018a, Barry et al., 2023, Clarke et al., 2023).

Silver trevally have been deemed eco-moderators (Chapter 5; Meyer et al., 2020), as they play an important role in moderating the impacts of bait and berley on other non-focal species inhabiting the Neptune Islands. The large aggregations of silver trevally (Chapter 4) spend extended periods of time in close proximity to operators (Chapter 2), outcompeting other species and consuming the berley at the surface before it reaches benthic species (Chapter 5; Meyer et al., 2020). Although negative impacts on the physiology, health, and fitness of silver trevally are limited (Chapter 5), there is the potential for provisioning to impact other species (i.e., limiting physiological process and condition; Brookhouse et al., 2013, Raubenheimer and Simpson, 2019), which at the Neptune Islands, is prevented through eco-moderation by the silver trevally. Occurrences of eco-moderators have been observed outside of wildlife tourism, with wild fishes around aquaculture pens consuming waste (i.e., uneaten feed and fish waste) and limiting the impacts of eutrophication on the benthic environment (Felsing et al., 2005, Fernandez-Jover et al., 2011). Benefits of eco-moderation also extends beyond species at the immediate impact site. For example, bait and berley used at the Neptune Islands is sourced from local tuna ranching around Port Lincoln ~60 km north of the Neptune Islands (Ellis and Kiessling, 2016), consisting of whole tuna that would typically need to be disposed of through other means. Much like fishery discards around the globe (Berg, 2019, Gilman et al., 2020, Viglia et al., 2022, Standal and Hersoug, 2023), disposal of human-mediated food sources can create additive pressures and impacts on wildlife (Votier et al., 2004, Bicknell et al., 2013, Oro et al., 2013), but supplying the tuna to the cage-diving industry prevents broader impacts. Organic matter and food waste in national parks has been provided to residents for feeding cattle previously, preventing the likelihood of wildlife feeding on the disposed waste (Manfredi et al., 2010) In the world of reduce, reuse, recycle (Abdul-Rahman and Wright, 2014), findings from this thesis support the use of eco-moderators to divert sources of food-based waste products, as opposed to its haphazard dispersal which acts as a resource pulse potentially impacting susceptible species (Felsing et al., 2005, Oro et al., 2013). However, detailed assessments of the response of wild species to a source of provisioning, like has been detailed in this thesis, is required to prevent health and fitness implications for eco-moderator species.

6.5 Conserve, cull, compromise: a Neptune Islands case study

Management of wildlife tourism is essential for ensuring sustainable practices and mitigation of impacts (Trave et al., 2017, Patroni et al., 2018), but requires the complex balance between conservation, animal welfare, economic benefits, and participant satisfaction (Meyer et al., 2021). A number of management frameworks have been developed and applied to wildlife tourism industries (Higginbottom et al., 2003, Buckley, 2009, Dubois and Fraser, 2013, Agyeiwaah et al., 2017, Leung et al., 2018). However, frameworks did not consider non-focal or wider ecosystem impacts until recently (Meyer et al., 2021). The Neptune Islands cage-diving industry is an example of adaptive management practices that have been implemented to balance impacts to animal welfare and the socioeconomic benefits of tourism, although regulations only consider the focal white sharks. This thesis has determined that the cage-diving industry in South Australia has led to shifts in the spatiotemporal distribution (Chapter 2), population size (Chapter 4), somatic growth (Chapter 5), and diet (Chapter 5; Meyer et al., 2020) of silver trevally. Using the findings from this thesis, I have updated the existing assessment of the Neptune Islands white shark cage-diving industry on non-focal species (Meyer et al., 2021), addressing key knowledge gaps identified in the previous assessment of this industry (Figure 30; Table 14).

South Australia's white shark cage-diving industry consisted of three operators, running tours ~265 days per year for >10,000 participants. The *tractability* score of the industry was reduced for non-focal species from somewhat high (+0.50) to slightly high (+0.30), and the negative score is now very low (-0.60). While the industry is small and highly regulated for the focal species, current regulations are only indirectly managing the non-focal species (Table 14). The use of provisioning that is attracting large numbers of silver trevally (Chapters 2 & 4) within a marine park is reducing public and political support for the industry, with operators calling for a cull, and customers experience being negatively impacted. *Socioeconomic values* remained unchanged from the previous assessment (somewhat high; +0.40; Table 14), as there has not been any indications that participants would not partake in cage-diving tours despite customer dissatisfaction because of the large number of silver trevally present (J Dennis pers. obs.). The industry is thus still providing substantial economic support, education, awareness of all species seen at the Neptune Islands, with non-focal species indirectly benefiting (Meyer et al., 2021). *Conservation outcomes* from the industry increased (+0.83 to +1) due to the influx of research opportunities on the non-focal silver trevally (Chapters 2, 3, 4, & 5), but also other non-focal species interacting with the industry (Rizzari et al., 2017, Clarke et al., 2022, Clarke et al., 2023). In addition, the Neptune Islands and industry may act as an *ecological haven* (see section 6.2), supporting the sustainability of the silver trevally population and reducing pressures from anthropogenic activities or impacts of resource limitation (see section 6.3). Meyer et al. (2021) identified a number of knowledge gaps in relation to the *animal welfare* and *ecosystem impacts* factors of the assessment, calling for an improved understanding of impacts on non-focal species, many of which have been addressed in this thesis (Table 14, Figure 30). The combination of positive and negative impacts identified through this thesis improved the positive scores for *animal welfare* (+0 to +0.20) due to good external physical condition and overall physiological condition of silver trevally (Chapter 5), and because they were still migrating away from the Neptune Islands during periods of low temperature (Chapter 2). Similarly, negative scores also improved (-0.65 to -0.5), as the severity of previously unknown effects were lessened (Table 14). Importantly, addressing unknowns for *ecosystem impacts* improved both positive (+0.15 to +0.30) and negative scores (-0.35 to -0.25), with silver trevally being identified as eco-moderators (see section 6.4). Overall, inclusion of findings from this thesis into the management framework not only reduced the number of knowledge gaps originally identified by Meyer et al. 2021 (i.e., 10 to 2), a key factor which limits the ability of managers to make informed decisions, but also improved both positive and negative scores for the cage-diving industry overall (Figure 30A, B).

Table 14. Updated Framework from Meyer et al. (2021) evaluating white shark Carcharodon carcharias cage-diving practices in South Australia, assessed by 26 factors within four categories: tractability, conservation outcomes, animal welfare, and ecosystem impacts. Scores are very high (+ +), somewhat high (+), somewhat low (–) or very low (– –), null impact (Ø), and unknown (U). Proportion scores calculated as the number of positive (++ = 1) and negative scores (– – = −1) divided by the count of potential scores for each category. Socioeconomic benefits were not included in this table as it remained unchanged. Red indicates negative impacts on silver trevally (*Pseudocaranx georgianus*), green indicates positive impacts, and orange indicates combined positive and negative impacts.

(Table on following page)

Factors	Focal	Non-focal (Meyer et al. 2021)	Non-focal (Dennis 2023)
Tractability			
Practice linked to conventions and guidelines	++ Industry management includes activity limits	+ indirect Industry guidelines indirectly manage nontarget species	+/– Industry guidelines indirectly manage nontarget species, however, should directly manage non-focal impacts
Feasible to regulate/monitor/intervene	+ Small industry with limited operator licences & an industry management plan	+ Small industry with limited operator licences, an industry management plan, & activity contained within a regulated marine protected area	+ Small industry with limited operator licences, an industry management plan, & activity contained within a regulated marine protected area
Public & political support	+/– Polarized support	+ indirect	+/– – Indirect for some species, industry calling for silver trevally to be culled, silver trevally impacting customers
Natural area stewardship	++	++	– – Attractant used in marine park, impacting non-focal species
Safe for the public	+	– Provisioned fish can be aggressive toward divers	– Provisioned fish can be aggressive toward divers
Proportion score	+0.70 –0.10	+0.50 –0.10	+0.30 –0.60
Conservation outcomes			
Contributes to understanding the species	++ History of providing opportunities for research	+ Providing opportunities for research	++ Provided opportunities for growing research
Contributes to population sustainability	Ø	++ Marine protected area, fish-based attractant nutritionally supports numerous species	++ Marine protected area, fish-based attractant nutritionally supports the increased growth, population size, and physiological condition of silver trevally
Does not facilitate illegal use (i.e., poaching)	+ Presence of operators provides area surveillance	++ Supports the marine protected area, presence of operators provides area surveillance	++ Supports the marine protected area, presence of operators provides area surveillance
Proportion score	+0.50 -0	+0.83 -0	+1 -0
Animal welfare			
Effects relatively few individual animals	+ Relatively few sharks interact with the industry	– – Many fish interact with the industry	– – ~4000 silver trevally interact with the industry
Does not cause physiological stress to animal	U/Ø	U/– Large aggregations potentiate stress from increased competition, or predation risk	+/– Trevally are in good physiological condition, but could potentiate stress from increased competition, or predation risk
Does not physically harm wildlife	- Occasional collisions with cages may cause injury	– Collisions with cages may cause minor injury	- Collisions with cages may cause minor injury
Does not facilitate harm to conspecifics	– Rare aggressive competition	– Some fish are aggressively competitive	+/– Some fish are aggressively competitive, however limited signs of harm observed in silver trevally
Does not facilitate disease	U/– Aggregations potentiate higher parasite load and disease transmission	U/– – Large aggregations potentiate higher parasite load and disease transmission	+/– Trevally were of good physiological condition, however, requires internal examination
Maintains normal migration and movement	– Increased residency	U/–	+/– Trevally Increased residency, reduced space use, but still undertook natural movements.
Does not facilitate predation	+ Few white shark predators, with a single incident of predation by an orca at this site	U/– No observed successful predations around diving boats Increased shark residency	– Observed successful predations around diving boats Increased shark residency

Factors	**Focal**	**Non-focal (Meyer et al. 2021)**	**Non-focal (Dennis 2023)**
		potentiates natural predations on pinnipeds & benthic elasmobranchs	potentiates natural predations on pinnipeds & benthic elasmobranchs
Maintains natural foraging & energy budget	+ + No change in diet or nutritional condition – Increase energy expenditure	– – Altered diet from consuming attractant	– Altered diet from consuming attractant, energy surplus due to no change in activity of silver trevally (opposite for kingfish) but were in good condition and growing larger.
Impacts from conditioned behaviour	U/– Potential reduced foraging range, reduced threat avoidance. Potentially conditioned to human interaction, but unlikely	U/– Conditioned fish are more aggressive. Reduced threat avoidance, including approaching boats, fishers & divers	– Trevally respond to olfactory cues. Conditioned fish are more aggressive. Reduced threat avoidance, including approaching boats, fishers & divers
Does not impact on mental state	U/– Potential frustration with failure to capture bait, may compromise natural learning opportunities U/+ Increased residency at rich hunting grounds	U/– Increased fear of predation and stress from competition	U/– Increased fear of predation and stress from competition
Proportion score	+0.29 –0.29	+0 –0.65	+0.2 -0.5
Ecosystem impacts			
Maintains suitable environment	+ Minimal traffic (3 boats max)	+ Minimal traffic (3 boats max) – Light pollution can attract nocturnal birds and squid U/– Potential noise pollution U/– Potential for nutrification from fish aggregations and attractant	+ Minimal traffic (3 boats max) – Light pollution can attract nocturnal birds and squid U/– Potential noise pollution +/– Trevally moderate impact of attractant. lack of nutrification from fish aggregations and attractant need to be confirmed
Does not strain natural resources	– Longer residency potentiates more predations + + Attractant is waste from local aquaculture	U/– Provisioned fish may strain resources when operators are absent +/– Attractant is waste from local aquaculture U/– Unbalanced pelagic fish assemblages	+/– Provisioned fish may strain resources when operators are absent, however populations did not show decline when absent for prolonged period + Attractant is waste from local aquaculture, preventing impacts on other species if dumped. U/– Unbalanced pelagic fish assemblages
Does not competitively exclude species	– Mid-trophic level elasmobranchs excluded	+ Unaltered benthic fish assemblages – Trevally and leatherjacket dominance likely to affect other species	+ Unaltered benthic fish assemblages + Trevally dominance has not affected abundance of other species.
Does not facilitate invasive species	Ø	Ø	Ø
Proportion score	+0.33 –0.17	+0.15 –0.35	+0.3 –0.25

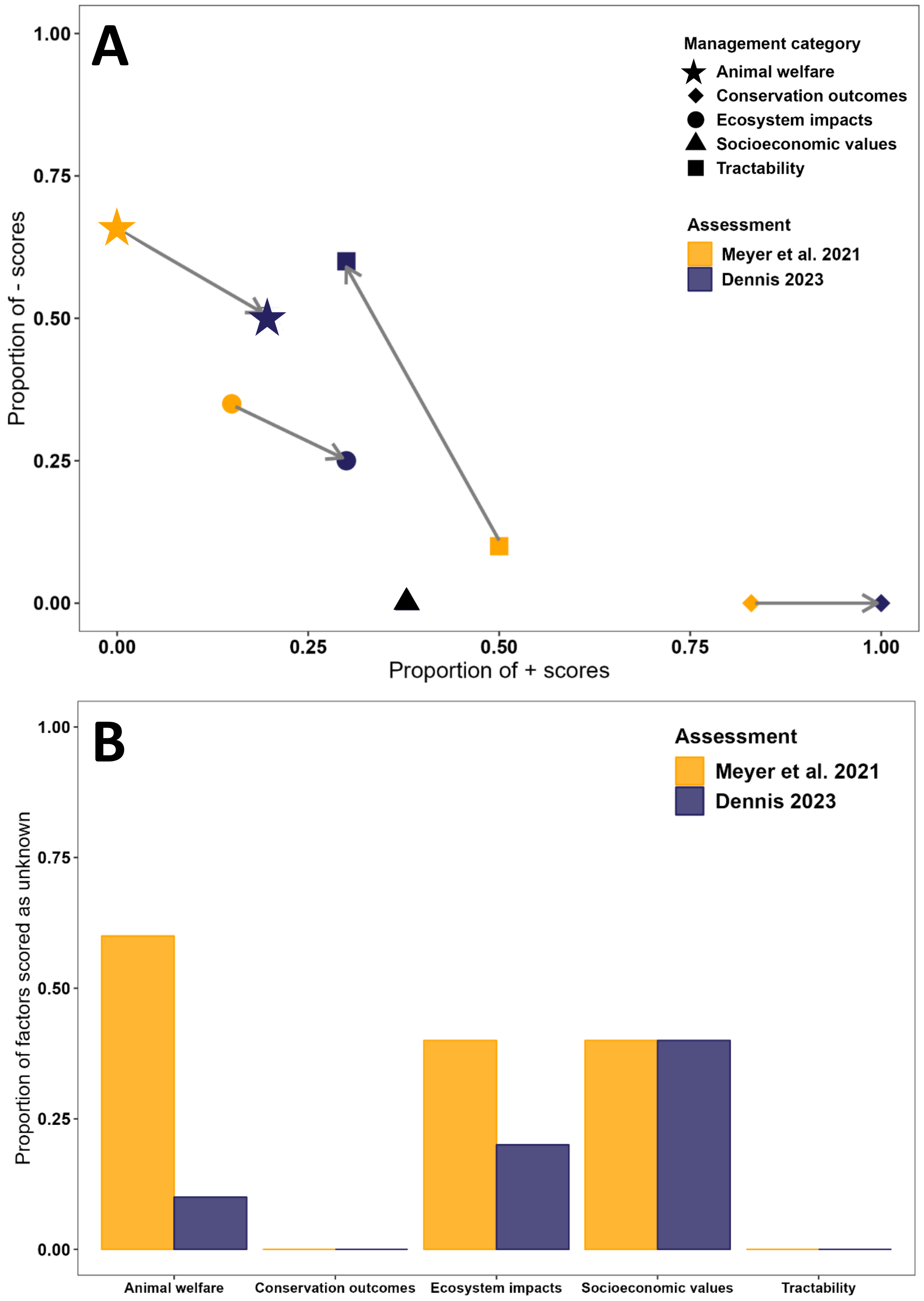


Figure 30. A. Updated proportion of known positive impacts (+ scores) and negative impacts (- scores) on non-focal species from cage-diving practices in South Australia for each management category. **B.** Updated proportion of factors within each category scored as unknown. Assessment scores from Meyer et al. 2021, and Dennis 2023 (this thesis). Symbols indicate management category. Socio-economic value is identical for both assessments. Arrows indicate change from Meyer et al. 2021 to Dennis 2023.

Cage-diving operators have raised concerns about the aggregations of silver trevally, which has the potential to lead to customer dissatisfaction, and even negative perception of the species and marine park outcomes (as per management framework, Table 14). One solution to reduce the number of silver trevally impacting customer satisfaction may be to reduce or cease the use of bait and berley. While removal of the provisioning from an already impacted site has the potential to cause further ecological implications (see section 6.3), effectiveness of the industry, facilitation of research, and the associated economic value may also be impacted. At the Neptune Islands, sound-based operators had a 37% chance of encountering sharks, compared to 75% with food-based provisioning (Figure 31A). The number of sharks sighted per day also increased with the use of food-based provisioning (sound-based: < 1 shark per day *versus* food-based provisioning: ~2–3 sharks per day; Figure 31B). Without the use of food-based provisioning, the successes of shark tourism would likely decrease, leading to poor customer satisfaction, potential financial impacts, and a loss of support for research that requires close encounters with focal and non-focal species. Another option may be the removal of silver trevally (i.e., culling or translocating), preventing the need for changes to provisioning. However, silver trevally act as eco-moderators, limiting the impacts of provisioning on other species (see section 6.4). Removing silver trevally may result in the provisioning influencing other species which may not be as transient or migratory as silver trevally (see section 6.2). Species which may be year-round residents at the Neptune Islands could be impacted, developing health and fitness impacts that were not observed for the silver trevally (see section 6.2–6.4). As the current impacts on the trevally are minimal, and they are essentially residing in an *ecological haven* (see section 6.2), current practices present the lowest ecological impacts compared to other provisioning scenario. Additionally, the minimal impacts of provisioning on the focal white sharks further supports the current practices, representing a holistic management approach of focal and non-focal species at the Neptune Islands.

While the known impacts are minimal, knowledge gaps have also been identified. Industry guidelines currently indirectly manage the non-focal species, but future guidelines should consider and directly manage impacts on non-focal species. Direct management efforts might include restrictions on anchorage location to reduce habituation by ensuring operators utilise more of the island, or reviewing current provisioning practices (i.e., type and quantity of provisioning) to better align with the natural diets of non-focal species. Alterations to pre-existing practices, does require prior assessment to ensure changes do not result in, or worsen effects on the non-focal individuals (i.e., ensure species are not dependent on provisioning). Future research understanding the daily energy expenditure of trevally would support modifications to provisioning, ensuring sufficient caloric value is supplied, mitigating potential negative impacts. In addition, understanding and identifying potential environmental impacts (i.e., eutrophication or repeated anchoring) on the benthic habitat should be prioritised by future research and policymakers. This may include determining concentrations of organic material in the sediment or impacts to the benthic environment, both of which would be alleviated through the proposed direct management efforts.

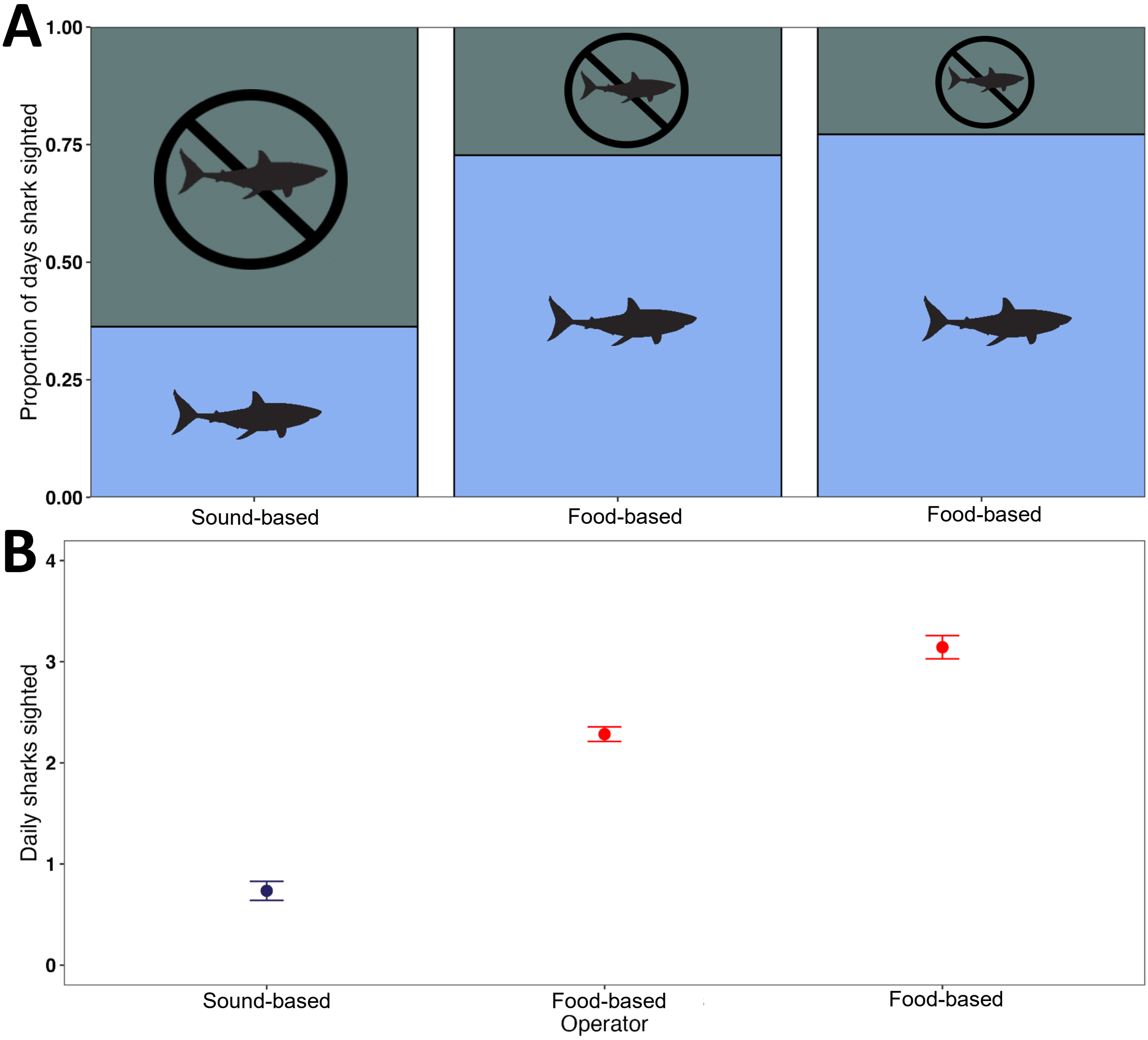
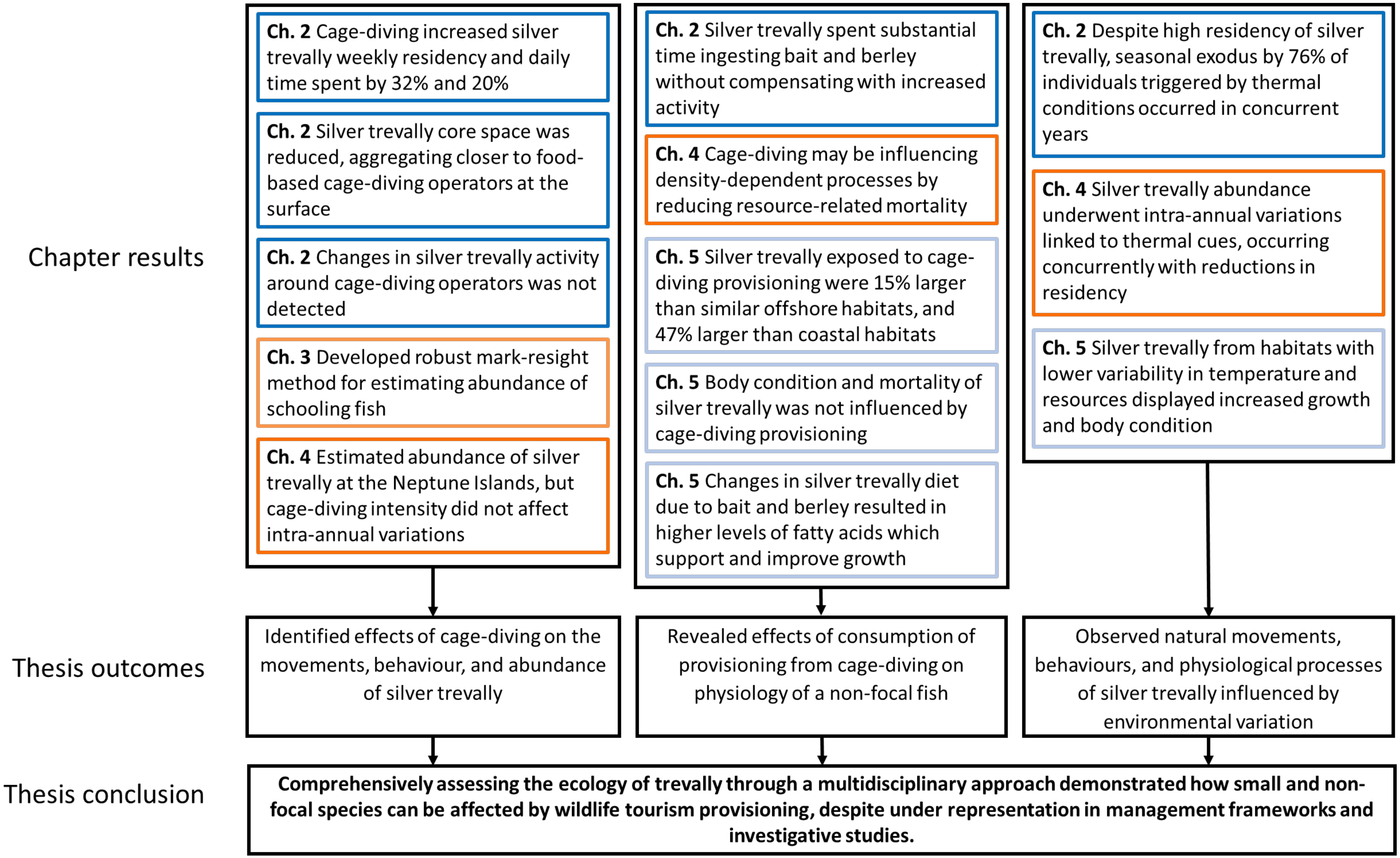


Figure 31. A. Proportion of total operating days from March 2020 to November 2023 when white sharks were sighted by sound-based (Adventure Bay Charters) and food-based (Calypso Star Charters; Rodney Fox Shark Expeditions) cage-diving operators at the Neptune Islands, South Australia**. B.** Daily number of sharks sighted by sound-based and food-based cage-diving operators. Error bars indicate standard error.

6.6 Conclusions

This is the first study to comprehensively assess the impacts of wildlife tourism on a non-focal species. My thesis aimed to determine the effects of cage-diving on silver trevally by: 1) identifying the effects on movements, behaviour, and abundance of silver trevally (Chapters 2, 3 & 4); 2) revealing the impacts of provisioning on the physiology of silver trevally (Chapters 2 & 5); and 3) observing natural movements, behaviours, and physiological processes of silver trevally exposed to provisioning (Chapters 2, 4 & 5; Figure 32). Findings from this thesis provide a baseline for impacts of supplemental feeding on a non-focal species. Despite the effects described in this thesis, exodus from the Neptune Islands during cold periods and the effect of temperature on population size indicates that silver trevally are still undergoing natural movements and behaviours triggered by temperature. I synthesised concepts of the Neptune Islands Group acting as an *ecological haven* for the silver trevally, which could potentially be leveraged to support at risk populations. Findings from this study were used to address knowledge gaps identified in the previous assessment of the sustainability and acceptability of white shark cage-diving industry, highlighting the importance of detailed understandings of both focal and non-focal species at tourism sites. Ultimately, consideration of non-focal species in tourism management is an essential component that continues to lack appropriate representation, underpinning any consideration of operations being labelled sustainable. Overall, my thesis comprehensively assess the ecology of silver trevally through a multidisciplinary approach, showing that small and non-focal species can be affected by provisioning, further highlighting the need for a more inclusive holistic ecosystem approach to wildlife research.



Chapter results

Ch. 2 Cage-diving increased silver trevally weekly residency and daily time spent by 32% and 20%

Ch. 2 Silver trevally core space was reduced, aggregating closer to food-based cage-diving operators at the surface

Ch. 2 Changes in silver trevally activity around cage-diving operators was not detected

Ch. 3 Developed robust mark-resight method for estimating abundance of schooling fish

Ch. 4 Estimated abundance of silver trevally at the Neptune Islands, but cage-diving intensity did not affect intra-annual variations

Ch. 2 Silver trevally spent substantial time ingesting bait and berley without compensating with increased activity

Ch. 4 Cage-diving may be influencing density-dependent processes by reducing resource-related mortality

Ch. 5 Silver trevally exposed to cage-diving provisioning were 15% larger than similar offshore habitats, and 47% larger than coastal habitats

Ch. 5 Body condition and mortality of silver trevally was not influenced by cage-diving provisioning

Ch. 5 Changes in silver trevally diet due to bait and berley resulted in higher levels of fatty acids which support and improve growth

Ch. 2 Despite high residency of silver trevally, seasonal exodus by 76% of individuals triggered by thermal conditions occurred in concurrent years

Ch. 4 Silver trevally abundance underwent intra-annual variations linked to thermal cues, occurring concurrently with reductions in residency

Ch. 5 Silver trevally from habitats with lower variability in temperature and resources displayed increased growth and body condition

Thesis outcomes

Identified effects of cage-diving on the movements, behaviour, and abundance of silver trevally

Revealed effects of consumption of provisioning from cage-diving on physiology of a non-focal fish

Observed natural movements, behaviours, and physiological processes of silver trevally influenced by environmental variation

Thesis conclusion

Comprehensively assessing the ecology of trevally through a multidisciplinary approach demonstrated how small and non-focal species can be affected by wildlife tourism provisioning, despite under representation in management frameworks and investigative studies.

Figure 32. Thesis overall conclusion and outcomes with each chapter's contribution

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APPENDICES

Supplementary material 1. Link to trevally impeding cage-diving tourist’s view.

https://drive.google.com/file/d/1eM8EDxxkodDmhY9EJHt6vQmhBVFszefk/view?usp=sharing

Supplementary material 2. Link to video of silver trevally bursting towards fresh baits thrown by the cage-diving industry.

https://drive.google.com/file/d/1jkJuGB21UgfWXB9HW90d7vHnucdRcrCI/view?usp=sharing

Supplementary material 3. Acoustic tag specifications.

V9AP transmitter settings were: 270–330s interval delay between high power transmissions, depth resolution of 0.1504 m and range of 34 m, accelerometer range of ± 4.9 m/s^2, and acceleration/depth transmission ratio of 3:1. Acceleration was sampled at 12.5 Hz for 15 seconds prior to each transmission and converted using the root mean square value of all three axes (activity = $\surd[X^2 + Y^2 + Z^2]$, averaged over time). The static contribution to the overall acceleration (g) was filtered out prior to root mean square calculation. The root mean square acceleration resolution was 0.01922 m/s^2.

Supplementary material 4. Link to video of swim pass survey conducted to resight ID tags for mark-resight abundance estimates.

https://drive.google.com/file/d/1xBoUugOTY05sglwVdIQt5DngMpVJNzWA/view?usp=drive_link

Supplementary table 1. R^2 values for each top-ranked model and each variables included in these models.

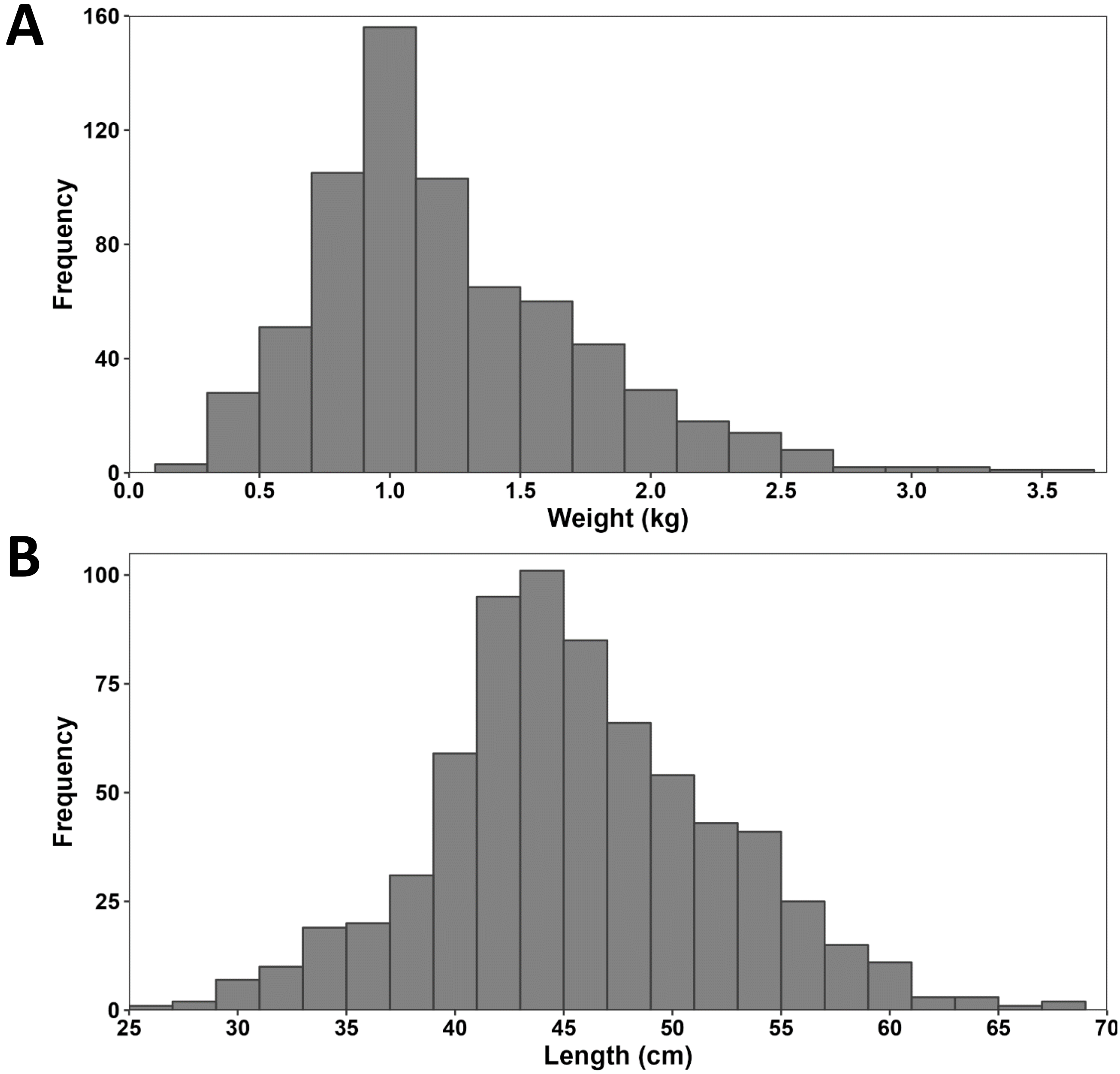
Model	**Variable**	**R^2 (%)**
Time spent	Full model	28.30
	Operator type	3.60
	Month	20.20
	TagID	4.40
Weekly Residency	Full model	31.70
	Operating days	2.50
	Month	25.50
	TagID	2.90
3DKUD-50 volume	Full model	47.10
	Operator presence	11.10
	Month	34.30
	TagID	2.20
3DKUD-95 volume	Full model	53.90
	Operator presence	9.10
	Month	38.80
	TagID	3.90
Distance	Full model	18.11
	Hour	3.42
	Operator type	8.16
	Hour*Operator type	12.84
	Month	5.37
	TagID	0.75
Depth	Full model	31.00
	Distance	1.38
	Hour	0.21
	Month	5.59
	Operator type	0.25
	Distance*Operator type	2.94
	TagID	28.28
Activity	Full model	17.01
	Depth	8.48
	Distance	0.027
	Hour	0.95
	Operator type	0.15
	Distance*Operator type	0.86
	Hour*Operator type	1.65
	Month	3.42
	TagID	9.29
Days since last boat	Full model	5.80
	Days since	0.70
	TagID	5.10

Supplementary table 2. Mark-resight model selection table for three mark-resight models (IELNE^{MR}, PLNE^{MR}, IELNE^{AC}) for two sampling years (2020; 2021): IELNE^{MR} and PLNE^{MR}: ID-tagged individuals and untagged individuals during surveys. IELNE^{AC}: Acoustic detections during surveys and untagged individuals during surveys. Model parameters are resighting probability (*p*), individual heterogeneity (σ), difference in population size and the mean population size (α), the mean population size (N^{-}),the super-population size (N^{*}), apparent survival (ϕ), the total number of unmarked individuals in the population (U), and the probability of transitioning from an unobservable state (γ''). Modelled as constant (.) or varying over time (t). 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; *w*AIC$_c$, model probability; Only the top 4 ranked models are presented for table clarity.

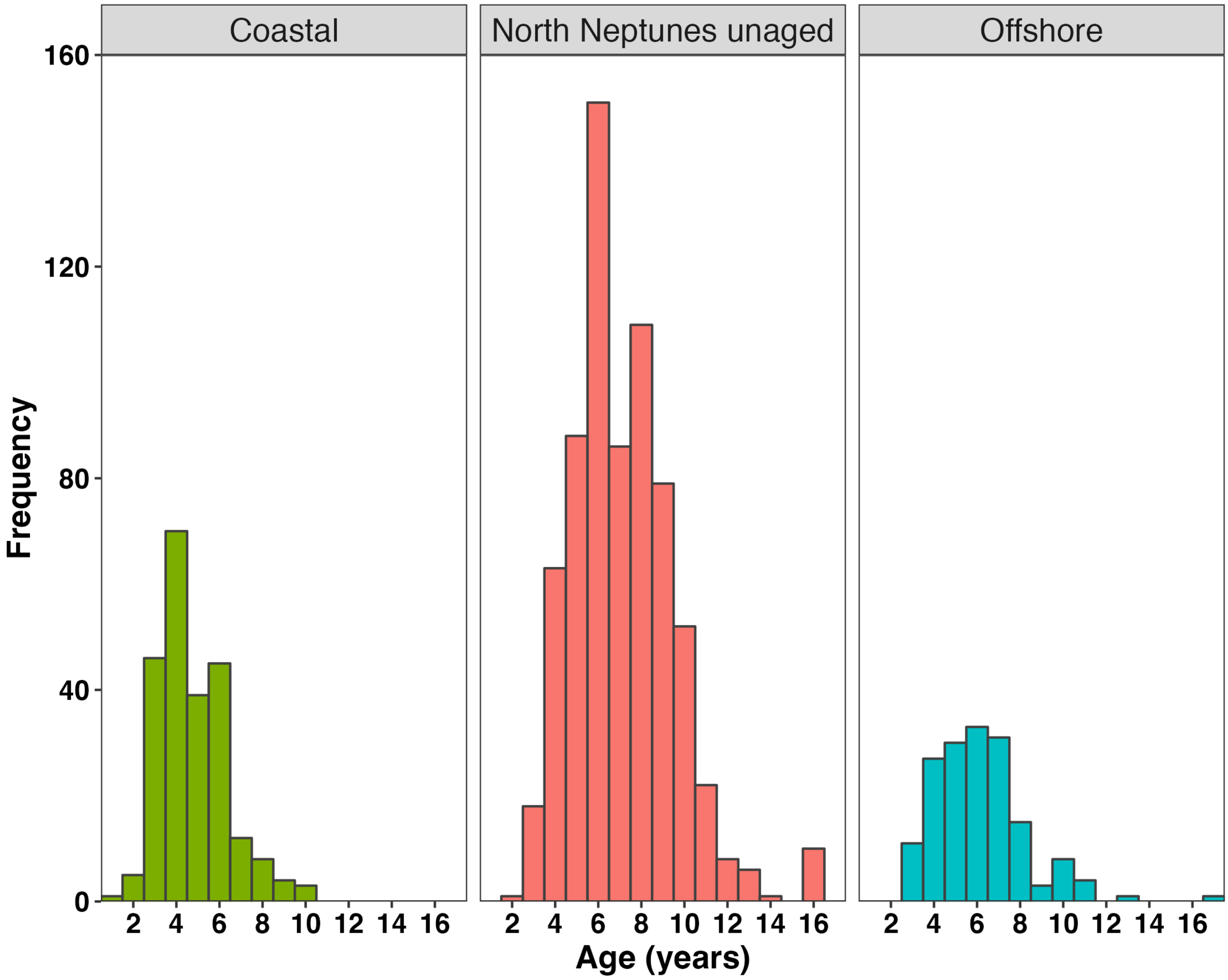
Model	AIC$_c$	ΔAIC$_c$	*w*AIC$_c$	Model likelihood	# Par	Deviance
IELNE^{MR}						
2020						
p(.) σ (0) α (0) N^{*}(t) N^{-} (t)	**2490.21**	**0**	**0.87**	**1**	**30**	**2402.21**
p(t) σ (0) α (0) N^{*}(t) N^{-} (t)	2494.05	3.84	0.13	0	41	2385.02
p(.) σ (0) α (.) N^{*}(t) N^{-} (t)	2518.06	27.84	0	0	31	2450.43
p(.) σ (0) α (t) N^{*}(t) N^{-} (t)	2530.41	40.23	0	0	40	2465.04
2021						
p(.) σ (0) α (0) N^{*}(t) N^{-} (t)	**3100.726**	**0**	**1**	**1**	**30**	**2779.17**
p(t) σ (0) α (0) N^{*}(t) N^{-} (t)	3104.736	4.01	0	0	41	3019.03
p(.) σ (0) α (.) N^{*}(t) N^{-} (t)	3181.556	80.83	0	0	31	3116.15
p(.) σ (0) α (t) N^{*}(t) N^{-} (t)	3199.077	98.35	0	0	40	3135.89
IELNE^{AC}						
2020						
p(t) σ (.) α (t) N*(t) N– (t)	**2577.358**	**0**	**1**	**1**	**41**	**2489.35**
p(t) σ (.) α (.) N*(t) N– (t)	2584.568	7.21	0	0	32	2501.54
p(.) σ (.) α (t) N*(t) N– (t)	2594.418	9.85	0	0	32	2510.65
p(.) σ (.) α (.) N*(t) N– (t)	2614.898	20.48	0	0	23	2594.54
2021						
p(t) σ (.) α (t) N*(t) N– (t)	**2639.25**	**0**	**1**	**1**	**69**	**2589.42**
p(t) σ (.) α (.) N*(t) N– (t)	2642.53	3.28	0	0	53	2601.25
p(.) σ (.) α (t) N*(t) N– (t)	2657.77	15.24	0	0	53	2610.59
p(.) σ (.) α (.) N*(t) N– (t)	2695.66	37.89	0	0	37	2661.21
PLNE^{MR}						
2020						
ϕ(.) σ (0) α (.) γ''(.) U(t)	**15815.72**	**0**	**1**	**1**	**12**	**15791.61**
ϕ(.) σ (0) α (t) γ''(.) U(t)	15867.34	51.62	0	0	19	15831.09
ϕ(t) σ (0) α (.) γ''(.) U(t)	15880.20	64.48	0	0	18	15844.05
ϕ(.) σ (0) α (.) γ''(t) U(t)	15889.15	73.43	0	0	18	15862.52
2021						
ϕ(.) σ (0) α (.) γ''(.) U(t)	**2550.14**	**0**	**1**	**1**	**14**	**2505.85**
ϕ(t) σ (0) α (.) γ''(t) U(t)	2583.06	32.92	0	0	22	2538.77
ϕ(t) σ (0) α (.) γ''(.) U(t)	2655.23	105.09	0	0	22	2594.70
ϕ(.) σ (0) α (.) γ''(t) U(t)	2666.64	116.51	0	0	30	2638.52

Supplementary table 3. Number of samples of silver trevally (*Pseudocaranx georgianus)* for different sampling habitats (North Neptune, Offshore, Coastal) and analysis types (Growth = length-at-age analysis, BIA = Bioelectrical Impedance Analysis, FA = Fatty acid analysis) in South Australia. Numbers in parentheses indicates location numbers on Figure 24.

Location	**Growth**	**BIA**	**FA**
North Neptune (1)	207	448	7
Offshore			
Liguana (2)	7	-	5
South Neptune (3)	73	144	-
The Pages (4)	52	47	10
Saunders Bank (5)	32	-	
Coastal			
Aldinga (6)	8	-	-
Arno Bay (7)	4	-	-
Cape Elizabeth (8)	13	-	-
Coffin bay (9)	8	-	-
Dangerous reef (10)	117	56	24
Point Turton (11)	27	-	-
Port Kenny (12)	22	-	-
The Passage (13)	34	-	



Supplementary figure 1. A. Weight frequency distribution of 700 randomly sampled silver trevally (*Pseudocaranx georgianus*) from the Neptune Islands Group Marine Park, South Australia. Weight was calculated using a bayesian length-weight relationship (weight = $10^{\log10(0.0141)}$ + 2.96 * $\log_{10}$(length)) for measured lengths. **B.** Total length frequency distribution of 700 randomly sampled silver trevally.



Supplementary figure 2. Age structures of silver trevally (*Pseudocaranx georgianus*) for different habitat types from South Australia. North Neptunes unaged age estimates calculated from an age-length-key using lengths of a random catch of individuals. Coastal n = 233 (8 locations), North Neptune unaged n = 694 (1 location), Offshore n = 164 (5 locations). Bin widths are 1 year.