Assessing the life history, ecological role and spatio-temporal movements of a neritic predator, the bronze whaler (*Carcharhinus brachyurus*)

by

Michael John Drew

Thesis Submitted to Flinders University for the degree of

Doctor of Philosophy

College of Science and Engineering

May 2018

Thesis declaration

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

Michael John Drew

Submitted for examination

October 2017

Table of Contents

List of Tables

2. SLOW LIFE HISTORY TRAITS OF A NERITIC PREDATOR, THE BRONZE WHALER (*CARCHARHINUS BRACHYURUS*)

3. ASSESSING THE SPATIO-TEMPORAL FORAGING DYNAMICS OF A TEMPERATE MARINE PREDATOR, THE BRONZE WHALER (*CARCHARHINUS BRACHYURUS*)

4. SEASONAL OCCURRENCE AND PHILOPATRY OF JUVENILE BRONZE WHALERS (*CARCHARHINUS BRACHYURUS*) IN A TEMPERATE INVERSE ESTUARY

5. THERMAL PREFERENCES AND COASTAL MIGRATIONS OF ADULT BRONZE WHALERS (*CARCHARHINUS BRACHYURUS*) IN TEMPERATE WATERS OF SOUTHERN AUSTRALIA

List of Figures

1. GENERAL INTRODUCTION

2. SLOW LIFE HISTORY TRAITS OF A NERITIC PREDATOR, THE BRONZE WHALER (*CARCHARHINUS BRACHYURUS*)

3. ASSESSING THE SPATIO-TEMPORAL FORAGING DYNAMICS OF A TEMPERATE MARINE PREDATOR, THE BRONZE WHALER (*CARCHARHINUS BRACHYURUS*)

4. SEASONAL OCCURRENCE AND PHILOPATRY OF JUVENILE BRONZE WHALERS (*CARCHARHINUS BRACHYURUS*) IN A TEMPERATE INVERSE ESTUARY

5. THERMAL PREFERENCES AND COASTAL MIGRATIONS OF ADULT BRONZE WHALERS (*CARCHARHINUS BRACHYURUS*) IN TEMPERATE WATERS OF SOUTHERN AUSTRALIA

Frontispiece

I dedicate this work to my wonderful parents, John and Stephanie Drew. Their love of nature and exploration was infectious for myself and my sisters, who all pursued careers in the natural sciences. Their willingness to show me every corner of this incredible country, instilled a deep fascination in its flora and fauna, and for that I will be eternally grateful.

Secondly, the drive to question the unknown was fueled by the stories and life work of Sir Hubert Wilkins, South Australia’s greatest unknown explorer. His unsurmountable achievements spurred by his desire to continually improve our understanding of earths atmospheric drivers, filled me with inspiration to pursue this challenging path.

Photo: Stephanie Drew

Logistical support and funding to support this study were provided by:

South Australian Research and Development institute (SARDI) Aquatic Sciences

Flinders University

Australian Research Council (ARC) (LP120100652)

Neiser Foundation

Mohamed Bin Zayed Species Conservation Fund

Nature Foundation of South Australia

Natural Research Management Board for the Mount Lofty Catchment

Scholarship funding was provided by:

Australian Postgraduate Award

Flinders University

Ministerial exemptions, animal ethics, and research permits

This study was undertaken under Flinders University's Animal Welfare Committee approval (Project number 360) and the State Ministerial Exemptions Section 115, 9902094, 9902064,

ABSTRACT

Many sharks are upper trophic level predators with wide-ranging distributions that play an integral role in the connectivity, maintenance, and stability of food webs. One such species is the bronze whaler (*Carcharhinus brachyurus*), which is a large-bodied species with a primarily temperate and coastal distribution in the Northern and Southern Hemispheres. Their coastal and nearshore distribution across southern Australia results in an overlap with anthropogenic stressors. However, information is limited for this wide-ranging predator and its vulnerability to the effects of fishing is poorly understood.

The overarching aim of this study was to assess the biology, ecological role, and movement of bronze whalers in temperate waters off southern Australia. I estimated the life history characteristics of bronze whalers by using vertebral growth counts to estimate age and biological data sampled from a seasonal commercial fishery. The ecological role and foraging ecology of bronze whalers in southern Australia was investigated by applying a combination of dietary assessment techniques, including stomach content and stable isotope analyses of muscle and liver tissue. Application of passive acoustic telemetry revealed insights into spatio-temporal patterns of occurrence, philopatry, and habitat use of juvenile bronze whalers in the inverse estuarine waters of northern Gulf St. Vincent. Broad-scale horizontal movements, and thermal and depth preferences of adult female bronze whalers were investigated using pop-up satellite archival tags.

Bronze whalers exhibited slow growth and a late ages-at-first maturity of 16 years for both males and females. Males matured at a smaller size than females. Fecundity estimated from four litters was low, ranging from 14 to 26 pups. Maximum age estimates were high for males and females at 25 and 31 years, respectively. Bronze whalers were identified as a generalist predator with a diverse prey field. Regional variations in prey diversity was evident with cephalopods (*Sepia novaehollandiae* and *Sepioteuthis australis*) and Australian sardine (*Sardinops sagax*) identified as the most important prey species. Fifty-six bronze whalers tagged with acoustic transmitters were monitored between 2009 and 2014 and showed a peak in seasonal presence in spring–early autumn (September–April). Philopatry to the study site was strong, with 77% of tagged sharks detected over multiple years. Time spent in the array was limited with a low estimate of mean residency index (mean Ri = 0.05 ± 0.01). Explanatory modelling indicated that water temperature and season had the most significant effect on presence, and juveniles exhibited the highest affinity to seagrass habitats (*Posidonia* spp.). Ten large bronze whalers (9 females and 1 unknown sex) ranging from 200–320 cm total length were tracked for 5–180 days (mean 106.5 ± 25.2 days) using pop-up satellite tags. Sharks tracked for >60 days moved from inshore waters (<50 m depth) to offshore shelf habitats (50–130 m depth) in late autumn, coinciding with the cooling of gulf and inshore coastal water temperatures. The maximum depth inhabited was 129 m, with four sharks inhabiting depths to >100m. Five sharks conducted broad-scale horizontal movements that covered distances ranging from ~200 km to coastal migrations of 1,600 km.

The findings of my study suggest that bronze whalers forage across several trophic levels and therefore play an important role in the ecosystem dynamics of temperate southern Australia gulf and shelf waters. The bronze whaler is a wide-ranging species that exhibit multi-jurisdictional movements from South Australia to Southeast Victorian and Western Australian waters. Sex- and stage-based segregation was evident within this population with shifts in habitat use occurring through life stages. Importantly, their predictable seasonal occurrence, coastal and neritic distribution, and slow life history traits combine to make the species potentially vulnerable to anthropogenic effects. The similarity in the life history characteristics of this species to the sympatric, highly migratory dusky shark (*C. obscurus*) which previous studies suggest is one of the most vulnerable shark species to extinction, highlights the need to ensure management and conservation improvements are considered for this important temperate marine predator. The findings of this study provided critical baseline biological and ecological information, that will be integrated into population assessments and ecosystem-based models recently developed for the southern Australian coastal, and shelf and oceanic waters.

ACKNOWLEDGEMENTS

First, and foremost, I would like to express an enormous amount of gratitude to my supervisors, Dr Charlie Huveneers and Dr Paul Rogers for their tireless work and persistence in helping me achieve something that I never thought that I could do. Paul Rogers you have an incredible skill set and are a highly capable and valuable scientist, you have provided me skills which have set me up for my working career. I can’t thank you enough for your patience and guidance through this process.

Charlie your work ethic is second to none, I still don’t even understand when you get time to sleep! Your continual support throughout this whole process has been unwavering, I also understand that I am not the most gifted of academics and you have continually supported me with the motivation to keep on going. I could not have done this study without your support and I will always be supremely grateful.

I would like to thank my colleges at SARDI in no particular order, Graham Hooper, Matt Lloyd, Tony Fowler, Mike Steer, Simon Goldsworthy, Johnathon Carroll, Bruce Jackson and Lachlan McLeay. Your support, encouragement and employment has always been greatly appreciated. I would like to thank the various members of the Southern Shark Ecology Group, Crystal Beckmann, Lauriene Escalle, Matt Heard and finally, Derrick Dapp for moral support and for the sleepless nights assisting with field work.

To all the countless volunteers, some of which are my good friends, Shea Cameron and Luke Sylvester, I can’t thank you enough of helping me with my diving, often not in ideal situations. I wouldn’t have been able to achieve what I have without your help. Additionally, I would like to extend my thanks to the various volunteers of Flinders University who helped me with laboratory work.

This research could not have happened without the support of the fisherman of South Australia, in particular I would really like to thank David Wilks, Wade Wheeler, Shane and Dan Frencsh, Kosta, Andrew and Bart Pisani and the infamous Darrin Brooks. I owe you all tremendously, and hopefully I have changed your opinions of what is to be expected out of a scientist.

To my dear friends who have all tolerated my absence and my often sleep deprived ramblings, you all have played a massive part in me finishing this ordeal and I will hopefully repay you all. To Alex Lloyd, Tom Steward, Ryan “Dad” Baring, Troy “Wonderboy” Rogers, Bill and Emma Howison and their amazing FIVE kids! A-ross and Esme Ross and the cutest little humans, Annie and Max and everyone from the House of Organics.

I couldn’t have done this without the support of my Family, Mum, Dad and Renee for the constant willingness to offer a hand and Megan for being the voice of reason on the other end of the phone. Your empathy and continual encouragement was one of the main reasons I continued to push even when I wanted to pack it in.

Publications resulting from this study:

Drew, Michael, Paul Rogers, and Charlie Huveneers. "Slow life-history traits of a neritic predator, the bronze whaler (*Carcharhinus brachyurus*)." *Marine and Freshwater Research* 68.3 (2017): 461-472.

The following publications resulted from side-studies completed during my PhD candidature:

Dapp, Derek R., Charlie Huveneers, Terence I. Walker, **Michael Drew**, and Richard D. Reina. "Moving from measuring to predicting bycatch mortality: predicting the capture condition of a longline-caught pelagic shark." *Frontiers in Marine Science* 2 (2016): 126.

Izzo, Christopher, Charlie Huveneers, **Michael Drew**, Corey J. A. Bradshaw, Stephen C. Donnellan, and Bronwyn M. Gillanders. "Vertebral chemistry demonstrates movement and population structure of bronze whaler." *Marine Ecology Progress Series* 556 (2016): 195-207.

Junge, Claudia, Stephen C. Donnellan, Charlie Huveneers, Corey J. A. Bradshaw, Alexis Simon, **Michael Drew**, Paul J. Rogers, Grant Johnson, Geremy Cliff, Matias Braccini, Rory McAuley, Clinton Duffy, Vic Peddemors, Paul Butcher, Scott C. Cutmore and Bronwyn M. Gillanders " Comparative population genomics confirms little population structure in two commercially important carcharhinid sharks." *In prep.*

Bradshaw, Corey J. A., **Michael Drew**, Thomas A. A. Prowse, Bronwyn M. Gillanders, Steven C. Donnellan and Charlie Huveneers. “Predicting sustainable shark harvest without stock assessments” *In prep*.

Huveneers, Charlie., Paul J. Rogers, and **Michael Drew**. “Monitoring shark species of conservation concern within the Adelaide metropolitan and Gulf St Vincent regions.” *Final Report to the Adelaide and Mount Lofty Ranges Natural Resources Management Board. SARDI Publication* F2013/000716 (2014): 1.

Rogers, Paul J., **Michael Drew**, Fred Bailleul and Simon D. Goldworthy. “Offshore survey of the biodiversity, distributions and habitat use of pelagic sharks in the Great Australian Bight”. *GABRP Research Report Number 7, Great Australian Bight Research Program,* August (2016). 77pp

Project extension was provided on the following websites:

Southern Shark Ecology Group website (www.southernsharkecologygroup.com.au)
AATAMS and IMOS acoustic telemetry database

1

GENERAL INTRODUCTION

Elasmobranch life histories

Many elasmobranchs (sharks, rays, and skates) have *K*-selected life history traits, characterised by slow growth, late maturity, low fecundity, high juvenile survival, and high longevity compared to the reproduction strategies of most ray fishes (Actinopterygii) (Walker 1998; Cortés 2000). The slow life history characteristics of sharks result in a low natural rate of population increase, which can have significant implications for populations subjected to additional unnatural mortality (Dulvy et al. 2014). The low potential for population increase causes many species to be vulnerable to overexploitation even under low levels of fishing pressure (Stevens et al. 2000; Dulvy et al. 2014). As a result, several shark populations have collapsed due to overfishing and may take decades to recover. Examples include the school or tope shark (*Galeorhinus galeus*) fisheries in California (Stevens et al. 2000) and Australia (Punt et al. 2000), and the western Atlantic Ocean dusky shark (*Carcharhinus obscurus*) fishery (Cortés et al. 2006).

Human effects on shark populations

Historically, sharks were captured by regional-scale artisanal and traditional fishers, primarily for their meat, skin, and teeth (Lack and Sant 2006). During the 1940s, the use of shark liver for squalene oil and vitamin A, led to the development of targeted shark fisheries (Lack and Sant 2006; Myers et al. 2007). The rapid advances and industrialisation of fishing fleets and equipment from the 1970s to the present day has seen shark exploitation intensify, with an almost four-fold increase in landings between the 1950s and 1990s (Bonfil 1994; Field et al. 2009; Worm et al. 2013). By 2010, the annual global catch of shark was 1.41 million tonnes, representing ~97 million sharks (Worm et al. 2013). The rise in shark landings was to meet the increased demand for their products (fins, livers, meat and cartilage) (Myers et al. 2007). More recently, sharks have been targeted for their fins, largely driven by the demand for fins to supply Asian markets, with an estimated 1.7 million tonnes of shark captured in 2000 to supply the Hong Kong fin market (Clarke et al. 2006). Between 2003 and 2011 the FAO reported a 15% decline in shark landings (Davidson et al. 2016). Explanations for this decline are unknown and could be attributed to a multitude of factors such as, improved management, reduced demand, reduction in targeting, gear changes, or the reduction of fishable biomass (Davidson et al. 2016). Davidson et al. (2016) suggested that improvements in management measures in the countries with the highest shark catches were unlikely to have had an immediate effect on shark landings, and that the reduction in catch was most likely the result of overfishing.

Global conservation measures

In addition to national management and fishing regulations, several regulatory treaties and measures have been implemented to avoid overexploitation and declining shark populations. The International Plan of Action for Sharks (IPOA-Sharks) is a nonbinding, legal instrument adopted by the FAO Committee on Fisheries (COFI) in 1999. This plan was established to ensure the conservation and management of sharks and their long-term sustainable use. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is an intergovernmental treaty that aims to ensure that international trade in specimens of wild animals and plants does not threaten their survival. It is the world’s primary mechanism for regulating international trade in endangered and threatened species. Fifty-two species of elasmobranchs are now listed in CITES Appendix I, II and III, with silky sharks (*C. falciformis*), thresher sharks (*Alopias* spp.), and devil rays (*Mobula* spp.) having been recently added in 2017. The Convention on Migratory Species of Wild Animals (CMS) is an intergovernmental treaty that aims to conserve migratory species throughout their range. Appendix I of CMS lists migratory species that are in danger of extinction, and Appendix II contains those species that need or would significantly benefit from international cooperation. A Memorandum of

Understanding (MoU) on the Conservation of Migratory Sharks was adopted under CMS in 2010 with the objective to “achieve and maintain a favourable conservation status for migratory sharks.” While many shark species are now listed on the CITES and CMS Appendices, and MoU, these instruments do not restrict domestic fishing effort or targeting of sharks and rays and the benefit of these measures for local shark populations is still to be determined. Many international resource treaties, e.g. the International Commission for the Conservation of Atlantic Tunas (ICCAT) or the Indian Ocean Tuna Commission (IOTC), and countries including Australia, New Zealand, Canada, United States, South Africa, Brazil, Costa Rica and Europe have restricted at sea shark finning. These regulations, however, often govern how sharks are taken rather than how many, and therefore require complementary management tools to ensure sustainable fishing practice (Clarke et al. 2013). Additionally, many countries that have implemented finning restrictions only represent a small portion of global chondrichthyan landings (Camhi et al. 2009).

Foraging ecology

Shark species are primarily mid- to upper-trophic level predators, with diverse and varying foraging strategies (Munroe et al. 2014a). In general, sharks are considered to have a broad prey field and occupy a large niche width, but many shark species have also been suggested to have a specialised diet. For example, whiskery sharks (*Furgaleus macki*) only feeds on cephalopods (Simpfendorfer et al. 2001a; Munroe et al. 2014a). Sharks often occupy the highest position in food webs and are therefore thought to exert significant top down influence on the structure and function of ecosystems (Baum et al. 2003b; Myers et al. 2007). Sharks have been shown to influence community structure in their ecosystems directly, through the mortality they inflict on their prey, and indirectly through sub-lethal risk effects that predators generate *via* behavioural changes in prey and competitors (Ruppert et al. 2013). These direct and indirect effects may impact the abundance and ecological function of species at the lowest levels in the food web (Ruppert et al. 2013). The wide-ranging nature of many shark species, also results in sharks frequenting multiple ecosystems and they play an important role in coupling and stabilising disparate food webs (Rooney et al. 2008). Ultimately, the predator-prey interactions between sharks and lower trophic species may lead to important changes to marine ecosystem function, productivity, and socioeconomic value (Holmlund and Hammer 1999; Halpern et al. 2008). Therefore, ascertaining and understanding the foraging dynamics of shark populations is critical for assessing their influence on the ecosystem. Traditionally, the foraging of a broad range of shark species has been investigated through the physical examination of the stomach contents (Hyslop 1980). Stomach content analysis facilitates a high degree of taxonomic precision into the recently consumed diet of the predator (Hyslop 1980). However, obtaining an adequate number of stomachs to describe the diet of a species can be difficult, in particular for a non-targeted species or one of conservation concern (Shiffman et al. 2012). More recently, the application of biochemical approaches for dietary analysis, such as stable isotope analysis allows the investigation of foraging over varying timescales, estimate trophic positions and identify prey sources, yet it lacks the prey specific resolution (Hussey et al. 2012). Dietary information is an important input into ecosystem-based models, which are used to assess the cumulative interactions within an ecosystem (Goldsworthy et al. 2013).

Movements and tracking

Understanding the movements and space use of marine species has historically been fraught with difficulties due to the concealing nature of the marine environment (Block et al. 2011; Hammerschlag et al. 2011). Advancements in tracking technology over recent decades have revealed insights into previously unknown behaviours, movements, and habitat use such as important areas for foraging, reproduction, and areas or times of increased vulnerability to anthropogenic threats (Hussey et al. 2015a). Telemetry studies have identified inter- and intra-species variations in habitat use and movement capabilities ranging from trans-oceanic migrations in white sharks (*Carcharodon carcharias*) (Duffy et al. 2012), shortfin mako (*Isurus oxyrinchus*) (Rogers et al. 2015), and whale sharks (*Rhincodon typus*) (Eckert et al. 2002) to highly residential species with limited home ranges, such as the nervous shark (*C. cautus*) (Escalle et al. 2015) and blacktip shark (*C. limbatus*) (Heupel et al. 2004).

The continual refinement and expanding range of tag capabilities allow researchers to investigate specific facets of a species ecology and physiology (Arnold and Dewar 2001). Currently, the three common electronic tags used in shark ecology research are passive acoustic transmitters, pop-up satellite archival tags, and satellite-linked platform transmitter terminals (Hussey et al. 2015a). Fine-scale movement studies have been transformed by the application of passive acoustic telemetry, which has identified philopatric behaviour, key areas for important life history events (reproduction and parturition), defined home ranges, and migratory patterns for several elasmobranch species (Heupel et al. 2006; Hussey et al. 2015a). Additionally, telemetry tags can also be used to investigate ambient physical parameters and physiological bio-logging of individuals (Hussey et al. 2015a). Acoustic tags can last for >10 years, depending on battery life and method of tag attachment, and can be used for studies across broad timescales, from hours to years (Hussey et al. 2015a). Broad-scale movements, migrations and habitat usage has been investigated with the application of satellite associated transmitters. Pop-up archival tags are mini-computers that are clock-integrated and designed to record high resolution light, water pressure, and temperature data at pre-programmed intervals (Sibert 2001; Hammerschlag et al. 2011). These tags allow for the investigation of habitat use and broad-scale movements by an individual and have been effectively used on species that seldom visit the surface. The horizontal displacement between tag deployment and detachment location can identify broad-scale movements for up to several years (Sibert 2001). However, deployment of these tags are typically 3–6 months, which allows for high resolution of data recorded and adequate battery life for the transmitting of data. After the pre-determined tag recording duration, the tag detaches, floats on the water surface, and transmits a summary of the archived data back to the user *via* a network of orbiting satellites (Arnold and Dewar 2001). If the tag can be recovered subsequent to the deployment all recorded data can be downloaded at a higher resolution than the transmitted data (Hammerschlag et al. 2011). Satellite-linked transmitters, are typically dorsal-fin mounted and transmit depth habitat and dive behaviour and radio signals used to estimate the location of the animal *via* orbiting satellites (Weng et al. 2005; Hammerschlag et al. 2011). Satellite-linked transmitters can last multiple years have been used to identify extensive trans-oceanic migrations, important diving behaviour, and habitat use and have identified key areas of importance for numerous large-bodied and highly mobile shark species (Arnold and Dewar 2001; Hammerschlag et al. 2011).

Carcharhinid biology

Carcharhinidae is the one of the most diverse chondrichthyan families, comprising of 56 species which inhabit most marine environments, from brackish estuaries to the pelagic open ocean (Weigmann 2016). Carcharhinids are fusiform in shape with a broad size range (<1 – >7 m) and possess viviparous reproduction (Last and Stevens 2009). Their life history characteristics when compared to teleosts are considered slow growing, late maturing, and of low fecundity (Cortés 2000). However, the life history characteristics of carcharhinids differ greatly between species and can even differs between populations within species (Lombardi-Carlson et al. 2003). Some small-bodied species possess fast growth rates compared to large-bodied species. For example, the Australian sharpnose shark (*Rhizoprionodon taylori*) reaches maturity after one year of rapid growth and has a maximum age of ~8 years (Simpfendorfer 1992). In contrast, the dusky shark (*C. obscurus*) reaches maturity at ~20 years of age, has low fecundity (mean of 9 pups per litter), and has a maximum life span of ~50 years, which led dusky sharks to be considered one of the most vulnerable species to overexploitation (Romine et al. 2009). The 55 species within the family are widely dispersed through most marine environments and thermal gradients. The majority (~95%) of carcharhinid species have tropical to warm temperate distributions, with ~5% inhabiting the temperate to sub-temperate thermal ranges (Weigmann 2016).

Carcharhinid fisheries

Carcharhinids are targeted worldwide through various fishing methods (long-lining, gill nets, drift nets, and drum lines) and caught as by-catch and retained as a result of their high-quality flesh and fins. Extensive fishing pressure over recent decades has been associated with reported declines of carcharhinid populations around the globe (Robbins et al. 2006; Baum and Blanchard 2010; Ferretti et al. 2010). Declines in relative abundance of ~70% of coastal carcharhinids, such as the dusky shark in the U.S. pelagic longline fishery have been reported between 1992–2005 (Baum and Blanchard 2010). The high catches of dusky sharks in the North West Atlantic and Gulf of Mexico through the 1990s has also seen severe declines in stocks (Romine et al. 2009). This species is now listed as vulnerable to extinction in the North West Atlantic and Gulf of Mexico on the IUCN red list (Cortés et al. 2006). Similarly, Robbins et al. (2006) identified an order of magnitude loss of whitetip (*Triaenodon obesus*) and grey reef shark (*C. amblyrhynchos*) populations on reefs outside of no-entry zones on the Great Barrier Reef (Robbins et al. 2006). Additionally, large declines of silky sharks (*C. falciformis*) (CITES appendix II listed) and blue sharks (*Prionace glauca*) captured as by-catch in the Atlantic and Indian Ocean long-line fisheries has been documented (Baum et al. 2003). However, the extent of the estimated decline by Baum et al. (2003) has been debated in literature (Burgess et al. 2006). Irrespective of the actual level of estimated declines, there is an overall agreement of large population losses for many carcharhinid (Dulvy et al. 2014). Many carcharinids due to their coastal distributions are also exposed to habitat degradation and pollution, and additional mortality through beach protection programs (Sumpton et al. 2011) and targeted by recreational anglers (Stevens et al. 2000).

Bronze whaler ecology, biology and global catches

The bronze whaler (*C. brachyurus*) or copper shark is a large-bodied (max 3 m total length) carcharhinid shark species that is found in both the Northern and Southern Hemispheres (Last and Steven 2009). Unlike most other carcharhinids, bronze whalers have a primarily temperate distribution in coastal and neritic waters, and mostly remain in relatively shallow depths of <100 m (Last and Stevens 2009). Life history characteristics of bronze whalers have been determined for the South African (Walter and Ebert 1991) and Argentinian (Lucifora 2003) populations, which identified this species to have slow growth, late maturity (19–20 years in South Africa and 21.7 years in Argentina for females) and low fecundity (mean ~16 pups) (Walter and Ebert 1991). Timing of parturition occurred during spring–summer in Argentinian, South African and Australian waters

(Walter and Ebert 1991; Lucifora et al. 2005; Rogers et al. 2013a; Drew et al. 2016). However, the periodicity of their reproductive cycle is still unknown.

Dietary studies in Argentina, South Africa, and Australia have shown that bronze whalers are considered to be generalist predators, with common prey species including locally abundant small pelagic teleosts and cephalopods, such as sardines (*Sardinops sagax*) and squid (*Sepioteuthis australis* and *Loligo reynaudii*) (Smale 1991; Lucifora et al. 2009; Rogers et al. 2012). Off Argentina, the presence of small-bodied elasmobranchs in the diet of large bronze whalers indicated an ontogenetic change in diet (Lucifora et al. 2009). Trophic position estimates in South Africa have determined that bronze whalers are a high order secondary consumer, similar to teleosts, such as the striped grunter (*Pomadasys striatus*) or similar body-sized carcharhinids, such as the spinner shark (*C. brevipinna*) (Hussey et al. 2014).

Genetic profiling has identified separate populations across the Southern Hemisphere, with genetically isolated stocks in South Africa-Namibia, Australia-New Zealand, and Peru (Benavides et al. 2011). Genetic mixing of the Australian bronze whaler stock is further supported by the broad-scale movements observed in a recreational tag and recapture study, which estimated some minimum long-range movements of >1000 km, through multiple state-managed jurisdictions (Rogers et al. 2013a). However, uncertainty regarding recreational fishers ability to accurately differentiate between bronze whalers and the sympatric dusky shark caused some speculation over these results and whether the long-range movements may have been undertaken by dusky sharks rather than bronze whalers (Rogers et al. 2013a). Some of the large estimates of movements may have been from tagged dusky sharks, which have also been identified as capable of extensive migrations (Rogers et al. 2013b). Furthermore, bronze whalers in South Africa have been identified to annual long-range northward movements from the Eastern Cape waters, exploiting the mass migration of African pilchards (*Sardinops sagax*) during the “sardine run” (Dudley and Cliff 2010).

In many parts of their distribution, a seasonal increase in occurrence has been identified, with both juveniles and adult females being captured in the inshore, coastal waters during the Southern Hemispheres spring–summer period in Argentina, Australia, and South Africa (Cliff and Dudley

1992; Lucifora et al. 2005; Rogers et al. 2013a). Off Argentina, bronze whalers are seasonally (spring–summer) targeted by shore-based recreational anglers and a small-scale commercial fishery (Chiaramonte 1998; Lucifora et al. 2005). In South Africa, bronze whaler aggregations have been identified to occur in the coolers waters off the Eastern Cape through the warm summer months (Smale 1991). In Australia, the increased seasonal presence of bronze whalers in the coastal waters of southern Australia has been identified by catch patterns in the recreational and commercial fisheries (Jones 2008; Rogers et al. 2013a).

Global whaler shark fisheries

Bronze whalers are commercially targeted in South Africa (Cliff and Dudley 1992), Australia (Jones 2008), and New Zealand (Francis 1998), with smaller targeted fisheries in Brazil, Uruguay, Argentina (Lucifora et al. 2005), Namibia (Kroese and Sauer 1998), and the Mediterranean (Duffy and Gordon 2003). In Argentina, bronze whalers represent one of two commercially targeted species that occurs seasonally in northern Patagonian coastal waters (Chiaramonte 1998). Reported catches are small during spring–summer periods, with 618 sharks captured over the 1993 and 1994 shark fishing seasons (Chiaramonte 1998; Lucifora et al. 2005). Recreational fishers also target this species over the same period (Chiaramonte 1998; Lucifora et al. 2005). In South Africa, bronze whalers comprise 29% of the catch in the beach net protection scheme along KwaZulu–Natal coast during the sardine run, which is the highest percentage of any shark species (Dudley and Cliff 2010). Bronze whalers are commercially targeted in relatively small numbers for both fins and flesh, with South Africa exporting much of its commercial catch as frozen fillets (Kroese and Sauer 1998). Namibia also lands small numbers of bronze whalers as part of their artisanal fisheries (Kroese and Sauer 1998). In New Zealand (NZ), bronze whalers are captured seasonally in a multi-species targeted fishery, with an average annual catch of ~27 tonnes between 1986–1997, with the highest maximum catch in 1995–1996 of 51 tonnes (Francis 1998).

In Australia, bronze whalers are predominantly a temperate species, inhabiting the southern Australian coast from Port Macquarie (New South Wales, NSW) around to Perth (Western Australia, WA) (Last and Stevens 2009) and are targeted across their distribution (McAuley et al. 2005; Jones 2008; Macbeth and Macbeth 2009; Fowler et al. 2016). However, due to their similarity in appearance to the sympatric dusky shark (*C. obscurus*), they are commonly misidentified by both commercial and recreational fishers. The difficulties in differentiating between the two species results in both species being grouped as whaler sharks in South Australia (SA), similarly, dusky sharks and bronze whalers have historically been described as bronze whalers in WA (McAuley et al. 2005; Jones 2008; Rogers et al. 2013a). In WA, commercial catches of bronze whalers are relatively low, representing ~3% of the annual whaler shark catch, with most catches recorded by the South western demersal gillnet fishery. In 2015, the total catch of dusky shark in WA was 154 tonnes, the 3% contribution of bronze whalers in the catches likely results in a total of ~5 tonnes of bronze whalers captured (McAuley et al. 2005; McAuley et al. 2015). This fishery uses demersal gillnets and long-lines that exclusively target neonates and juvenile sharks up to three years in age. During the 1990s, 89% of dusky shark catches was composed of 1–2-year old sharks (McAuley et al. 2015).

In NSW, bronze whalers are captured in the ocean trap and line fishery (OTL) (Macbeth and Macbeth 2009). Until 2005, catches were grouped as whaler sharks due to the difficulties in identifying sharks to the species level. Average annual whaler shark catches were approximately 165 tonnes per year until 2005–2006 when catches rose by 200% leading to the implementation of new management strategies (Macbeth and Macbeth 2009). These included a implementation of a total allowable commercial catch (TACC) for large shark species, maximum catch limits per trip, and permits for fishers specifically targeting sandbar shark (*C. plumbeus*) (Macbeth and Macbeth 2009). Improvements in the recording of catches to species level were also introduced through improved education of commercial fishers. On-board observer surveys showed that the majority of catches consisted of sandbar sharks (35%), with the dusky shark making up 15% of the total number of sharks landed and bronze whalers only comprising 1% of catches (Macbeth and Macbeth 2009). The fisher-dependent catch-reporting system indicated that bronze whaler catches were < 5 tonnes annually, with a peak in landings in 2007/08, of ~12 tonnes (Macbeth and Macbeth 2009).

In SA, whaler sharks are an economically important component of the South Australian Marine Scalefish (MSF) fishery (Fowler et al. 2016). The MSF is primarily an owner-operator multi-species commercial industry with the majority of fishers targeting sharks with longlines and gillnets (Jones 2008). South Australia has a targeted whaler shark fishery which seasonally fishes for bronze whalers and dusky sharks in coastal waters. The commercial catch composition is dominated by bronze whalers, with an estimated 10% of catches being dusky sharks (McAuley et al. 2015). Catches of both species are commonly termed "whalers" by the commercial fishers due to their similar appearance and difficulties in differentiating the two species (Rogers et al. 2013a). Whaler sharks are caught as by-catch in the Commonwealth managed gill-net hook and trap, Spencer and Gulf St. Vincent prawn trawls, small pelagic purse seine and Lower Lakes and Coorong swing net fisheries, and are targeted as prize game fish by recreational fishing sector (Jones 2008; Fowler et al. 2016). Annual whaler shark catches have averaged ~80 tonnes over the past 20 years (Jones 2008; Fowler et al. 2016) . A peak in catches was recorded in 2009–2010, with a landed trunk weight of 155 tonnes. Since the 2009–10 peak in catches, total landed biomass has receded back to ~70 tonnes per annum (Fowler et al. 2016). The catch composition mostly consists of juvenile sharks < 1.5 m, that are targeted in the spring–summer months (Rogers et al. 2013a). Relatively small catches of large female sharks occurred in the northern and southern Gulf waters over the same period (Rogers et al. 2013a). Currently, there are no size or catch restrictions for whaler sharks in the commercial fishery, enabling the targeting of sharks through their life history stages. However, in 2012, the maximum number of long-line hooks, primary gear used to target whaler sharks, was changed from 400 to 200 within the gulf waters of South Australia to restrict catches of snapper (*Pagrus auratus*). Annual whaler shark catches are assessed by fishery managers using state-wide harvest (kg), targeted and non-targeted effort (fisher days), and targeted catch per unit effort (CPUE) based trigger points (± 20% change) (Jones 2008). In South Australia, bronze whalers are targeted by the recreational fishing sector for both consumption and as sport fishing. In 2000–01, the estimated catch of whaler sharks by recreational fishers was ~57.2 tonnes, which was ~30% of the total whaler shark catches for that year (Jones 2008; Fowler et al. 2016). Limited gear and catch restrictions have been enforced on the recreational fishing sector, with a ban on shark fishing on Adelaide's metropolitan beaches during the daytime and a reduction in maximum hook size to 16/o and leader thickness to 1.6 mm stainless steel wire. In 2016, South Australian fishery management implemented changes to the fishing limits for the recreational sector, enforcing a daily limit of one whaler shark or a maximum of three per boat if three persons are onboard. Currently, the status and resilience of bronze whalers in South Australia is unknown and it is uncertain the level of impact that targeted and non-targeted fisheries is having on this population.

Background and aims

Bronze whalers have received limited scientific attention globally, with the majority of biological and ecological information collected from South Africa, Argentina, and Australia. This study was conceived to address the gaps in knowledge identified in a review of the fishery status for whaler sharks in South Australian waters (Jones 2008) and to build on recent work by Rogers et al. (2012; 2013a). The overarching objective of my thesis is to improve our understanding of the biology and ecology of bronze whalers in southern Australia to inform decision-making processes and minimise the potential detrimental effects of anthropogenic activities, including fishing.

To achieve this overall objective, the main aims of this study were to further our knowledge and understanding of:

1) The biological characteristics of bronze whalers in southern Australia;
2) The ecological role and importance of bronze whalers in southern Australian temperate ecosystem dynamics; and
3) The spatio-temporal variations in population distribution and movements within the coastal waters of southern Australia.

To fulfil each aim, I have completed four thesis chapters (excluding this introductory chapter and a general discussion chapter [Chapter 6]), each with specific goals which link to an aim and can be visualised in Figure 1.

Thesis structure

This thesis is comprised of a general introduction (Chapter 1) and four data chapters (Chapters 2–5) that are described in further detail below. This culminates with a synthesis of the key findings in the general discussion (Chapter 6).

Chapter 1: Introduces background information relevant to bronze whaler shark fisheries, biology, diet and movement, and their vulnerability to anthropogenic threats. This chapter describes the overarching aims and objectives of the study, the thesis structure, and a synopsis of the individual chapters.

Chapter 2: I modelled vertebral age count data with corresponding length and maturity data to estimate the life history characteristics of bronze whalers in the temperate waters of South Australia Life history information was then used in an age- and stage-based population model (Bradshaw et al. in review) to provide information to support sustainable fisheries. This chapter has been published in *Marine and Freshwater Research* (Appendix 1).

Chapter 3: I investigated the foraging ecology of bronze whalers over varying spatial and temporal scales by applying a multi-method approach of stomach content analysis and stable isotope analysis of liver and muscle tissue. This important ecological information was applied to broader-scale ecosystem modelling during the Great Australian Bight Research Program.

Chapter 4: I used passive acoustic telemetry to assess the seasonal occurrence and philopatry of juvenile bronze whalers in a temperate inverse estuary. Juvenile bronze whalers were monitored over a four-year period to investigate patterns of seasonal residency, philopatry, diurnal activity, habitat preferences, and to identify important nursery grounds. This information will improve our understanding of how bronze whalers use the sheltered waters of northern Gulf St. Vincent, and provides important baseline spatio-temporal information for future management and conservation measures. Information on fine-scale movements and spatio-temporal occurrence was documented in two published reports (Appendix)

Chapter 5: I used pop-up satellite archival tags to investigate the thermal preferences and coastal migrations of adult bronze whalers in the temperate coastal waters of southern Australia.

Chapter 6: The general discussion provides a synthesis of the key findings of this study, with a focus on discussing the implications of the outcomes of each data chapter. This chapter discusses some of the remaining key gaps in knowledge and future research priorities.

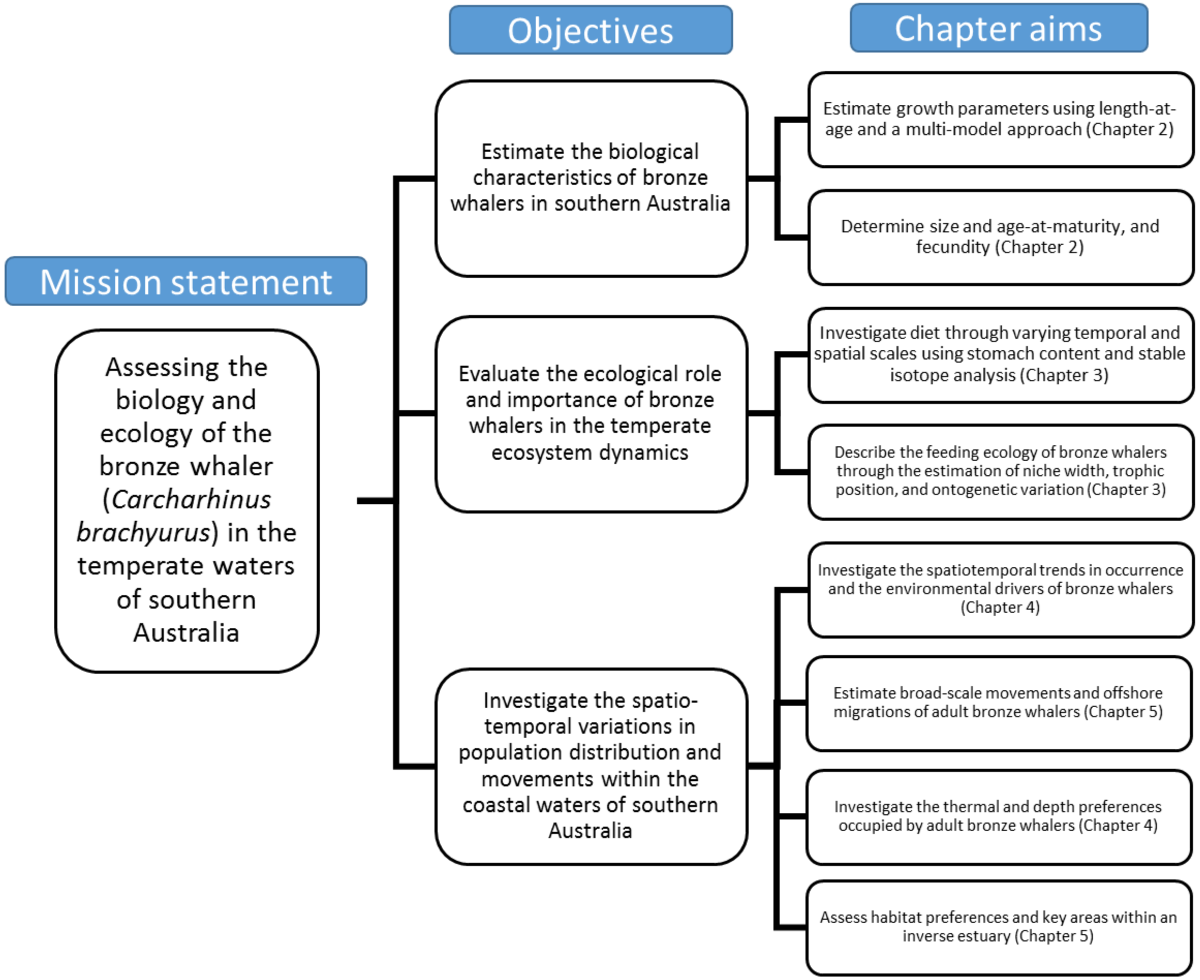


Figure 1.1 PhD structure with general objectives and chapter specific aims

2

SLOW LIFE HISTORY TRAITS OF A NERITIC PREDATOR, THE BRONZE WHALER (*CARCHARHINUS BRACHYURUS*)

Abstract

Intra-species plasticity in the life history characteristics of sharks leads to the need for regional estimates to accurately determine shark resilience to anthropogenic effects. This study provides the first length-at-age, growth and maturity estimates for the bronze whaler (*Carcharhinus brachyurus*) from southern Australia. Age estimates were obtained from vertebral sections from 466 sharks spanning 50–308 cm in total length (TL). Maximum estimates of age for males and females were 25 and 31 years. The model of best fit was the three-parameter Logistic model for females (L_∞ = 308 cm TL, k = 0.15, α = 742) and for males (L_∞ = 317 cm TL, k = 0.13, α = 782). Males matured at a similar age (16 years), but smaller size than females (224 vs. 270 cm TL). Growth parameters and age-at-maturity were similar to those estimated for genetically isolated bronze whaler populations and for the sympatric dusky shark (*C. obscurus*). The southern Australian bronze whaler population is long lived, slow growing and late maturing. These life history parameters are necessary to undertake demographic analyses to assess the resilience of bronze whalers to fishing, and provide an example of a wide-ranging elasmobranch with similar life history characteristics across isolated populations.

A manuscript based on this chapter was published in Marine and Freshwater Research (Vol 68-3, 2017 pg. 461–472).

Introduction

The bronze whaler (*Carcharhinus brachyurus*) (Günther, 1870) is a large-bodied coastal shark, with a patchy cosmopolitan distribution throughout the Northern and Southern Hemispheres (Cliff and Dudley 1992; Compagno 2001; Last and Stevens 2009; Rogers et al. 2013a). Although bronze whalers are reported to occur in tropical waters, the species is mostly found in temperate and subtropical marine ecosystems (Garrick 1982; Smale 1991). Bronze whalers are targeted throughout their range by commercial and recreational fishers for their high quality flesh and fins, and for sport (Jones 2008), and reportedly caught in Argentina (Chiaramonte 1998; Lucifora et al. 2005), Australia (Rogers et al. 2013a), New Zealand (Francis 1998), South Africa (Smale 1991; Cliff and Dudley 1992), and the Mediterranean (Duffy and Gordon 2003).

The comparatively low economic value of bronze whaler fisheries has resulted in the species receiving minimal scientific attention compared to other elasmobranchs that are targeted by larger commercial fisheries, such as the gummy shark, *Mustelus antarcticus* (Günther, 1870), or dusky shark, *C. obscurus* (Lesueur, 1818) (Walker 1994; Natanson et al. 1995; Simpfendorfer et al. 2002; Dudley et al. 2005; Geraghty et al. 2013; Natanson et al. 2014). Some life history characteristics of bronze whalers have been described for populations in the coastal waters of the South West Atlantic (Argentina) and South West Indian Oceans (South Africa) from commercial or recreational fisheries, and shark meshing programs (Walter and Ebert 1991; Lucifora et al. 2005). Mitochondrial DNA analysis has shown that populations from these regions and Australia are genetically isolated (Benavides et al. 2011). The slow growth patterns, large size-at-maturity, and corresponding low reproductive output are similar to that of the sympatric dusky shark (Walter and Ebert 1991; Simpfendorfer et al. 2002). The dusky shark has been the subject of multiple studies of its life history characteristics (Natanson et al. 1995; Simpfendorfer et al. 2002; Dudley et al. 2005; Geraghty et al. 2013; Natanson et al. 2014), with demographic analyses and stock assessments identifying this species as one of the most vulnerable sharks to overexploitation (McAuley et al. 2007; Romine et al.

2009). This has raised concerns about the comparative susceptibility of bronze whalers and the need to assess management measures to ensure the sustainability of target fisheries.

In Australia, the largest proportion of bronze whaler catch comes from the South Australian Marine Scalefish Fishery (MSF) which takes ~80 tonnes year^{-1} (Fowler et al. 2016). This seasonal (October–May) targeted fishery captures both dusky sharks and bronze whalers (Rogers et al. 2013a). The estimated proportion of dusky sharks in catch samples was lower (<20%) than bronze whalers, but varied spatially and temporally (Jones 2008; Rogers et al. 2013a). Whaler sharks are also taken as bycatch and considered to be a 'pest' species by the aquaculture industry (Jones 2008).

Growth rates, age, and reproductive output are key population parameters (Cailliet and Goldman 2004), and are required for most demographic analyses and fisheries stock assessments based on age-structured population models (Pauly 1987). Inaccurate age determination can lead to major errors in stock assessment and estimation of resilience to fishing (Hoenig and Gruber 1990; Officer et al. 1996; Campana 2001). While some life history parameters have been estimated for bronze whalers from the South West Atlantic and South West Indian Oceans, this information is lacking for the Australian population. The life history information of a species in one location cannot be assumed to be representative of other regional populations (Parsons 1993; Harry et al. 2011). Large regional variations in growth estimates have been found in blacktip sharks (*C. limbatus*) (Smart et al. 2015) and the scalloped hammerhead (*S. lewini*) (Harry et al. 2011; Drew et al. 2015).

The aims of this study were to estimate the length-at-age and growth parameters for bronze whalers from southern Australia to provide key demographic information necessary to assess the resilience of this population to fishing and inform fisheries management. Growth parameters were combined with size-at-first maturity to provide preliminary information on the maturity of bronze whalers. Our findings were then compared to life history traits of other regions, and to those of the sympatric dusky shark from Australian waters.

Methods

SAMPLE COLLECTION

Biological samples were collected during the Austral Spring–Autumn (September–May) between September 2009 and March 2014 through a combination of fisheries-dependent and independent sampling. Bronze whalers were mainly caught using commercial floating longlines in the South Australian Marine Scalefish Fishery. Longlines consisted of floating rope or mono-filament main-lines with 1.2–1.7 mm stainless steel leaders with up to 400 16/0 steel circle hooks attached to the main-line with a stainless steel clip. Management of longline fisheries changed the maximum hook limit to 200 in 2012. Main-lines were up to 8 km long, anchored, and marked at each terminal end with 20 to 70 cm diameter rubber floats. Hooks were spaced along the main-line at intervals of 10–20 m apart with small floats every two hooks. Samples were also obtained from recreational fishers who used suspended baits under balloons using heavy tackle (30–80 lb line) and leaders of 1.5–1.7 mm nylon-coated wire attached to 12/0 or 14/0 J-style hooks. Scientific longlines were deployed using similar gear as the commercial longlines, but with a reduced number of hooks (~110 hooks) and a main-line of 1.1–1.7 km in length. Commercial samples were collected from the Eastern Great Australian Bight and adjacent gulf waters (West Coast, Spencer Gulf and Gulf St. Vincent), which is part of the South East Indian Ocean (Fig. 2.1). Samples obtained from the recreational fishery and scientific surveys were obtained from the South East region and Northern Gulf St. Vincent (Fig. 2.1). Hereafter, the sample location for this region will be referred to as the southern Australia population.

The sex of each shark was determined by noting the presence of claspers in males. Length measurements were recorded to the nearest centimetre including total length (TL), pre-caudal length (PCL), fork lengths (FL), and trunk length (TKL). Linear regressions of TL on FL, PCL, and TKL were determined using data pooled across sexes. In situation when TL could not be measured during sampling, e.g., due to fisher processing sharks before TL could be measured (n = 79), TL was estimated using the regression for the next largest measurement, which was mostly PCL.

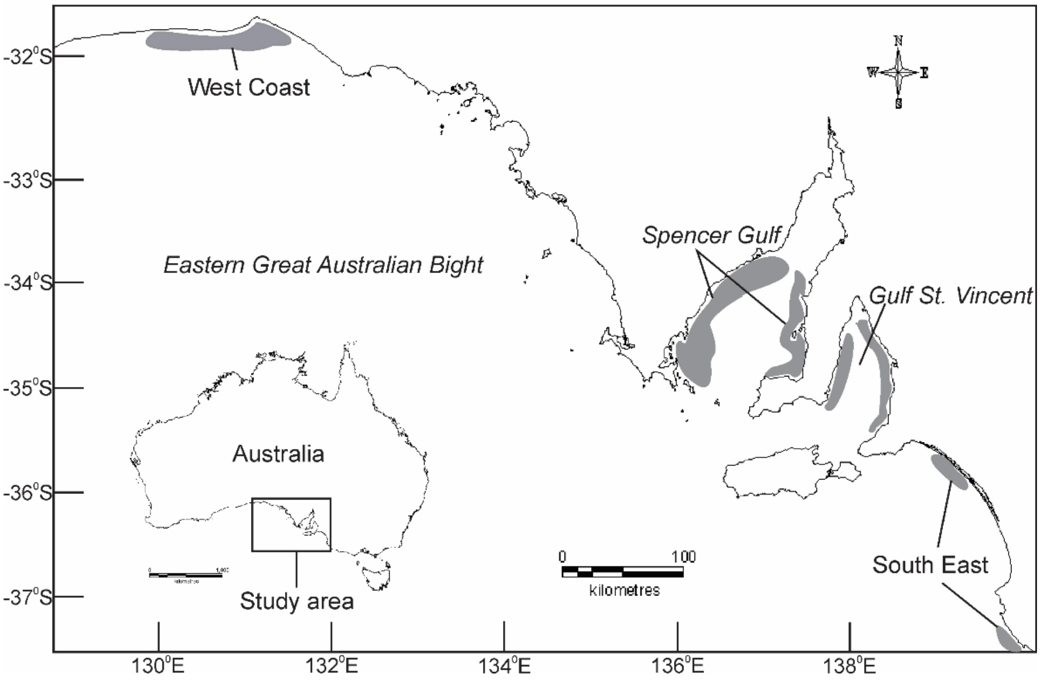


Figure 2.1 Map of Australia and South Australian coastal waters, fishing areas where vertebral samples of bronze whalers were collected are indicated in grey.

VERTEBRAE PREPARATION

A vertebral section, consisting of one to six vertebrae (centra), was collected from the region immediately posterior to the cranium. Removal of vertebrae anterior to the first dorsal fin (i.e. the largest vertebrae) was avoided as it may lower the market value of the trunk. The vertebrae were frozen until further processing and analysis. In the laboratory, vertebrae were thawed, excess muscle, connective tissue, and neural and ventral arches were removed and individual vertebrae were separated (Cailliet 1990; Goldman 2005; Cerna 2009). Individual centra were soaked in a solution of 5% sodium hypochlorite for periods ranging from 15 to 120 minutes depending on the size of the vertebrae to aid in the removal of intervertebral cartilage connective tissue on the *corpus calcareum* (Carlson and Baremore 2005; Piercy 2007). Vertebrae were then rinsed thoroughly under fresh water and left to air dry for ~24 hours.

One whole centrum from each individual was embedded in clear casting resin and sectioned sagittally by cutting through the focus of the vertebrae (Cailliet and Goldman 2004) using a low speed Gemmasta lapidary saw with a 150 mm x 0.06 mm pro-slicing diamond encrusted blade. The ~0.6 mm sections were washed in freshwater, cleaned, wiped with alcohol, and fixed to clear glass slides using Crystal bond temporary adhesive I509 (Proscitech). Thin cut sections were viewed under a dissecting microscope (Olympus SZ-PT) using transmitted light with varying magnifications (1–6.3 x) to accommodate the varying size range of the sections.

Growth bands were counted on one half of each vertebral section. A single growth band was defined as including one fully formed opaque band and one fully formed translucent band (Cailliet and Goldman 2004). The angle of change along the *corpus calcareum*, which identifies a change in growth rate, was considered the birth mark (Cailliet and Goldman 2004). Following the examination of vertebral sections from prenatal embryos from three litters, the presence of a translucent pre-birth band was identified slightly before the angle of change. Therefore, the first translucent band prior to the angle of change was considered as time zero. A pre-birth band was also identified for bronze whalers in South Africa (Walter and Ebert 1991). The timing of parturition was determined to be seasonal in Spring–Summer (November–February) based on the capture of pregnant female sharks and neonates with open umbilical scars (Jones 2008; Rogers et al. 2013a). Partial ages were estimated by adjusting the date of capture in relation to a theoretical birth date (Branstetter 1987; Piercy 2007; Kneebone et al. 2008). Since the birth date of bronze whalers was estimated to be between November and February, the theoretical birth date of 1 January was assigned for age estimations. To calculate partial age, the date of capture was converted to Julian days and divided by 365.25 days to estimate the fraction of the final year. This portion of the year was subsequently added to the growth counts.

Prior to undertaking the final two growth band counts and to ensure reproducible counts, two readers counted the number of growth bands from a subset of 50 vertebrae until their average percent error (Beamish and Fournier 1981) reached a constant repeatable value (± 0.5%). To assess between reader bias both readers counted a subset of 220 vertebrae from sharks across the size range. During reading, counts that disagreed by more than two bands between readers were repeated. If the two readers could not agree on a count that was within two growth bands that sample was classified as unreadable and discarded. Most counts agreed to within two years but agreement within four years was considered acceptable in fish aged ≥14 years and above (Bishop et al. 2006). The final count of the primary reader was used to generate the final age and to estimate growth rate parameters (Bishop et al. 2006).

PRECISION AND BIAS

The precision of band counts and reproducibility of counts were calculated using Average Percent Error (APE) (Beamish and Fournier 1981) and the Coefficient of Variation (CV) (Chang 1982). Within and between reader bias was estimated from the percent agreement (Cailliet 1990) where PA= [number agreed/number read]×100, and percent agreement (PA= [±1 yr]) for length groups of 10 cm to evaluate precision (Conrath 2002). Bowker's test of symmetry was used to test for within and between reader bias (Hoenig et al. 1995; Evans and Hoenig 1998). Age-bias plots were constructed to visually inspect bias for within and final between reader counts (Cailliet 1990).

VERIFICATION AND VALIDATION

Marginal increment ratio (MIR) is a ratio of the width of the last band on the outer edge of the centrum to the width of the last fully formed growth band (Conrath 2002). The measurements of growth bands were made using Imagepro V9.0 image analysis tool through an Olympus MZ5 dissecting microscope. Specimens under the age of one were not used for increment analysis because of the lack of fully formed growth bands (Goldman 2005). The centrum edge analysis (CEA) was used as an additional tool to verify the timing and frequency of growth band deposition. During age determination, the centrum edge of each vertebra was classed as either opaque or translucent (Kusher et al. 1992). The proportion of opaque and translucent band was plotted against the month of capture to determine seasonal changes in growth.

Wild bronze whalers were also chemically marked with oxytetracycline (OTC) to validate the periodicity in growth band deposition, as part of a scientific longline and movement study in the

Northeast of Gulf St Vincent (Fig. 2.1) between September 2009 and November 2014. Fifty-eight juvenile bronze whalers were captured and injected with OTC to chemically mark vertebrae at a dose of 20mg/kg (Huveneers et al. 2014). Prior to release, date and time, sex, and total length were recorded, and sharks were externally tagged with a plastic head conventional identification tag (Hallmark^{TM}, Hindmarsh Valley, South Australia) to allow for future identification when recaptured.

GROWTH MODELS

A multi-model inference (MMI) information theoretical approach was used to determine the most appropriate growth model, with an *a priori* set of six candidate models fitted to the length-at-age data (Burnham and Anderson 2002; Katsanevakis and Maravelias 2008). The candidate set consisted of the traditional three-parameter von Bertalanffy (VBGM - von Bertalanffy 1938), Gompertz (Gompertz 1825), and logistic growth models (Ricker 1979), along with their respective two-parameter (2P) equivalents (2P VBGM – Fabens 1965; 2P Gompertz – Gompertz 1825; 2P logistic – Ricker 1979). In the two-parameter growth models, the length-at-birth (L_0) and point of inflection (α) were fixed at 68 cm TL, based on published lengths at birth and the observed smallest recorded shark during this study (Walter and Ebert 1991; Lucifora et al. 2005). Model parameters were estimated by non-linear least-squares using packages *nlstools* in R assuming additive normal error structure (R Development Core Team 2013). Individual model performance was evaluated using the small sample bias adjustment form of the Akaike's (1973) Information Criterion (AIC_c) (Burnham and Anderson 2002; Katsanevakis and Maravelias 2008). The best model was determined to be the one with the lowest AIC_c value. Delta AIC_c (Δ AIC_c) and Akaike's weights (w_i) were calculated to conduct comparisons of individual model fits (Burnham and Anderson 2002). Models with ΔAIC_c of 0–2 had substantial support, those with ΔAIC_c of 3–7 had considerably less support, and those with $\Delta AIC_c>10$ had no support. Akaike's weights (w_i) represent the probability of choosing the correct model from the set of candidate models. The 95% confidence intervals around the best fit parameter estimates were derived from 10,000 re-sampled data sets using the bias-corrected accelerated boot strap method (Harry et al. 2011).

REPRODUCTIVE CHARACTERISTICS

Dissected specimens were visually inspected to assess their reproductive condition and classed with maturity indices (Huveneers et al. 2007). Males were considered mature when their claspers were fully calcified (Clasper index =3). Females were considered mature when the ovaries contained yellow follicles > 30 mm in diameter (Ovary index = 3–5), or when the uteri were enlarged tubular structures with thickened walls (Uterus index = 3–6). The sex and total length of embryos from each litter (or sub-sample of a litter) were recorded. The overall sex ratio of embryos was tested for significant variation from a ratio of 1:1 using a chi-square goodness-of-fit test.

Results

SAMPLE COLLECTION AND LENGTH REGRESSIONS

Vertebral centra were collected from 466 bronze whalers comprising of 259 females (50–308 cm TL) and 196 males (53–281 cm TL) (Fig. 2.2). A pre-natal translucent band was present on the centrum edge on the vertebrae of 22 near-term embryos from three litters. This band was evident slightly before the angle of change on the centrum edge, therefore, the first band after the angle of change was considered to be the first growth band.

All length based regressions were statistically significant with all correlation coefficients > 0.95:

TL = 0.830 * (FL) +22.544 R^2=0.99 n=391

TL = 1.364 * (PCL) – 35.924 R^2=0.98 n=212

TL = 1.655 * (TKL) + 30.418 R^2=0.96 n=68

PRECISION AND BIAS

The banding pattern was well defined for bronze whalers resulting in consistent band counts by both readers (Fig. 2.3). The number of bands could not be agreed on for three vertebrae that were discarded. APE, CV, and PA ± 1 between the final two counts of the primary reader were 4.9, 7.1, and 91.0%, respectively (Figure S2.1, Supplementary material). The Bowker's test of symmetry showed no significant bias between the final counts of the primary reader (X^2_{41}= 53.9; P = 0.085). The APE, CV, and PA±1 values between the final counts of both readers were 6.8, 9.7, and 79.1%, respectively (Figure S2.1, Supplementary material). The Bowker's test of symmetry showed no significant bias between the final counts of both readers (X^2_{49}= 44.36; P = 0.662). Between and within reader biases were relatively low considering the high growth counts. No systematic bias was recorded suggesting that consistent and repeatable interpretation of the banding pattern had been achieved.

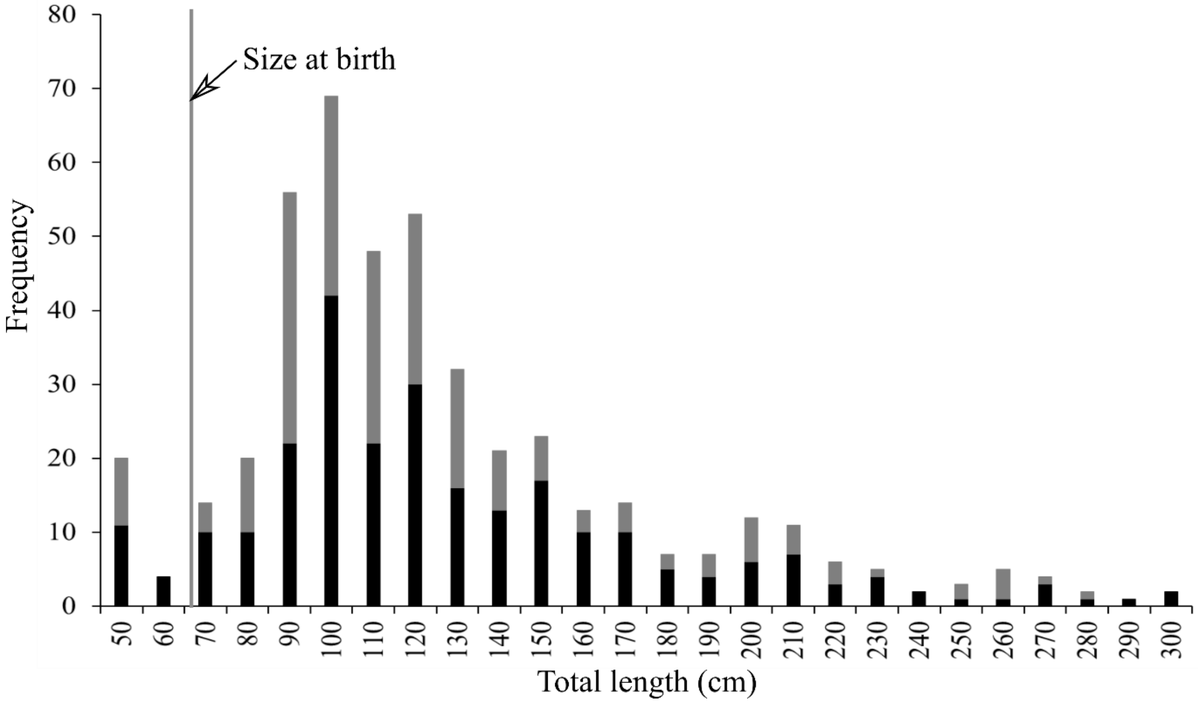


Figure 2.2 Length–frequency distribution of bronze whalers specimens used for vertebral aging. Grey bars represent males, black bars represent females. Bars before the size-at-birth lines are the sizes of prenatal embryos.

Figure 2.3 Image of bronze whaler vertebral thin-cut section (22 years old). White dots denote a translucent growth band, black dot indicates the birth band or Age 0.

VERIFICATION

Centrum edge analysis and MIR values were not estimated for the months of June to September due to the lack of availability of samples in the seasonal fishery (October–May). Centrum edge analysis was performed on 460 vertebral sections for bronze whalers. During the Austral warmer months (December–March) a high percentage (>70%) of vertebrae had translucent edges (Fig. 2.4b). In the comparatively cooler months (October–November and April–May), there was a higher percentage of vertebrae with opaque edges (Fig. 2.4b). Vertebrae sampled in May had 100% opaque edges. The monthly trend in centrum edge width suggests that a translucent band is deposited during the Austral summer (December–March) and that an opaque band is deposited when the water is cooler during the Austral winter (Fig. 2.4b). Marginal increment ratios were measured for 275 vertebrae that were sampled during the months of November to May. No clear pattern in monthly increment ratios was evident (Fig. 2.4a). In summary, the results from this method of post-capture verification were inconclusive and did not indicate any periodicity in band formation.

None of the 58 chemically marked sharks were recaptured preventing validation of the periodicity of band formation. In the absence of a conclusively verified periodicity in growth band formation, an annual cycle was assumed based on the previous findings for bronze whalers in South Africa (Walter and Ebert 1991) and on the validated annual band deposition of the sympatric dusky shark (Simpfendorfer et al. 2002). The implications of this are examined in the discussion

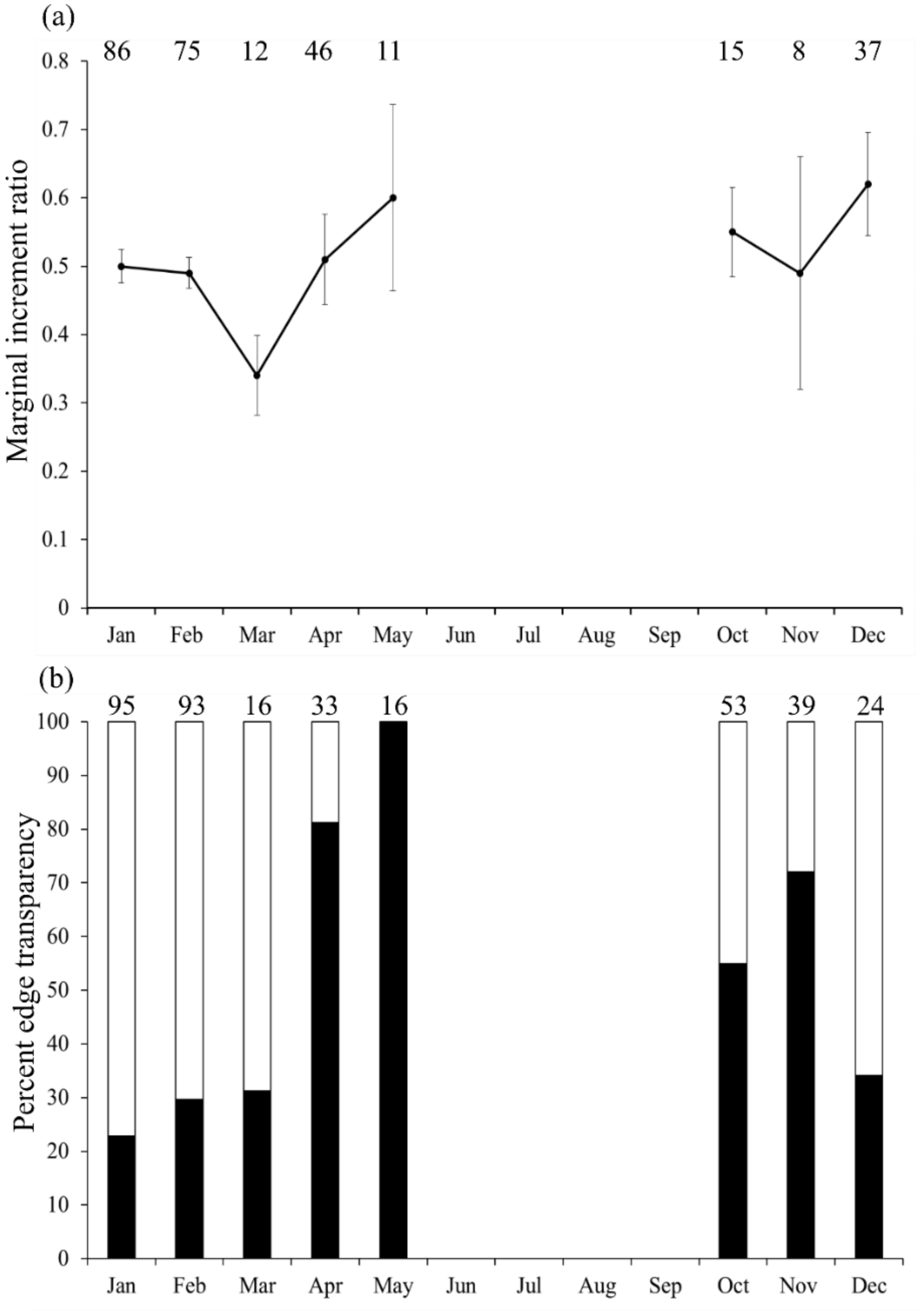


Figure 2.4 (a) Mean monthly marginal increment ratio and (b) centrum edge analysis plotted against month of capture for bronze whalers. Monthly means (closed circles); numbers at top of graph represent sample size, error bars represent standard error. Monthly percentage of translucent centrum edge (open squares). Monthly percentage of opaque centrum edge (closed squares).

GROWTH MODELS

The highest estimates of age for male and female bronze whalers were 25 and 31 years (265 and 308 cm TL), respectively (Fig 2.5a). The three-parameter Logistic model provided the best fit to the male, female, and combined length-at-age estimations (55%, 42% and 63% Akaike's weight, respectively) (Table 2.1). The three-parameter Gompertz model provided good fit for males, females and both sexes combined (34%, 23%, and 31% Akaike's weight, respectively). The two parameter Logistic models provided poor fits to the length-at-age data and the two and three-parameter von Bertalanffy models were poor fits to the length-at-age data for females and both sexes combined (Table 2.1). The estimated asymptotic length for the three-parameter Logistic model for both sexes combined (306 cm TL) and for females (308 cm TL) was similar to the largest observed total length (308 cm TL), but was much higher for males.

Table 2.1 Six growth models fit to length-at-age data of bronze whalers from South Australia. Model of best fit (bold) has the lowest value of Akaike information criterion (AIC). *w*, AICc percentage weight; Δ, delta AICc values. The estimated model parameters are provided as: L_∞, asymptotic total length; L_0, length at birth; α, point of inflection for the logistic models; *k*, growth coefficient; r.s.e., residual standard error. CI is the 95% confidence interval, which is provided for estimated model parameters

Sex	Model	AIC	Δ	*w* (%)	L_∞ (cm)	CI	L_0	CI	α	CI	*k*	CI	r.s.e.
Combined sexes	VB3	5404	23.8	0	491	(437–579)	65	(62–68)			0.029	(0.02–0.04)	14.15
n = 434	VB2	5406	25.8	0	547	(495–620)					0.025	(0.02–0.03)	14.14
	GOM3	5382	1.4	31.3	343	(329–360)	71	(68–73)			0.086	(0.08–0.09)	13.86
	GOM2	5385	4.7	6.1	330	(321–344)					0.093	(0.09–0.10)	13.94
	LOG3	**5380**	**0.0**	**62.6**	**306**	**(296–318)**			**75**	**(73–77)**	**0.143**	**(0.13–0.15)**	13.79
	LOG2	5420	40.2	0	287	(280–293)					0.168	(0.16–0.17)	14.28
Female	VB3	3065	18.2	0	457	(400–532)	63	(60–67)			0.034	(0.03–0.04)	13.40
n = 246	VB2	3069	22.1	0	518	(460–596)					0.027	(0.02–0.03)	13.49
	GOM3	3048	1.2	23.1	340	(323–358)	70	(66–72)			0.089	(0.08–0.10)	12.94
	GOM2	3047	0.4	34.7	334	(321–347)					0.093	(0.09–0.10)	12.93
	LOG3	**3047**	**0.0**	**42.3**	**308**	**(298–321)**			**74**	**(72–76)**	**0.146**	**(0.14–0.15)**	12.92
	LOG2	3066	19.6	0	293	(285–300)					0.167	(0.16–0.17)	13.10
Male	VB3	2406	4.4	6.1	973	(531–2122)	72	(67–76)			0.011	(0.01–0.03)	11.90
n = 188	VB2	2407	5.0	4.6	610	(471–886)					0.021	(0.01–0.03)	11.94
	GOM3	2403	0.9	34.3	383	(330–457)	76	(71–80)			0.069	(0.06–0.08)	11.75
	GOM2	2412	10.1	0.4	322	(300–350)					0.092	(0.08–0.10)	11.99
	LOG3	**2402**	**0.0**	**54.7**	**317**	**(290–357)**			**78**	**(75–82)**	**0.126**	**(0.11–0.14)**	11.73
	LOG2	2426	24.1	0	275	(263–289)					0.171	(0.16–0.18)	12.18

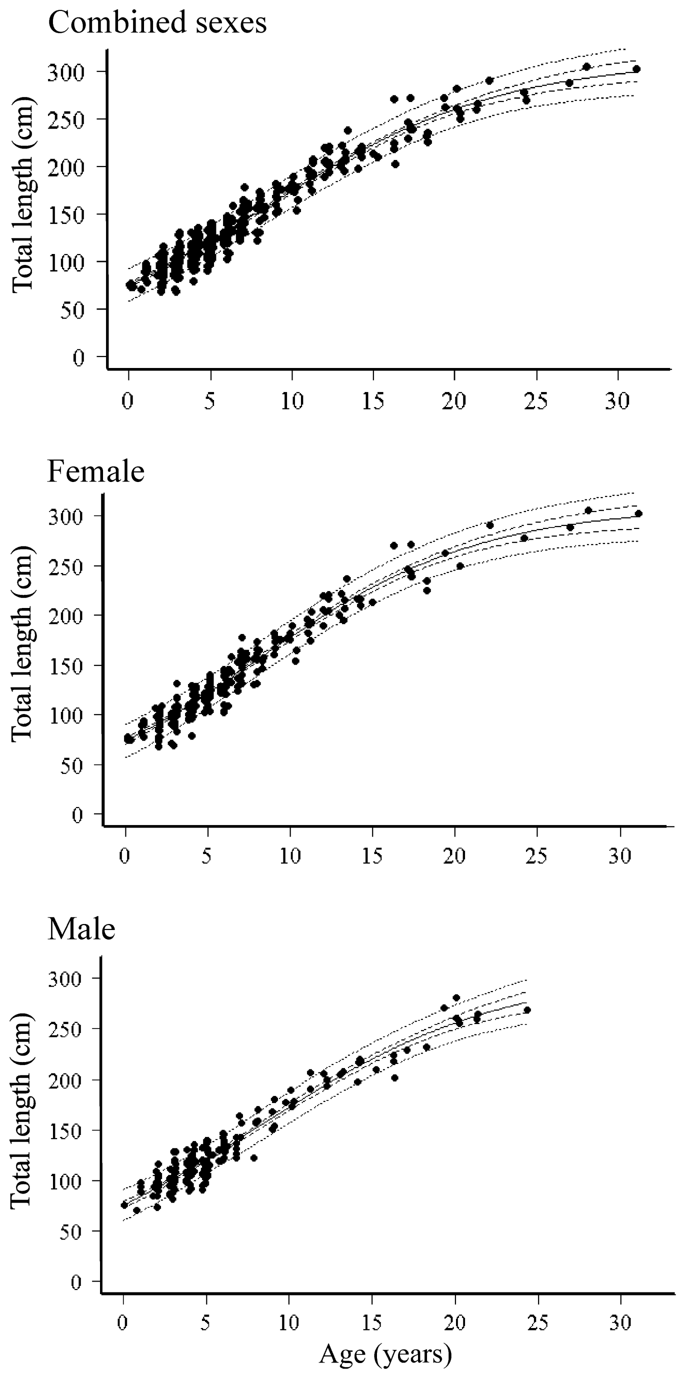


Figure 2.5 Models of best fit for length-at-age for bronze whalers in South Australian waters. Combined sex, three-parameter logistic model (top); female three-parameter logistic model (middle); and male three-parameter logistic model (bottom). Growth curve (solid line) with 95% confidence limits (longer dashed line) and 95% prediction limits (shorter dashed line) are presented.

REPRODUCTIVE PARAMETERS

During the study, four pregnant female sharks were captured by commercial and recreational fishers (Table 2.3). Pregnant sharks were caught within the reported parturition period between October and February (Jones 2008; Rogers et al. 2013a), and had embryos ranging from 37–67 cm TL. The size ranges for three litters were 58–63 cm TL in January, 61–66 cm TL in February, and 50–60 cm TL in January (Table 2.3). A further litter, from a shark caught in late February, was not considered to be fully developed. The embryo size range was 37–46 cm TL (Table 2.3). The number of embryos per litter ranged from 14–26 pups, with a mean of 21 pups (± 2.65, standard error). The embryonic sex ratio was 1.15:1 skewed towards males, but was not significantly different from the expected 1:1 sex ratio (X_1^2 = 11, P > 0.05). The smallest out of seven captured free-swimming sharks with an open umbilical scar was 68 cm TL (range 68–77 cm TL; mean 72 ±11.9 cm TL).

Total length, age, and maturity were available for 138 males (75–281 cm TL) and 193 females (68–302 cm TL). Seventeen mature sharks were sampled throughout the study (8 males and 9 females), which was too small to confidently estimate length- and age-at-maturity (L_{50} and A_{50}). The youngest mature male and female was 224 cm and 271 cm TL, respectively, and both were 16 years old. The oldest immature male and female sharks were 17 (229 cm TL) and 20 years (250 cm TL), respectively.

Table 2.2 The estimated life-history parameters for bronze whalers for temperate populations globally. The estimated model parameters are provided as: L_0, length at birth; L_∞, asymptotic total length; k, growth coefficient. L_0 for the 2P von Bertalanffy model point of inflection for the 3P Logistic models are indicated by asterisks

Author	Sex	Model	Number of specimens	L_0 (cm)	L_∞ (cm)	k	Age-at-first maturity (years)	Size-at-first maturity (cm)	Max age (years)	Location
Present study	Combined	3P Logistic	434	75*	306	0.143				Southern Australia
	Male		188	78*	317	0.126	16	224	25	
	Female		246	74*	308	0.146	16	270	31	
Walter and Ebert (1991)	Combined	2P von Bertalanffy	61	74	385	0.039				South-western Indian Ocean
	Male						13	200	30	
	Female						20	229	25	
Cliff and Dudley (1992)	Male		534					196		South-western Indian Ocean
	Female		770					207		
Smale (1991)	Male		189					206		South-western Indian Ocean
	Female		87					244		
Lucifora et al. (2005)	Male		96					210		South-western Atlantic Ocean
	Female		207					215		

Table 2.3 Fecundity and embryo information for the four gravid female bronze whalers captured in southern Australian coastal waters between 2009 and 2014

Date	Location	Mother TL (cm)	Litter size	Females	Males	Size range TL (cm)	Mean TL (cm)
30 Jan. 2009	Eastern Gulf St Vincent	288	19	10	9	50–60	57
9 Feb. 2010	Eastern Spencer Gulf	302	20	10	10	61–66	63
4 Nov. 2012	Eastern Spencer Gulf	295	26	14	12	58–63	60
20 Feb. 2014	Southern Spencer Gulf	280	14	7	7	37–46	43

Discussion

The present study provides the first estimates of age, growth, and reproductive parameters for bronze whalers from southern Australia. Slow growth was ascertained for bronze whalers from southern Australia, taking eight years to reach 150 cm TL, and with maturity occurring at 16–17 years for males and 16–20 years for females. Bronze whalers are long-lived with several individuals aged ≥ 25 years, including one female aged 31 years, which represents the oldest bronze whaler recorded worldwide. Parturition is likely to occur during the Austral spring to summer (November to February), with mature sharks producing an average of 21 pups per litter (based on four litters).

The clarity of growth bands on the thin cut sections allowed consistent and accurate ageing between and within readers. Clear banding formation aided in the agreement of 98% of the vertebrae counts with only three vertebrae omitted due to inconsistent counts between readers.

Marginal increment ratio showed no consistent patterns of periodicity in growth band deposition. This may be partially explained by the gaps in sampling, due to the seasonally targeted fishery. In addition, the standard error of MIR was relatively large for two months (May and November), which was due to the variations in outer band widths at the edge of the *corpus calcareum*. Although MIRs are frequently used as verification techniques, it does not often result in periodicity being determined (Carlson et al. 1999; Wintner et al. 2002; Santana and Lessa 2004) and alternative methods are frequently recommended such as chemical marking. In this study, chemical marking was attempted with 58 bronze whalers marked with oxytetracycline and released over a four-year period (2009–2013), however, no sharks were recaptured.

The centrum edge analysis provided evidence to suggest growth bands were deposited with annual periodicity with a translucent band deposited during the warmest months and an opaque band deposited during the Austral winter. This finding is consistent with sympatric temperate teleost species (Fowler and Short 1998) and with the closely related dusky shark (Simpfendorfer et al. 2002). Annual growth band deposition was validated for Australian dusky sharks based on 34 OTC-injected sharks at liberty for up to 1,481 days (Simpfendorfer et al. 2002). In addition, the only previous study investigating the age and growth of bronze whalers in the South West Indian Ocean also assumed that growth bands were deposited annually (Walter and Ebert 1991). Incorrectly specifying the frequency of growth band deposition (e.g. annual instead of biannual) can effectively lead to a halving or doubling of *k* estimates. This has implications for the accuracy of demographic models that use these estimates, which can then have flow-on effects for subsequent management and conservation measures. As such, validation of growth increments in vertebrae of bronze whalers should be considered a high priority in future studies. The recapture of chemically-marked sharks and a spread of samples covering all months of the year would be necessary to confirm annual band deposition in bronze whalers from southern Australia. Although this could not be directly validated during this study, it was assumed that band deposition in vertebrae of bronze whalers is annual, following results from the centrum edge analysis and Walter and Ebert (1991).

The size frequency of the sharks sampled during this study was skewed toward neonates and small juveniles (70–160 cm TL), with only a small number of sharks >2.5 metres captured. A size bias within the samples can influence the results from the growth models which can be a common issue when using samples obtained from commercial fisheries (Simpfendorfer et al. 2002; Thorson and Simpfendorfer 2009). The limited number of large individuals in this study led to unrealistic asymptotic total length estimates by some growth models. In all cases, for combined sexes, males, and females, the two- and three-parameter von Bertalanffy models over-estimated the asymptotic total length. This is likely due to the almost linear growth through the first 15 years in both sexes, which is better suited to Logistic and Gompertz models. This study showed that both von Bertalanffy growth models were more sensitive to the lack of large individuals compared to the Gompertz and Logistic models. Additional large sharks are required to estimate asymptotic total length more accurately, however, sharks over 220 cm TL are less frequently encountered in the South Australian gulfs (chapter 4), making sampling of this size class difficult.

The life history characteristics obtained from the present study are supported by previous studies from temperate regions throughout the species' distribution, e.g., South West Atlantic (Lucifora et al. 2005) and South West Indian Oceans (Walter and Ebert 1991; Lucifora et al. 2005) (Table 2.2, Fig. 2.6). The previous age and growth study of bronze whalers in the South West Indian Ocean (Walter and Ebert 1991) only used the two-parameter von Bertalanffy growth model based on 61 sharks. Their growth curve was compared with the two-parameter von Bertalanffy growth curve from this study to allow direct comparison and avoid differences due to the type of model selected. Both curves were similar up to 15 years (Fig. 2.6a). After 15 years, the growth curves differ, with South African bronze whalers being smaller than the southern Australian population for a specific age. This is likely due to differences in the number and size of large individuals between the two studies and to the von Bertalanffy growth curve being a less suitable model for linear growth leading to an over-estimate of the modelled size-at-age in large individuals.

Age-at-first maturity for the southern Australia population of bronze whalers was similar for both sexes (16 years), however, the eldest immature female shark was estimated to be 20 years of age suggesting that the age-at-maturity maybe higher in females. This was supported by Walter and Ebert (1991) in the South West Indian Ocean, which identified ages-at-first maturity of 13 years for males and 20 years for females. In the South West Altantic ages-at-maturity were higher for males (20 years) and marginally older for females (21.7 years). Both studies lacked sufficient sample sizes of mature animals of both sexes to fit a logistic curve and estimate the size or age at which 50% of the population is mature (L_{50} and A_{50}).

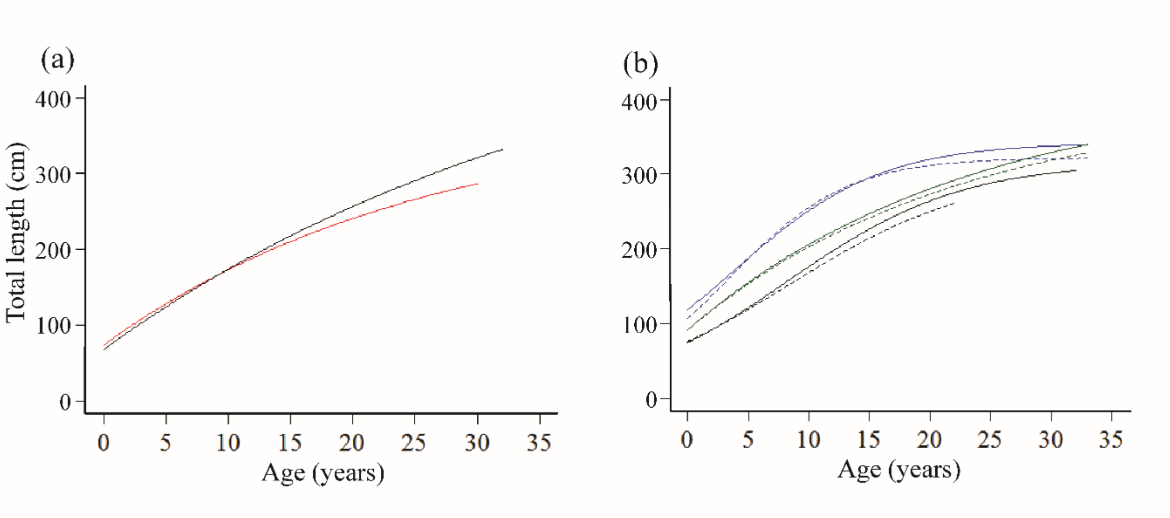


Figure 2.6 Von Bertalanffy growth curves of bronze whalers for combined sexes for (a) South Australia (black) and South Africa (red) based on Walter and Ebert (1991). (b) Comparison of bronze whaler and dusky shark growth curves estimated from samples collected in Australian waters. Models of best fit are provided for bronze whalers from South Australia (black; present study), dusky sharks from Western Australia (green; Simpfendorfer et al. 2002) and dusky sharks from New South Wales (blue; Geraghty et al. 2013). Dashed line represents males, continuous line represents females.

Length-at-maturity has been estimated for the South West Indian Ocean and South West Atlantic oceans (Table 2.2) (Smale 1991; Cliff and Dudley 1992; Lucifora et al. 2005). Length-at-first maturity for male bronze whalers from the southern Australia population (224 cm TL) aligns with the estimates from Cliff and Dudley (1992) (228–255 cm TL), but was higher than the South West Atlantic population (200–220 cm TL) (Lucifora et al. 2005) and other estimates from the South West Indian Ocean (200–230 cm TL) (Smale 1991; Walter and Ebert 1991). Length-at-first maturity for female bronze whalers from southern Australia (271 cm TL) was larger than estimates from other regions. The South West Atlantic population had the smallest size range of female maturity (215–223 cm TL) (Lucifora et al. 2005), while the size range for length-at-first maturity from the four studies in the South West Indian Ocean were larger (229–247 cm TL) (Smale 1991; Walter and Ebert 1991).

Parturition period in the present study occurred during the Austral spring to summer (November to February), which fell within the previously reported period of (September to February) for other temperate regions (Smale 1991; Cliff and Dudley 1992; Lucifora et al. 2005; Jones 2008). These present estimates are based on a small sample size of four gravid females (Table 2.3) and the capture of seven free swimming sharks with open umbilical scars. Anecdotal evidence of catches of gravid female bronze whalers by both commercial and recreational fisherman during October to December in the Gulf waters of South Australia additionally supports the suggested timing of parturition (Drew et al. unpublished data). The present study recorded the largest litter size of 26 pups, but the mean litter size of 21 was close to or within the range of previous estimates (Table 2.3): 7–23 (Garrick 1982), 8–20 (mean 15, n = 46; Cliff and Dudley 1992), 17–24 (n = 4; Chiaramonte 1998), 16 (n = 2; Lucifora et al. 2005). The duration of parturition has been estimated for the South West Indian Ocean population as 12 months and the timing of reproduction is reportedly biennial (Walter and Ebert 1991; Cliff and Dudley 1992). These life history traits could not be determined for the southern Australia population and would require a larger sample size of mature female sharks. The life history traits presented by this study combined with the reproduction estimates from the South West Indian Ocean raises concerns over the resilience of bronze whalers, which could have implications for future fishery management discussions. Female bronze whalers first reach maturity at 16 years, with a mean fecundity of 21 pups and a ~1:1 sex ratio. Assuming a biennial reproductive cycle (Cliff and Dudley 1992), the production of females could be as low as ~10 pups biennially or ~50 female pups every decade after reaching maturity at ~16 years (or 270 cm TL). The oldest estimation of age for bronze whalers was 31 years from a 308 cm TL female, which is the longest total length recorded for this species worldwide. It is unrealistic that this animal represents the maximum age limit for bronze whalers, but it is plausible that maximum longevity would be likely to be <40 years. Such low production of female pups, slow growth, and late fecundity combined with a predictable seasonal distribution during which the species can be commercially and recreationally targeted (Lucifora et al. 2005; Jones 2008) has implications for bronze whalers resilience to fishing mortality and susceptibility to other anthropogenic effects.

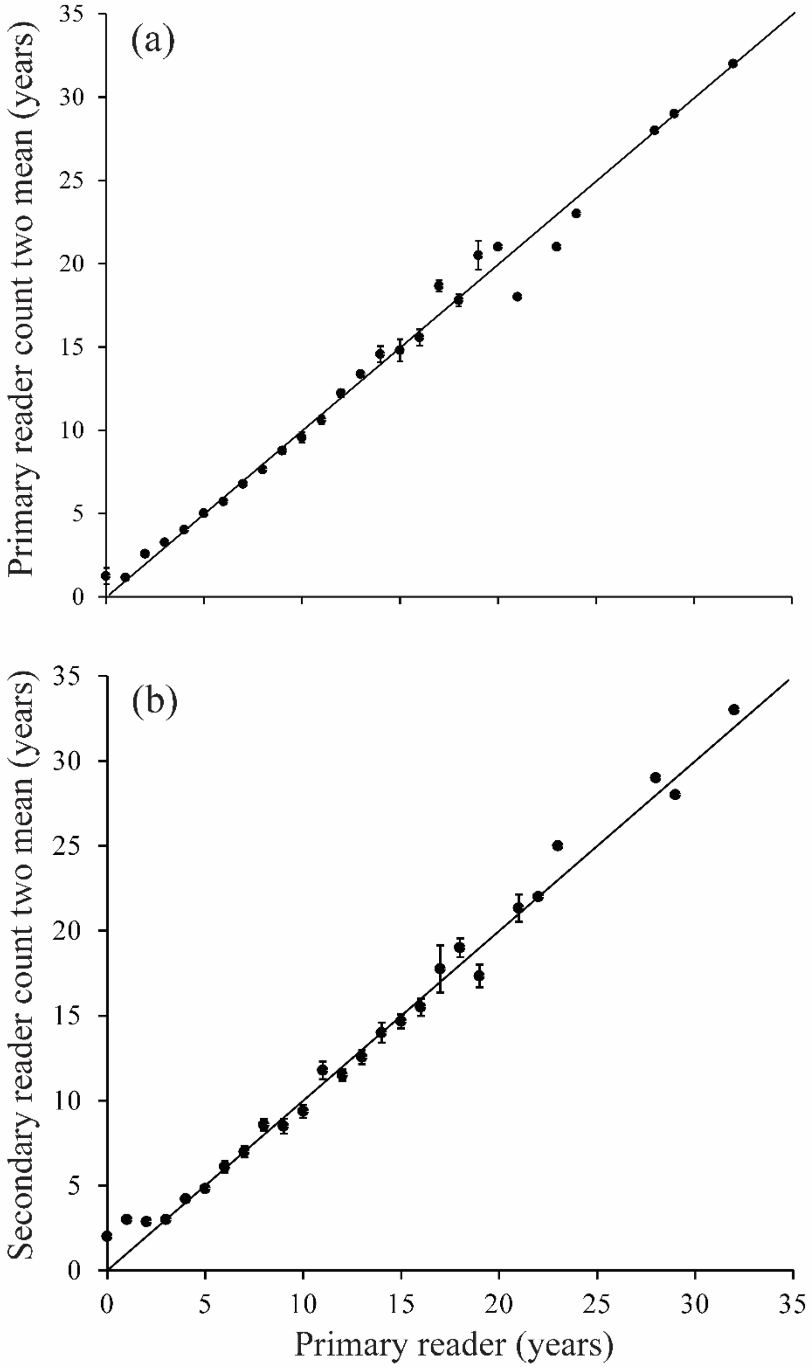
Regional variations in life history traits within species are increasingly being documented in wide-ranging elasmobranchs (Driggers et al. 2004; Drew et al. 2015; Smart et al. 2015). In the case of bronze whalers, however, the three populations of bronze whalers for which life history characteristics are available (South West Atlantic, South West Indian Ocean, and southern Australia), have relatively similar life history traits, even though bronze whalers from these areas form genetically discrete populations (Benavides et al. 2011). The similarities between the three isolated regions are not limited to life history traits, but many similarities can be found in oceanographic conditions, diet, and seasonal philopatry for bronze whalers (Smale 1991; Lucifora et al. 2005).

The present growth curve of bronze whalers is comparable to that of the sympatric dusky shark (Simpfendorfer 1999; Simpfendorfer et al. 2002) (Fig. 2.6b). Although a more recent study found that dusky sharks sampled from South East Australia grows faster than those from Western Australia (Geraghty et al. 2013), the authors suggest that such discrepancy is driven by differences in sample size and length-distribution rather than true plasticity in growth. In Australia, age-at-maturity is also similar between the two sympatric species, with bronze whalers maturing at 16–20 years and dusky sharks maturing at 17–23 years (Simpfendorfer et al. 2002). In contrast, the fecundity of the two species is vastly different as bronze whalers give birth to an average of twice as many pups as dusky sharks (~21 vs ~10 pups, respectively; McAuley et al. 2007). Considering that previous studies have identified dusky sharks as highly susceptible to overfishing due to their life history traits (McAuley et al. 2007; Romine et al. 2009) and that bronze whalers have comparable life history traits aside from higher fecundity, it may be plausible that bronze whalers possess a similar, low resilience to fishing pressure. As a result of their low resilience to fishing pressure, annual population declines of 3–13% were estimated for the South West Atlantic Ocean population (Lucifora 2003).

The present study provides the first estimates of age, growth, and age-at-first maturity for bronze whalers from southern Australia. The estimated life history traits of late maturity, slow growth and low fecundity, combined with their seasonal coastal distribution have raised concern over their resilience to anthropogenic effects. This highlights the potential vulnerability of bronze whalers to cumulative human impacts and the need for an assessment of their resilience to fishing mortality.

Acknowledgments

The authors would like to thank the members of Marine Scalefish Fishery research group for their support and guidance. Thanks to Alastair Harry for his assistance with statistical analysis and thanks goes to commercial fishers from the South Australian Marine Scalefish fishery for their cooperation and assistance in sample collection. Chris Lamont is thanked for his assistance with the second counts of samples. Financial support was provided by Flinders University and Australia Postgraduate Award. This research was funded through the Australian Research Council (ARC) (LP120100652).



Supplementary Figure S2.1 Age-bias plots for the primary reader final counts (a) and the final counts of both readers (b). Error bars represent the standard error

3

ASSESSING THE SPATIO-TEMPORAL FORAGING DYNAMICS OF A TEMPERATE MARINE PREDATOR, THE BRONZE WHALER (*CARCHARHINUS BRACHYURUS*)

Abstract

Large-bodied sharks can be critical for coupling disparate habitats and food webs, which has been identified as central for ecosystem stability. Understanding the role of sharks and their associated predator-prey relationships is also integral to the development of multi-species ecosystem models. This study combined stomach content (SCA) and stable isotope analysis (SIA) from multiple tissues to investigate the feeding ecology of the bronze whaler (*Carcharhinus brachyurus*) in the temperate waters of southern Australia. A total of 212 stomachs, 101 liver and 108 muscle tissue samples were collected from fishery catches over three years, during the Austral spring-summer seasons. Stomach content analysis suggested that bronze whalers are a generalist predator with a highly diverse prey field, with cuttlefish (*Sepia novaehollandiae*), southern calamari (*Sepioteuthis australis*), and Australian sardine (*Sardinops sagax*) being the most important species (36%, 21%, and 18% index of relative importance, respectively). Regional differences in diet composition were evident, although no size- or sex-based variation was identified. Isotope mixing models and regional food web bi-plots showed that *S. sagax* were the most important prey species. Trophic position estimate of 4.49, categorised bronze whalers as a secondary consumer and this was similar to previous estimates for the South African population. The combination of tissues and methods of dietary analysis allowed diet to

be investigated over varied temporal scales and revealed short-term variations in diet through liver tissue SIA and SCA. Feeding ecology information has been integrated into ecosystem-based fishery models and provide further information for the conservation of an important marine predator in temperate southern Australian coastal waters.

Introduction

The ability of predators to move between discrete habitats and shift foraging between locally abundant prey species is central for coupling energy flow among distinct food webs components. Such species that migrate or have broad-scale movements effectively link food webs throughout their range promoting ecosystem stability (Rooney et al. 2006; Rooney and McCann 2012). For example, the mobility of ground-dwelling predators in the grasslands of a Kenyan savanna is known to couple the canopy and understory (Pringle and Fox-Dobbs 2008), while deer link both fringe agricultural land and dense natural scrub in Japanese forests and grasslands (Takada et al. 2002). Similarly, in the aquatic realm, Killer whales (*Orcinus orca*) predating on sea-otters (*Enhydra lutris*) link inshore and pelagic habitats and lead to indirect effects on kelp forest community structure (Estes et al. 1998). Energy flow and linkages between contrasting habitats in freshwater lakes and streams are also widely reported (Post et al. 2000; Schindler and Scheuerell 2002; Seminoff et al. 2007).

Large-bodied sharks are considered highly mobile, upper-trophic level predators which can consume a diverse range of prey species (McCauley et al. 2012; Hussey et al. 2015a). As a result of wide-ranging movements, large sharks have the potential to act as vectors coupling disparate habitats through exploiting abundant prey species across their range. A study of predators at Palmyra Atoll found that blacktip reef sharks (*Carcharhinus melanopterus*) and grey reef sharks (*C. amblyrhynchos*), derived resources from lagoon, fore reef and pelagic habitats (McCauley et al. 2012). Equally, tiger sharks (*Galeocerdo cuvier*) in Australian and Hawaiian waters were found to undertake broad scale movements between contrasting habitats with increased spatio-temporal occurrence as a result of a temporal diet specialisation (Meyer et al. 2010; Fitzpatrick et al. 2012). In Australia, tiger sharks exploited an increased abundance of nesting green turtles (*Chelonia mydas*) during summer around Raine Island (Fitzpatrick et al. 2012), while the abundance of sharks at French Frigate Shoals in Hawaii, increased seasonally to opportunistically exploit fledging albatross (Meyer et al. 2010). Tagged tiger sharks from Hawaii then dispersed large distances through multiple habitats out into the open ocean (Meyer et al. 2010). The foraging ecology and broad-scale movements of tiger sharks provides evidence for the role of sharks to couple food webs. Quantifying dynamic predator-prey interactions and spatio-temporal variation in predator foraging behaviour is consequently necessary to derive data to inform ecosystem-based models examining the effects of human activities in marine environments (Pikitch et al. 2004; Barnett et al. 2010; Goldsworthy et al. 2013).

Traditionally, the diet or feeding ecology of sharks was assessed through stomach content analysis (SCA) (Cortés 1997). SCA offers a high degree of taxonomic precision and prey physiology data through identifying actual prey consumed, but can be limited by variable digestion rates. As a result, SCA essentially provides a "snap shot" of recently consumed prey items (Hyslop 1980; Cortés 1997). In addition, a large number of sampled stomachs are required to accurately quantify diet over the spatial and temporal range of a target species (Hussey et al. 2011). This scale of sampling can be confounded by a high percentage of empty stomachs (Shiffman et al. 2012) and moral issues with sampling sufficient animals of non-exploited species or those that may be considered imperilled (Shiffman et al. 2012).

Advances in biochemical approaches (Stable isotope (SIA) and fatty acid analyses) and genetics are providing alternative techniques to assess diet and feeding ecology over varying temporal scales (Parnell et al. 2010; Phillips 2012). These approaches allow assessment of diet through non-lethal and cost-effective methods, but lack the dietary resolution of SCA (Shiffman et al. 2012). Consequently, a combined SCA and biochemical/genetic approach is now viewed as the most comprehensive method to assess diet (Hussey et al. 2011; Layman et al. 2012). For SIA, the rate of isotope incorporation into tissues has been shown to vary widely among tissues dependent on metabolic turnover (Pinnegar and Polunin 1999). As a result, temporal shifts in feeding ecology can be investigated through analysing isotope values in tissues with different metabolic turnover rates (MacNeil et al. 2005; Logan and Lutcavage 2010; Matich et al. 2011; Kim et al. 2012). Isotopic incorporation rates can be as short as three to six months for blood (Kim et al. 2012) and liver (MacNeil et al. 2005) to over a year for muscle tissue (Tieszen et al. 1983; Pinnegar and Polunin 1999; Hussey et al. 2010; Matich et al. 2011; Kim et al. 2012).

The bronze whaler (C*archarhinus brachyurus*) is a large-bodied, long-lived (Drew et al. 2017), neritic species that is widely distributed throughout the temperate waters of the northern and southern hemispheres (Last and Stevens 2009). Feeding ecology of bronze whalers has been investigated in the South West Atlantic (Argentina) (Lucifora et al. 2009) and South West (South Africa) (Smale 1991; Cliff and Dudley 1992) and South East Indian Ocean (Australia) (Rogers et al. 2012). In Argentina, SCA identified an ontogenetic shift in the diet of bronze whalers with an increase in small bodied elasmobranchs in the diet of adult sharks. However, small pelagic teleosts such as Engraulidae and Atherinopsidae species were identified as key prey items for both juveniles and adults (Lucifora et al. 2009). Off South Africa's Eastern Cape, bronze whalers consumed a broad range of prey, although the Cape Hope squid (*Loligo reynaudii*) was the most important prey item for both adult and juvenile sharks (Smale 1991). In contrast the diet of bronze whalers captured in beach protection nets in northern KwaZulu-Natal, 1000km north of the Eastern Cape, was dominated by African sardines (*Sardinops sagax*), a result of sharks seasonally exploiting the high abundance of sardines during their annual northward migration (Dudley and Cliff 2010). Similar to other regions, SCA identified that bronze whalers in southern Australia are generalist feeders, with a preference for small pelagic teleosts and cephalopod species (Rogers et al. 2012). Long range movements of bronze whalers > 1000 km's have been identified in southern Australia from acoustic telemetry and tag and recapture data, highlighting the potential for coupling resources across multiple habitats within their range (Rogers et al. 2013a; Huveneers et al. 2014) similar to South Africa. Currently, in southern Australia little information exists on how bronze whalers feeding ecology varies seasonally and regionally, and how spatio-temporal variations in prey abundances may explain movement patterns of this large-bodied predator.

To assess temporal and spatial variation in the feeding behaviour of bronze whalers off southern Australia, a combined SCA and SIA approach was adopted. Specifically, I investigated ontogenetic shifts in diet and then by sampling across a large spatial scale at three regional sites in inshore and offshore waters (northern Gulf St. Vincent, eastern Spencer Gulf and Southern Spencer Gulf), spatial and temporal variation in foraging ecology were quantified. Trophic position, niche width and the contribution of key prey items to the diet of this highly mobile shark species were quantified across regions. These findings further our understanding of the ecology of bronze whalers in temperate waters off Southern Australia but also highlight the importance of considering the movements, and seasonal occurrence of predators and prey to define ecological roles.

Methods

SAMPLE COLLECTION

Bronze whales were sampled during the Austral autumn–spring (September 2009 and March 2014) through a combination of fisheries-dependent (South Australian Marine Scalefish Fishery and recreational fishers) and independent sampling (scientific longlines). For the commercial fishery, sharks were sampled from longlines consisting of floating rope or mono-filament main-lines with 1.2–1.7 mm stainless steel leaders with up to 200–400 16/o steel circle hooks attached to the main-line with a stainless steel clip. Main-lines were up to 8 km long and marked at each terminal end with 20 to 70 cm diameter rubber floats. Anchors at each end of the main line were used to minimize drifting of gear during sets. Hooks were spaced along the main-line at intervals of 10–20 m apart with small floats every two hooks. For the recreational fishery, sharks were caught using suspended baits under balloons, heavy tackle (30–80 lb line) and leaders of 1.5–1.7 mm nylon-coated wire attached to 12/o or 14/ o J-style hooks. Finally, scientific longlines were deployed using similar gear to that of the commercial longlines, but with a reduced number of hooks (~110 hooks) and a main-line of 1.1–1.7 km in length. All sampling of sharks targeted the three focal study regions within South Australian Gulf waters: Gulf St. Vincent (GSV), Eastern Spencer Gulf (ESP), and Southern Spencer Gulf (SSP) (Fig. 3.1).

On capture, the sex of each shark was determined by the presence (males) or absence (females) of claspers. Length measurements were recorded to the nearest centimetre and included total length (TL), pre-caudal length (PCL), fork length (FL), and trunk length (TKL). Linear regressions of TL on FL, PCL, and TKL were determined using data pooled across sexes. When TL could not be measured, e.g., due to fisher processing sharks before TL could be recorded (n = 79), TL was estimated using the regression for the next largest measurement, which was mostly PCL (Drew et al. 2016). For all captured sharks, the entire stomach was removed and stored frozen. Tissue samples were taken for SIA (Table 3.1) for a subset of sharks, sampled within the three regions (GSV, ESP, and SSP) and across the size range of individuals encountered. Approximately five grams of muscle and liver tissue were sampled; muscle samples were collected posterior of the cranium, where the head is separated from the carcass by commercial fishers and liver were collected from the lower section of the right or left lobe. Tissue samples were either frozen immediately after collection or stored on ice until they were stored in a -20^{0}C freezer. Known prey species of bronze whalers identified from SCA were sampled from defined habitats (seagrass, reef, benthic and pelagic habitats) within each study region. In addition, three representative baseline species (*Crassostrea gigas*, *Melicertus latisulcatus* and *S. sagax*) (Table 3.3) were sampled from each region in an attempt to delineate unique regional isotopic sources. Muscle tissue from prey items and baseline species were sampled from commercial fishing vessels, fish markets, scientific surveys, and from recreational fishers (Table 3.2).

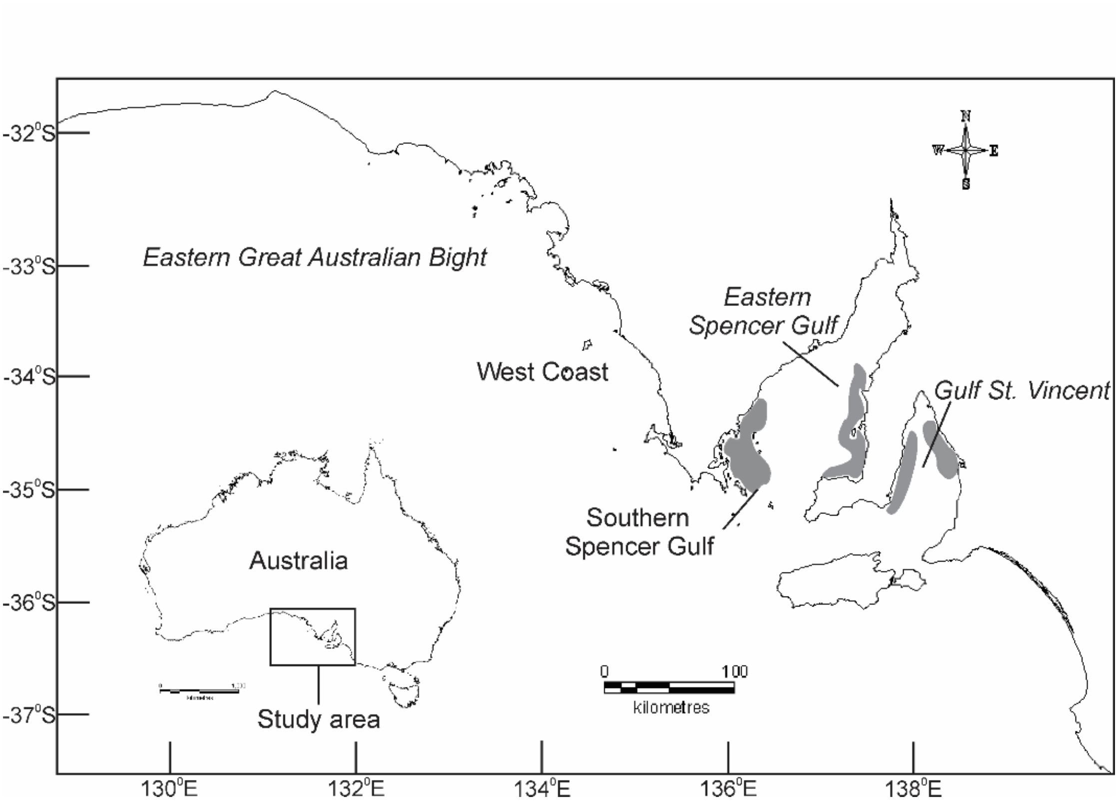


Figure 3.1 Map of South Australia, sampling areas are coloured grey and split into three regions. Southern Spencer Gulf (SSP), Eastern Spencer Gulf (ESP) and Gulf St Vincent (GSV).

Table 3.1 Samples numbers used for stomach content analysis (SCA) and stable isotope analysis (SIA). Muscle = muscle tissue samples for SIA; Liver = liver tissue samples for SIA; GSV = Gulf St. Vincent; ESP = eastern Spencer Gulf; SSG = southern Spencer Gulf; >1200 = no. of sharks greater than 1200 mm TL; <1200 = no. of sharks less than 1200 mm TL

	Region	**Total**	**Male**	**> 1200**	**< 1200**	**Female**	**> 1200**	**< 1200**
SCA	**GSV**	105	38	15	23	67	29	38
	ESP	64	29	11	18	35	13	22
	SSG	43	18	11	7	25	19	6
	total	212	92	37	48	120	61	66
Muscle	**GSV**	33	14	4	10	19	4	15
	ESP	34	16	4	12	18	11	7
	SSP	34	15	12	3	19	16	3
	total	101	45	20	25	56	31	25
Liver	**GSV**	34	14	4	10	20	5	15
	ESP	36	17	12	5	19	11	8
	SSP	38	17	14	3	21	18	3
	total	108	48	30	18	60	34	26

Table 3.2 Prey items and indices identified through stomach content analysis. N number counted; %N numerical importance; F frequency item occurred; F% percentage of frequency of occurrence; W= total weight of items; W% percentage of weight; IRI Index of relative importance; IRI% percentage of Index of relative importance; GII geometric index of importance.

	N	**N%**	**F**	**F%**	**W (grams)**	**w%**	**IRI**	**IRI%**	**GIII**
Chordata									
Unidentified ascidian	1.00	0.17	1.00	0.47	9.00	0.04	0.10	0.00	0.40
Crustaceans									
Brachyura	1.00	0.17	1.00	0.47	5.00	0.02	0.09	0.00	0.39
Isopoda	7.00	1.22	7.00	3.29	1.51	0.01	4.04	0.14	2.61
Jasus edwardsii	1.00	0.17	1.00	0.47	26.95	0.13	0.14	0.00	0.45
Ovalipes australiensis	2.00	0.35	2.00	0.94	16.36	0.08	0.40	0.01	0.79
Portunus pelagicus	3.00	0.52	3.00	1.41	180.57	0.85	1.94	0.07	1.61
Benthic Cephalopod									
Octopus berrima	7.00	1.22	6.00	2.82	10.13	0.05	3.58	0.12	2.36
O. maorum	1.00	0.17	1.00	0.47	0.20	0.00	0.08	0.00	0.37
Sepia apama	60.00	10.47	46.00	21.60	1024.32	4.83	330.43	11.30	21.30
S. braggi	1.00	0.17	1.00	0.47	5.10	0.02	0.09	0.00	0.39
S. novaehollandiae	139.00	24.26	74.00	34.74	1276.57	6.02	1051.87	35.98	37.54
Sepioteuthis australis	77.00	13.44	50.00	23.47	2567.91	12.11	599.65	20.51	28.30
Unidentified cephalopod	5.00	0.87	4.00	1.88	19.83	0.09	1.81	0.06	1.64
Unidentified sepia	6.00	1.05	6.00	2.82	206.99	0.98	5.70	0.19	2.79
Small pelagic teleost									
Arripis georgianus	3.00	0.52	3.00	1.41	38.61	0.18	0.99	0.03	1.22
A. truttaceus	10.00	1.75	9.00	4.23	988.08	4.66	27.06	0.93	6.14
Engraulis australis	1.00	0.17	1.00	0.47	5.36	0.03	0.09	0.00	0.39
Etrumeus teres	21.00	3.66	2.00	0.94	1105.88	5.21	8.34	0.29	5.67
Sardinops sagax	95.00	16.58	34.00	15.96	3616.98	17.05	536.86	18.37	28.63
Scomber australasicus	3.00	0.52	3.00	1.41	164.14	0.77	1.83	0.06	1.56
Unidentified small pelagic teleost	12.00	2.09	10.00	4.69	449.40	2.12	19.78	0.68	5.14
Benthic teleost									
Achoerodus gouldii	1.00	0.17	1.00	0.47	1660.87	7.83	3.76	0.13	4.89
Aldrichetta forsteri	4.00	0.70	4.00	1.88	410.24	1.93	4.94	0.17	2.60
Chelmonops curiosus	1.00	0.17	1.00	0.47	34.50	0.16	0.16	0.01	0.47
Chrysophrys auratus	4.00	0.70	4.00	1.88	538.22	2.54	6.08	0.21	2.95
Genypterus tigerinus	1.00	0.17	1.00	0.47	555.04	2.62	1.31	0.04	1.88
Girella zebra	1.00	0.17	1.00	0.47	373.55	1.76	0.91	0.03	1.39
Haletta semifasciata	1.00	0.17	1.00	0.47	76.34	0.36	0.25	0.01	0.58
Hyporhamphus menanochir	11.00	1.92	9.00	4.23	196.34	0.93	12.02	0.41	4.08
Mugilidae sp.	1.00	0.17	1.00	0.47	17.60	0.08	0.12	0.00	0.42
Parequula melbournensis	2.00	0.35	2.00	0.94	23.46	0.11	0.43	0.01	0.81
Platycephalus bassensis	1.00	0.17	1.00	0.47	219.48	1.03	0.57	0.02	0.97
Platycephalus sp.	7.00	1.22	7.00	3.29	1204.44	5.68	22.68	0.78	5.88
Pseudocaranx georgianus	1.00	0.17	1.00	0.47	19.15	0.09	0.12	0.00	0.42
Scolecenchels australis	7.00	1.22	7.00	3.29	138.81	0.65	6.17	0.21	2.98
Scorpis aequipinnis	1.00	0.17	1.00	0.47	12.03	0.06	0.11	0.00	0.40
Sillago schomburgkii	1.00	0.17	1.00	0.47	58.40	0.28	0.21	0.01	0.53
Sillago sp.	5.00	0.87	5.00	2.35	267.34	1.26	5.01	0.17	2.59
Sphyraena novaehollandiae	5.00	0.87	4.00	1.88	608.40	2.87	7.03	0.24	3.24
Syngnathidae Sp.	1.00	0.17	1.00	0.47	3.29	0.02	0.09	0.00	0.38
Thamnaconus degeni	1.00	0.17	1.00	0.47	12.94	0.06	0.11	0.00	0.41
Upeneichthys vlamingii	3.00	0.52	3.00	1.41	264.31	1.25	2.49	0.09	1.83
Large pelagic teleost									
Thunnus sp.	1.00	0.17	1.00	0.47	201.18	0.95	0.53	0.02	0.92
Unidentified teleost									
Unidentified teleost	39.00	6.81	39.00	18.31	1347.88	6.35	240.98	8.24	18.17
Elasmobranch									
Myliobatis tenuicaudatus	3.00	0.52	3.00	1.41	388.00	1.83	3.31	0.11	2.17
Orectolobus sp.	1.00	0.17	1.00	0.47	118.52	0.56	0.34	0.01	0.69
Parascyllium Sp.	1.00	0.17	1.00	0.47	35.72	0.17	0.16	0.01	0.47
Rajidae sp.	4.00	0.70	4.00	1.88	327.21	1.54	4.21	0.14	2.38
Squatina australis	1.00	0.17	1.00	0.47	11.89	0.06	0.11	0.00	0.40
Trygonorrhina fasciata	1.00	0.17	1.00	0.47	89.65	0.42	0.28	0.01	0.62
Unidentified elamsobranch	4.00	0.70	4.00	1.88	263.27	1.24	3.64	0.12	2.20
Urolophus sp.	1.00	0.17	1.00	0.47	12.81	0.06	0.11	0.00	0.41

Table 3.3 Mean Stable isotope analysis values for shark tissue by region and mean of prey items. The SIAR group identifies the prey category that prey item has been grouped in; H & O = herbivorous and omnivorous; GSV = Gulf St. Vincent; ESP = eastern Spencer Gulf; SSG = southern Spencer Gulf; SD = standard deviation

Species	SIAR group	No. of samples	Tissue	Region	δC^{13}	SD	δN^{15}	SD
Carcharhinus brachyurus		33	Muscle	GSV	-17.18	0.71	13.94	1.01
C. brachyurus		34	Muscle	ESP	-17.21	0.99	13.03	0.86
C. brachyurus		34	Muscle	SSP	-17.83	1.35	13.60	0.80
C. brachyurus		34	Liver	GSV	-17.60	1.08	12.16	1.21
C. brachyurus		36	Liver	ESP	-17.84	1.03	11.43	0.94
C. brachyurus		38	Liver	SSP	-18.53	1.41	11.92	0.84
Melicertus latisulcatus		5	Muscle	GSV	-17.56	0.80	9.43	1.60
Notolabrus tetricus	reef	5	Muscle	GSV	-21.04	0.63	12.33	0.76
Scorpis aequipinnis	reef	5	Muscle	GSV	-20.89	1.32	12.46	1.14
Meuschenia hippocrepis	reef	5	Muscle	GSV	-19.97	0.62	10.84	0.54
Sepioteuthis australis	cephalopod	5	Mantle	GSV	-14.29	1.69	10.66	0.44
Sphyraena novaehollandiae	carnivorous	5	Muscle	GSV	-16.85	2.31	12.65	1.11
Chrysophrs auratus	carnivorous	5	Muscle	GSV	-17.38	1.70	11.86	1.16
Hyporhamphus menanochir	H & O	5	Muscle	GSV	-14.81	2.38	8.86	0.98
Sillaginodes punctatus	H & O	3	Muscle	GSV	-16.65	0.67	10.88	0.05
Sepioteuthis australis	cephalopod	3	Muscle	GSV	-18.20	0.65	10.44	1.18
Posidonia angustifolia		5	Seagrass	GSV	-9.33	0.76	6.25	0.48
Crassostrea gigas		5	Muscle	GSV	-18.58	0.23	4.55	0.32
M. latisulcatus		5	Muscle	ESP	-18.50	0.46	7.16	1.07
N. tetricus	reef	5	Muscle	ESP	-20.44	0.70	11.54	0.73
C. gigas		5	Muscle	ESP	-19.83	0.28	4.09	0.29
S. australis	cephalopod	5	Muscle	ESP	-16.14	1.34	11.44	0.46
S. novaehollandiae	carnivorous	5	Muscle	ESP	-17.36	0.48	11.66	0.65
Arripis georgianus	H & O	5	Muscle	ESP	-16.12	1.14	11.76	0.82
H. menanochir	H & O	5	Muscle	ESP	-17.80	1.50	11.97	1.85
S. punctatus	H & O	5	Muscle	ESP	-16.28	0.78	10.71	0.67
Acanthaluteres brownii	reef	5	Muscle	ESP	-17.00	0.71	6.12	0.18
Platycephalus speculator	carnivorous	3	Muscle	ESP	-17.28	0.09	11.78	0.42
P. bassenis	carnivorous	2	Muscle	ESP	-16.86	0.41	11.68	0.12
Posidonia species.		5	Seagrass	ESP	-11.48	0.37	3.17	1.24
Haletta semifasciata	H & O	5	Muscle	ESP	-15.07	1.14	8.54	0.39
Meuschenia scaber		5	Muscle	ESP	-17.78	0.48	8.56	0.33
M. freycineti		6	Muscle	ESP	-16.10	1.11	9.31	0.45
Notolabrus parilus		2	Muscle	ESP	-15.82	0.34	11.72	0.02
A. truttacea	carnivorous	5	Muscle	ESP	-18.95	0.41	13.71	1.08
C. gigas		5	Muscle	SSP	-20.10	0.32	4.28	0.20
Sardinops sagax	small pelagic	5	Muscle	WC	-19.95	0.16	11.38	0.70
Nototodarus gouldi	cephalopod	4	Muscle	WC	-17.27	0.28	11.77	0.86
S. sagax	small pelagic	5	Muscle	SSP	-20.69	0.16	9.73	0.40
P. conatus	carnivorous	5	Muscle	SSP	-19.09	0.11	14.58	0.34

STOMACH CONTENT ANALYSIS

Stomachs were thawed prior to analysis, washed in running water using 0.5 mm sieves and total contents weighed to the nearest 0.01 gram. Prey identification was based on intact and remaining hard items, including cephalopod beaks, fish otoliths, and internal and external skeletal material, combined with shape and anatomical features. Prey were identified to the lowest taxon using reference guides (Lu and Ickeringill 2002). Contents identified as bait via prominent hook marks or knife cuts were excluded from the analysis. The number of empty stomachs together with the number of stomachs containing only bait were recorded and expressed as a percentage of the total number examined (vacuity index, %V). Prey items were categorised into a broad functional prey groups (chordata, crustacean, benthic cephalopod, unidentified cephalopod, benthic teleost, large pelagic teleost, small pelagic teleost, unidentified teleost and elasmobranchs). Each item was weighed to the nearest ± 0.01 grams. Cephalopod beaks were grouped into pairs, weighed and recorded as one individual.

STOMACH CONTENT - DATA ANALYSIS

Cumulative prey curves were generated for the number of prey items and trophic groups to assess if the quantity of stomachs collected was adequate to describe the diet of bronze whalers (Ferry and Cailliet 1996). The order in which stomachs were analysed was randomised 10 times and the number of new prey items counted for each randomisation (Rogers et al. 2012; Espinoza et al. 2015). The mean number of prey items (± standard deviation, SD) and functional prey groups (± SD) per stomach were plotted against the number of stomachs sampled and a three-parameter von Bertalanffy growth curve fitted to the data, with L_{inf} representing the theoretical maximum number of species or trophic group that bronze whalers consumed. If the estimated L_{inf} was less than the observed number of species or functional prey groups, it was considered that an adequate number of samples had been obtained to describe the total diet.

The contribution of different prey items or functional prey groups to the diet of bronze whalers was determined by the percent numerical importance (%N) (Hyslop 1980), percent frequency of occurrence (F%) (Hynes 1950; Hyslop 1980), and percent weight (W%) (Pillay 1952; Hyslop 1980). Using these three indices, the Index of relative importance (IRI) (Pinkas 1971), expressed as a percentage (IRI%) (Cortés 1997) and the geometric index of importance (GII) (Assis 1996) was calculated for comparison with previous studies (Rogers et al. 2012).

$$\mathrm{IRI} = (\%\mathrm{N} + \%\mathrm{W})\ x\ \%\mathrm{F}$$

$$\mathrm{GII} = (\%\mathrm{N} + \%\mathrm{W} + \%\mathrm{F})/\sqrt{3}$$

Analysis of bronze whaler diet by sex and size and among regions (GSV, ESP, and SSP) was performed using permutational multivariate analysis of variance (PERMANOVA, 4999 permutations) (Primer version 7.0.6). Prior to running the PERMANOVA, mean IRI prey values were fourth-root transformed and a Bray-Curtis similarity resemblance matrix constructed. Shark sex and size were included in the analysis as categorical variables; male and female and <120cm TL or >120 cm TL, the size at which differences in movement patterns are known to occur that could potentially influence the prey consumed in different habitats (Huveneers et al. 2014). If either sex or size were identified to have a significant effect among regions, a pairwise test using 4999 permutations was undertaken. Similarity of percentages (SIMPER) analysis was used to determine the prey species that contributed the most to the similarities and dissimilarities between significant variables.

STABLE ISOTOPE SAMPLES - LABORATORY ANALYSIS

Tissue samples for all predator, prey and baseline species were freeze-dried for 48–96 hours and lipids were extracted using chloroform and methanol (2:1) (MacNeil et al. 2005). For sharks, tissues samples were not water washed, but it was assumed lipid extraction would remove most urea (Hussey et al. 2012). Stable isotopes ratios of 13C/12C and 15N/14N were determined by a Thermo Finnigan Delta Plus mass spectrometer at the Great Lakes Institute of Environmental Research (GLIER) in Canada (Espinoza et al. 2015). Ratios of heavy to light isotopes were expressed in δ according to the following equation: X=(RSample / RStandard − 1) × 1000 (‰), where X was the heavy isotope, Rsample is the ratio of heavy to light isotope in the sample, and Rstandard was the ratio of heavy to light isotope in the reference standard (Espinoza et al. 2015). Pee Dee Belemnite and atmospheric N2 were used as standard reference materials for carbon and nitrogen, respectively (Espinoza et al. 2015). Laboratory and National Institute of Standards and Technology (NIST) standards were analysed every 12 samples to determine analytical precision (Espinoza et al. 2015). The analytical precision (standard deviation) for NIST standard 1577c (bovine liver, n = 93) and an internal laboratory standard (tilapia muscle, n = 93) were 0.07‰ and 0.11‰ for δ13C and 0.11‰ and 0.11‰ for δ15N (Espinoza et al. 2015).

STABLE ISOTOPE - DATA ANALYSIS

Non-metric dimensional scaling plots were created using bronze whaler δC^{13} and δN^{15} data for region and sex for liver and muscle tissue separately. A PERMANOVA (4999 permutations) was performed on muscle and liver carbon and nitrogen stable isotope data using a non-transformed Euclidean distance resemblance matrix, with region and sex as fixed factors. Size was excluded from the analysis given insufficient samples per size class (Table 3.1). If significant differences were found, a pairwise test using 4999 permutations was conducted as for the SCA analyses.

To assess variation in muscle and liver δC^{13} and δN^{15} values of bronze whalers as a measure of ontogenetic changes in foraging location and diet, respectively, isotope data were plotted against body length and linear regressions were performed.

To examine individual and regional level variation in the diet of bronze whalers, inter-tissue variation in isotope values were estimated by calculating the residual δC^{13} and δN^{15} values between muscle and liver for each individual. Prior to this, the isotope values for muscle and liver were standardised to account for fractionation. Trophic enrichment factors (TEF) are the difference in isotopic composition between the consumer and prey, which varies between species and tissue type. Muscle tissue data were adjusted by the mean of the individual prey adjusted TEF's calculated from the slope coefficients in Hussey et al. (2014) and Caut et al. (2009) ($^{15}N = 2.83$ and $^{13}C = 0.83$) while liver tissue was adjusted by a fixed value of 1.5 for ^{15}N and 0.22 for ^{13}C (Caut et al. 2009; Hussey et al. 2011).

Individual inter-tissue residual values were plotted against body length and the mean residual ± SD for each region presented. A single factor ANOVA was used to test for statistical differences between tissues for each isotope (δC^{13} and δN^{15}) for each region.

To examine the trophic role of bronze whalers within the three gulfs, trophic position (TP) was calculated using both a scaled ΔN^{15} approach (TP_{scaled}; Hussey et al 2014a, b), and the traditional additive method of Vander Zanden and Rasmussen (1999; $TP_{addititive}$) (Vander Zanden et al. 1999). The scaled approached was calculated as follows;

$$TPscaled = \frac{\log(\delta N15lim - \delta N15base) - \log(\delta N15lim - \delta N15tp)}{k} + \alpha \qquad (1)$$

Where δN^{15}lim is the dietary δN^{15} value at which N^{15} incorporation and N^{15} elimination are equal, 21.9

$$TPadditive = \alpha + \frac{(\delta N15consumer - \delta N15base)}{\Delta n} \qquad (2)$$

where δN^{15}consumer is the δN^{15} value of the consumer of interest, δN^{15}base is the δN^{15} value of a known baseline consumer; α is the tropic position of the baseline organism; and Δn the trophic enrichment factor (TEF) of 2.3‰ for muscle tissue according to Hussey et al. (2011).

Three independent baseline consumers (*C. gigas* TP=2.5, *M. latisulcatus* and *S. sagax* TP=3) and a combination of the three baselines were used to estimate the trophic position of bronze whalers using muscle tissue to limit bias associated with using a single species (Hussey et al. 2015b).

To visually assess the relative role of bronze whalers relative to potential sympatric prey consumed in each sampling region, bi-plots of mean (± SD) δC^{13} and δN^{15} values are presented (Fig. 4). Isotope values of all prey items were adjusted to account for the TEF of shark muscle and liver tissues as described above.

STABLE ISOTOPE MIXING MODELS

To examine niche space and temporal variation in niche occupied by bronze whalers in each focal region, isotopic niche was calculated for muscle and liver tissue data. Bayesian ellipses, a measure of isotopic niche space or the trophic diversity consumed by bronze whalers in each region were constructed in the R package, Stable Isotope Bayesian Ellipses (SIBER) (Jackson et al. 2011). Bayesian isotopic ellipse area (SEAb) and corrected areas for small sample sizes (SEAc) were estimated to allow a comparison of niche overlap among regions. Differences in SEAb were considered significant if the 95% credible interval ellipses did not overlap.

The proportional contribution of primary prey items/functional prey groups to the diet of bronze whalers was then estimated for both tissue types across all regions using the R package SIAR (Stable Isotope Analysis in R) (Jackson et al. 2011) (R Development Core Team 2015). The SIAR isotope mixing model incorporates uncertainties within the consumer and prey isotope data and that of TEFs (± SD). All prey selected as source contributions for the isotope mixing models were identified as primary prey from stomach content data (Rogers et al. 2012). To determine prey sources were unique, A PERMANOVA was run on the non-transformed prey stable isotope values using a Euclidean distance matrix. Species with overlapping isotope values were categorized into biologically relevant groups based on species type and habitat resulting in four distinct prey categories: reef teleosts, small pelagic teleosts, herbivorous and omnivorous species, and carnivorous species (Table 3.3).

Results

STOMACH CONTENT ANALYSIS

A total of 306 stomachs from bronze whalers were sampled, with 212 containing prey items (Table 3.1) and a vacuity index of 31%. Fifty-two different prey items were identified and categorised into nine functional prey groups (Table 3.2). Prey diversity was high and ranged from small crustaceans to large pelagic teleosts and demersal elasmobranchs.

The cumulative prey curve for the lowest taxonomic level did not reach an asymptote (Fig. 3.2a), but the cumulative prey curve for the functional prey groups indicated that a sample size of 212 stomachs was sufficient to describe the diet of bronze whalers at this taxonomic level (Fig. 3.2b). The von Bertanlanffy curve fit to both the lowest taxonomic level and functional prey group data agreed with the cumulative prey curves with L_{inf} estimates of 58.13 for the lowest taxonomic level and 8.1 for the trophic group level, which was less than the observed number of functional prey groups.

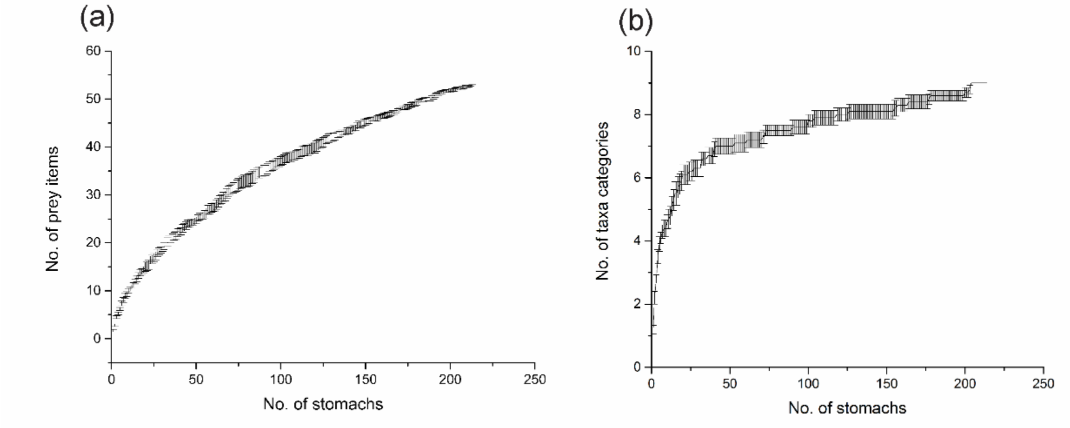


Figure 3.2 Cumulative prey curves showing the relationship of the number of stomachs to the number of identifiable prey items (left) or trophic groups (right). Error bars represent the standard error of the means.

The most important prey species contributing to total diet of bronze whalers (with IRI% > 10%) were the cephalopods, *S. apama, S. novaehollandiae* and *S. australis*, and the small pelagic teleost, *S. sagax* (Table 2). Additional important species from the benthic teleost group were flathead (*Platycephalus* spp.) (IRI%= 0.78) the Southern Garfish (*Hyporhamphus melanochir*) (IRI%= 0.41) and snook (*Sphyraena novaehollandiae*) (IRI%= 0.24). Australian Salmon (*Arripis truttaceus*) (IRI%= 0.93) and maray (*Etrumeus teres*) (IRI%= 0.29) from the small pelagic teleost group also contributed to the diet of bronze whalers (Table. 3.2). Rays species were also identified in the diet in relatively low numbers, such as, the southern eagle ray (*Myliobatis tenuicaudatus*) (IRI%= 0.11) and Rajidae sp. (IRI%= 0.14).

Non-metric multidimensional scaling revealed no visual clustering or separation of diet between sexes, sizes, or regions (Fig. S3.1 Supplementary material). PERMANOVA found a significant difference in diet by region (p< 0.001), but not by sex (p= 0.11) or size (p= 0.06). PERMANOVA pairwise tests by region estimated that GSV and ESP were significantly different from SSP (p= 0.001 for both regions respectively), but were not significantly different from each other (p= 0.15). SIMPER analysis showed the diet of bronze whalers from GSV and ESP were the most similar (dissimilarity = 85.5%), while bronze whalers from SSP had a more distinct diet (dissimilarity = 89.5% from ESP and 90.1% from GSV). Differences between regions were mostly driven by fish, and cephalopods with *S. sagax* and *S. novaehollandiae* contributing ~32% of the difference between SSP and the other two regions.

STABLE ISOTOPE ANALYSIS

A total of 101 muscle and 108 liver samples (108 Individuals) were collected from bronze whalers (Table 3.1) and mean (± SD) isotope values calculated for 34 potential prey items (Table 3.3). Estimated mean $\delta^{13}C$ and $\delta^{15}N$ values for both shark tissues showed large variation, with the highest variation in $\delta^{13}C$ values for the SSP (Fig. 3.3). NMDS plots of muscle $\delta^{13}C$ and $\delta^{15}N$ values showed no separation or clustering by region or sex (Fig. S3.2 Supplementary material); liver $\delta^{13}C$ and $\delta^{15}N$

values showed minor separation among regions, but no distinct clustering was apparent between sexes (Fig. S3.2 Supplementary material).

PERMANOVA found no significant differences in $\delta^{13}C$ and $\delta^{15}N$ values of muscle or liver between sexes (p=0.092 and 0.176 respectively) and no significant differences in the δC^{13} and δN^{15} of muscle between regions (p= 0.078). In contrast, $\delta^{13}C$ and $\delta^{15}N$ values of liver were significantly different among all regions (p= 0.002), with ESP the most different to GSV and SSP (p=0.014 and 0.005 respectively).

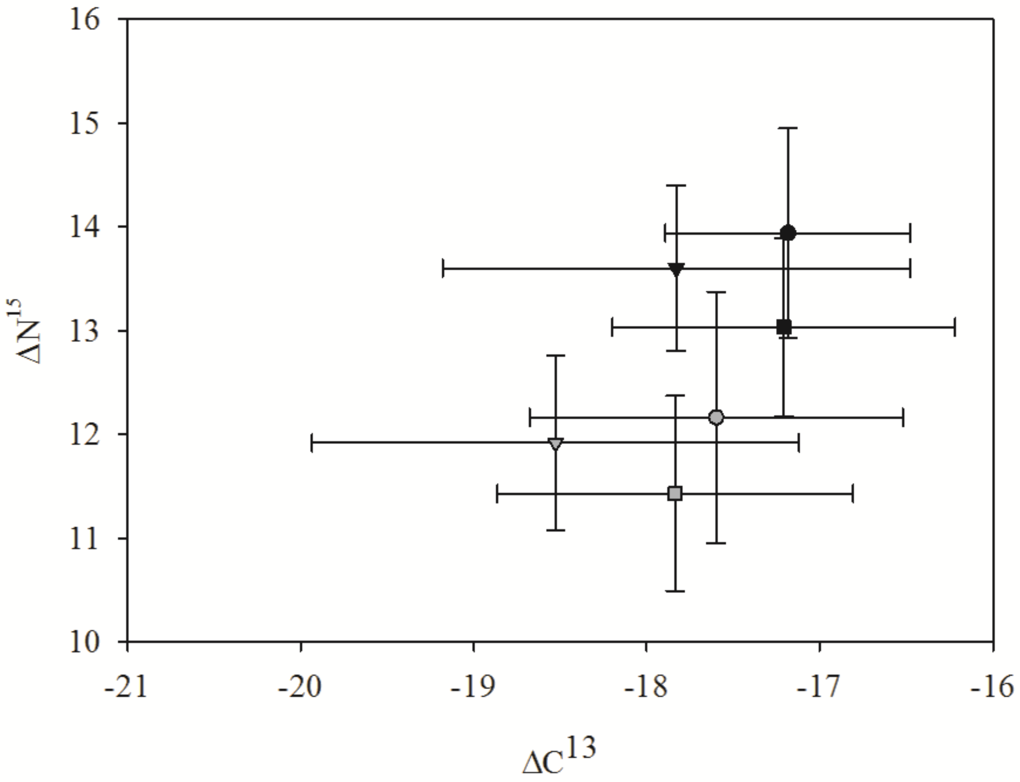


Figure 3.3 Bi-plots of the mean stable isotope values (+SD) of bronze whaler muscle (black) and liver (grey) tissue from the three regions. Triangle = southern Spencer Gulf, square = eastern Spencer Gulf and circle = Gulf St. Vincent.

The linear relationships between total length and $\delta^{13}C$ and $\delta^{15}N$ values for muscle and liver tissue were not significant, suggesting no ontogenetic shift in foraging location and diet for bronze whalers (68 and 295 cm TL) (Fig. 3.4a-d).

No significant differences were found in the inter-tissue variations between regions for both δC^{13} and δN^{15} ($p= 0.083$ and 0.087, respectively). The mean residual values of δC^{13} for each region were ~0, with the highest variation in δC^{13} standard deviation values for SSP (Fig. 3.6a). Mean residual values for δN^{15} differed slightly between regions, with the highest variation in standard deviation in GSV samples (Fig. 3.6b). This is likely driven by some high δN^{15} muscle values for young of year sharks with a maternal meddling legacy of their mothers isotope signatures still present. The two sharks that were effected by their maternal isotope signatures were removed from the SIA mixing models.

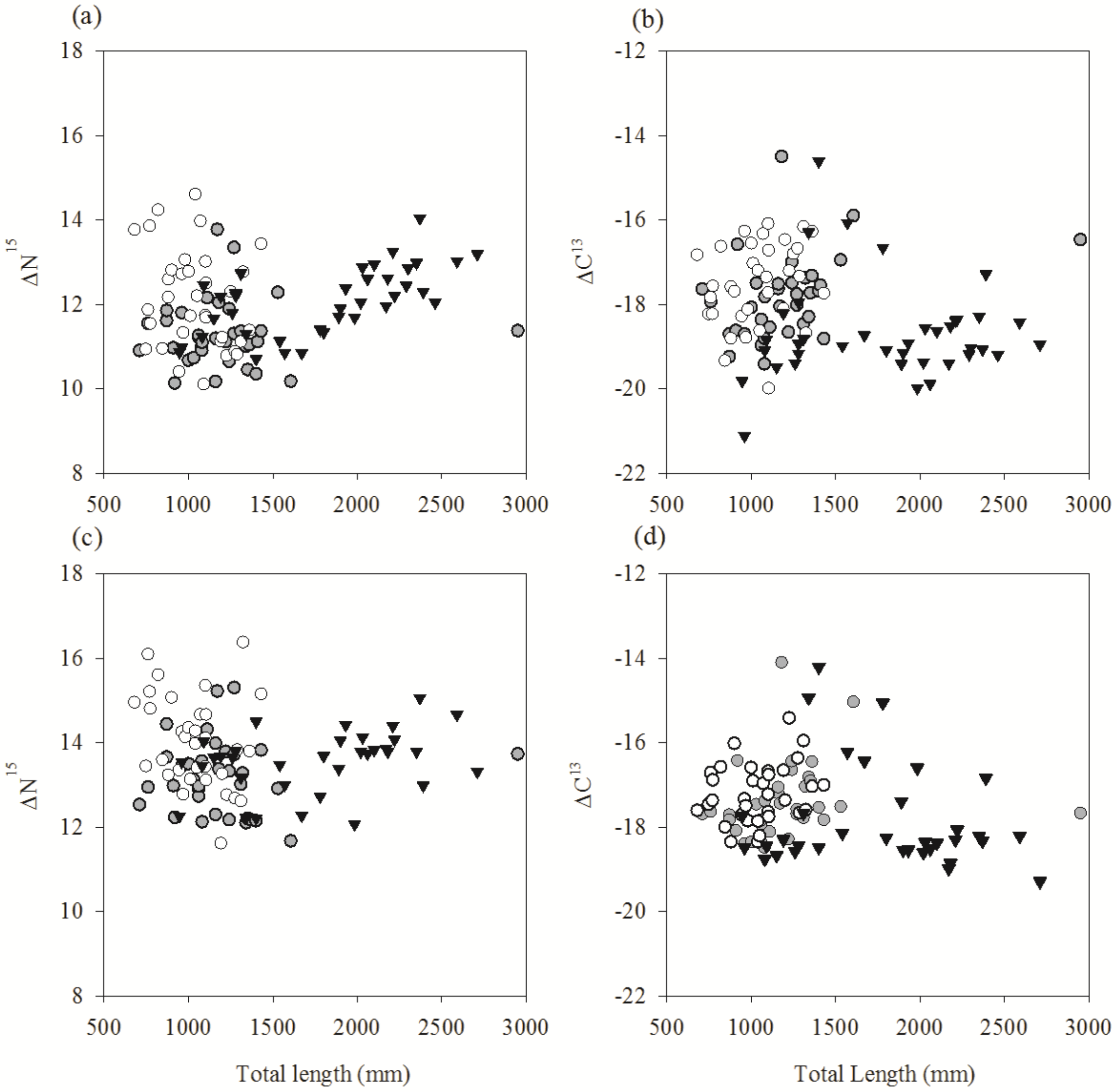


Figure 3.4 Stable isotope (δC^{13} and δN^{15}) tissue signatures of bronze whalers plotted against total length (mm). a) muscle tissue δC^{13} vs total length (mm), b) muscle tissue δN^{15} vs total length (mm), c) Liver tissue δC^{13} vs total length (mm) and d) liver tissue δN^{15} vs total length (mm). White circles = GSV, Grey circles = ESP and black triangles = SSP.

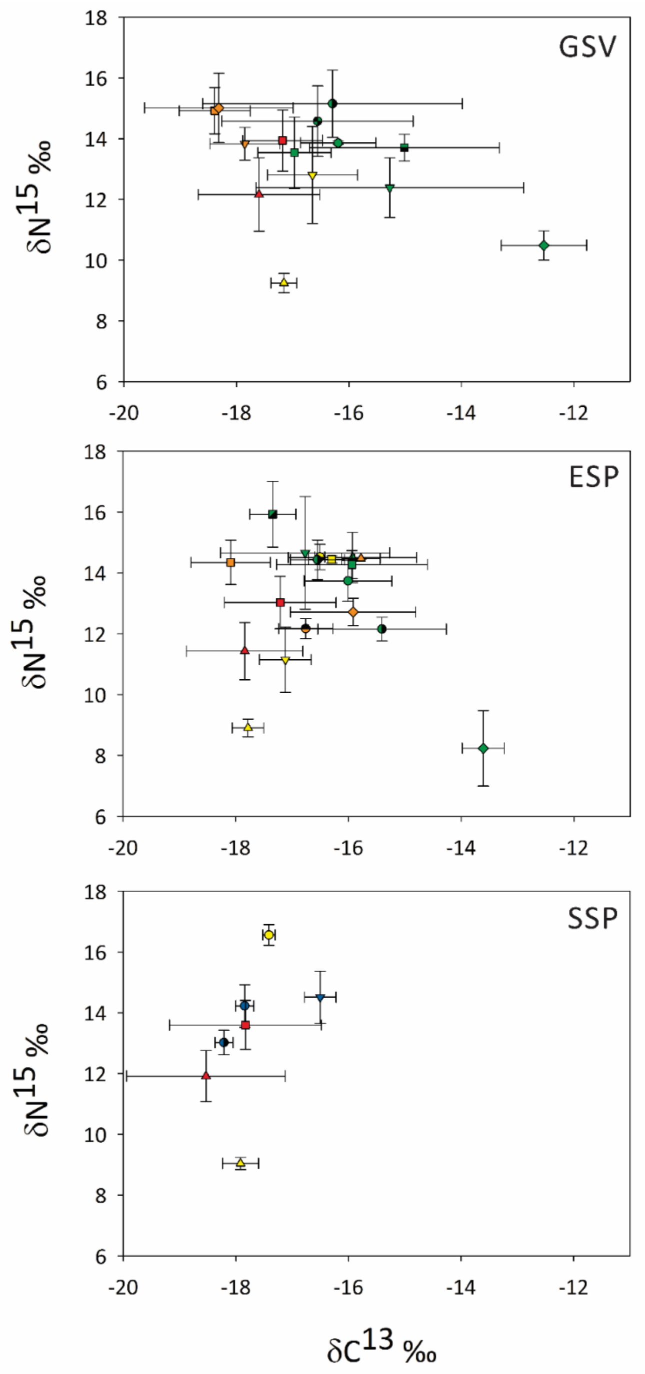


Figure 3.5 Bi-plots of the mean stable isotope values (+SD) of bronze whaler and sympatric prey species with prey categorized by habitat. a) GSV, b) Eastern Spencer Gulf and c) Southern Spencer gulf. The colour represent the habitat that the prey item resides, yellow = benthic/ sediment, green = seagrass, blue = pelagic, brown = reef and red represents shark tissue. Error bars are the standard deviation of the values around the mean.

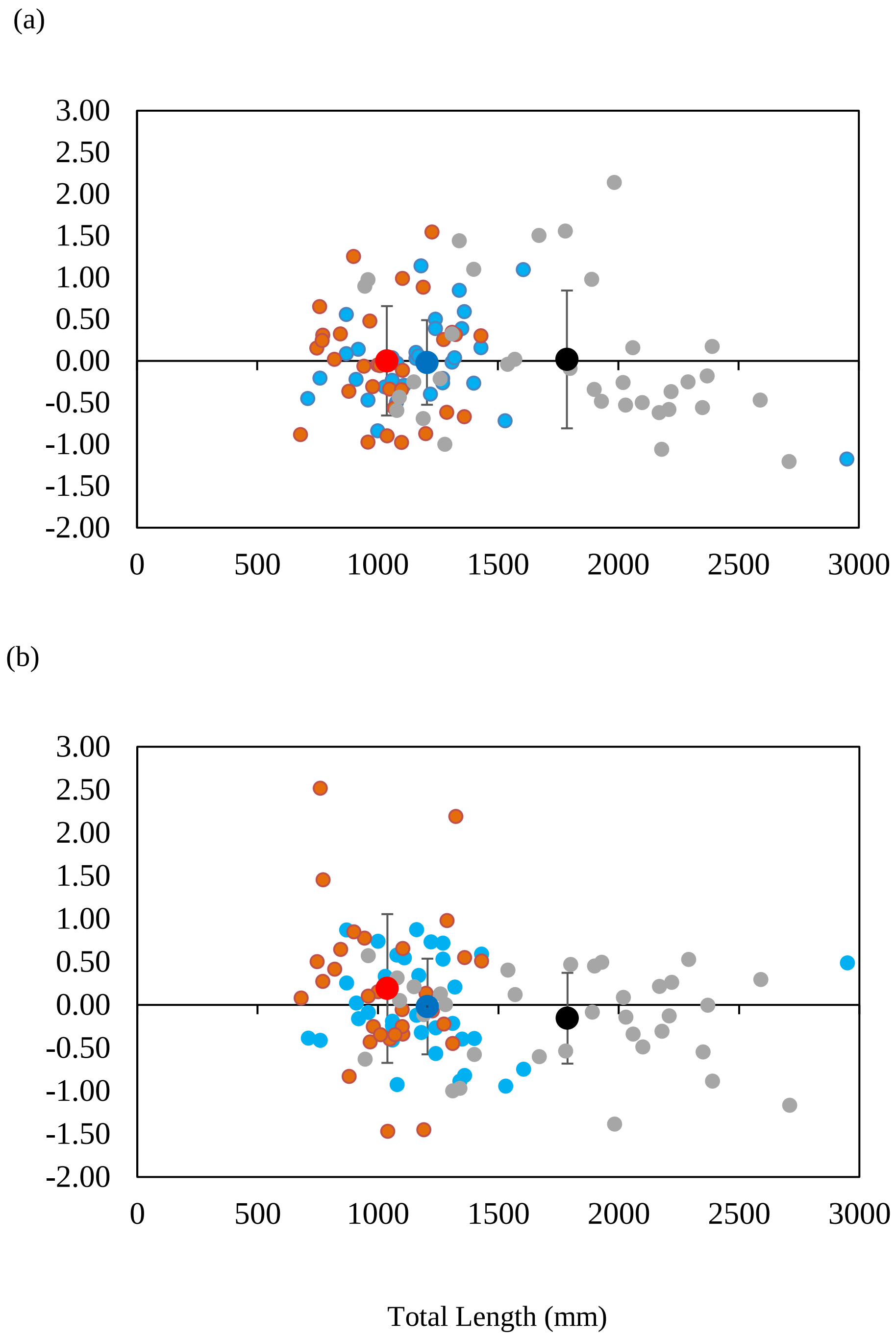


Figure 3.6 Inter-tissue stable isotope (δC^{13} and δN^{15}) residual variations for each individual bronze whaler. Plots are ordered in increasing total length within each region. a) The between tissue residual variation of each individual for δC^{13}; b) The between tissue residual variation of each individual for δN^{15}; orange dots = GSV; red dots = GSV mean residual value; light blue dots = ESP; dark blue dot = ESP mean residual; grey dots = SSP; black dots = SSP mean residual.

Table 3.4 Trophic position estimates from multiple baseline species. Combined is the mean of all three baseline species, δN^{15} values used a single baseline value in the equations. SD is the standard deviation of the means represented.

Baseline consumer	Trophic Position	SD	Method
Melicertus latisulcatus	4.55	0.38	Scaled
Crassostrea gigas	4.84	0.38	Scaled
Sardinops sagax	3.98	0.38	Scaled
Combined	4.46	0.38	Scaled
M. latisulcatus	5.30	0.42	Constant DTDF
C. gigas	6.53	0.42	Constant DTDF
S. sagax	4.32	0.42	Constant DTDF
Combined	5.38	0.42	Constant DTDF

Trophic position estimates for bronze whalers using a combination of baseline species were 4.46 ± 0.38 and 5.38 ± 0.42 for the scaled and constant TEF equations (Table 3.4). Trophic position estimates for the constant TEF equation were consistently higher than those estimated using a scaled TEF equation when using individual and combined baseline species (Table 3.4). The differences in TP estimates between baseline species was higher for the constant TEF equation (maximum difference of 2.3 TP) than for the scaled equation (maximum difference of 0.86 TP). The individual baseline species that generated the lowest TP estimates was *S. sagax* for both equations, while the highest TP estimates were from *C. gigas* (Table 3.4).

Bronze whalers occupied a large niche width for both liver and muscle isotope data (Fig. 3.7a, b). There was a large overlap in Bayesian standard ellipses for muscle δ^{13}C and δ^{15}N values for all regions (Fig. 3.7a). The bivariate mean (95% CI) per region was overlapping between SSP and ESP, but not with GSV. Similarly, Bayesian standard ellipses for liver isotope data for each region also showed large overlap, but the bivariate mean (95% CI) did not overlap among regions (Fig. 3.7b).

The SIAR isotope mixing model for muscle δ^{13}C and δ^{15}N values of all sharks combined found that small pelagic fishes contributed the most to the diet of bronze whalers (~70%) followed by the herbivorous and omnivorous fish group (~25%), while the two remaining groups (reef fish and carnivorous fish had low contributions of ~5–10%) (Fig 3.8a). When considering liver tissue δ^{13}C and δ^{15}N values, the dominant prey were herbivorous and omnivorous fish (~55%) and small pelagic teleosts (~40 %) (Fig 3.8b).

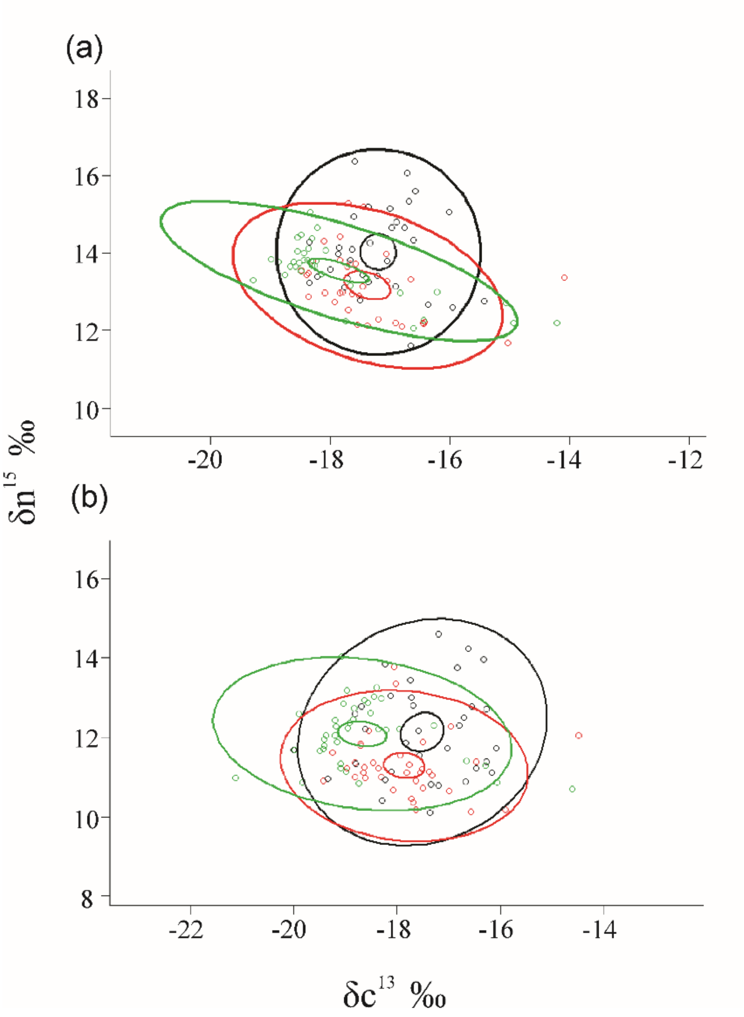


Figure 3.7 Standard Bayesian ellipses for niche width both tissues of bronze whalers. a) Bayesian ellipses of muscle (a) and liver (b) tissue niche width by region. Outer large circles represent the standard Bayesian ellipses, the smaller circles represent the mean value with its 95% confidence intervals. Green = SSP, black = GSV and red = ESP.

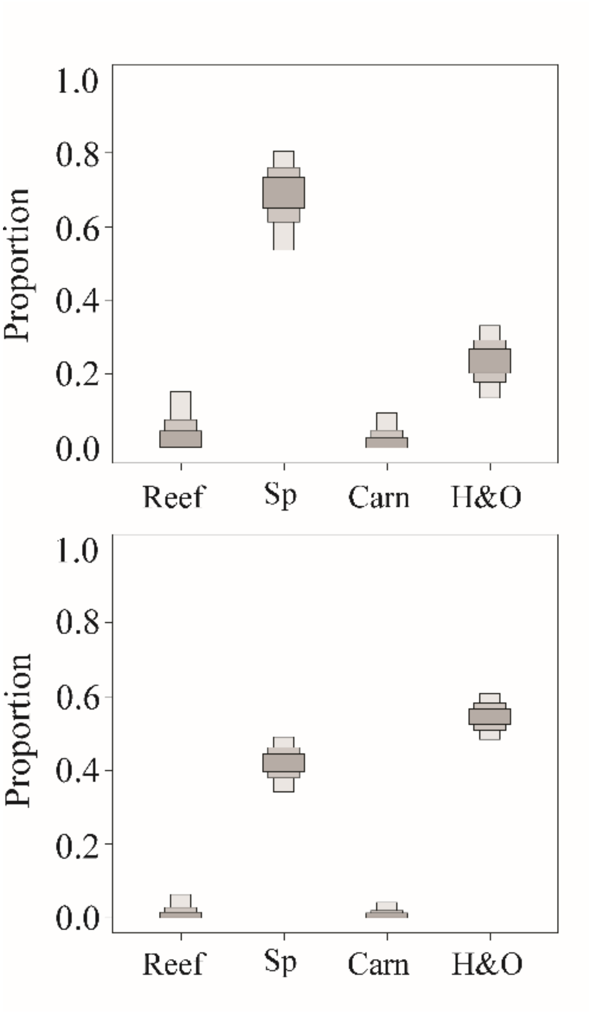


Figure 3.8 SIAR mixing model plots of prey proportion to the diets of bronze whalers. Prey proportions of muscle tissue are on the top and liver tissue on the bottom. R = reef fish species; SP = small pelagic teleosts; Carn = secondary consuming teleosts; H&O = herbivores and omnivores

Table 3.5 The mean values for inter- tissue variations in isotope signatures between regions. Δ represents the difference in mean isotope values.

	Muscle δC^{13}	**Liver δC^{13}**	**Δ δC^{13}**	**Muscle δN^{15}**	**Liver δN^{15}**	**Δ δN^{15}**
GSV	-17.17	-17.53	0.36	13.98	12.19	1.79
ESP	-17.37	-17.82	0.44	13.17	11.30	1.87
SSP	-17.85	-18.62	0.77	13.54	12.05	1.49
Total	-17.47	-17.99	0.52	13.56	11.85	1.72

Discussion

Understanding the feeding ecology of a predator can identify critical predator-prey relationships, which can reveal insights into habitat use, broad-scale movements, and shifts in life histories. Such information is integral for developing ecosystem models and for understanding the effects of changing populations due to natural events or anthropogenic threats. We found that bronze whalers in southern Australia is a generalist forager with a large niche width, but primarily feeding on *S. sagax* and locally abundant cephalopods (*S. novaehollandiae*, *S. australis*, and *S. apama*), supporting previous findings in southern Australia (Rogers et al. 2012), South Africa (Smale 1991; Cliff and Dudley 1992) and Argentina (Lucifora et al. 2009). The high contribution of lower order prey species to diet of bronze whalers, such as *S. sagax* irrespective of body length resulted in a lack of ontogenetic variation and a trophic position estimate associated with lower order carnivorous teleosts, suggesting that large bronze whalers can exert direct top down pressure on lower trophic level species than would be expected based on total length. The temporal scale at which diet was assessed, affected whether regional variations was observed. The overall similar diets but observed regional variation when assessed based on tissues with fast turnover rates aligns with seasonal movements of bronze whalers from continental shelf waters to coastal areas where diet is more restricted to the specific region and habitat frequented. The information provided has further improved the knowledge of the ecological role of bronze whalers within the temperate marine environment.

PREY SPECIES DIVERSITY

Prey diversity was high for bronze whalers with 52 different items identified through SCA. Prey species identified ranged from benthic crustaceans to pelagic teleosts and small bodied elasmobranchs, which expresses bronze whalers ability to exploit various habitats. The highly diverse prey assemblage categorises bronze whalers as a generalist feeder, similar to the sympatric dusky shark (*C. obscurus*) (Rogers et al. 2012).

The large estimates of niche width from SIA of muscle and liver tissues also supported the diverse prey assemblages suggested by SCA. Niche widths (50 % confidence intervals) strongly overlapped between regions for both tissues, suggesting that over a longer time frame bronze whalers prey assemblages are highly diverse, irrespective of the region sampled. The large niche width estimates for bronze whalers reflect both their broad generalist feeding strategy and their highly mobile nature, allowing for extensive movements between different habitat and prey fields.

Although, prey species diversity was high, both methods of SCA and SIA identified several important prey species such as, small pelagic teleosts (*S. sagax*) and locally abundant cephalopods species (*S. australis, S. novaehollandiae* and *S. apama*). Sharks sampled in the two northern gulf regions were identified to have similar prey assemblages, with benthic and demersal teleosts species such as *Platycephalus* sp., *A. truttaceus, S. novaehollandiae,* and *Sillago* sp. contributing to the diet of bronze whalers. The southern gulf region of SSP prey assemblage was significantly different from both ESP and GSV regions due to the high abundances of *S. sagax* identified in the stomach contents.

The highest contributing prey groups for both muscle and liver tissue estimated from the isotope mixing models, were small pelagic teleosts and herbivorous and omnivorous teleosts. Although the proportional contribution of small pelagic and herbivorous and omnivorous teleosts changed between liver and muscle tissue, both groups were the most important to the assimilated diet. The high estimated contribution of small pelagic teleosts to the diet of bronze whalers highlights the role that this shark species may play in the population dynamics of small pelagic teleosts in the coastal waters of southern Australia (Goldsworthy et al. 2013).

The dominance of small pelagic teleosts and cephalopods in the diet of bronze whalers has previously been identified in southern Australia (Rogers et al. 2012), in the South West Atlantic (Lucifora et al. 2009), and South West Indian Oceans (Smale 1991; Cliff and Dudley 1992). The dominance of the South African sardine (*Sardinops sagax*) in the stomach contents of bronze whalers off South Africa was, however, biased by the high seasonal abundance of *S. sagax* during winter (June–August) as *S.*

sagax migrate to warmer waters, which coincides with the majority of *C. brachyurus* catches (Cliff and Dudley 1992; Dudley and Cliff 2010). A study based on sharks caught outside of the sardine migration season, showed that the Cape Hope squid (*Loligo reynaudii*) instead, dominated the diet off the Eastern Cape of South Africa of both adult and juvenile bronze whalers (Smale 1991). The findings in the previous studies outside of Australia are based on samples collected over a short seasonal scale over multiple years and decades, which may reflect the selective targeting of prey by bronze whalers at that point in time (Munroe et al. 2014a). These previous findings were also impeded by the limitations of SCA, which only provides information about recent feeding events and is affected by variations in digestion rates. In the present study, the lower importance of cephalopods based on SIA, suggests that the slower digestion rate of hard parts may have previously led to an over estimation of cephalopods in studies relying on SCA only.

REGIONAL VARIATION

Regional differences in prey species were identified through SCA and liver tissue SIA, but not muscle SIA. A significant difference between the northern gulf regions ESP and GSV and the southern gulf region of SSP was identified through SCA and liver tissue SIA. Both methods estimate diet over a short timeframe, with SCA representing diet over the past few days and liver tissue representing prey assimilation over the previous of 3–6 months (MacNeil et al. 2005; Logan and Lutcavage 2010). As bronze whalers are generalist foragers, the regional variations in diet likely reflect a regionally distinct prey field which is primarily driven by contrasting habitats where sampling occurred. The sampling areas in the upper gulf regions of GSV and ESP are predominately shallow water (>20 m) with large sea grass meadows, scattered sandy benthos, and isolated patches of low profile reef (Bryars et al. 2008; Shepherd et al. 2008). Southern Spencer Gulf is characterised by deeper water (~50 m) with silt benthos and scattered sea grass and reef ecosystems (Seddon et al. 2000). The prey species diversity was greater for the two upper gulf regions (GSV and ESP) with numerous small pelagic, cephalopod, herbivorous, and carnivorous teleosts. The SSP region shares the same species diversity, however, this region is more abundant in small pelagic teleosts, i.e. *S. sagax*, than the other two regions, and supports Australia's largest small pelagic fishery (Ward et al. 2006). This difference in small pelagic teleost abundance likely explain the difference in the diet of bronze whalers from SSP (Rogers et al. 2012). The high consumption of small pelagic teleosts in the SSP is additionally supported by a lower mean δN^{15} value which is likely driven by the diet being dominated by small pelagic teleosts, which have a lower δN^{15} value. The higher δN^{15} values for the upper gulf regions are likely due to the foraging on higher trophic level consumers, such as cephalopods (*S. australis, S. novaehollandiae* and *S. apama*) and carnivorous teleosts (*Platycephalus* sp., *S. novaehollandiae*), which was identified through SCA.

The isotope mixing model for regions combined shows difference in the diet of bronze whalers according to the type of tissue used for SIA. The mixing model based on muscle tissue suggests that small pelagic teleosts are the highest contributing group to the diet of bronze whalers, while herbivorous and omnivorous teleosts were as important as small pelagic teleosts when based on liver tissue. The discrepancy is linked to the difference in prey assimilation rate between tissues. The shorter prey assimilation rate in liver tissue suggests that during the previous 3–6 months the sampled sharks were consuming more herbivorous and omnivorous teleosts, which are in high abundances in the northern gulf and coastal waters. In contrast, the results of the mixing model from the muscle tissue indicates that, over a longer time frame, bronze whalers are consuming a high proportion of small pelagic teleosts which are most abundant offshore and in the southern gulf waters (Ward et al. 2006). This variation in prey group contributions between tissues suggests seasonal variations in habitat. This change in prey contribution to the diet of bronze whalers aligns with the increased seasonal abundances of this species within the gulf and coastal waters over the Austral Spring–summer months (September–April). This is supported by movement and residency studies showing that bronze whalers have their highest residency in GSV over the Austral summer and relatively low residency throughout the remainder of the year (Huveneers et al. 2014)(chapter 4). Pop-up satellite archival data also shows that large bronze whalers (>2 m TL) leave the gulf waters when Austral winter approaches (May–June) (Huveneers et al. 2014; chapter 5).

ONTOGENETIC VARIATION

Our results do not show any evidence of ontogenetic variation in the diet of bronze whalers. The lack of linear relationship between δN^{15} and total length for both tissues contradicts the ontogenetic shift observed in the South West Atlantic, where the contribution of elasmobranchs in bronze whalers diet increased with body size (Lucifora et al. 2009). Although a small number of sharks >2.5 m TL was sampled in our study, ontogenetic changes would have been expected to occur between neonates and sharks of ~2 m TL. Ontogenetic shifts with increasing body size is common for large-bodied shark species and has been shown in a broad range of species including tiger shark (*Galeocerdo cuvier*) (Lowe et al. 1996; Simpfendorfer et al. 2001b), sevengill shark (*Notorynchus cepedianus*) (Ebert 2002), sandbar shark (*C. plumbeus*) (McElroy et al. 2006; Ellis and Musick 2007), and white shark (*Carcharodon carcharias*) (Estrada et al. 2006). Bronze whalers might challenge this paradigm, as their key prey species was low in δN^{15} irrespective of body length. In bronze whalers, while the maximum size of the prey items increases with shark body size, the minimum prey size and highest contributing prey species remain the same throughout shark's growth. The lack of ontogenetic variation and high contribution of small pelagic teleosts to their diet suggests that bronze whalers may therefore have a direct effect on the lower trophic levels of the temperate marine environment Such lack of ontogenetic diet shifts has previously been observed in a similar carcharhinid species, the silky shark (*C. falciformis*) in the eastern Pacific Ocean (Duffy et al. 2015). The use of N^{15} isotopes signatures to identify changes in trophic level feeding with increased body length might lead to spurious results in shark species that continue to feed on lower order species throughout ontogeny.

TROPHIC POSITIONS

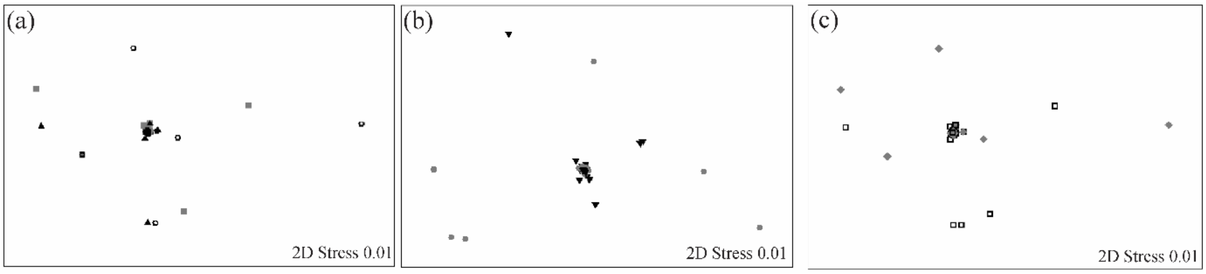
Trophic positions were estimated using the constant TEF and scaled TEF equations with multiple baseline species. The constant TEF equation proposed by Post (2002) has been widely applied to estimate TP through SIA. Post's (2002) method assumes that each trophic level has the same magnitude of trophic enrichment. However, the trophic enrichment value used in the equation varies between studies, with the three main values of N^{15} trophic enrichment for shark studies being 3.4‰ (Zanden and Rasmussen 2001; Post 2002), 2.3‰ (Hussey et al. 2010), and 3.7‰ (Kim et al. 2012). The scaled TEF equation is based on the concept of a narrowing enrichment value of N^{15} as the trophic level increases (Hussey et al. 2014). The constant TEF estimations of TP for all baseline species individually and combined was higher than estimates from the scaled equation. The constant TEF method overestimated the trophic position for bronze whalers in southern Australia at 5.38, which would place bronze whalers into the same trophic level as white sharks (*C. carcharias*). This is likely incorrect as the two species are known to feed on prey from differing trophic levels (Hussey et al. 2014). The scaled equation estimated a more conservative TP of 4.45, which is similar to the only other TP estimate from SIA for bronze whalers (Hussey et al. 2014). The variability in TP estimations from a single baseline shown in this study highlights the importance of using multiple baseline species to reduce individual baseline species bias. Region-specific baselines are additionally integral to accurately determine the TP of any species, as intra-species variation in N^{15} has been identified for many fish and shark species (Munroe et al. 2014b).

CONCLUSION

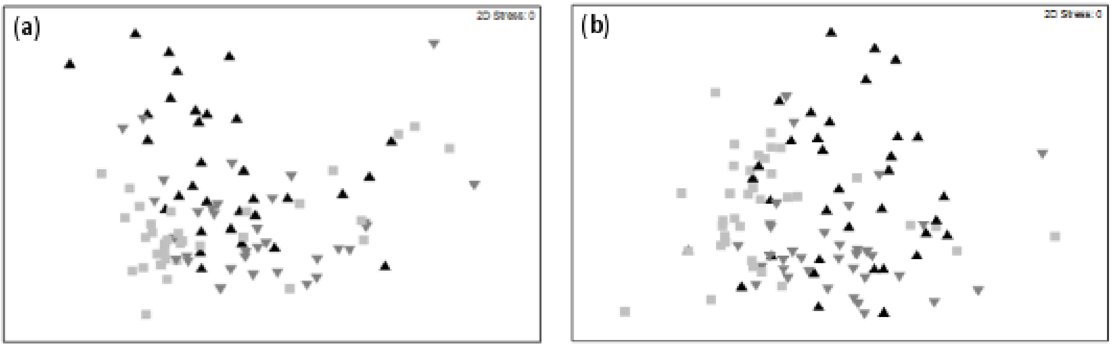
In this present study, we investigated the foraging ecology of bronze whalers in the coastal waters of southern Australia to further improve our understanding of the ecological contribution of this large-bodied shark species. We identified that bronze whalers have a diverse prey field, occupies a large niche space, and is a generalist forager that consumes prey from a broad range of habitats within its range. Bronze whalers consume a high proportion of small pelagic teleosts and cephalopods irrespective of body length, resulting in a lack of ontogenetic variation. Regional variations in diet over short time frames was identified through SCA and SIA, although diet did not vary across the sampling regions over a longer time frame. Inter-habitat movement was inferred through changes in prey group contributions between both tissues isotope mixing models. The combination of dietary analysis techniques and sampling over a greater temporal and spatial scale, has increased our understanding of the temporal and spatial variability in foraging, which has further improved our understanding of the ecological importance of bronze whalers to the gulf and neritic waters of southern Australia. The critical dietary information provided can be applied to further ecosystem based models and has improved our understanding of the feeding ecology of an important predator in the temperate marine environment.

Acknowledgments

The authors would like to thank the fishermen of the Marine Scalefish Fishery within South Australian coastal waters for kindly providing assistance in obtaining access to samples. The authors also thank the South Australian Research and Development Institute (SARDI) for their in kind support and additional thanks goes to Matthew Lloyd, William Jackson and the members of the Marine Scalefish Fishery Research group for their assistance in sampling. Thanks to Anna Hussey at the GLIER lab for processing the stable isotope samples and assistance with sample preparation. Thanks to Sasi Nayar and Michelle Braley from the SARDI Phytoplankton Biology and Analytical team for the processing samples. The authors would also like to acknowledge the numerous Flinders University undergraduate students for their assistance in the laboratory processing.



Supplementary Figure S3.1 Non-metric multidimensional scaling plots for bronze whaler stomach content analysis for sex (a), size (b) and region (c).



Supplementary Figure S3.2 Non-metric multidimensional scaling plots for bronze whaler stable isotope analysis for sex (a) and region (b).

4

SEASONAL OCCURRENCE AND PHILOPATRY OF JUVENILE BRONZE WHALERS (*CARCHARHINUS BRACHYURUS*) IN A TEMPERATE INVERSE ESTUARY

Abstract

Assessing the movements and habitat use of wide-ranging predators is critical for understanding their role within an ecosystem and vulnerability to anthropogenic threats. The bronze whaler (*Carcharhinus brachyurus*) is a large-bodied, slow growing shark species that is widely distributed throughout temperate Australian waters. Currently, habitat use, spatial-temporal presence and fine-scale movements information is unknown for southern Australian inshore coastal waters which can identify periods of increased vulnerability to anthropogenic effects. This study investigated the spatio-temporal patterns of occurrence, habitat use, and residency of bronze whalers in Gulf St. Vincent, South Australia. Fifty-six bronze whalers were tagged with acoustic transmitters from 2009–2014 and monitored for periods of up to 55 months (range: 516–1634 days; mean ± standard error: 825 ± 47). The seasonal presence of bronze whalers peaked in spring–early autumn (September–April). Philopatry to the array was high, with 77% of tagged sharks detected over multiple years and 36% detected over three years. A low estimate of mean residency index (Ri = 0.05 ± 0.01) indicated that time spent within the array was limited. Water temperature and season had the most significant effect on shark presence, which increased with water temperature. Chesson's electivity index showed bronze whalers exhibited the highest affinity to seagrass (*Posidonia* spp.), suggesting that this habitat plays an important role in the early life history stages of bronze whalers. The philopatric behaviour and

seasonal occurrence of bronze whalers in the North East Gulf St. Vincent, combined with catches being dominated by neonates and juveniles provide evidence that the area might be used as a nursery ground. The low productivity and slow life history traits of bronze whalers combined with its nearshore seasonal occurrence result in this species being susceptible to anthropogenic threats, which highlights the need for further vulnerability assessments.

Introduction

Quantification of the extent and drivers of animal movement and site fidelity within critical areas is becoming increasingly important, as ecosystems are exposed to growing pressures from anthropogenic influences and strengthening environmental variability (Hughes et al. 2003; Halpern et al. 2008). The corollary is that aquatic ecosystems can be thrown out of balance, with implications for a range of species through direct or indirect effects (Pinnegar et al. 2000; Maxwell et al. 2013). Understanding the distribution and habitat use of aquatic organisms is paramount for predicting behavioural responses to anthropogenic and environmental changes and to the management and conservation of species and habitats (Pikitch et al. 2004).

Species particularly at risk of being affected by anthropogenic effects are sharks and rays because of their life history characteristics, which often result in slow intrinsic rates of population increase and to their extinction risk being substantially higher than most other vertebrates (Smith et al. 1998; Stevens et al. 2000; Dulvy et al. 2014). Depletion of some shark populations has raised concerns over the sustainability of shark populations and their fisheries (Dulvy et al. 2014), as well as the stability of ocean ecosystems (Ferretti et al. 2008; Ferretti et al. 2010; Ruppert et al. 2013). Despite well-documented concerns about the sustainability of a range of shark populations and their potential vulnerability to fisheries (Baum et al. 2003a), population assessments for many shark species have not been conducted. Population assessments rely on high-quality catch and effort data, and require information on population structure, extent of movements and migratory patterns, and residency to determine how the spatio-temporal dynamics of sharks affect their resilience to anthropogenic and environmental changes (Chapman et al. 2015). This is particularly pertinent for species with a nearshore coastal distribution which may result in a high degree of overlap with human activities and therefore in an increased exposure to targeted and non-targeted mortality (Speed et al. 2010).

The bronze whaler (*Carcharhinus brachyurus*) is a large-bodied (up to 3 m total length) shark species with a primarily coastal, temperate, and neritic distribution in the Northern and Southern Hemispheres

(Last and Stevens 2009). The species life history characteristics has been described as slow growing, late maturing, and with a low reproducing output (Walter and Ebert 1991; Drew et al. 2016). Bronze whalers are taken in small-scale fisheries in discrete regions of their range (Walter and Ebert 1991; Francis 1998; Chiaramonte 1998; Drew et al. 2016). In Australia, bronze whalers are caught throughout their range in New South Wales (NSW), Victoria, (Vic), South Australia (SA), and Western Australia (WA), with the largest catches from SA where bronze whalers are seasonally targeted by longline fishers within the Marine Scalefish Fishery (MSF) (Rogers et al. 2013a). The vulnerability to extinction of bronze whalers was assessed using a fuzzy logic model, giving bronze whalers a vulnerability index of 78 on a scale from 1 to 100, with 100 being most vulnerable (Rogers et al. 2013a). Currently, no population assessments have been undertaken to determine the resilience of this bronze whaler population to anthropogenic or environmental pressures. Movement and site fidelity of bronze whalers are poorly understood, with previous studies inferring seasonal occurrences through patterns in commercial and recreational catches (Lucifora et al. 2005; Jones 2008; Rogers et al. 2013a) or beach meshing programs (Dudley and Cliff 2010). Seasonal increases in abundance have been linked to fluctuations in ambient water temperatures (Lucifora et al. 2005), opportunistic exploitation of migrating pelagic teleost schools (Dudley and Cliff 2010), or the use of nursery areas (Rogers et al. 2013a). In South Australia, tag-recapture information from conventional identification tags deployed by recreational fishers suggested a seasonal increase in occurrence in October–March and that movements were characterised by site philopatry and long-range dispersal of up to ~2300 km (Rogers et al. 2013a). However, the seasonal nature of the recreational fishery, inherent biases of tag-recapture data, and the inability of recreational fishers to discern between bronze whalers and the sympatric dusky shark (*C. obscurus*) limited the conclusions drawn from those data. New information using a method providing data other than catch and recapture locations was required to better understand the residency and extent of movement of *C. brachyurus* in South Australia. Understanding how sharks use their environment has been transformed by the application of passive acoustic telemetry, which has revealed new insights into philopatry, key areas for reproductive events, fine-scale habitat use, extent of home ranges, and migratory patterns (Heupel et al. 2006; Hussey et al. 2015a).

The aim of this study was to describe the movements and site fidelity of bronze whalers in one of South Australia’s gulfs using acoustic telemetry. Specifically, we (1) assessed the level of residency of bronze whalers within key areas of Gulf St. Vincent (GSV); (2) identified preferred habitat; and (3) described the spatio-temporal occurrence of bronze whalers and determined which environmental factors influenced residency patterns of bronze whalers in GSV.

Methods

STUDY SITE

Gulf St. Vincent is a large semi-enclosed inverse estuary connected to the South East Indian Ocean *via* Investigator Strait and Backstairs Passage (Bryars et al. 2008; Shepherd et al. 2008) (Fig. 4.1). The gulf is ~170 km in length and ~50 km wide at its largest extent, shallow in depth (max 40 m), and strongly influenced by tidal flow, seasonal variations in water temperature, and swell from the Southern Ocean (Kämpf et al. 2010). Gulf St. Vincent has a diverse range of habitats that include reef, seagrass, mangroves, and silt benthos (Shepherd et al. 2008). Predominant habitats are seagrass meadows comprising of *Posidonia*, *Zostera*, and *Amphibolis* spp., and silty benthos (Bryars et al. 2008). The eastern boundary of GSV is adjacent to the largest urban settlement in South Australia and has ports for commercial and recreational fishing.

The study sites were located in four main regions, including North West (NW), North East (NE), Metropolitan (Metro), and Aldinga Reef (Aldinga) which is a IUCN category II protected area (Fig. 1). The North West region has an average depth of 20 m, where the benthos is predominately silt and is an important area for demersal teleost species, potential preys of bronze whalers (Chapter 3). The North East region is shallower in depth (max ~12 m) with abundant seagrass (*Posidonia* spp.) meadows where juvenile bronze whalers have been historically targeted (Jones 2008). The Metropolitan region consists of patchy seagrass and sand habitats with river and urban storm water runoffs, ship wrecks, and artificial reefs (max ~22 m). The Aldinga Reef Aquatic Reserve which is part of the Encounter Marine Park, supports the largest high-profile reef ecosystem in the gulf and has been a marine protected area since 1971 (max ~25 m) (Shepherd 2008).

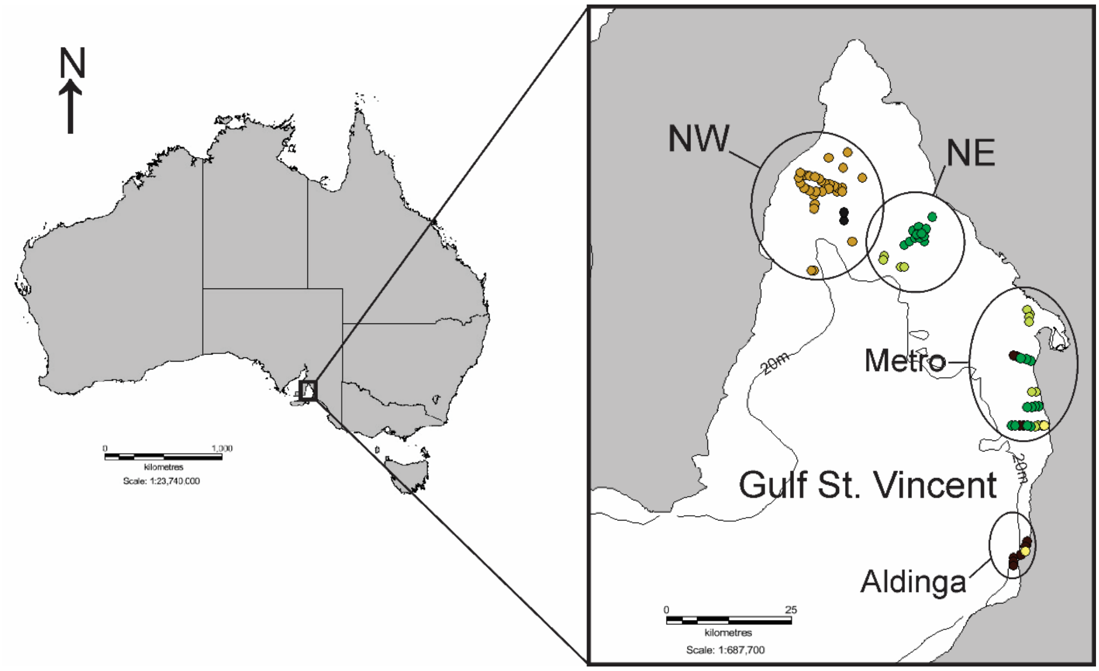


Figure 4.1 Acoustic receiver layout in Gulf St. Vincent (GSV). South Australia. NW = North West GSV receiver array; NE = North East GSV receiver array; Metro = metropolitan receiver array; Aldinga = Aldinga Reef receiver array. Colour dots denote habitat type at that receiver station, black dot = wreck; dark green = seagrass; yellow = sand; light green = mixed seagrass and sand habitat; light orange = silt benthos; brown = natural and artificial reef.

ACOUSTIC ARRAY

A total of 77 acoustic receivers (VR2W, Vemco Ltd, Nova Scotia) were deployed between October 2009–June 2014 in the NE, NW, Metro, and Aldinga regions (Fig. 4.1). The initial array, deployed in 2009, consisted of 15 receivers, which gradually increased to 27, 48, and 70 in 2010, 2011, and 2012. In the final two years of the study 2013–2014, 68 receivers were deployed. The variations in the number of receivers deployed throughout the study was the result of receivers being added or removed due to a lack of detections or logistical challenges in recovery. Receivers were coated in anti-fouling paint, and either attached to a 1.8 m long steel post that was hammered into the substratum to at least 0.6–0.8 m depth, or attached to a post embedded within a 70–90 cm diameter concrete-filled car tyre. All receivers were serviced and downloaded annually.

ENVIRONMENTAL VARIABLES

Environmental data from 1 Jan 2011 to 30 June 2014 were obtained to assess correlations with shark presence/absence. Water temperatures were recorded using three water temperature loggers (Hobo V2, OneTemp Pty. Ltd.) attached to the receiver moorings and data were downloaded annually during receiver maintenance. Two temperature loggers were deployed in the North West region and one in the North East region. The mean water temperature across the three loggers was calculated and used for modelling. Moon illumination data were downloaded from NOAA (http://aa.usno.navy.mil/data/docs/MoonFraction.php). Hourly tidal height (metres) and wind speed (km.h$^-$1) data at Outer Harbour, located on the northern extent of the Metropolitan region, were obtained from the Australian Bureau of Meteorology (http://www.bom.gov.au). Maximum daily tidal ranges were calculated from the difference between daily maximum and minimum tidal heights for Outer Harbour. Although environmental variables were not available for each of the four regions, temporal fluctuations in moon illumination, tidal range, wind strength, and water temperature are considered consistent across the study site.

SHARK TAGGING

Sharks were captured for tagging using floating longlines, and by rod and line. Longlines consisted of floating rope main-lines with ~100, 1.7 mm stainless steel leaders. Leaders consisted of 2 m lengths of nylon-sheathed 2 mm stainless steel wire, with a 16/o stainless steel circle hook and a stainless steel clip. Leaders were baited with Western Australian salmon (*Arripis truttaceaus*), sea mullet (*Mugil cephalus*), or snook (*Sphyraena novaehollandiae*). The rope main-line (8 mm) was up to 2.2 km long and was anchored and marked at each terminal end with a float and flashing beacon. Leaders were evenly spaced along the main-line at intervals of 7–12 m with small floats attached every two leaders. Longlines were deployed on sunset and checked every two hours. Some sharks were also captured off the Metropolitan coast using rod and reel. Baits were suspended under balloons using heavy tackle

(30–80 lb braided line) and leaders of 1.5–1.7 mm nylon-sheathed wire attached to 12/o or 14/o J-style hooks.

Upon capture, sharks >1.8 metres were restrained alongside the vessel using a small rubber sling. Sharks <1.8 metres were brought on-board the vessel and restrained on a wet foam mattress. Seawater was circulated across the gills of each shark using a water pump to ensure continuous oxygenation during handling. A small incision (1.5–2 cm) was made posterior to the pelvic fins. A Vemco V16-6H tag (transmission delay 50–110 s) was inserted into the body cavity. The incision was stitched using 2–3 non-continuous external sutures (3/0 Monosyn absorb violet 70 cm, needle tapercut). Oxytetracycline was injected into the dorsal musculature at a dose of 20 $ml.kg^{-}1$ to reduce the chance of infection. A plastic head conventional identification tag (Hallprint™, Hindmarsh Valley, South Australia) was inserted into the muscle below the first dorsal fin to identify in the event of a recapture. The total length (TL) of each shark was measured to the nearest 1 cm. The maturity of males was assessed based on the degree of clasper calcification (Huveneers et al. 2007). Female maturity was assessed based on published size-at-maturity estimates (Walter and Ebert 1991; Drew et al. 2016). Two sharks were externally tagged under the first dorsal fin in the dorsal musculature using a pole and stainless steel applicator. Two V16-6H tags were affixed to a stainless steel dart tag (Hallprint™, Hindmarsh Valley) using fast setting epoxy (Knead it®), these sharks were tagged externally.

DATA ANALYSIS

To determine the detection range of receivers, a sentinel tag was attached to an anchored buoy-line and suspended in the water column at distances varying between 136 m and 1100 m from multiple receiver locations. The sentinel tag was deployed in the NE and Metro regions for 2–7 days throughout the study. The number of recorded detections was then divided by the number of expected detections to calculate detection probability. Range testing indicated a maximum detection range of ~900 m and a 50% detection probability at ~500 m (Fig. S4.1 Supplementary material).

A tagged shark was considered to be present in a monitored area if two or more detections were recorded over a 24-hour period by at least one receiver. Site fidelity was quantified using a residency index (Ri) and calculated for each region and the four regions combined. Residency was calculated by dividing the number of days a shark was present by the monitoring period (from tagging day to the end of the study). The residency index ranged from 1 to 0, where 1 represents 100% residency, and 0 indicates that the shark was never detected within the array. An analysis of covariance (ANCOVA) was used to examine if residency index varied between sexes, with TL as a covariate.

A roaming index was used to investigate space use and the extent of movements by tagged sharks. The roaming index was calculated by dividing the total number of receivers each shark visited by the maximum number of deployed receivers (77) throughout the study. Although, the number of deployed receivers varied through time, all sharks could potentially have been detected by a maximum of 77 receivers as the battery life of the V16-6H tags lasted throughout the study period. The relationship between roaming index and sex was examined using an ANCOVA with TL as a covariate.

Spatio-temporal variation in habitat use by tagged sharks was assessed by examining the standardised number of detections across hours and months. Acoustic detectability is affected by variations in environmental conditions, potentially biasing the probability of detecting a tagged shark in the proximity of a receiver (Payne et al. 2010; Huveneers et al. 2016). A corrected detection frequency (referred to as standardised number of detections) for each hour and month bin was calculated for each shark using the formula from Payne et al (2010). Standardised detection frequency is represented by SDF, B is the mean detection frequency in each 24-hour bin for control tags and μ is the overall mean hourly detection frequency. The mean detection frequency across all 24 hourly bins is b (Payne et al. 2010).

$$\mathrm{SDF}_b = \frac{B_b}{\mu}$$

Receivers were assigned to one of six habitats based on the diver observations when deploying and servicing the receivers, video footage, and habitat maps (Tanner 2005) (Fig. 4.1): seagrass, sand, mixed (mix of seagrass and sand), silt, shipwrecks, and reef (natural and artificial). I used the Chesson's index to calculate the electivity of habitat used by bronze whalers (Escalle et al. 2015).

Generalised Linear Mixed-effect Models (GLMM) were used to examine relationships between biological (size and sex) and environmental factors (season, water temperature, wind, tidal range, and moon illumination) and residency patterns of bronze whalers. Individual sharks were included in the model as the 'random effect'. The error structure of GLMM corrects for non-independence of statistical units due to shared temporal structure, and permits the 'random effects' variance explained at different levels of clustering to be decomposed. The response variable (shark presence) represented whether an individual shark was detected and hence a binomial distribution was selected for the model. Validity of the models was determined by examination of the distribution of the response variable, a visual inspection of the residuals for the saturated models, and an ANOVA test between the fitted and residual values. GLMM were fitted using detection data from 1 Jan 2013 to 30 June 2014, as this was the period during which the maximum number receivers at any one time (68) were deployed. Model performance was assessed using Akaikes Information Criterion (AIC) and candidate models were compared against a null model (*No*)

$$No = glmer\ (presence \sim 1 + (1|Tag\ no)).$$

Models were evaluated using maximum likelihood ratio tests. Models were tested for multicollinearity using the 'Variance Inflation Factor (VIF)' in the *AED* package (Zuur et al. 2009), with a maximum VIF value of 3 indicating collinear factors. If factors were collinear, one would be removed from the model (Table 4.4). Over-dispersion of the full model was tested using the dispersion_glmer function in the *lme4* package. Over-dispersion was determined by the criteria of a score <1 indicated the model was not over-dispersed. A set of 125 candidate models (Table S1, Supplementary material) were fitted with a unique combination of factors. Mixed-effect models were implemented using the 'glmer' function from the *lme4* library (Bates, 2010) (R Development core team 2016).

Results

Fifty-six bronze whalers comprising of 23 males, 31 females, and 2 unknown sex were tagged with acoustic transmitters. Individuals ranged in size between 74–275 cm TL (male: 74–155 cm TL: female: 97–275 cm TL) (Fig. 4.2). The size structure of sharks captured for tagging was dominated by small juveniles, with 83% of tagged sharks <150 cm TL. All but two of the tagged sharks were captured in the NE region, with the remaining two sharks tagged in the Metro region.

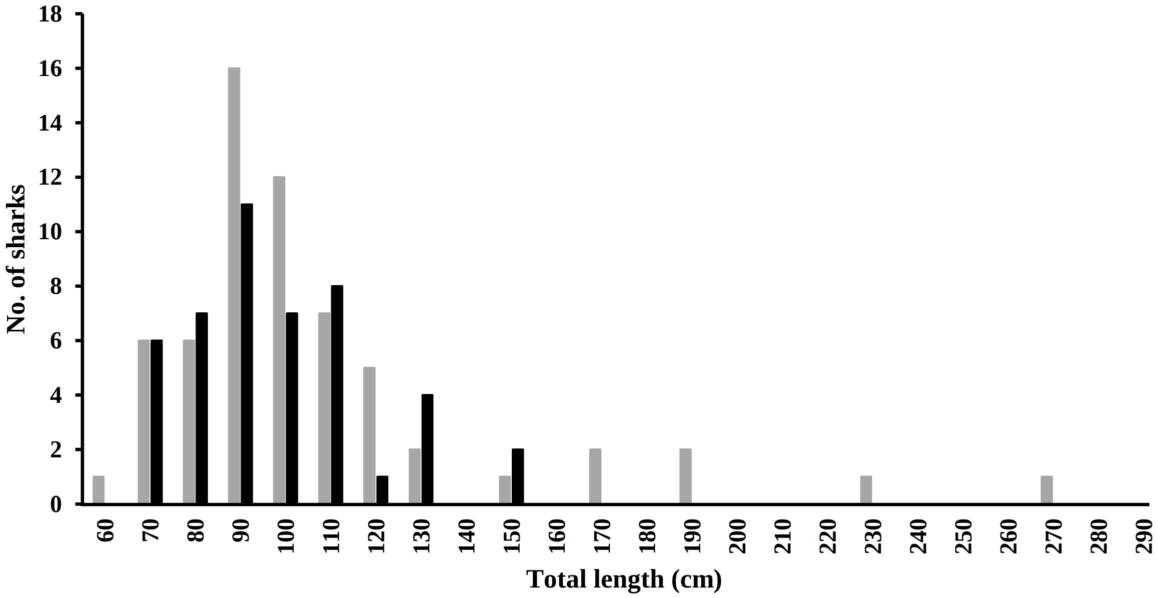


Figure 4.2 Length-frequency of *C. brachyurus* captured in northern Gulf St. Vincent. Grey bars represent female sharks and black represents males.

DETECTIONS

Of the 56 tagged sharks, 51 (91%) were detected. Four sharks were detected by only one receiver for extended periods of time (range of 13–36 months), indicating they may have died close to the receivers following capture and tagging. The assumed death of one tagged shark near one of the acoustic receivers as a result of the near continuous detections over a 36 month period allowed the estimation of temporal variation in detectability (Payne et al. 2010). This tag was thereafter referred to as ‘sentinel tag’ and was detected on 796 days over a 1096-day period. Diel and seasonal patterns in detections were observed, with the highest number of detections during the daytime (6:00–19:00) (Fig. S2a, Supplementary material) and through winter (June–August) (Fig. S2b, Supplementary material). Data from the presumed dead sharks were not included in further analyses.

A total of 61,533 detections were recorded for 47 sharks over the 52-month period between March 2010 and June 2014. Total detections per shark ranged from 2–7511 (mean ± s.e. 1480 ± 251.4 detections per shark). The mean number of days that sharks were detected was 36.6 ± 4.46 days and ranged 1–127 days. Tagged sharks were detected in the array for up to a maximum of 1434 days (shark 26) (Table 4.1). Philopatry over the duration of the study was evident with 77% of the sharks detected over multiple years (Table 4.1) and 36% detected over three consecutive years, while 6% were detected across four consecutive years (Table 4.1).

RESIDENCY

Residency was estimated for 45 individuals, as the release date of the two externally tagged sharks was not available. Residency was generally low and ranged from <0.01 to 0.21 with a mean of 0.05 ± 0.01 (Table 4.1). Mean residency estimates by region were 0.003, 0.013, 0.039, and 0.011 for Aldinga, Metro, NE, and NW, respectively (Table 4.1) (Fig. 4.3). There was a significant effect of total length on residency (ANCOVA, $F_{39} = 4.10$, $P = 0.049$), but not for sex (ANCOVA, $F_{39} = 1.26$, $P = 0.294$) (Fig. 4.4a). Roaming index values ranged from 0.01–0.62; the shark with the highest roaming index visited 62% of the 77 receivers (0.21 ± 0.02; n = 47; Table 4.2). There was no significant effect of body size (Fig. 4.5) (ANCOVA, $F_{39} = 0.78$, $P = 0.384$) or sex (ANCOVA, $F_{39} = 0.35$, $P = 0.710$) on roaming index (Fig. 4.4b).

Table 4.1 Summary of bronze whaler biological and acoustic detection indices in Gulf St. Vincent 2010–2014. ID code = unique acoustic transmitter identifier, Conv. ID = external ID tag number, Last Det. = last day shark was detected within the array, β= detection period in days, # years = number of years shark has been detected during study period, # days = the number of day detected in study period, Total Det. = total number of detections, DAL = days at liberty after tagging till the end of the study period, R_o = roaming index, Residency = residency index.

Shark No.	ID code	Sex	TL (cm)	Date tagged	Last Det.	β	# years	# days	Total Det.	DAL	R_o	Residency				
												Total	Aldinga	Metro	NE	NW
1	30716	Male	137	18/10/2011	21/10/2012	369	2	6	92	1009	0.09	0.006			0.006	0.002
2	30717	Male	115	3/11/2011	4/01/2014	793	4	95	3197	993	0.21	0.096		0.001	0.094	0.001
3	30718	Male	95	19/10/2011	6/10/2013	718	3	41	1578	1008	0.13	0.041			0.042	
4	30719	Female	106	3/11/2011	3/05/2014	912	3	14	194	993	0.23	0.014			0.007	0.005
5	30721	Female	103	3/11/2011	9/12/2012	402	2	52	919	993	0.25	0.052		0.003	0.041	0.008
6	30723	Male	92	3/11/2011	19/01/2012	77	2	11	197	993	0.05	0.011			0.012	
7	30725	Male	89	3/11/2011	3/11/2011	0	1	1	7	993	0.03	0.001			0.001	
8	30727	Female	190	3/11/2011	4/12/2011	31	1	5	47	993	0.12	0.005		0.001	0.003	0.002
9	33178	Female	130	29/11/2012	22/04/2014	509	3	18	111	601	0.05	0.03			0.028	
10	33180	Female	79	5/12/2012	25/06/2014	567	3	125	7511	595	0.44	0.21		0.012	0.139	0.064
11	33182	Male	155	6/12/2012	22/12/2012	16	1	1	2	594	0.01	0.002				0.002
12	33183	Female	156	6/12/2012	8/01/2014	398	3	24	778	594	0.35	0.04			0.01	0.03
13	33184	Female	88	10/01/2013	24/06/2014	530	2	2	123	559	0.13	0.004	0.002		0.002	
14	33187	Female	119	24/01/2013	27/12/2013	337	1	17	785	545	0.13	0.031			0.029	
15	33188	Female	104	24/01/2013	8/03/2014	408	2	55	2888	545	0.4	0.101		0.013	0.068	0.022
16	33189	Female	90	24/01/2013	26/03/2014	426	2	331	5420	545	0.23	0.607		0.029	0.094	0.002
17	33190	Female	92	24/01/2013	13/04/2014	444	2	39	2325	545	0.21	0.072		0.002	0.061	0.006
18	33191	Male	90	24/01/2013	11/01/2014	352	2	25	1423	545	0.39	0.046		0.028	0.011	0.011
19	33193	Male	115	21/02/2013	4/05/2014	437	2	27	1510	517	0.23	0.052		0.002	0.052	0.002

Shark No.	ID code	Sex	TL (cm)	Date tagged	Last Det.	β	# years	# days	Total Det.	DAL	R_o	Residency				
												Total	Aldinga	Metro	NE	NW
20	33194	Female	104	22/02/2013	17/03/2014	388	2	68	2799	516	0.39	0.132	0.004	0.089	0.033	
21	33195	Female	99	22/02/2013	16/05/2013	83	1	59	4441	516	0.27	0.114		0.008	0.105	0.002
22	33196	Female	101	22/02/2013	24/03/2014	395	2	83	3928	516	0.27	0.161	0.006	0.008	0.147	
23	33197	Male	85	22/02/2013	2/05/2014	434	2	70	3032	516	0.62	0.136		0.041	0.056	0.05
24	49134	Female	110	31/01/2010	11/01/2012	710	3	44	1182	1634	0.3	0.027		0.012	0.01	0.002
25	49135	Female	106	31/01/2010	26/12/2011	694	2	13	185	1634	0.08	0.008		0.002	0.007	
26	49138	Female	123	31/01/2010	4/01/2014	1434	4	23	569	1634	0.3	0.014		0.001	0.01	0.003
27	49141	NA	NA	20/05/2011*	24/01/2014	NA	4	76	2602	NA	0.31	NA			NA	NA
28	49142	Male	154	24/11/2010	18/12/2013	1120	3	60	1286	1337	0.17	0.045			0.048	0.001
29	49143	NA	NA	13/02/2012*	1/04/2014	NA	3	89	1871	NA	0.45	NA		NA	NA	NA
30	49145	Male	114	13/01/2011	30/04/2011	107	1	3	170	1287	0.05	0.002		0.003		
31	49150	Female	92	31/01/2011	1/11/2011	274	1	5	136	1269	0.06	0.004		0.002	0.002	
32	49151	Male	85	31/01/2011	2/03/2011	30	1	1	9	1269	0.01	0.001		0.001		
33	52472	Female	173	23/11/2012	11/11/2013	353	2	12	364	607	0.12	0.02			0.018	0.002
34	52634	Female	136	14/02/2012	8/01/2014	694	3	37	1656	890	0.25	0.042		0.001	0.044	
35	52635	Female	115	4/04/2012	7/01/2014	643	3	51	4256	840	0.31	0.061		0.011	0.05	
36	52636	Female	103	14/02/2012	27/11/2013	652	2	43	1072	890	0.35	0.048		0.015	0.034	0.001
37	52637	Male	104	14/02/2012	13/10/2013	607	2	85	3743	890	0.53	0.096		0.022	0.052	0.029
38	52638	Male	99	15/02/2012	16/12/2012	305	1	25	724	889	0.3	0.028	0.001	0.022	0.001	0.001
39	52639	Male	114	15/02/2012	23/12/2013	677	2	55	3542	889	0.43	0.062	0.001	0.019	0.036	0.006
40	52640	Male	95	15/02/2012	29/08/2012	196	1	38	1422	889	0.16	0.043	0.001	0.001		0.039
41	52645	Female	121	23/11/2012	1/12/2012	8	1	3	89	607	0.08	0.005			0.007	
42	52646	Female	232	23/11/2012	6/01/2014	409	3	25	492	607	0.21	0.041	0.005		0.033	0.005
43	52647	Male	86	23/11/2012	9/05/2014	532	3	55	210	607	0.04	0.091			0.087	
44	52648	Male	124	29/11/2012	9/05/2014	526	3	33	110	601	0.01	0.055			0.055	
45	52650	Female	103	29/11/2012	24/06/2014	572	3	21	479	601	0.21	0.035	0.005	0.023	0.002	0.005

Shark No.	ID code	Sex	TL (cm)	Date tagged	Last Det.	β	# years	# days	Total Det.	DAL	R_o	Residency				
												Total	Aldinga	Metro	NE	NW
46	52652	Male	79	29/11/2012	20/06/2014	568	2	3	20	601	0.04	0.005		0.003		0.002
47	52653	Female	122	29/11/2012	19/10/2013	324	2	4	305	601	0.14	0.007		0.002	0.005	

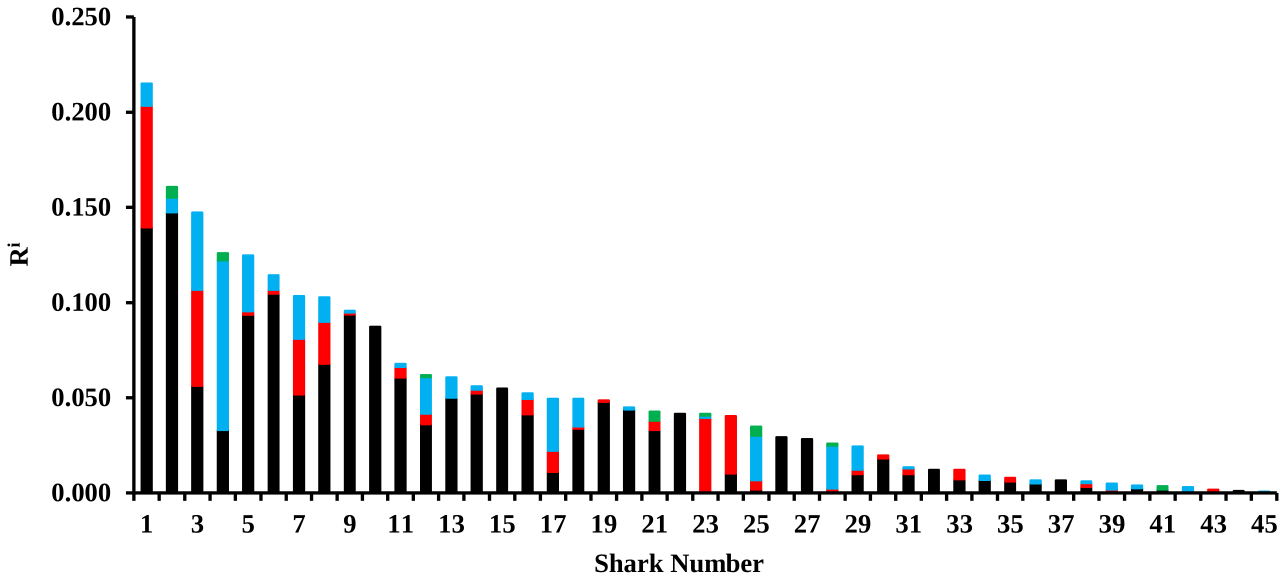


Fig 4.3 Residency index (Ri) for each detected bronze whaler in GSV split by region. Colour denote regions, black = NE; red = NW; blue = Metro; green = Aldinga

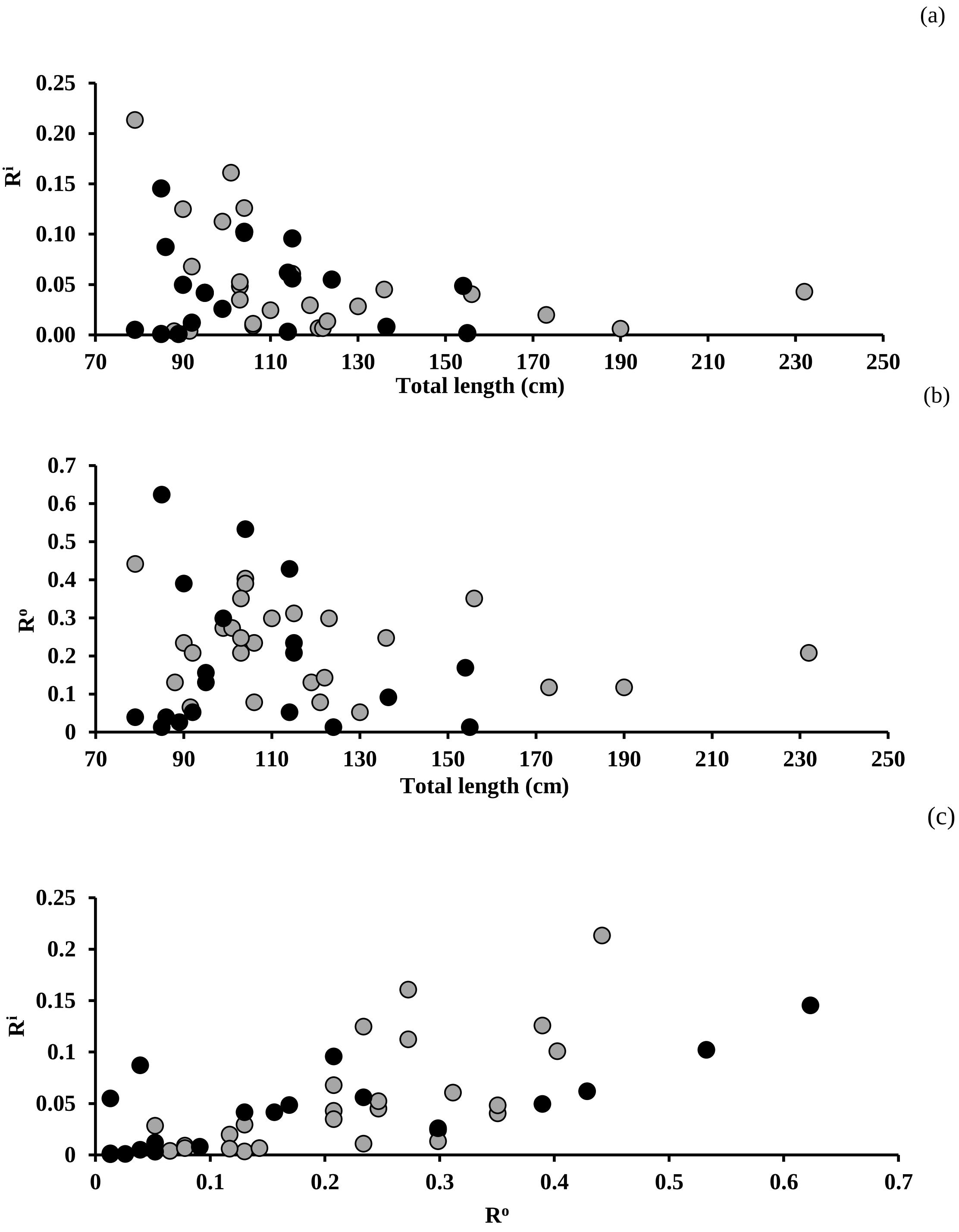


Figure 4.4 (a) Residency index (Ri) by total length (cm), (b) Roaming index (Ro) by total length (cm), (c) Roaming index (Ro) vs residency index (Ri) for juvenile bronze whalers in GSV. Black dots = males, grey dots = females.

Table 4.2 Habitat electivity of juvenile bronze whalers in Gulf St. Vincent. No. receivers = the number of receivers deployed in each habitat; α = Chesson's electivity index; se= standard error; mean = mean number of detections in a specific habitat per shark

Habitat	No. receivers	α	se	mean	se
Reef	10	0.07	0.02	131.5	38.4
Sand	1	0.02	0.01	23.5	4.7
Seagrass	24	0.39	0.02	1030.1	187.1
Silt	27	0.04	0.01	207.5	51.5
Wreck	2	0.18	0.14	13.1	2.6
Broken	13	0.10	0.03	90.7	33.5

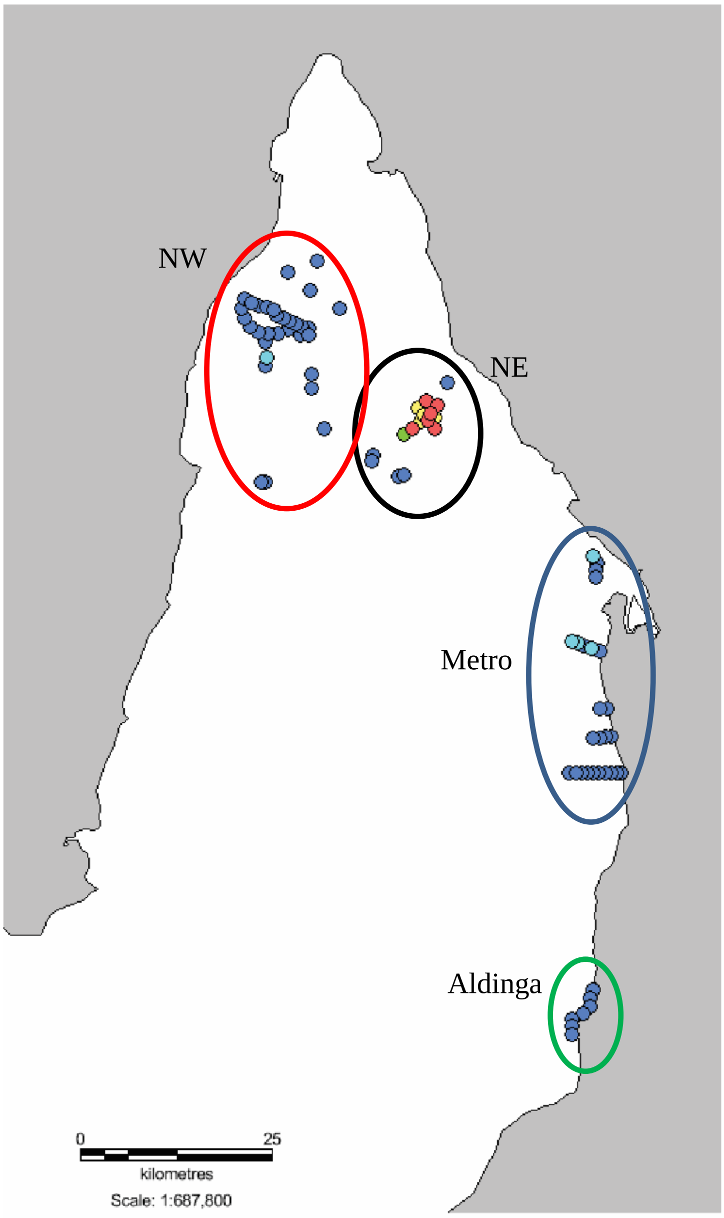


Figure 4.5 The number of detections by tagged sharks at each station. The colour of dots denote the category or number of detections, dark blue = <1,000 detections; light blue = 1,000 – 2,000 detections; green = 2,000 – 3,000 detections; yellow = 3,000 – 4,000 detections; red = >4,000 detections.

SPATIO-TEMPORAL VARIATION IN DETECTIONS

Seventy-four percent of the detections were recorded on receivers within the NE region of Gulf St. Vincent (Fig. 4.5). The region with the second highest percentage of detections was the Metro (16%), followed by NW (9%), and Aldinga (0.4%) (Fig. 4.5). The number of individual sharks detected was also highest in the NE region, with 20 or more individuals detected by at least 11 of the 17 receivers deployed within the region (Fig. 4.6a). The Metro, NW, and Aldinga regions had less sharks detected than in the NE region. In the NW region, 9 of the 28 receivers detected >10 sharks (Fig. 4.6a). In the Metro region, 10 of the 26 receivers detected >10 shark. Only five sharks were detected by the Aldinga array over the three years of receiver deployment (Fig. 4.6a).

The NE region had the highest number of detections per shark across receivers, with ten receivers having >100 detections per shark (Fig. 4.6b). Receiver ‘LS 16’ had the most detections with 275 detections per shark (Fig. 4.6b). In the other regions, only a few receivers had >100 detections per sharks, ’Agros 1’ had 130 detections per shark in the NW region and ’Out’ had 141 detections per shark in the Metro region (Fig. 4.6b).

Overall, the standardised number of detections increased from 19:00 to 6:00, with the highest mean number of detections per hour at 1:00–2:00. The diurnal pattern was strongest in the NE region (Fig. 4.7). The number of sharks detected per hour was consistent across the 24-hours in the NW, Metro, and Aldinga regions (Fig. 4.7). There was a strong seasonal pattern in the standardised number of detections (Fig. 4.8) and the number of sharks detected per month (Fig. 4.8). Both increased from September to April and peaked in December.

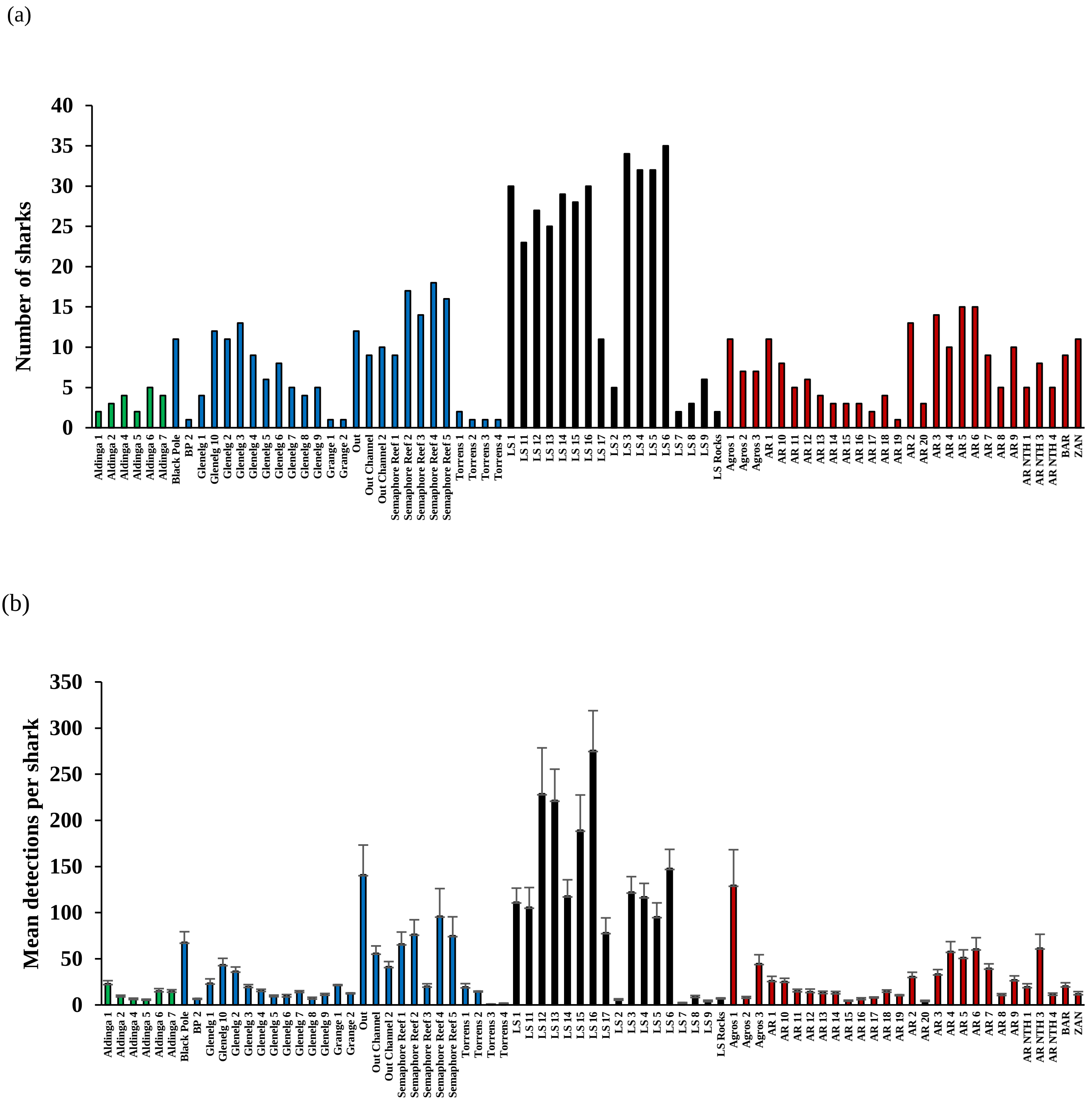


Figure 4.6 (a) The number of tagged juvenile bronze whalers detected per station in GSV for 2010–2014. (b): The mean number of detections by tagged juvenile bronze whalers detected per station in GSV for 2010–2014. Black = NE; Red = NW; Blue = Metro; Green = Aldinga.

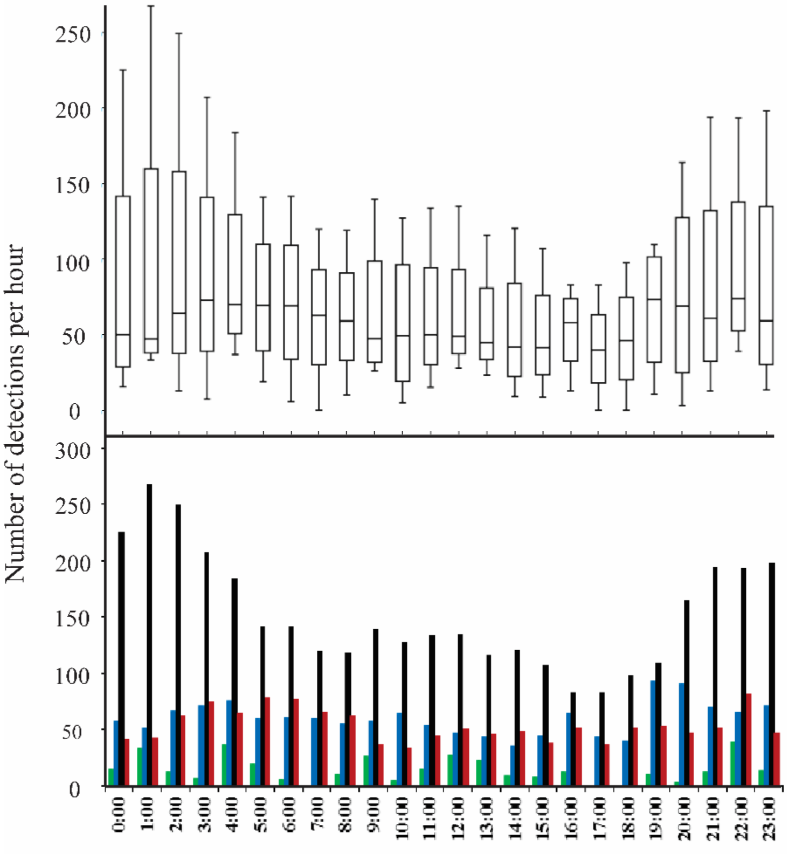


Figure 4.7 (top) The mean number of detections per hour for tagged juvenile bronze whalers in the greater GSV for 2010–2014. (bottom) Standardised number of detections per hour for the detected juvenile *C. brachyurus* in each region for 2010-2014. Error bars are standard error, boxes represent the 25% and 75% confidence intervals, dash = median value and black outlined circle is the mean value. Black = NE; Red = NW; Blue = Metro; Green = Aldinga.

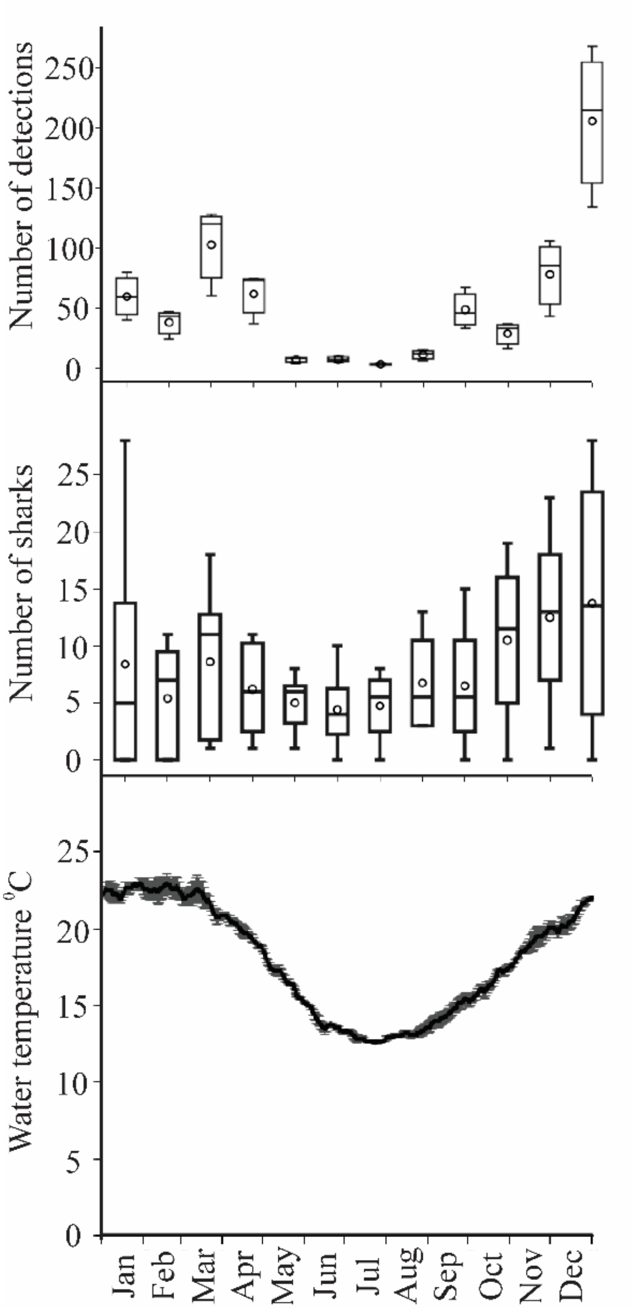


Figure 4.8 The mean number of detections (top) and tagged sharks (middle) per month for juvenile bronze whalers and the mean water temperature (°c) (bottom) in the greater GSV for 2010–2014. Error bars are standard error, boxes represent the 25% and 75% confidence intervals, dash = median value and black outlined circle is the mean value.

HABITAT ELECTIVITY

Seagrass beds had the highest number of detections with 1030 ± 187.1 detections per shark, followed by silt (207 ± 51.5 detections per shark) (Table. 4.2). Chesson's electivity index showed that bronze whalers had a high affinity to only the seagrass habitat (0.39 ± 0.02), with a low affinity for shipwrecks (0.18 ± 0.14) and mixed habitats (0.10 ± 0.03). The three remaining habitats of silt, reef, and sand were an order of magnitude lower in electivity (< 0.1) (Table 4.2).

INFLUENCE OF BIOLOGICAL AND ENVIRONMENTAL DRIVERS

No collinearity was identified between factors included in the full model. The generalised linear mixed-effects model that best explained the presence of bronze whalers in GSV included the factors of season, total length, water temperature, wind, and moon illumination (AIC= 6709.7, Dev= 6695.7) (Table 4.4). Water temperature and season were highly significant in all models and best explained the residency patterns of bronze whalers in GSV. Wind speed and moon illumination were less significant drivers (Table 4.4). Sex, total length, and maximum tidal difference had the least effect in model fits to shark presence. As water temperature, moon illumination, and wind speed increased the probability of sharks being present within the receiver array increased (Fig. 4.9). A higher probability of shark presence was also identified during spring and summer (Fig. 4.9). The intensity of wind speed and moon illuminated correlated with a small increase in shark presence (Fig. 4.9). Total length, tidal range, and sex had negligible effects on shark presence (Fig. 4.9).

Table 4.3 Variation inflation factors calculated for all factors included in the full Generalised linear mixed effects model

Factor	VIF value
Month	1.84
Season	2.63
TL	1.05
Sex	1.05
Temp	2.21
Tide	1.00
Moon	1.00
Wind	1.03

Table 4.4 Generalized linear mixed model results and model factors. Random factor Tag_ID not added to all models below. * = factor was significant in model; AIC = Akaikies information criterion; BIC = Bayesian information criterion; LogLik= log likelihood; Dev = deviance; DF.Resid = degrees freedom residuals.

No.	Model	AIC	BIC	LogLik	Dev	DF.Resid
1	season* + TL + temp* + wind* + moon*	6709.7	6763.8	-3347.8	6695.7	16826
2	season* + temp* + wind* + moon*	6710.1	6756.5	-3349.1	6698.1	16827
3	season* + TL + moon* + temp* + tide + wind*	6710.6	6772.5	-3347.3	6694.6	16825
4	season* + TL + sex + temp* + moon* + wind*	6711.6	6773.5	-3347.8	6695.6	16825
5	season* + sex + temp* + wind* + moon*	6712.1	6766.2	-3349	6698.1	16826
6	season* + TL + sex + temp* + tide + wind* + moon*	6712.6	6782.2	-3347.3	6694.6	16824
7	season* + moon + sex + temp* + tide + wind*	6713	6774.9	-3348.5	6697	16825
8	season* + temp* + wind*	6716.9	6755.6	-3353.4	6706.9	16828
9	season* + TL + temp* + tide + wind*	6717.4	6771.5	-3351.7	6703.4	16826
10	season* + temp* + tide + wind*	6717.9	6764.3	-3352.9	6705.9	16827

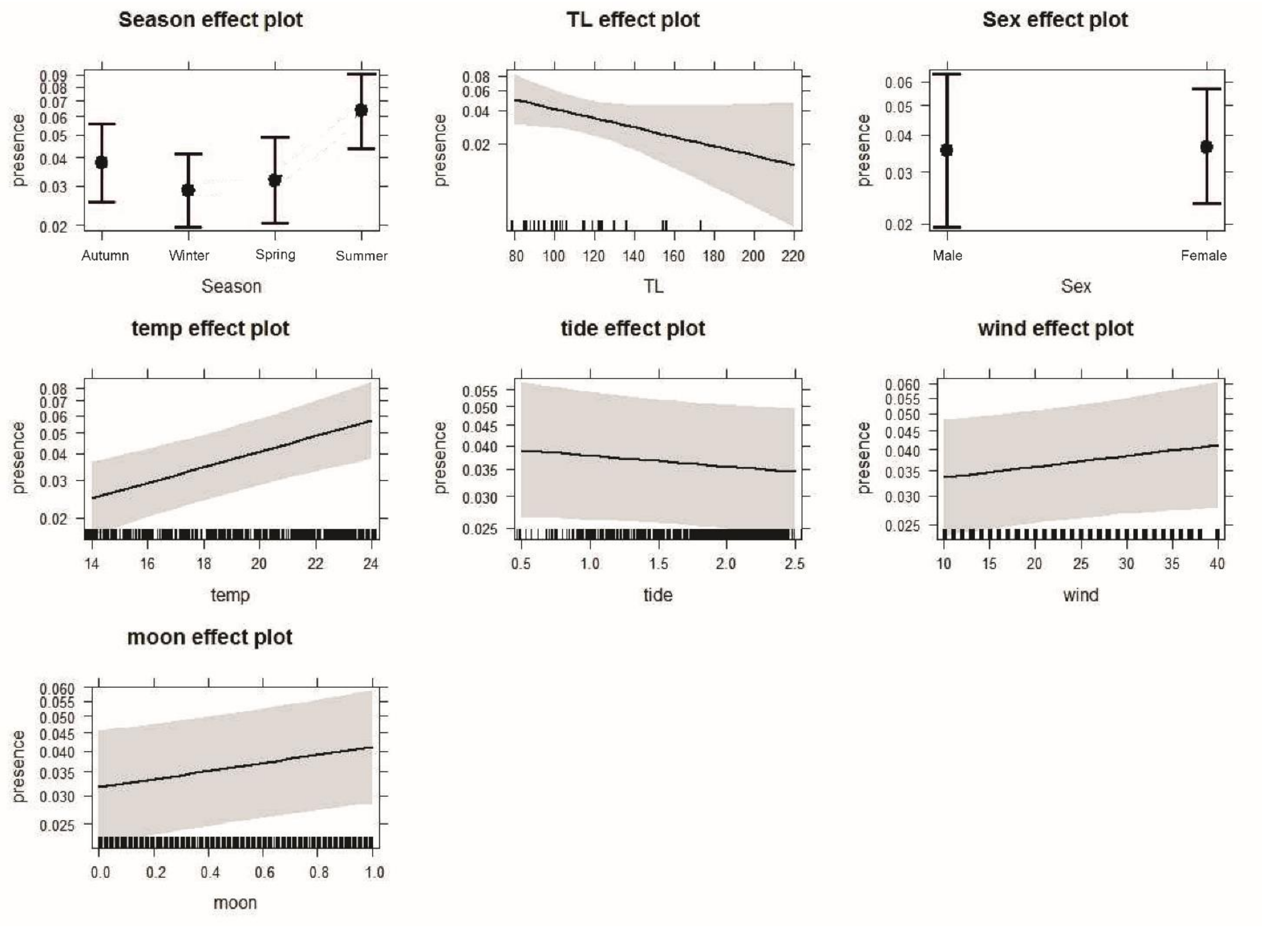


Figure 4.9 Partial residuals for factors in Generalised linear mixed effect models.

Discussion

Passive acoustic telemetry coupled with the examination of environmental correlations provided valuable new insights into the spatio-temporal patterns in occurrence, and ecological and biological drivers of bronze whalers presence in the unique inverse estuarine waters of GSV. This study was the first to investigate fine-scale movement, habitat use, and site fidelity of this important marine predator in these waters which have a large overlap with anthropogenic influences. Juvenile bronze whalers exhibited philopatry in GSV, with a majority of tagged sharks returning over multiple years and up to four years. The NE GSV region detected the most sharks and had the highest number of detections, which is characterised by shallow seagrass meadows, resulting in seagrass habitat having the largest electivity. Peaks in shark presence was influenced by season and fluctuations in water temperature, with shark numbers and amount of time spent within the monitored region peaking during the austral late spring to early autumn (September–April). Shark presence and time spent within GSV rapidly declined during the austral winter (May–August), which coincides with the cooling of gulf water temperatures. Philopatric behaviour and increased presence of bronze whalers during October–March, and catches being dominated by young-of-the-year and small juveniles indicate that NE GSV is an important habitat during summer in the early life history stages of bronze whalers (Chapter 2).

PHILOPATRIC BEHAVIOUR

The long-term duration of this study (2009–2014) facilitated the investigation of the philopatric behaviour of bronze whalers. The seasonal annual return of 77% of tagged juveniles over multiple years, and up to four years, supports the philopatry of juvenile bronze whalers suggested based on tag-recapture data from conventional tags (Rogers et al. 2013a) and that the monitored area is ecologically important to juvenile bronze whalers. Philopatric behaviour to coastal regions is common in elasmobranchs, with a review of philopatry in sharks showing a tendency to return to specific areas in 31 species (Chapman et al. 2015). Philopatric behaviour can result from multiple factors such as a sharks temporally exploiting an abundant prey source, e.g., tiger sharks (*Galeocerdo cuvier*) feeding on fledging albatross (Gallagher et al. 2011), or returning to a natal ground for parturition, e.g., blacktip reef sharks (*C. melanopterus*) (Mourier and Planes 2013) , or to a mating ground, e.g., lemon sharks (*Negaprion brevirostris*) (Feldheim et al. 2004). In the case of bronze whalers in southern Australia, philopatry by juveniles to GSV and in particular the NE region is likely the combination of seasonal increased gulf water temperatures, prey availability and abundances, and the use of seagrass habitats as a seasonal nursery ground.

TEMPORAL OCCURRENCE

The increase in presence of bronze whalers in South Australia's coastal and gulf waters from summer to early autumn was first suggested in a review of the fishery status for whaler sharks (Jones 2008). In the present study, we identified an annual seasonal increase in detections during spring to early autumn (September–April), which coincided with seasonal increases in the gulf water temperatures (Fig. 8c). Maximum waters temperatures in the northern gulf reach sub-tropical temperatures of 24°C during summer (January–February) and then drop to as low as 11°C during midwinter (June–July) (Petrusevics 1993). This was supported by the GLMM showing that season and water temperature had the largest effect on the presence of bronze whalers. From this study, it is not possible to decipher if the increased presence of bronze whalers is directly driven by seasonal water temperature fluctuations or indirectly through other changes associated with increased water temperature (e.g. changes in prey fields). Seasonal fluctuations in water temperature have also been suggested to influence the occurrence of bronze whalers within the inshore coastal waters of Argentina and South Africa (Smale 1991; Cliff and Dudley 1992; Lucifora et al. 2005). In Argentina, increased recreational catches of juveniles and large female bronze whalers suggest a seasonal increase of bronze whalers during summer months (Lucifora et al. 2005). Off South Africa, nutrient rich, cool upwelled water supports the annual north-ward migration of sardines (*Sardinops sagax*) from the Eastern Cape to the KwaZulu-Natal coast (Cliff and Dudley 1992). This sardine migration results in large sardine schools forming close to the coast, attracting many marine predators including bronze whalers, as they opportunistically forage and exploit the schooling teleosts (Cliff and Dudley 1992; Dudley and Cliff 2010).

Wind speed and moon illumination also positively affected the patterns of occurrence of bronze whalers. As wind velocity increases, it can lead to the resuspension of particulate matter and increase turbidity in shallow coastal waters (Kessarkar et al. 2009). Such turbid waters may improve hunting and foraging success of bronze whalers, as prey may have a reduced ability to avoid predators. As bronze whalers in the present study were primarily small juveniles, it is also plausible that they preferred shallow turbid waters to avoid predation from large sympatric species such as adult dusky sharks (*C. obscurus*) and white sharks (*Carcharodon carcharias*). Turbidity has previously been identified as a key environmental variable influencing the presence, movement, and space utilisation of multiple juvenile shark species, including as an anti-predator strategy (Heithaus 2004; Gutteridge et al. 2011; Yates et al. 2015).

Increased moon illumination correlated with a rise in shark presence and suggested that bright night time conditions increase shark presence in the array. Dietary studies showed that cephalopods and small pelagic teleosts were key dietary species for juvenile bronze whalers (Smale 1991; Rogers et al. 2012; Chapter 3). Many of these species, e.g., southern calamari (*Sepioteuthis australis*), take refuge in seagrass during the day and hunt during the night. The nocturnal feeding activity by these species makes them more vulnerable to predation and likely results in bronze whalers increasing their predatory activity during periods of bright moon illumination to benefit from the visual advantage provided by the moonlight. Enhanced moon illumination correlated with an increase in the presence of silky sharks (*C. falciformis*) on reef systems in the Red Sea, where the extra ambient light during full moon conditions were hypothesised as an extension of diurnal behaviour which aided in predation success (Clarke et al. 2011). The effect of a full moon also influenced habitat selection and increased mean depth usage of grey reef sharks (*C. amblyrhynchos*) in Palau, Micronesia, as a response to distribution patterns of their prey or a predator avoidance strategy (Vianna et al. 2013).

A review of 166 shark movement studies, showed that the majority of studies (>50%) identified an expanded range and increased activity during the crepuscular period, but that this pattern was not evident during the night (Hammerschlag et al. 2017). In contrast, the present study suggests increased activity in bronze whalers during the night with a peak in detections at 1–2 am, in particular within the NE GSV region. The increase in bronze whaler presence during the night, in particular in the NE GSV region is likely as response to the predation of primarily nocturnal species in this area. For example, the foraging strategy and diet of the southern garfish (*Hyporhamphus melanochir*) varies diurnally, with garfish primarily feeding on plankton on the surface during the night, which likely increase their susceptibility to predation (Earl et al. 2011).

HABITAT USE

This study identified that seagrass meadows are important to the ecology of juvenile bronze whalers. Dietary studies of bronze whalers in South Australia (Rogers et al. 2012; Chapter 3) and throughout their range (Smale 1991; Lucifora et al. 2009) showed that the bronze whaler has a broad and highly diverse prey field, with key prey species being small pelagic teleosts (i.e. *Sardinops sagax*), cephalopods (i.e. *Sepioteuthis australis*), and demersal teleosts (i.e. *Platycephalus spp*.) (Smale 1991; Lucifora et al. 2009; Rogers et al. 2012). These species are commonly associated with complex seagrass meadows and patchy sand and seagrass habitats, which provides support for the patterns of habitat use of bronze whalers observed in this study. Seagrass habitats within GSV have been receding over recent decades due to various anthropogenic effects (Tanner 2005). There has been an estimated 28–80% loss of seagrass habitat along GSV’s metropolitan coastline between 1949–1993 (Edyvane 1999). This extensive loss of seagrass habitats causes concern over the potential negative effect on bronze whaler population because of their strong association with seagrass habitats.

RESIDENCY

Bronze whalers show seasonal, diurnal, and philopatric patterns of residency in GSV. However, the amount of time spent within the receiver array was relatively low, resulting in a low mean residency index. The receivers were deployed in areas with high commercial and recreational catches of bronze whalers, and where these sharks are frequently sighted (Jones 2008). However, the surface area covered by the acoustic receivers (~154 km^2) was relatively small in comparison to the size of GSV (~6800 km^2). The low residency observed was unexpected and suggests that the home range of bronze whalers was greater than the area acoustically covered and extends across a greater proportion of GSV.

The low residency of bronze whalers over an extensive receiver coverage (~154 km^2) was markedly different to the residency patterns displayed by reef-associated species of the same family. For example, blacktip reef sharks (*C. melanoterus*), nervous sharks (*C. cautus*), sharptooth lemon sharks (*N. acutidens*), spottail sharks (*C. sorrah*), and blacktip shark (*C. limbatus*) all exhibit high residency within areas of similar or smaller size than the area covered in the present study (Heupel et al. 2004; Papastamatiou et al. 2009; Knip et al. 2012; Speed et al. 2012; Escalle et al. 2015; Chin et al. 2016; Speed et al. 2016). While the above species are contrasting in body size, life history strategies, and in habitat use compared to bronze whalers, other large-bodied species such as Caribbean reef sharks (*C. perezi*) and grey reef sharks (*C. amblyrhynchos*) have also been shown to have high residency within restricted areas (Chapman et al. 2005; Heupel et al. 2010; Field et al. 2011). The high residency within a small area or a reef system might be related to the centralised high productivity of reef systems (Meekan and Choat 1997) and the ability of these species to source and consume enough food and energy within a restricted areas (Mourier et al. 2016; Roff et al. 2016). In the temperate southern Australian gulf waters, prey species are more broadly dispersed than in coral reef ecosystems, which may necessitate predators to occupy and forage across wider areas than in tropical locations. As bronze whalers in GSV was found to prefer seagrass, the home range and extent of movement of the tagged sharks to source adequate food provisions may have been across a larger number of seagrass meadows than monitored in this study. The coverage of seagrass or mixed seagrass and sand bottom was ~130 km^2, which represents ~5% of the 2,440 km^2 total seagrass coverage within GSV (Bryars et al. 2008). The logistical inability to cover all seagrass habitat within

GSV has likely resulted in our low estimates of residency. I attempted to mitigate this issue by focusing on key areas within the gulf and by incorporating receivers maintained by a concurrent study on the movement of snapper (*Pagrus auratus*) (Fowler et al. 2017). The high mobility and roaming of bronze whalers is supported by the relatively high (40%) percentage of sharks visiting >25% of the stations, with two individuals visiting 50% of the 77 stations available. The large number of stations visited and the associated broad movements (>40 km) provides evidence of juvenile bronze whalers highly mobile nature and wide-ranging capabilities.

NURSERY GROUNDS

Neonate and juvenile bronze whalers preferentially used seagrass areas in NE GSV compared to three other regions and six different habitats in GSV. Sharks also returned to the study site seasonally (September–April), exhibiting philopatric behaviour across the study period and for up to four years. Sharks caught during the present study and by the commercial fishery consisted primarily of neonates and small juveniles (Drew et al. 2017). In addition, the small number of mature female bronze whalers captured in northern GSV in late spring–summer have either had late-term embryos or evidence of recent parturition (Rogers et al. 2013a; Drew et al. 2017). Combined, these lines of evidence suggest that northern GSV, and in particular seagrass meadows in NE GSV, are ecologically important to bronze whalers and may act as a nursery area for the species. The northern gulf waters of South Australia were first suggested to be a nursery area based on commercial catches by Jones (2008) and further substantiated by recreational fishing tag-recapture data analysis in Rogers et al. (2013). The present study provides additional support that northern GSV is a pupping or nursery area for bronze whalers in late spring–summer.

The findings from the present study might not seem to fulfil the criteria for a nursery area proposed by Heupel et al. (2007). This is likely related to the difficulties collecting the necessary empirical data to test these criteria when nursery areas extend over a large spatial scales vs. standard nursery areas that are typically constrained spatially e.g., within small reef lagoons and tidal creeks by lemon sharks

(Wetherbee et al. 2007) or small mangrove fringed coastal bays used by up to eight shark species (Simpfendorfer and Milward 1993). For example, the overall low residency in the present study seemingly goes against Heupel’s second criteria of sharks remaining or returning for extended periods (Heupel et al 2007). The observed low levels of residency were likely due to temperate ecosystem having greater dispersion of prey items compared to the centralized activity of coral reef systems, leading juvenile bronze whalers to have large home range beyond that monitored by the acoustic receivers to meet nutritional needs (even though up to 68 receivers were deployed at key areas). Regardless of our inability to adequately fulfil one of the criteria proposed by Heupel et al (2007), the findings from the present study support previous studies and suggest that the northern seagrass habitats of GSV are important and potential pupping or nursery area for the southern Australian population of bronze whalers.

FISHERIES IMPLICATIONS

Bronze whalers in southern Australia exhibit slow growth, late maturity, and low fecundity (Chapter 2). These life history characteristics likely result in the species having a low rebound potential and likely susceptible to overfishing. This southern Australian population are also subjected to low levels of fishing mortality, with commercial and recreational catches in being ~80 t and ~50 t per annum respectively. The philopatric behaviour and predictable seasonal patterns of occurrence in the inshore coastal waters of GSV also render bronze whalers vulnerable to spatially concentrated fishing (Chapman et al. 2015), especially as current fishing pressure targets these sharks during their known seasonal peaks in presence. The combination of these factors highlights the need for further vulnerability assessments into the sustainability of the bronze whaler shark fishery.

CONCLUSION

Using passive acoustic telemetry, this study identified important spatio-temporal trends in occurrence, habitat use, and the drivers behind the seasonal presence of juvenile bronze whalers in the waters of GSV. Results indicated that the seagrass habitats of northern GSV are a critical habitat in the early life stages of bronze whalers and should be considered as a seasonal nursery area. This study provided critical ecological information of an important marine predator within the gulf and coastal waters of southern Australia. This information will be integral for future management and conservation measures.

Acknowledgments

All shark tagging complied with the animal ethics standards of Flinders University animal ethics guidelines (ethics approval #E360).

The authors would firstly like to thank the members of the Southern Shark Ecology Group, in particular Matthew Heard, Derek Dapp, Crystal Beckmann, and Lauriane Escalle. We would also like to thank SARDI Aquatic Sciences for their in-kind support with logistics throughout this project, in particular Anthony Fowler, Michael Steer and Simon Goldsworthy. We would especially like to thank, Shea Cameron and Luke Silvester of Flinders University for their assistance with receiver maintenance. The South Australian Royal Life Savers jet boat patrol group with their assistance in receiver maintenance. This project was jointly funded by the Australian Post-graduate Award to MD, the Adelaide & Mount Lofty Ranges Natural Resources Management Board, the Neiser Foundation, the Nature Foundation of South Australia Inc, and the Tracking Research for Animal Conservation Society (TRACS). Some of the acoustic receivers were provided by the Institute of Marine and Antarctic Studies, the University of Adelaide, the Department of the Environment, Water and Natural Resources, and the Integrated Marine Observing System (IMOS) Animal Tracking Facility. IMOS is supported by the Australian Government through the National Collaborative Research Infrastructure Strategy and the Super Science Initiative.

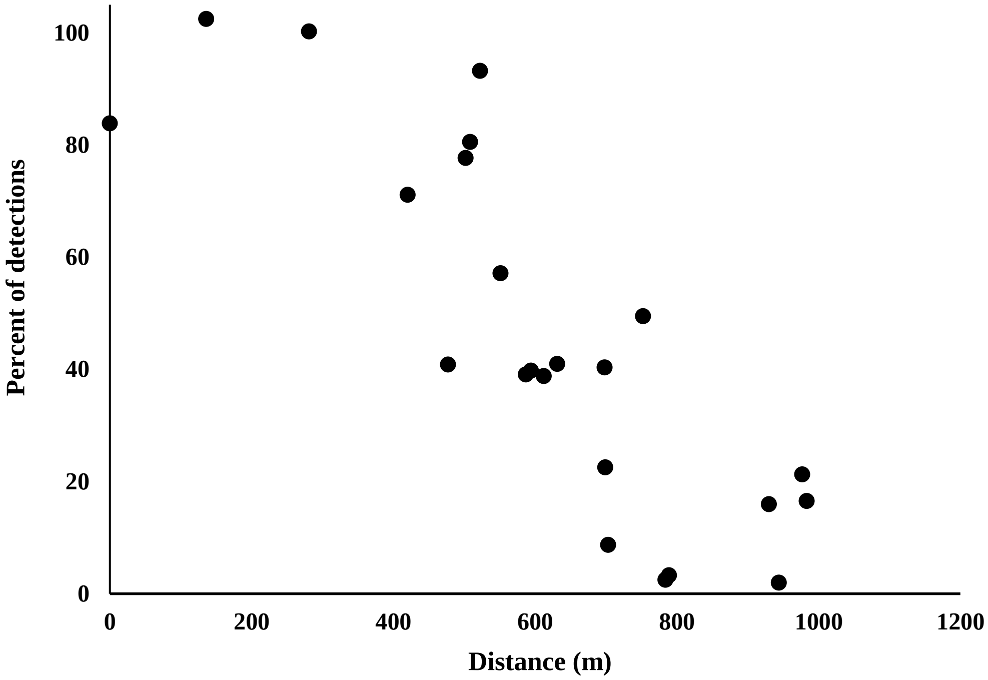
Supplementary table 4.1 Generalized linear mixed model results and model factors. Random factor Tag_ID not added to all models below. * = factor was significant in model; AIC = Akaikies information criterion; BIC = Bayesian information criterion; LogLik= log likelihood; Dev = deviance; DF.Resid = degrees freedom residuals.

No.	Model	AIC	BIC	LogLik	Dev	DF.Resid
1	season* + TL + temp* + wind* + moon*	6709.7	6763.8	-3347.8	6695.7	16826
2	season* + temp* + wind* + moon*	6710.1	6756.5	-3349.1	6698.1	16827
3	season* + TL + moon* + temp* + tide + wind*	6710.6	6772.5	-3347.3	6694.6	16825
4	season* + TL + sex + temp* + moon* + wind*	6711.6	6773.5	-3347.8	6695.6	16825
5	season* + sex + temp* + wind* + moon*	6712.1	6766.2	-3349	6698.1	16826
6	season* + TL + sex + temp* + tide + wind* + moon*	6712.6	6782.2	-3347.3	6694.6	16824
7	season* + moon + sex + temp* + tide + wind*	6713	6774.9	-3348.5	6697	16825
8	season* + temp* + wind*	6716.9	6755.6	-3353.4	6706.9	16828
9	season* + TL + temp* + tide + wind*	6717.4	6771.5	-3351.7	6703.4	16826
10	season* + temp* + tide + wind*	6717.9	6764.3	-3352.9	6705.9	16827
11	season* + TL + sex + temp* + wind*	6718.4	6772.6	-3352.2	6704.4	16826
12	season* + TL + sex + temp* + tide + wind*	6719.4	6781.3	-3351.7	6703.4	16825
13	season* + sex + temp* + tide + wind	6719.8	6773.9	-3352.9	6705.8	16826
14	season* + TL + temp* + moon*	6739.5	6785.9	-3363.7	6727.5	16920
15	season* + temp* + moon*	6739.9	6778.6	-3365	6729.9	16921
16	season* + TL + temp* + tide + moon*	6740	6794.1	-3363	6726	16919
17	season* + temp* + tide + moon*	6740.4	6786.8	-3364.2	6728.4	16920
18	season* + TL + sex + temp* + moon*	6741.5	6795.6	-3363.7	6727.5	16919
19	season* + sex + temp* + moon*	6741.9	6788.3	-3364.9	6729.9	16920
20	season* + TL + sex + temp* + tide + moon*	6742	6803.9	-3363	6726	16918
21	season* + sex + temp* + tide + moon*	6742.4	6796.5	-3364.2	6728.4	16919
22	TL + temp* + tide + wind* + moon*	6742.5	6796.6	-3364.2	6728.5	16826
23	temp* + wind* + moon*	6742.9	6781.6	-3366.5	6732.9	16828
24	temp* + tide + wind* + moon*	6742.9	6789.3	-3365.5	6730.9	16827
25	TL + sex + temp* + wind* + moon*	6744.5	6798.6	-3365.2	6730.5	16826
26	moon* + TL + sex + temp* + tide + wind*	6744.5	6806.3	-3364.2	6728.5	16825
27	sex + temp* + wind* + moon*	6744.9	6791.3	-3366.4	6732.9	16827
28	sex + temp* + tide + wind* + moon*	6744.9	6799	-3365.4	6730.9	16826
29	season* + TL + temp*	6745.5	6784.2	-3367.8	6735.5	16921
30	season* + temp*	6746	6776.9	-3369	6738	16922
31	season* + TL + temp* + tide	6746.1	6792.5	-3367	6734.1	16920
32	season* + temp* + tide	6746.6	6785.2	-3368.3	6736.6	16921
33	season* + temp* + tide	6746.6	6785.2	-3368.3	6736.6	16921
34	season* + TL + sex + temp*	6747.5	6793.9	-3367.8	6735.5	16920

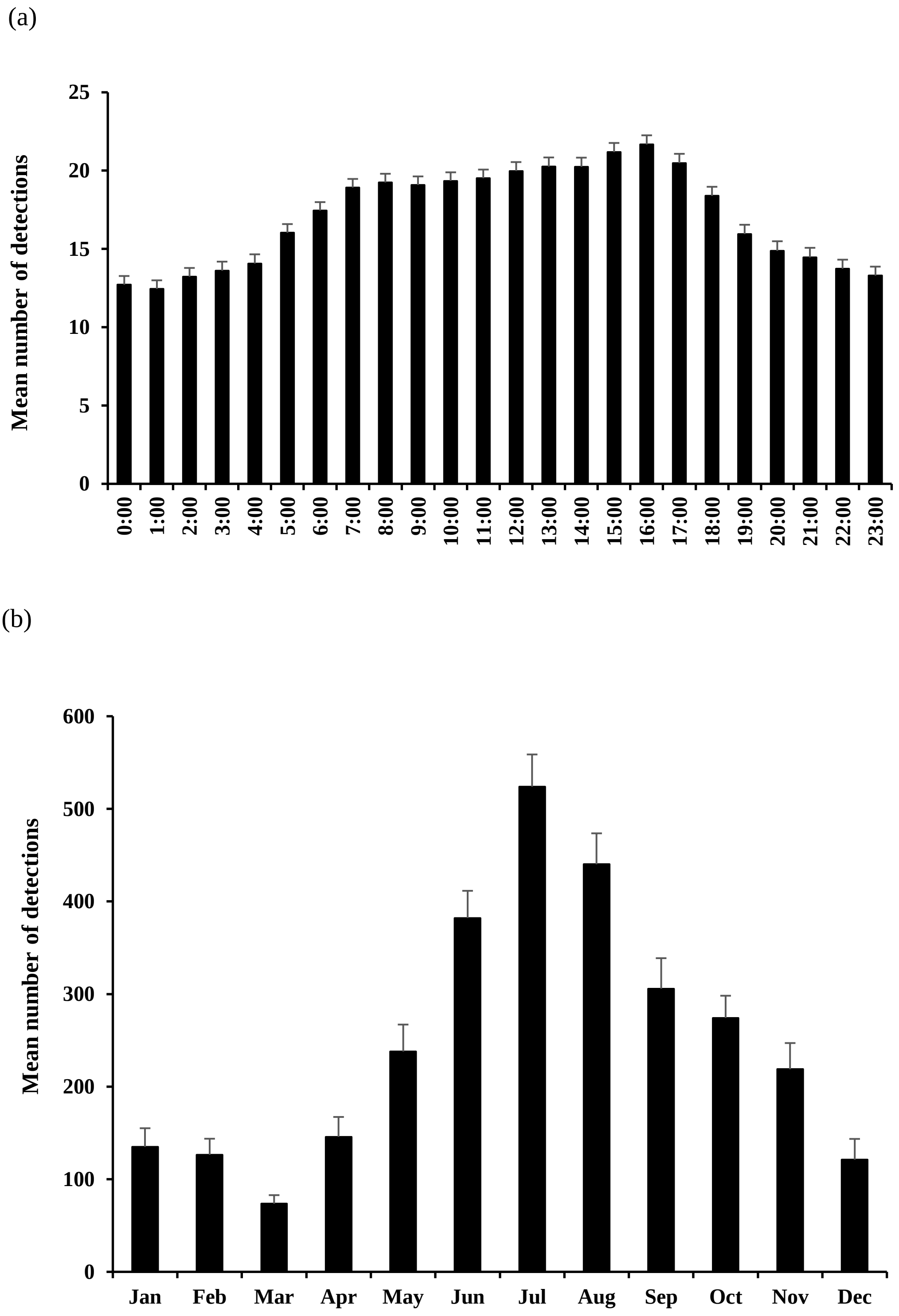
35	season* + sex + temp*	6747.9	6786.6	-3369	6737.9	16921
36	TL + sex + temp* + tide	6748.1	6802.2	-3367	6734.1	16919
37	season* + sex + temp* + tide	6748.5	6794.9	-3368.3	6736.5	16920
38	TL + temp* + tide + wind*	6749.4	6795.8	-3368.7	6737.4	16827
39	temp* + tide + wind*	6749.9	6788.5	-3369.9	6739.9	16828
40	temp* + tide + wind*	6749.9	6788.5	-3369.9	6739.9	16828
41	TL + sex + temp* + wind*	6751.4	6797.8	-3369.7	6739.4	16827
42	TL + sex + temp* + tide + wind*	6751.4	6805.5	-3368.7	6737.4	16826
43	sex + temp* + wind*	6751.8	6790.5	-3370.9	6741.8	16828
44	sex + temp* + tide + wind*	6751.8	6798.2	-3369.9	6739.8	16827
45	sex + temp* + tide + wind*	6751.8	6798.2	-3369.9	6739.8	16827
46	temp* + tide + moon*	6777.2	6815.8	-3383.6	6767.2	16921
47	TL + temp* + moon*	6777.5	6816.1	-3383.7	6767.5	16921
48	temp* + moon*	6777.9	6808.8	-3385	6769.9	16922
49	TL + sex + temp* + tide + moon*	6778.7	6832.9	-3382.4	6764.7	16919
50	TL + sex + temp* + tide + moon*	6778.7	6832.9	-3382.4	6764.7	16919
51	sex + temp* + tide + moon*	6779.1	6825.5	-3383.6	6767.1	16920
52	TL + sex + temp* + moon*	6779.4	6825.9	-3383.7	6767.4	16920
53	sex + temp* + moon*	6779.8	6818.5	-3384.9	6769.8	16921
54	TL + temp* + tide	6782.8	6821.4	-3386.4	6772.8	16921
55	temp* + tide	6783.2	6814.2	-3387.6	6775.2	16922
56	TL + temp*	6783.4	6814.3	-3387.7	6775.4	16922
57	temp*	6783.8	6807	-3388.9	6777.8	16923
58	TL + sex + temp* + tide	6784.7	6831.2	-3386.4	6772.7	16920
59	sex + temp* + tide	6785.2	6823.8	-3387.6	6775.2	16921
60	TL + sex + temp*	6785.4	6824.1	-3387.7	6775.4	16921
61	sex + temp*	6785.8	6816.7	-3388.9	6777.8	16922
62	sex + temp*	6785.8	6816.7	-3388.9	6777.8	16922
63	season + TL + tide + wind* + moon*	6798	6852.1	-3392	6784	16826
64	TL + tide + wind* + moon*	6798.5	6844.9	-3393.3	6786.5	16827
65	season + tide + wind* + moon*	6798.5	6844.8	-3393.2	6786.5	16827
66	season + TL + wind* + moon*	6798.9	6845.3	-3393.4	6786.9	16827
67	tide + wind* + moon*	6799	6837.6	-3394.5	6789	16828
68	TL + wind* + moon*	6799.3	6837.9	-3394.6	6789.3	16828
69	season + wind* + moon*	6799.3	6838	-3394.7	6789.3	16828
70	wind* + moon*	6799.7	6830.7	-3395.9	6791.7	16829
71	season + TL + sex + moon* + tide + wind*	6800	6861.8	-3392	6784	16825
72	season + sex + tide + wind* + moon*	6800.4	6854.5	-3393.2	6786.4	16826
73	sex + tide + wind* + moon*	6800.9	6847.3	-3394.4	6788.9	16827
74	season + TL + sex + wind* + moon*	6800.9	6855	-3393.4	6786.9	16826

75	TL + sex + wind* + moon*	6801.3	6847.7	-3394.6	6789.3	16827
76	season + sex + wind* + moon*	6801.3	6847.7	-3394.6	6789.3	16827
77	sex + wind* + moon*	6801.7	6840.3	-3395.8	6791.7	16828
78	season + TL + tide + wind*	6806.5	6852.9	-3397.2	6794.5	16827
79	season + tide + wind*	6806.9	6845.6	-3398.5	6796.9	16828
80	season + tide + wind*	6806.9	6845.6	-3398.5	6796.9	16828
81	TL + tide + wind*	6807.2	6845.9	-3398.6	6797.2	16828
82	season + TL + wind*	6807.3	6846	-3398.6	6797.3	16828
83	season + wind*	6807.7	6838.7	-3399.9	6799.7	16829
84	tide + wind*	6807.7	6838.6	-3399.8	6799.7	16829
85	TL + wind*	6807.9	6838.9	-3400	6799.9	16829
86	wind*	6808.4	6831.6	-3401.2	6802.4	16830
87	season + TL + sex + tide + wind*	6808.5	6862.6	-3397.2	6794.5	16826
88	TL + sex + tide + wind*	6809.2	6855.6	-3398.6	6797.2	16827
89	season + TL + sex + wind*	6809.3	6855.7	-3398.6	6797.3	16827
90	sex + tide + wind*	6809.6	6848.3	-3399.8	6799.6	16828
91	season + sex + wind*	6809.7	6848.3	-3399.8	6799.7	16828
92	sex + wind*	6810.3	6841.3	-3401.2	6802.3	16829
93	TL + tide + moon*	6826.8	6865.5	-3408.4	6816.8	16921
94	tide + moon*	6827.2	6858.2	-3409.6	6819.2	16922
95	season + TL + tide + moon*	6827.7	6874.1	-3407.9	6815.7	16920
96	TL + moon*	6828.2	6859.1	-3410.1	6820.2	16922
97	TL + moon*	6828.2	6859.1	-3410.1	6820.2	16922
98	season + tide + moon*	6828.2	6866.8	-3409.1	6818.2	16921
99	moon*	6828.6	6851.8	-3411.3	6822.6	16923
100	sex + tide + moon*	6829.2	6867.9	-3409.6	6819.2	16921
101	season + TL + moon*	6829.2	6867.8	-3409.6	6819.2	16921
102	season + moon*	6829.6	6860.6	-3410.8	6821.6	16922
103	season + moon*	6829.6	6860.6	-3410.8	6821.6	16922
104	season + TL + sex + tide + moon*	6829.7	6883.9	-3407.9	6815.7	16919
105	TL + sex + moon*	6830.2	6868.8	-3410.1	6820.2	16921
106	sex + moon*	6830.6	6861.5	-3411.3	6822.6	16922
107	season + TL + sex + moon*	6831.2	6877.6	-3409.6	6819.2	16920
108	season + TL + sex + moon*	6831.2	6877.6	-3409.6	6819.2	16920
109	season + sex + moon*	6831.6	6870.2	-3410.8	6821.6	16921
110	TL + tide	6834.8	6865.7	-3413.4	6826.8	16922
111	tide	6835.2	6858.4	-3414.6	6829.2	16923
112	season + TL + tide	6835.4	6874.1	-3412.7	6825.4	16921
113	season + tide	6835.9	6866.8	-3413.9	6827.9	16922
114	TL	6835.9	6859.1	-3415	6829.9	16923

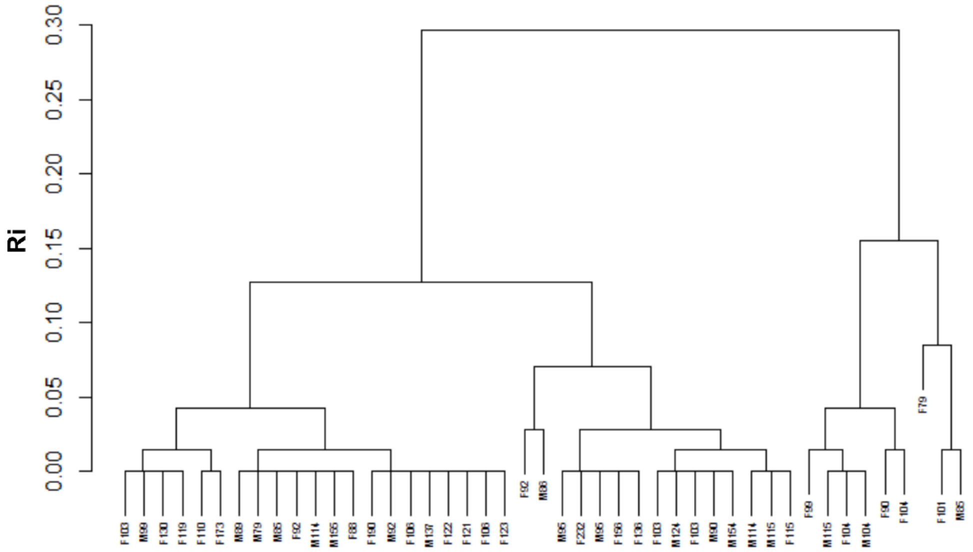
115	presence ~ 1 + (1 | Tag_id)	6836.4	6851.8	-3416.2	6832.4	16924
116	season + TL	6836.7	6867.6	-3414.3	6828.7	16922
117	TL + sex + tide	6836.8	6875.4	-3413.4	6826.8	16921
118	sex + tide	6837.1	6868.1	-3414.6	6829.1	16922
119	season	6837.1	6860.4	-3415.6	6831.1	16923
120	season + TL + sex + tide	6837.4	6883.8	-3412.7	6825.4	16920
121	season + sex + tide	6837.8	6876.5	-3413.9	6827.8	16921
122	TL + sex	6837.9	6868.9	-3415	6829.9	16922
123	sex	6838.3	6861.5	-3416.2	6832.3	16923
124	season + TL + sex	6838.7	6877.4	-3414.3	6828.7	16921
125	season + sex	6839.1	6870	-3415.5	6831.1	16922
126	season + sex	6839.1	6870	-3415.5	6831.1	16922



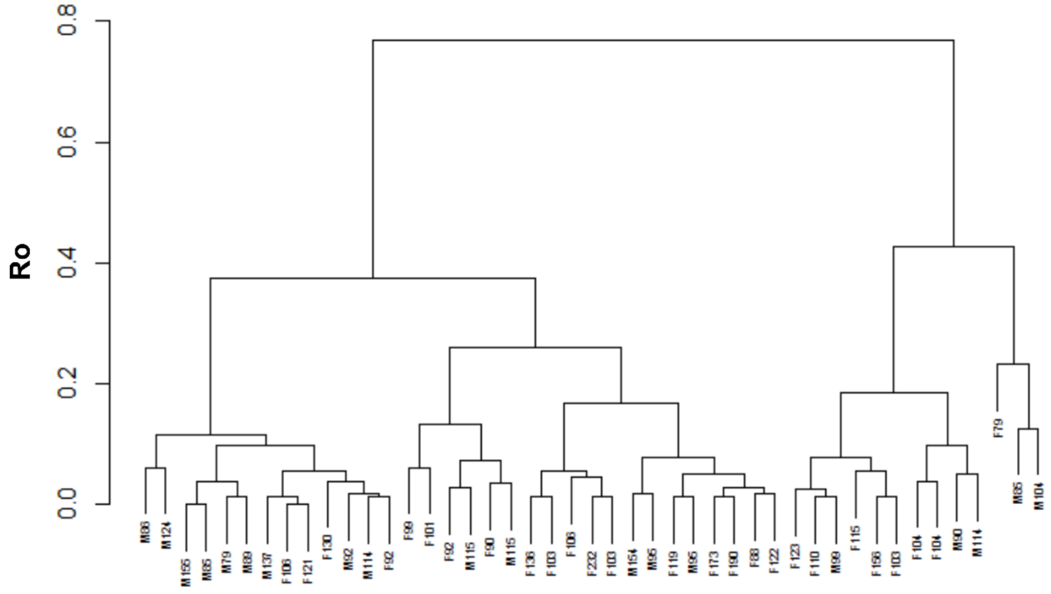
Supplementary Figure S4.1 Acoustic receiver and tag range testing for tag detectability in Gulf St. Vincent.



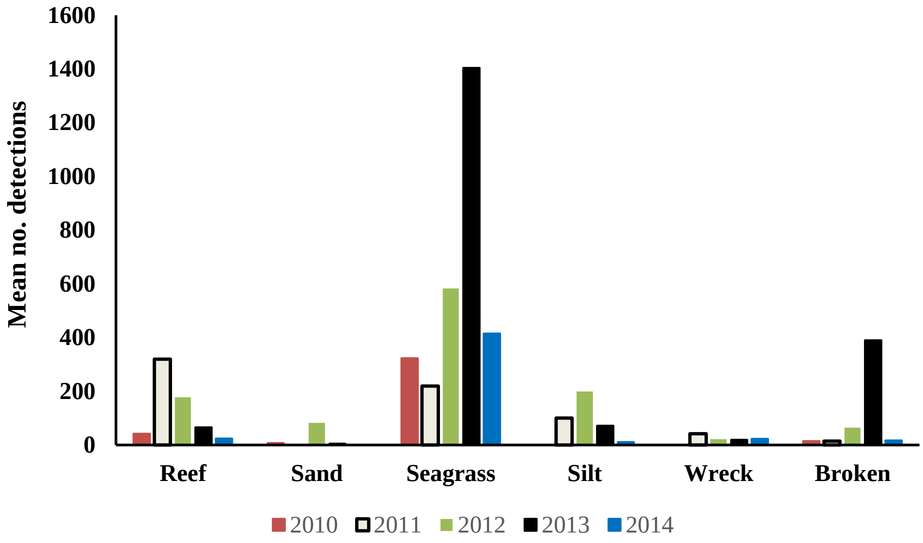
Supplementary Figure S4.2 Temporal patterns in sentential tag detections for northern Gulf St. Vincent used for calculating the standardisation factor for adjusting temporal variations in tag detectability. (a) The mean number of detections per hour over a 24-hour period. (b) The mean number of detections per month, errors bars = standard error.



Supplementary Figure S4.3 Dendrogram of residency indices (Ri) of tagged juvenile bronze whalers in Gulf St. Vincent.



Supplementary Figure S4.4 Dendrogram of roaming indices (Ro) of tagged juvenile bronze whalers in Gulf St. Vincent.



Supplementary Figure S4.5 The mean number of detections per habitat type over the study period 2010-2014

5

THERMAL PREFERENCES AND COASTAL MIGRATIONS OF ADULT BRONZE WHALERS (*CARCHARHINUS BRACHYURUS*) IN TEMPERATE WATERS OF SOUTHERN AUSTRALIA

Abstract

Many large shark species have broad spatial distributions and can exert significant influence on the structure and function of ecosystems. Determining the movements and habitat use of sharks is, therefore, critical for understanding their role in regulating, stabilising, and coupling marine food webs. We used two types of pop-up satellite archival tags to investigate the horizontal movements, depth, and temperature preferences of adult bronze whalers (*Carcharhinus brachyurus*) in the coastal temperate waters of southern Australia during 2011–2016. Ten large bronze whalers (9 females and 1 unknown sex) ranging 200–320 cm total length were tracked for 5–180 days (mean 106.5 ± 25.2 days). Minimum horizontal displacement ranged from ~200 km to 1,600 km (mean 330.5 ± 156.4 km). Sharks tracked for >60 days concurrently moved from inshore waters (<50 m) to offshore habitats (50–130 m) in late autumn, coinciding with the cooling of gulf and inshore coastal water temperatures. In inshore waters, the thermal habitat ranges of tagged sharks was large (13–24°C) and individuals spent 45% of their time within the top 10 m during both day and night. Bronze whalers occupied a smaller thermal range (15–19° C) in the offshore habitat and spent 85% of time between 10 and 60 m and only ~5 % of time at the surface. Four sharks dived deeper than 100 m, with the maximum depth recorded being 129 m. The seasonal and predictable inshore occurrence of adult

female bronze whalers renders them vulnerable to anthropogenic influences and when coupled with slow life history traits raises concerns about the status of this commercially targeted species.

Introduction

The understanding of movement, habitat usage, and trophic ecology is critical for the effective management and conservation of marine species (Pikitch et al. 2004). This is particularly true for predatory species, as they play an important role in food web structure and dynamics by regulating, coupling, and stabilising disparate ecosystems (Rooney et al. 2006). Historically, the tracking of animals was restricted to terrestrial species, due to the vagrant, cryptic, and concealing nature of the aquatic environment and the species within it (Hammerschlag et al. 2011). However, the advent and continuing refinement in marine telemetry capabilities has revealed insights into unknown ecological behaviours, habitat usage, and transoceanic migrations (Sims 2010; Block et al. 2011; Hussey et al. 2015a).

Many large-bodied shark species occupy high trophic position in food webs and can routinely undertake broad movements from regional scales, e.g., dusky sharks (*Carcharhinus obscurus*) (Hoffmayer et al. 2010; Rogers et al. 2013b), bull sharks (*C. leucas*) (Brunnschweiler et al. 2010; Daly et al. 2014) and sand tiger sharks (*C. taurus*) (Teter et al. 2015) to transoceanic migrations, e.g. tiger shark (*Galeocerdo cuvier*) (Heithaus et al. 2007; Werry et al. 2014), basking shark (*Cetorhinus maximus*) (Skomal et al. 2009), salmon shark (*Lamna ditropis*) (Weng et al. 2008), short-fin mako (*Isurus oxyrinchus*) (Rogers et al. 2015), and white sharks (*Carcharodon carcharias*) (Bonfil et al. 2005; Bruce et al. 2006; Weng et al. 2007; Domeier and Nasby-Lucas 2008). The drivers influencing broad-scale movements and spatio-temporal shifts in habitat use has been linked to predator-prey dynamics, predator avoidance, thermal preferences, and philopatry to key life history areas (Sims et al. 2008; Meyer et al. 2009; Cartamil et al. 2010; Humphries et al. 2010; Fitzpatrick et al. 2012). Critically, the knowledge of broad-scale movements and migratory pathways also highlights spatial areas and temporal periods of increased vulnerability to natural predation and to cumulative anthropogenic affects (Hammerschlag et al. 2011; Chin et al. 2012). Currently, many shark populations are reportedly in decline, which combined with their slow life history traits and low resilience to fishing pressure causes concern over the sustainability of fisheries that target them or take them as bycatch (Ferretti et al. 2010; Dulvy et al. 2014). Knowledge of movement ecology and therefore, habitats or periods of increased vulnerability is fundamental to the effective management and or protection of exploited species.

The bronze whaler is a large-bodied, primarily temperate species with a Northern and Southern Hemisphere distribution (Last and Stevens 2009). Available genetic information suggests the Australian population is one stock, with a distribution extending from the mid-coast of New South Wales through the south to the Southwest of Western Australia (Last and Stevens 2009; Benavides et al. 2011). South Australia has the largest targeted fishery, which seasonally targets bronze whalers in the coastal and gulf waters during the spring–summer months (September–April) (Jones 2008; Drew et al. 2016). The fishery predominately catches juvenile bronze whalers and large sharks are less frequent in catches (Rogers et al. 2013a). The few large sharks caught in northern gulf waters were mature females that were either pregnant or had recently given birth (Rogers et al. 2013a; Drew et al. 2016). Previous studies of the life history characteristics of bronze whalers showed that the species is slow growing, late maturing, and with low fecundity (Walter and Ebert 1991; Drew et al. 2016). As a result, bronze whalers are likely to be vulnerable to anthropogenic pressures, including fishing (Walter and Ebert 1991; Drew et al. 2016).

A fine-scale movement study of juvenile bronze whalers in Gulf St. Vincent, South Australia, identified philopatric behaviour, and low levels of seasonal residency and site fidelity during spring–autumn (Chapter 4). Habitat modelling predicted that water temperature fluctuations and season had a significant effect on juvenile bronze whaler occurrence (Chapter 4). Fluctuations in water temperature has also been linked as a potential driver of bronze whaler movement in other regions. Off Argentina, the occurrence of bronze whalers during summer has been linked to seasonal increase in water temperature (Lucifora et al. 2005). Off South Africa, the flow of cool, nutrient rich waters from the Eastern Cape creates a mass migration of sardines (*Sardinops sagax*). Bronze whalers exploit this migration commonly known as the “sardine run” and move up the east South African coast along with the sardines (Dudley and Cliff 2010). Similarly in South Australia, stomach content and stable isotope analyses revealed the diet of bronze whalers was dominated by sardines (*S. sagax*) (Chapter 3; (Rogers et al. 2012). However, the motivations behind large bronze whaler movement in southern Australia is currently unknown. Previous research on bronze whalers in southern Australia has been primarily focused on juveniles as adult sharks were rarely encountered. Understanding the movements of the adult, breeding component of this population is integral for establishing the sustainability of the fishery and conservation of the species. The aim of the present study was to describe the long-range movements, and quantify thermal and depth preferences of adult bronze whalers over contrasting habitats and seasonal time scales. This information will help further our knowledge of this important component of the bronze whaler population in this temperate southern marine ecosystem.

Methods

TAGGING

Ten pop-up satellite archival tags (PSAT; 8x PTT-100; Microwave Telemetry (MT), Columbia, MD, USA; 2x Mini-pat archival tags, Wildlife Computers (WC), Redmond, WA, USA) were deployed on large adult bronze whalers from commercial and recreational fishing vessels. On board commercial fishing vessels, sharks were tagged either while free-swimming or while hooked on a longline targeting bronze whalers and dusky sharks. Free-swimming sharks were tagged by enticing sharks alongside the vessel using bait (West Australian Salmon, *Arripis truttaceus*). Commercial long-lines consisted of floating rope or mono-filament main lines with 1.2–1.7 mm stainless-steel leaders, with up to 200 16/o stainless steel circle hooks attached to the main line with a stainless-steel clip. Main lines were up to 8 km long, anchored, and marked at each terminal end with 20–70-cm-diameter rubber floats. Hooks were spaced along the main line at intervals of 10–20 m apart, with small floats every two hooks (Drew et al. 2016). Recreational fishers captured sharks on a rod and reel. They suspended baits under balloons with heavy tackle (14–36 kg line) and leaders of 1.5–1.7 mm nylon-coated wire attached to 12/o or 14/o J-style hooks (Drew et al. 2016). PSAT were tethered to an umbrella dart-tag head using either ~5 cm of 130 kg monofilament crimped to 10 cm of 1.7 mm plastic sheathed stainless-steel cable or only using the 1.7mm stainless-steel cable (Rogers et al. 2013b). The entire tether was then covered in heat-shrink plastic tubing (Rogers et al. 2013b).

Tethered PSAT were implanted in the dorsal musculature of sharks using a tagging pole when sharks were close to the vessel. The body weight of the tagged individuals was >80 kg, estimated by published length-weight regressions (Cliff and Dudley 1992), and the weight of the tags were ~0.07 kg, therefore we were satisfied the swimming behaviour was not impacted by the trailing tag. Sex was determined for nine of the ten sharks by observing the presence or absence of claspers, one shark’s sex was undetermined. Total length (TL) was measured to the nearest cm or estimated to the nearest 10 cm by comparing the shark to a known length along the gunwale of the vessel. Maturity of sharks was assessed by using size-at-maturity estimates from Drew et al. (2016).

All tags were programmed to release 180 days after deployments. The MT PTT-100 PSATs were pre-programed to record depth, temperature, and transmitted light at 15-min intervals. The resolution of the recorded data for depth was ± 5.4 m and for temperature was ± 0.18°C. The WC Mini-pat tags were programmed to record temperature, depth, and light at 10-min intervals. The archived data were binned into three-hour summaries. Depth resolution was ± 0.5 m and temperature resolution was ± 0.05°C. All tags were equipt with a constant pressure switch which was set to trigger if the tag remained at constant pressure (± 5m) for 72 hours. The recorded archived data and tags location was transmitted via the ARGOS satellite network once the tag reached the surface. No tags were recovered after detachment, and all data sets used were satellite-transmitted data (Table 5.1).

Table 5.1 Tagging and biological information for ten bronze whalers in southern Australia. DAL = days-at-liberty after tag deployment, Dist = is the minimum calculated distance travelled between tag deployment and pop-up locations.

Shark No.	Tag No.	TL (cm)	Sex	Tag date	Tag latitude (S)	Tag longitude (E)	Pop-up date	Pop-up latitude (S)	Pop-up longitude (E)	DAL	Dist (km)	% Data obtained
1	42958	310	F	6/12/2011	35.27	136.80	16/12/2011	35.25	137.07	10	29	98%
2	102368	300	F	6/12/2011	35.26	136.82	10/12/2011	35.27	136.95	4	19	84%
3	52468	270	F	7/2/2012	34.52	137.44	6/8/2012	33.92	132.94	181	482	85%
4	139899	300	NS	3/1/2016	35.78	137.78	5/2/2016	35.76	137.80	33	2	100%
5	139000	330	F	15/2/2015	35.65	137.65	14/8/2015	35.25	135.66	180	198	66%
6	139001	290	F	31/12/2014	35.69	137.78	28/6/2015	34.97	135.69	179	210	67%
7	139002	200	F	19/11/2014	34.26	137.39	18/5/2015	37.92	140.28	180	582	71%
8	139003	270	F	15/2/2016	35.92	138.09	15/8/2016	34.37	122.42	181	1620	68%
9	144878	260	F	3/1/2017	35.67	137.68	6/3/2017	35.87	137.95	62	72	54%
10	144879	280	F	4/1/2017	35.76	137.83	28/2/2017	35.56	135.77	55	91	80%

DATA ANALYSIS

Diel period (day/night) was calculated based on civil daily sunrise and sunset times for Adelaide, South Australia obtained from the Geoscience Australia website (2017) (http://www.ga.gov.au/geodesy/astro/sunrise.jsp). Day was considered as the period between one hour after sunrise and one hour before sunset. Likewise, night was considered the period between one hour after sunset and one hour before sunrise. We excluded crepuscular periods due to the relatively small contribution of data obtained (~7% of detections).

Horizontal movements were assessed using transmitted light-based estimates of longitude based on sunrise and sunset times and calculated by MT proprietary algorithms. To estimate error in longitude, we compared MT light-based estimated longitudes to ARGOS class 3 location estimates from drifting tags following the release from tagged sharks. The difference between light-based position estimates and ARGOS position data for longitude and latitude was tested using a Wilcoxon signed-rank test (IBM SPSS Statistics Version 24).

Minimum horizontal displacements of sharks were calculated between the deployment location and the first transmitted satellite locations following release and surfacing of tags (Fig. 5.1). Positions between release and pop-up location were not calculated due a low number of reliable position estimates based on light-based data from the WC Mini-pat tags. Tag deployment, pop-up locations were plotted and minimum horizontal displacements travelled measured in MapInfo Professional GIS software (Version 12.5; Pitney Bowes Software, North Sydney, NSW, Australia).

Vertical habitat use was analysed for individual bronze whalers using binned time series data. Depth and temperature data were grouped into 10 m and 1°C bins, respectively. Histograms of percentage of time spent at each depth and temperature bin was split into day and night, and inshore and offshore waters based on longitude and maximum depth. The inshore region was defined as the waters of Spencer Gulf and Gulf St. Vincent, Backstairs Passage, and Investigator Straight between Cape Borda and Cape Willoughby on Kangaroo Island (Fig. 5.1). The offshore region is considered all areas East of Cape Willoughby (138.10°E) and West of Cape Borda (136.70°E) (Fig. 5.1). Timing of tagged sharks leaving the inshore areas was determined by cross-referencing the maximum depth and longitude position data. Depths >60 m were considered offshore based on bathymetry for the region. Kolmogorov–Smirnov (KS) tests were used to assess if depth and temperature distributions were different between day vs. night and between inshore vs. offshore. Statistical analyses were performed in the R statistical language using the *dgof* and *graphics* package (R Development core team, 2017).

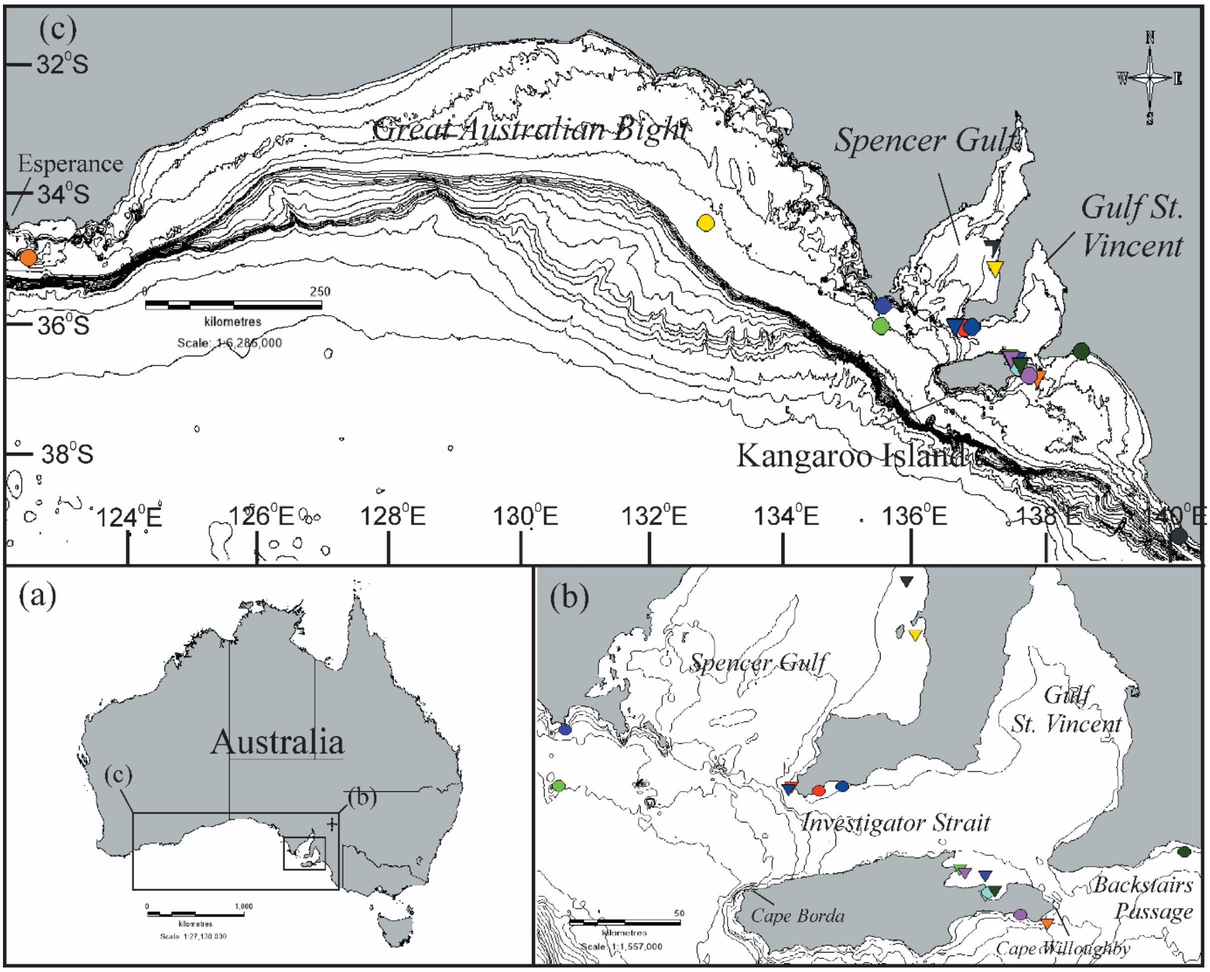


Figure 5.1 Pop-up archival tag deployement and detachment locations for ten tagged large bronze whalers (*Carcharhinus brachyurus*) in southern Australia. Triangles represent tagging locations and circles represent tag detachment locations identified through argos satellite locations.

Depth- and time-integrated thermal habitat profiles were constructed for individual bronze whalers using paired temperature and depth data in OCEAN DATA VIEW software with the Data-Interpolating Variational Analysis (DIVA) gridding tools filter (ver. 4: Alfred Wegener Institute, Bremerhaven, Germany) oceanographic profiling software (Schlitzer, 2016).

Water temperature data were downloaded from the IMOS data portal (https://portal.aodn.org.au/search) for the Australia National Mooring Network (ANMN). Mean water temperature data plots were calculated for two moorings, the southern Spencer Gulf mooring (SAM8SG, 35.25°S and 136.69°E) at ~40 m depth and the offshore Coffin Bay mooring (SAM5CB, 34.93°S and 135.05°E) at ~90 m depth from 1 January 2011 to 31 December 2014. Water temperature and estimated longitude were plotted for sharks with >60 day deployments to investigate shifts in habitat use in the inshore and offshore regions.

Results

Ten PSAT tags were deployed during the Austral summer months December–February (2011–2016) on nine females and one unknown sex (size range 200–330 cm TL) bronze whalers (Table 5.1) in the inshore, coastal waters of South Australia. According to size-at-maturity estimates for the region (Drew et al. 2016) nine of the ten sharks were mature. All sharks were released in good condition, with only minor hook injuries present upon release. Five tags (Shark 3, 5, 6, 7 and 8) were retained for 180-days and five tags released prematurely (Shark 1, 2, 4, 9 and 10). The mean days at liberty for all deployments was 106.5 ± 25.2 (mean ± standard error).

For the five tags that released prematurely, depth data prior to tags popping-up suggest that the release was due to the triggering of the pre-set constant pressure switch. In all cases, the long period prior to the premature release (e.g., >60 days) or resighting of tagged sharks after the tag had popped-up suggest that the release was not due to mortality linked to capture and tagging, but to sharks swimming within ± 5 m depth range.

Horizontal movements

Mean positional error estimated from the drifting tags post-release was 1.467 ± 0.228° (163 ± 25 km; range 39–447 km) for latitude and 0.298 ± 0.045° (27 ± 4 km; range 14–69 km) for longitude. Estimates of latitude were not used in subsequent further analyses. No significant difference was identified between MT's algorithm light-based position estimates and ARGOS estimates of longitude position (Wilcoxon test: z= -1.639 p = 0.101).

The furthest horizontal displacement was 1,620 km (shark 8) over 180 days-at-liberty, representing a minimum distance travelled of 9 km day^{-1} (Fig. 5.1). Based on tags which reach full-term deployment, the mean distance travelled was 330.5 ± 156.4 km, with all full-term tag deployments travelling ~200 km or greater (Table 5.1). All sharks tracked for > 60 days performed inshore to offshore movements (Fig. 5.1).

Five tags remained attached to bronze whalers for the full six-month duration. Based on the distance between tagging and pop-up locations, the five individuals travelled a range of distances from regional-scale movements of ~200 km to large-scale migrations of >1,600 km. The furthest distance travelled was ~1620 km by shark 8, which spanned from Northeast of Kangaroo Island to east of Esperance (Western Australia) (Fig. 5.1; Table 5.1). Longitudinal estimates also suggest that this shark had travelled further west almost reaching Albany (Western Australia) (~120°E) before returning to the pop-off location (Fig. 5.2). Sharks 3 and 7 were tagged in the eastern Spencer Gulf and both travelled a minimum horizontal displacement of ~500 km, with shark 3 swimming ~500 km west to the offshore Great Australian Bight (GAB) waters (Fig. 5.1; Table 5.1). Shark 3 also appears to have moved further west (~132°E) than its pop-up location (Fig. 5.2). Therefore, the estimated minimum distanced travelled for these two sharks are likely to be underestimates. Shark 7 travelled a minimum distance of ~500 km into the waters of the Bonney Coast in Southeast South Australia (~141°E) (Fig. 5.2), which is a productive region characterised by seasonal upwelling through summer (Fig. 5.1; Table 5.1). Sharks 5 and 6 had full-term tag deployments and conducted regional-scale movements.

These sharks were tagged in the NE corner of Kangaroo Island and travelled a minimum distance of ~200 km to offshore southern Eyre Peninsula (South Australia) (Fig. 5.1; Table 5.1). They appear to have spent most time in the waters of Investigator Strait and the northern coastline of Kangaroo Island then moved into offshore waters ~60 days before tag pop-up. However, longitude estimates for shark 5 showed a rapid westward movement out to ~132°E and returning to ~136°E within a week (Fig. 5.2). Shark 4 was at liberty for 33 days, but remained within the tagging area until premature tag detachment (Fig. 5.1; Table 5.1).

Longitudinal data showed that sharks are moving from inshore to offshore habitats by the end of the Austral Autumn (May–June) (Fig. 5.2), which aligns with the rapid cooling of southern Gulf water temperatures (Fig. 5.2).

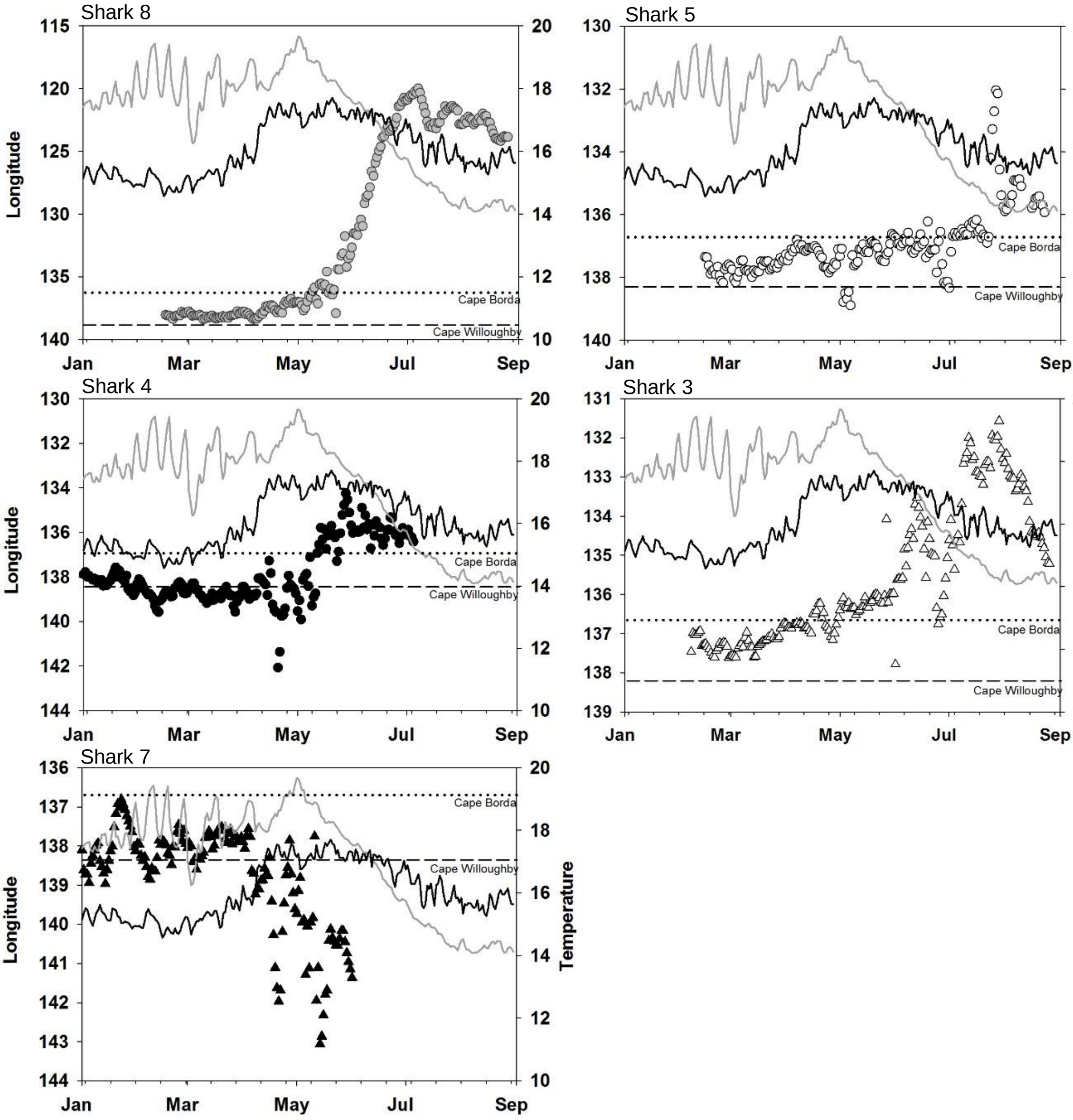


Figure 5.2 Daily longitudinal and mean thermal habitat plots for five tagged large bronze whalers in the temperate waters of southern Australia. Circles and triangles represent daily individual shark longitudinal values, solid grey (southern Spencer Gulf) and sold black (offshore Coffin Bay) line represents mean daily water temperature data from 2010 – 2014. Dashed lines represent geographical landmarks of Cape Borda and Cape Willoughby which represent the east and west limits of inshore waters.

DEPTH PROFILES

The deepest depth recorded was 129 m (Shark 3), with four sharks (Shark 3, 5, 7, 8) recording depths >110 m (Table 5.2). Mean depth across the ten tagged bronze whalers was 22.6 ± 9.3 m. Depth frequency distribution was not significantly different between day and night for the inshore or offshore habitats, but was significantly shallower in the inshore habitat (17.1 ± 5.3 m for day and 13.45 ± 2.13 m night) compared to the offshore habitat (46.2 ± 14.6 m for day 42.10 ± 5.08 m for night) (Fig. 5.3; Table 5.3). This was mostly driven by shark 5, 6, and 8 that spent most of their time (95%, 38% and 77%, respectively) in the upper twenty metres of the water column in the inshore habitat compared to the offshore habitat where depth distribution was relatively homogeneous with sharks spending 80–90% of the time between 20–60 m during both day and night (Fig. 5.4, Table 5.3).

THERMAL PREFERENCES

The mean temperature occupied by all bronze whalers across all habitats was 18.6°C ± 0.6 °C (range 12.9–24.3°C). Similarly to depth distribution, thermal preferences was not significantly different between day and night for the inshore or offshore habitat. The water temperatures were significantly different between the inshore (19.2°C ± 0.6°C) and offshore habitats (16.7°C ± 0.5°C) during day and night periods (Fig. 5.5; Table 5.3). This was mostly driven by data for sharks 5 and 6, which inhabited a large thermal ranges of 12–24°C in the inshore habitat, and a narrower thermal range in the offshore habitat (Fig. 5.6). Whilst offshore, these sharks spent ~80% of their time within 14–16°C, and only ~5 % of their time in waters >16°C (Fig 5.6.).

Table 5.2 Temperature and depth information recorded from transmitted PSAT data for ten tagged large bronze whalers in the temperate coastal waters of southern Australia.

Shark No.	Temp / depth pairs	Depth records	Max depth (m)	Mean depth inshore (m)	Mean depth offshore (m)	Temp records	Temp min (˚C)	Temp max (˚C)	Mean temp inshore (˚C)	Mean temp offshore (˚C)
1	926	987	26.9	10.6		1014	18.1	20.0	19.2	
2	296	296	22.0	5.4		296	17.9	22.2	19.0	
3	9326	10475	129.1	22.8	62.9	10067	15.9	22.0	19.6	17.3
4	3355	3355	16.1	5.6		3355	19.1	23.9	21.4	
5	5240	7760	110.2	6.4	29.8	8099	12.9	23.6	19.2	15.8
6	5599	7958	83.4	25.5	40.1	7987	14.6	24.3	18.9	16.8
7	6313	8507	112.9	21.6	37.6	8646	13.5	22.0	19.1	16.3
8	5570	8258	112.9	15.8	55.6	8259	13.8	20.2	18.7	17.6
9	193	385	40.0	13.1		384	17.6	23.6	21.3	
10	3455	4175	73.5	21.7		4223	14.1	22.2	19.3	

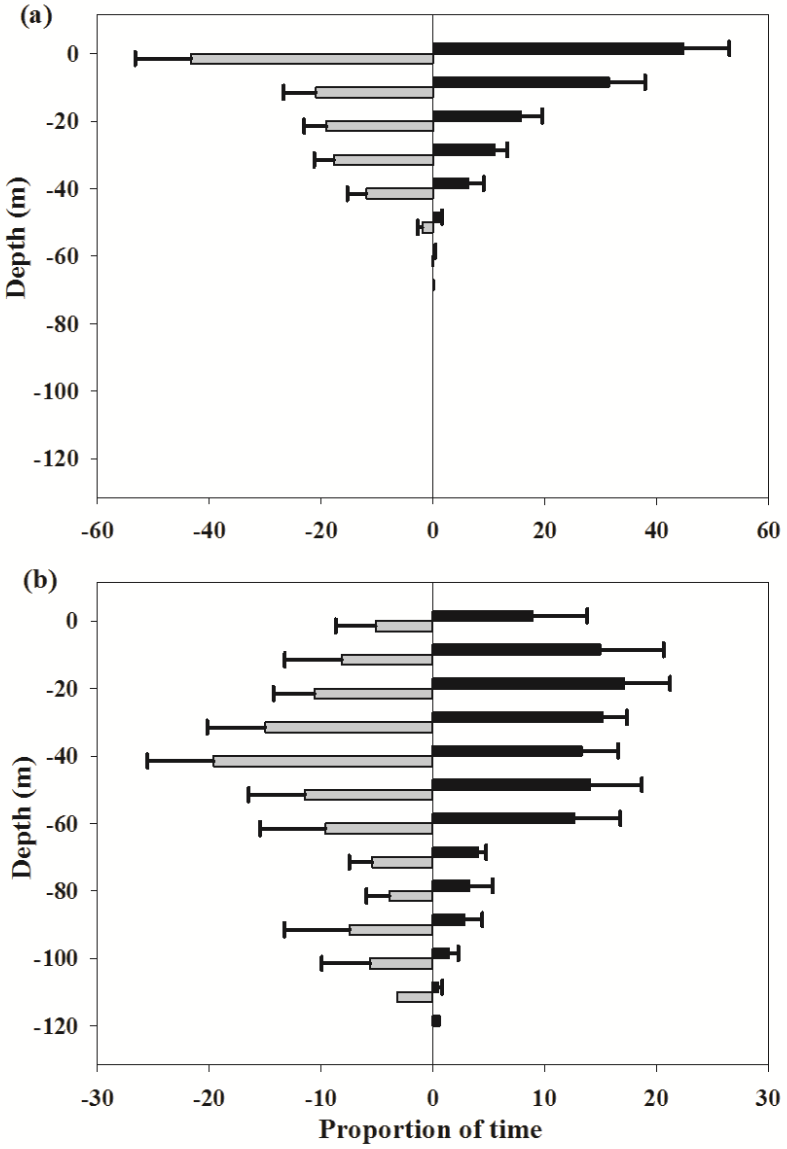


Figure 5.3 The mean inshore (a) and offshore (b) percentage of time spent at depth distributions during the day (grey) and night (black) for large bronze whalers in southern Australia waters. Error bars represent standard error.

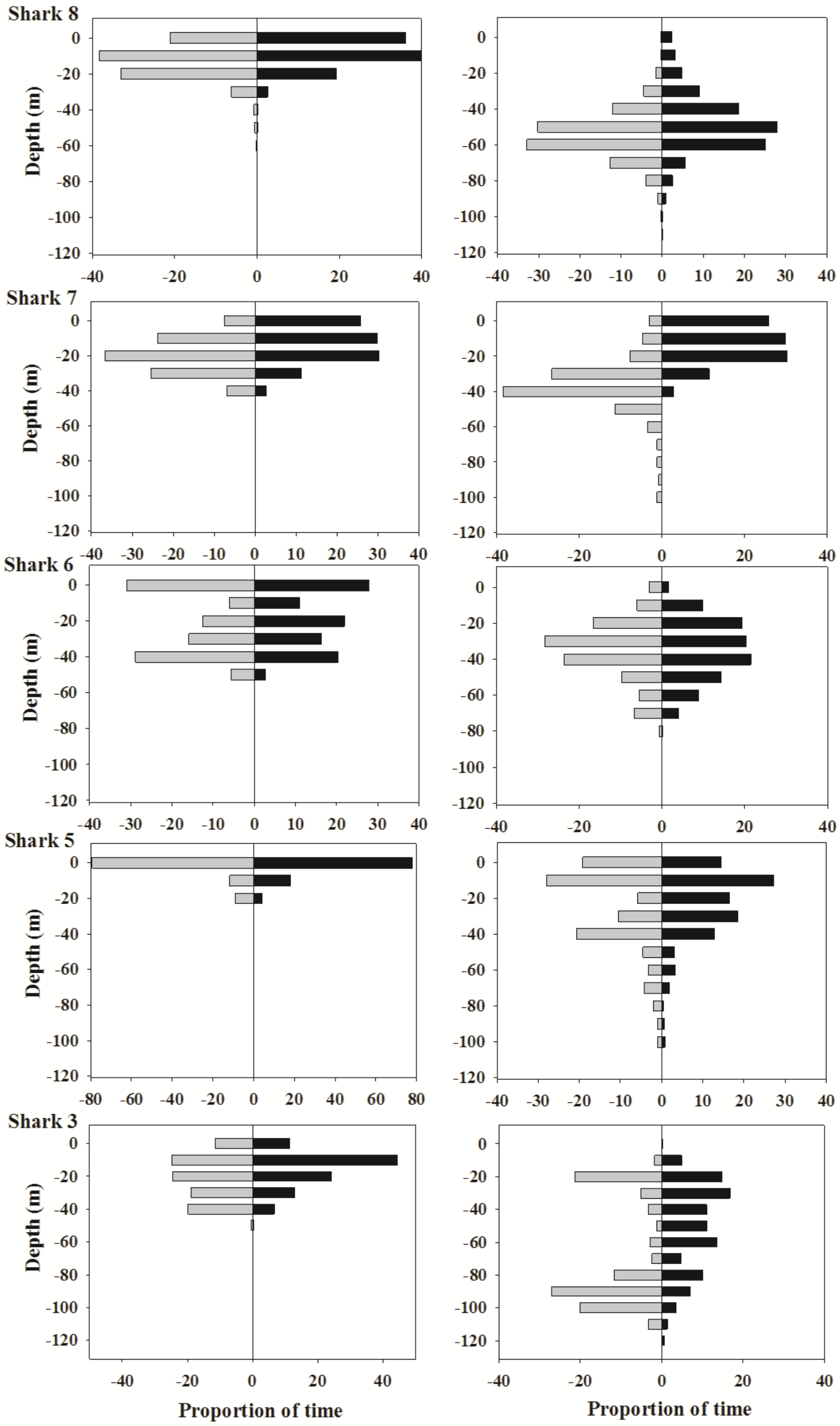


Figure 5.4 Individual shark inshore (left) and offshore (right) percentage of time spent at depth distributions during the day (grey) and night (black) for five tagged large bronze whalers in southern Australia.

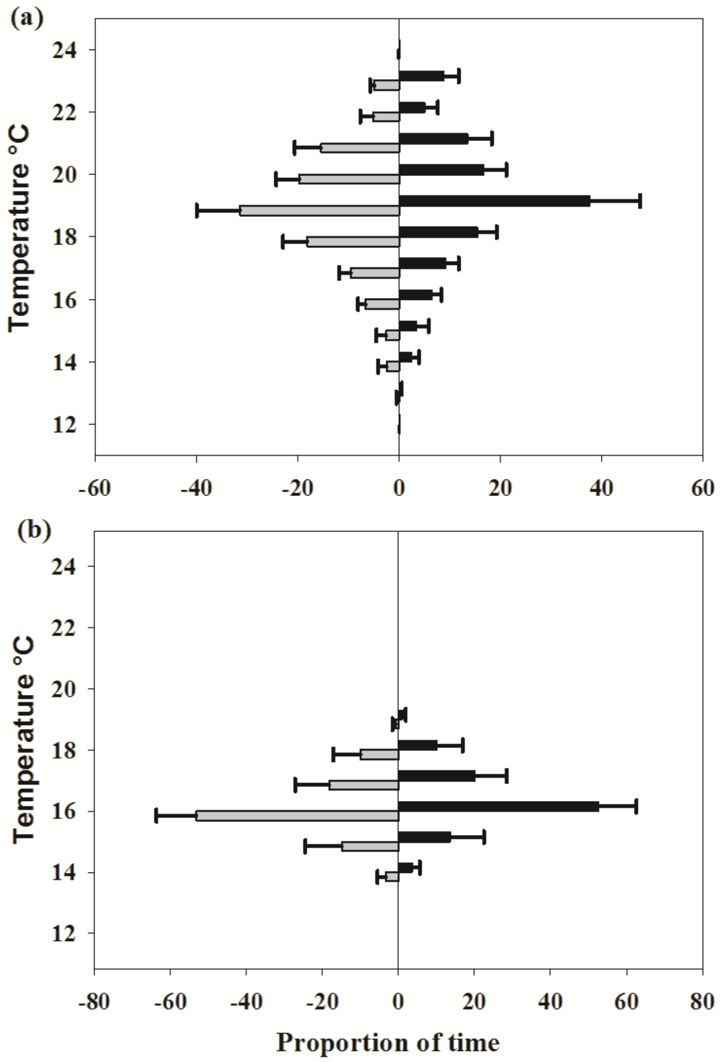


Figure 5.5 The mean inshore (a) and offshore (b) percentage of time spent at temperature distributions during the day (grey) and night (black) for tagged large bronze whalers in southern Australia. Error bars represent standard error.

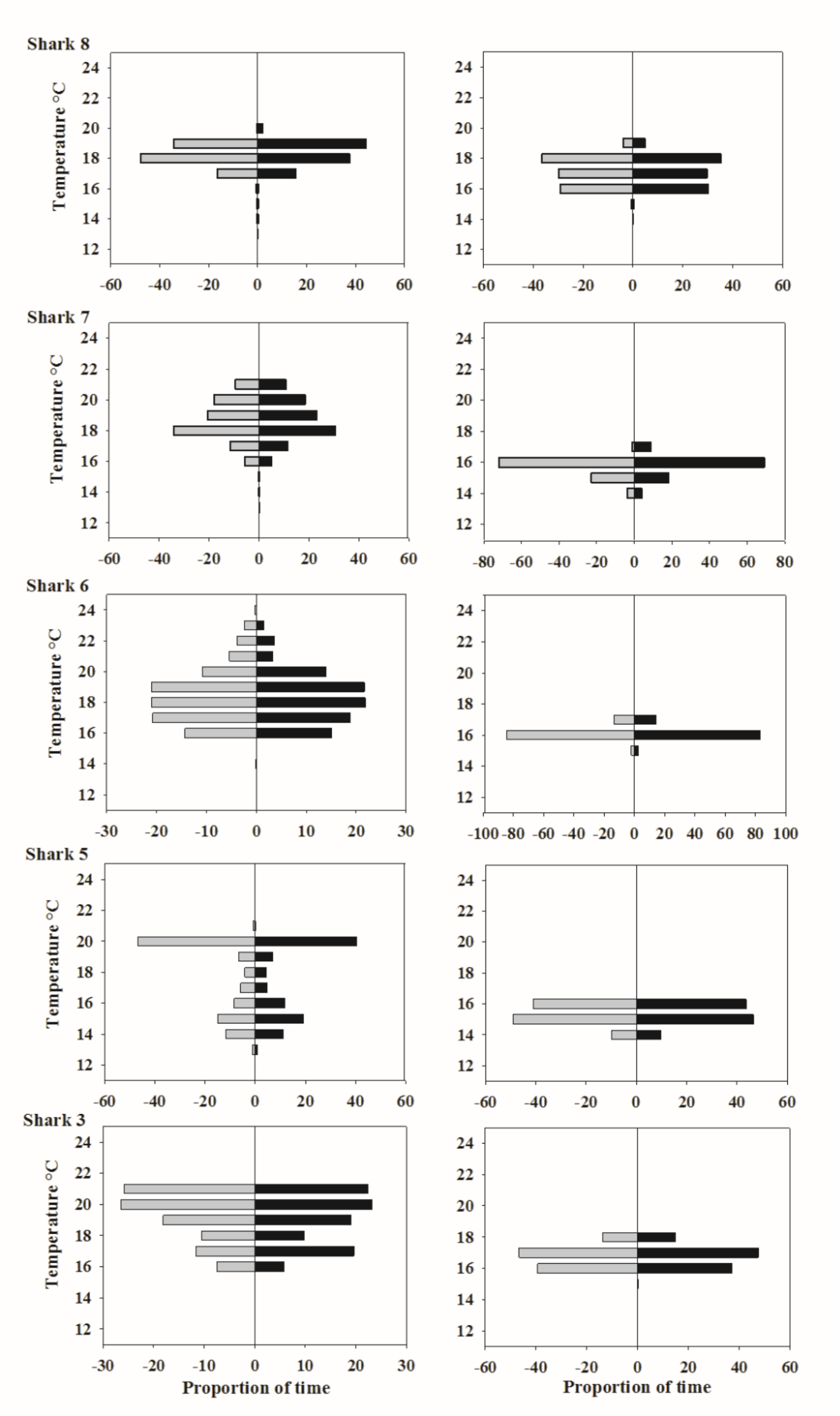


Figure 5.6 Individual shark inshore (left) and offshore (right) percentage of time spent at temperature distributions during day (grey) and night (black) for five tagged large bronze whalers in southern Australia.

Table 5.3 The results of the Kolmogorov–Smirnov (KS) tests for depth and temperature and inshore and offshore habitat usage. D = maximum distance in cumulative fraction between of the two distributions, *P* value = represents the significance of the difference between the two distributions.

	Depth								**Temperature**							
	Inshore Day vs Night		Offshore Day vs Night		Day Inshore vs Offshore		Night Inshore vs Offshore		Inshore Day vs Night		Offshore Day vs Night		Day Inshore vs Offshore		Night Inshore vs Offshore	
Shark No.	**D**	***P***	**D**	***P***	**D**	***P***	**D**	***P***	**D**	***P***	**D**	***P***	**D**	***P***	**D**	***P***
1	0.077	1.000							0.090	1.000						
2	0.077	1.000							0.308	0.570						
3	0.154	0.998	0.385	0.299	0.461	0.125	0.538	**0.046**	0.154	0.998	0.077	1.000	0.231	0.879	0.231	0.879
4	0.077	1.000							0.077	1.000						
5	0.077	1.000	0.230	0.879	0.615	**0.015**	0.692	**0.003**	0.077	1.000	0.077	1.000	0.615	**0.015**	0.538	**0.046**
6	0.154	0.998	0.154	0.998	0.230	0.879	0.230	0.879	0.154	0.998	0.077	1.000	0.615	**0.015**	0.615	**0.015**
7	0.077	1.000	0.461	0.125	0.461	0.125	0.077	1.000	0.077	1.000	0.154	0.998	0.385	0.291	0.385	0.291
8	0.154	0.998	0.230	0.879	0.384	0.291	0.461	0.125	0.154	0.998	0.077	1.000	0.154	0.998	0.154	0.998
9	0.154	0.998							0.154	0.998						
10	0.154	0.998							0.154	0.998						
Mean	0.154	0.998	0.308	0.588	0.538	**0.046**	0.538	**0.046**	0.154	0.998	0.384	0.291	0.538	**0.046**	0.538	**0.046**

Daily thermal and depth profiles and associated movements

Thermal range and depth profiles were investigated on a daily scale for five sharks (3, 5, 6, 7, and 8) with full-term tag deployments (Fig. 5.7). All tags were deployed on sharks in the inshore gulf or coastal waters within the southern straits of South Australia during the Austral summer months. Similar trends in habitat use were identified for all five individuals. Sharks remained within the inshore gulf and shallow waters of the southern straits, using the entire water column and traversing a warm water mass (19–24°C) in December–May. As the ambient water temperatures within the gulf and Investigator Strait declined below 18°C in May–June, sharks moved to deep, offshore regions. When in the offshore neritic habitat, sharks occupied a mixed water mass (16–18°C) (Fig. 5.7). In the offshore regions, maximum depths of dives were ~120 m and water temperature was consistent across this depth range with limited dives under the mixed layer or in areas of cool waters. All sharks spent limited time in waters <15 ˚C.

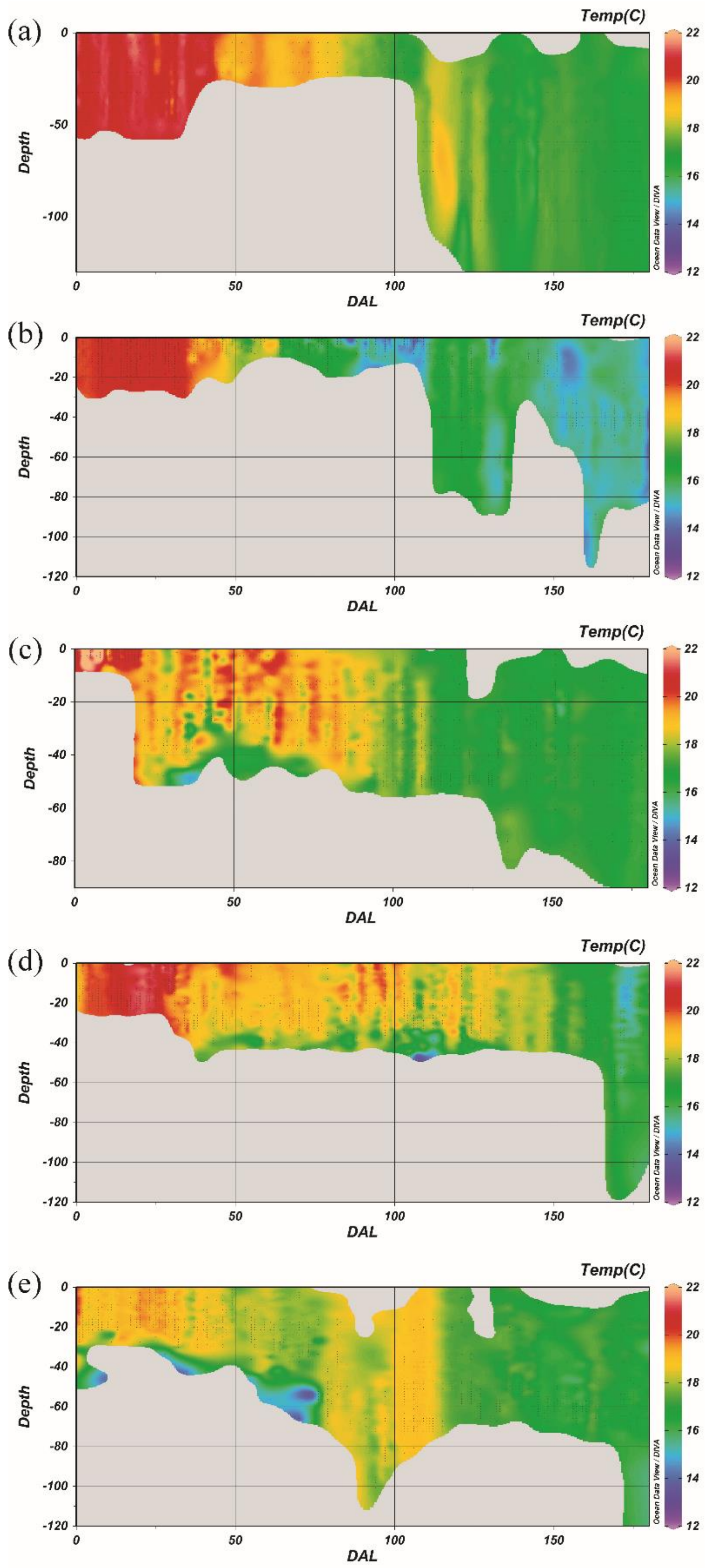


Figure 5.7 Daily thermal range and depth plots for five tagged large bronze whalers in the temperate waters of southern Australia. (a) = shark 3, (b) = shark 5, (c) = shark 6, (d) = shark 7 and (e) = shark 8. DAL= Days at liberty after tag application.

Discussion

This study is the first to use PSATs to describe temperature and depth habitat use, and broad-scale horizontal movements of adult female bronze whalers. Tagged sharks travelled 200–1,620 km from the South Australian gulfs with their departure aligning with the cooling of inshore coastal waters and the intrusion of eastward flowing Leeuwin Current and GAB warm pool waters into the eastern GAB shelf ecosystem (McClatchie et al. 2006; Petrusevics et al. 2009). Patterns of depth and thermal preferences by bronze whalers varied between inshore and offshore continental shelf waters. In the inshore habitats, most time in both day and night was spent at or near the surface and sharks endured a large thermal range of 12–24°C. In the offshore habitat, sharks spent most time between 20–60 m and the thermal range was narrower and more consistent at 16–18°C. Tag pop-up locations combined with relatively shallow maximum depths inhabited indicate that bronze whalers are primarily a coastal and neritic species, compared to the sympatric dusky shark which reaches depths of >300 m and move more than twice as far as bronze whalers within the same period (Rogers et al. 2013a).

The region where tags were deployed were previously hypothesised to represent juvenile nursery areas as neonates and small juvenile bronze whalers have been captured in and displayed philopatry and site fidelity to these regions (Rogers et al. 2013a; Huveneers et al. 2014). The tracking of small juvenile bronze whalers in Gulf St. Vincent identified that the northern gulf waters are nursery grounds (Chapter 4). The timing of the tagging and residency of the mature females within inshore waters coincide with bronze whaler parturition period (Rogers et al. 2013a; Drew et al. 2016). Fisheries-dependent and independent sampling has also shown that gravid females are found in the inshore coastal and gulf waters during the Austral spring–summer (chapter 2). These findings suggest that females might migrate in the coastal waters of South Australia to give birth. The present study, therefore, supports that the seasonal occurrence of female bronze whalers in the inshore South Australian region is likely related to their reproductive cycle. However, studies on the diet of bronze whalers have shown that the movements and migrations of this species can also be linked to the abundance of food resources (e.g., exploitation of mass prey events) (Cliff and Dudley 1992; chapter

3). At this stage, it remains unclear if the presence of large female bronze whalers in the inshore coastal waters of the South Australian gulfs are linked to their reproductive cycle and to give birth, to their foraging ecology, or a combination of both.

HORIZONTAL MOVEMENTS

The accuracy of positional estimates was determined by calculating the error between highest quality ARGOS locations of drifting tags to the positions generated by light-based estimates. The level of error was lower for longitudinal position estimates (27 ± 4 km) compared to latitudinal estimates (163 ± 25 km). Low rates of error for longitudinal positions have been previously described by Teo et al. (2004) with 80 to 94% of light-based longitude estimates within 1° of ARGOS positions for salmon sharks (*Lamna ditropis*) and blue sharks (*P. glauca*). Furthermore, Rogers et al. (2013) determined that longitude position estimates (15.03 ± 12.74 km) for PSAT tagged dusky sharks was sufficient to describe their movement in southern Australia. The low estimates of error for longitude combined with the East–West direction of the southern facing Australian coastline, determined that longitudinal positions were acceptable for describing movement of bronze whalers in southern Australia.

Long-range movements by juvenile bronze whalers in southern Australia have been previously identified through conventional identification tag and acoustic telemetry studies. Rogers et al. (2013) estimated minimum movements between capture locations of up to 2,400 km with several sharks having travelled ~1,000 km, in east and west directions from South Australia. Some of these long-range movements may have, however, been undertaken by dusky sharks due to morphological similarities between the sympatric bronze whaler and dusky shark making species identification difficult. The only confirmed long-range movement of bronze whalers in Australia was obtained from a female bronze whaler (1.9 m) tagged with an acoustic tag that travelled between northern Gulf St. Vincent to Corner Inlet, Victoria, covering a minimum distance of ~1,600 km, similar to the maximum distance travelled in the present study. The same shark was redetected two years later in the Corner Inlet receiver array (Bruce and Bradford, unpublished data). The broad extent of movement and migratory capabilities demonstrated by bronze whalers supports findings from genetic analyses, which identified a single Australian wide population (Benavides et al. 2011; Junge et al. In Prep). Long-range movements of >1,000 km by bronze whalers have also been identified in South Africa (Cliff and Dudley 1992). Bronze whalers migrate north from the Eastern Cape waters off South Africa in a response to the mass migration of schooling small pelagic teleosts, known as the “Sardine run” (Cliff and Dudley 1992; Dudley et al. 2010). The large bronze whalers annually migrate to opportunistically exploit the mass aggregations of schooling sardines and then return back to the cooler waters off the Eastern Cape (Cliff and Dudley 1992).

Long-range migrations were identified for the sympatric dusky sharks tagged in the same inshore gulf waters of southern Australia. Comparatively, the similar-sized dusky sharks travelled greater distances and further north in Western Australia into warm sub-tropical and tropical waters (Rogers et al. 2013b). Although dusky sharks are a sympatric species, their distribution extends well into tropical waters (Last and Stevens 2009). On the East coast of Australia short term tracking of large dusky sharks also identified long-range movements and maximum distance travelled of up to 89 km per day (Barnes et al. 2016). In South Australia, pelagic sharks such as the blue sharks, thresher sharks, short-fin mako, and white sharks are known to undertake long-range movements (Bruce et al 2006; Rogers et al. 2015; Heard et al. in press). However, these pelagic species use contrasting habitats such as, off the continental shelf or along the shelf slope, compared to the coastal and shallow depth distribution of bronze whalers. Large-scale migrations are not limited to pelagic and large-bodied shark species, but can also be undertaken by smaller-bodied species living in other habitats. For example, the Port Jackson shark (*Heterodontus portusjacksoni*) is a small-bodied demersal shark that has been recorded to undertake return migrations of ~1,200 km along the eastern coastline of Australia (Bass et al 2017).

DEPTH PATTERNS

The vertical depth profiles of bronze whalers changed between inshore and offshore habitats. When present in inshore waters, the mean depth profiles for day and night were similar, with most of the time spent in the upper 10 m of the water column. The inshore waters between Cape Willoughby (138.10°E) and Cape Borda (136.70°E) (Fig. 5.1) have a maximum depth of ~50 m and an average depth of ~20 m in the gulfs (Bruce and Short 1990). Apart for shark 5, depth distribution of bronze whalers span the entire water column and their mean depth was ~17 m for day and 13 m for night. This information combined suggests that bronze whalers use the entire water column when inshore. In the offshore habitat, bronze whalers spent less time at the surface compared to inshore, and spend most of the time between 10 and 60 m during day and night periods. Dives to >100 m were not common for the ten tagged female bronze whalers, except for shark 3, which spent a greater proportion of time at 80–110 m. Some of the shallow depth usage by adult bronze whalers in the offshore habitats may have occurred around offshore islands and reefs in the coastal waters of southern Australia. The depth profiles of bronze whalers in southern Australia are contrasting to the depth profiles of the sympatric dusky sharks off the southern and eastern Australian coastline (Rogers et al. 2013b; Barnes et al. 2016). Dusky sharks tagged in both locations of Australia spent more time at greater depths than bronze whalers in this study (Rogers et al. 2013b; Barnes et al. 2016). Tagged dusky sharks spent ~40% of their time between 50–100 m and had maximum depth dives of 355 m in southern Australia (Rogers et al. 2013b) and spent 46% of their time in >60 m and dived to a maximum depth of 498 m off eastern Australia (Barnes et al. 2016).

Studies on the feeding ecology of bronze whalers have consistently shown that they primarily feed on pelagic species such as sardines and cephalopods (Smale 1991; Lucifora et al. 2009; Rogers et al. 2012). Stable isotope models estimated that ~50% of the diet of bronze whalers in southern Australia is comprised of small pelagic teleosts (e.g. *Sardinops sagax*) (Chapter 3). These species are abundant in the offshore habitat, through the southern Gulf and shelf waters of southern Australia (Ward et al. 2006). These species are known to undertake diel vertical migrations spending most time at depth during the day and migrating to the surface at night (Giannoulaki et al. 1999; Watanabe et al. 2006; Hagan and Able 2008). However, no diel differences were observed in bronze whalers in either inshore and offshore habitats, which is likely the result of the relatively shallow depths occupied and their ability to quickly transverse through the entire water column.

THERMAL PREFERENCES

Inshore waters, in particular in the gulfs, have large thermal variability between seasons due to their shallow depths and northward extension into the arid zone where they are exposed to high air temperatures through summer (Vaz et al. 1990). As a result, the upper gulf waters can reach sub-tropical temperatures as high as 24°C at the end of summer and drop to as low as 11°C in winter. During summer, the elevated water temperatures develop into a frontal zone, which builds at the mouth of Spencer Gulf from December and peaks in March (Petrusevics et al. 2011). This frontal zone leads to limited oceanographic exchange between the gulf and shelf waters (Petrusevics et al. 2011). The frontal zone holds the dense warm sea water in the gulfs until the rapid cooling of the gulf water temperatures through autumn into winter (May–June) (Petrusevics et al. 2011). The thermal range experienced by adult bronze whalers in the inshore habitat from tagging in summer (December–February) aligns with these seasonal fluctuations in water temperatures. The timing of departure of large female bronze whalers from the inshore waters, identified through estimates of longitude and exceeding maximum depths for inshore waters, aligns with the timing of the break-down of the frontal zone.

In the offshore shelf environments, the heavily mixed, warmer water mass which bronze whalers reside in is the result of the eastward moving Leeuwin Current / GAB warm pool (McClatchie et al. 2006). The Leeuwin Current transports tropical-warm water masses down the West Australian coast, around Cape Leeuwin heading eastward into the southern Australian shelf waters (Petrusevics et al. 2009). East of 129°E, the Leeuwin Current is termed the South Australian Current (Petrusevics et al. 2009), which extends out to the continental shelf slope. The South Australian Current flows at its strongest through winter (June–August) and is characterised by a mixed water mass down to a thermocline of 200 m with temperatures range of 16–19°C and a mean of 17°C (Petrusevics et al.

2009). The timing of movement from inshore to offshore, the offshore temperature ranges, and the daily thermal depth plots suggest that the five sharks with full-term tag deployments moved into this warm water mass. The avoidance of <16°C water indicates that movement from the cool inshore to warm offshore waters in late autumn to early winter may be related to temperature patterns. Juvenile bronze whalers also have a seasonal presence in the South Australian gulfs influenced by water temperature, with juvenile sharks more often occurring in Gulf St. Vincent during periods of high water temperatures (chapter 4). Additionally, tag and recapture data from recreational fishers in southern Australia also identified a seasonal occurrence in the inshore waters which was believed to be driven by seasonal fluctuations of water temperatures (Rogers et al. 2013a). Seasonal fluctuations of water temperature is also hypothesised to influence occurrence of bronze whalers in other parts of its range such as in Argentina (Lucifora et al. 2005) and South Africa (Cliff and Dudley 1992).

Model projections in the GAB suggest that water temperatures are rising and will increase by 1.5–3°C by the year 2070 (Hobday and Lough 2011). Pearce and Feng (2007) have also documented an increased warming and rise in salinity but overall weakening of the Leeuwin Current into the GAB. Based on these models, the projected water temperatures of the Leeuwin Current into the GAB could be as high as 21°C, with water temperatures in the gulfs reaching >25°C. Currently, the implications of climate change and its effects on predators that inhabit the SE Indian Ocean and gulf waters is poorly understood (Pistevos et al. 2015). The effect of increased water temperatures on bronze whalers in southern Australia could potentially impact the timing of movements between habitats which could lead to flow on effects through the temperate ecosystem and food web dynamics (Goldsworthy et al. 2013). The continual and steady increase of water temperatures into the GAB may also result in the extension of ranges for warm-temperate and tropical species such as dusky sharks, sand bar sharks, and tiger sharks. An influx of species could create spatial overlaps, increased competition, and predation. Ultimately, the effect that increasing water temperatures will have on bronze whalers and the temperate marine ecosystem is uncertain, although the narrow thermal trigger for the migration out of the gulf waters (<16°C) for bronze whalers were surprising in the context of the current rate of warming and the apparent lack of plasticity in response to large-scale environmental changes.

POPULATION STRUCTURE

Size- and sex-segregation is well-documented in large-bodied shark species (Mucientes et al. 2009) and has been identified in short-fin makos in the South Pacific Ocean (Mucientes et al. 2009), scalloped hammerheads (*Sphyrna lewini*) (Klimley 1987), and white sharks in the Pacific Ocean (Domeier and Nasby-Lucas 2012). In Western Australia, a latitudinal gradient in size of large dusky sharks was identified in the north and north west of the state (Braccini 2017). The lack of large male bronze whalers in inshore waters identified by this study and Drew et al. (2016) provides evidence for size- and sex-based segregation in this species off southern Australia. The small number of mature males sampled in Drew et al. (2016) were from catches in the southern Spencer Gulf waters, suggesting that adult males may reside outside of targeted areas and seldom visit the inshore coastal and gulf waters (Drew et al. 2016). Commercial fishers provided anecdotal reports of large schools of adult male sharks swimming in the offshore islands and far west coast of South Australia. Adult male bronze whalers are also regularly seen at the Neptune Islands (~40 km offshore) during summer (C Huveneers per obs).

This study provided the first movement and habitat use information on a rarely encountered and poorly understood component of the southern Australian bronze whaler population. The predictable seasonal inshore occurrence of adult females during spring–summer exposes them to increased vulnerability to anthropogenic effects, which combined with slow growth and low levels of biological productivity highlights concern over the current status of this population. This movement and habitat use information will be important for future management and conservation measures of this important marine predator.

Acknowledgments

All work during this study was conducted under the Flinders University animal ethics approval (E360). Funding support was provided by the Mohamed bin Zayed species conservation fund, the Neiser Foundation and the Save Our Seas Foundation. The authors would like to thank SARDI - Aquatic Sciences for their in-kind support, in particular Simon Goldsworthy and the Threatened, Endangered and Protected Species Sub-Program and Matthew Hoare of the Offshore Crustaceans Sub-Program. We thank Brad Smith, Paul Williams, members of the Adelaide Game Fishing Club, Shane and Daniel Frensch, Kostas Andrelious, and Peter Hickmann who assisted in tagging the bronze whaler sharks in this study.

6

GENERAL DISCUSSION

This study provides critical baseline biological and ecological information for an important marine predator in the temperate waters off southern Australian. Data has been incorporated into population assessments and ecosystem-based models to ensure the future sustainability for this species, and to support ecosystem based fishery management. Throughout the study, I addressed three broad objectives: 1) Estimate the biological characteristics of bronze whalers in southern Australia, 2) Evaluate the ecological role and importance of bronze whalers in the southern Australia ecosystem, 3) Investigate the spatio-temporal variations in population distributions within the coastal waters of southern Australia. These objectives were addressed in the four data chapters of this thesis, and the key findings relating to each objective and their broad implications are discussed below.

ESTIMATE THE BIOLOGICAL CHARACTERISTICS OF BRONZE WHALERS IN SOUTHERN AUSTRALIA

This research estimated the previously unknown life-history parameters for the Australian bronze whalers population, which represents the only estimates for this species outside of South Africa and Argentina (Walter and Ebert 1991; Cliff and Dudley 1992; Lucifora et al. 2005; Lucifora et al. 2009). Previous studies off South Africa and Argentina showed that, similar to many large-bodied shark species, bronze whalers possess '*K*-selected' life-history traits typified by long life spans, slow growth, late maturity, and low fecundity. However, intra-species plasticity in the life-history characteristics of sharks highlights to the need for regional estimates to accurately determine population resilience to anthropogenic effects (Parsons 1993; Smart et al. 2015). Bronze whaler growth rates in southern Australia were slow and among the slowest for a carcharhinid species (Walter and Ebert 1991). Such slow growth may be attributed to the primarily temperate distribution of bronze whaler, which results in the species spending most of its time in cooler waters than 95% of other carcharhinid species that are mostly distributed in warm-temperate and tropical regions (Compagno 2001). This study showed that the bronze whaler has a long life span of at least 31 years. The largest sharks sampled during this study were near the maximum reported size (~3 m) for this species (Last and Stevens 2009). However, age and growth studies have shown that age estimates of long-lived sharks can be severely underestimated and that band deposition may not be consistent through an individual's life span (Francis et al. 2007; Passerotti et al. 2014; Cailliet 2015; Harry 2017). This suggests that the maximum age estimates for this study may actually be an under estimate, regardless, age estimates of >30 years indicates that bronze whalers are a long lived shark species.

Size- and age-at-maturity estimated in this study were preliminary and largely restricted to estimates of size- and age-at-first-maturity due to low sample size of large sub-adult and adult sharks. The size structure of the sharks sampled consisted of primarily small juvenile sharks, with 70% of sharks <1.5 m. Small juveniles are targeted within the Marine Scalefish fishery of South Australia, as they can be sold at a higher price than large sharks. Large sharks >2 m were rarely encountered in this inshore targeted fishery and are often released upon capture by fishers due to logistical difficulties related to landing them from small vessels and comparatively low market value. This made obtaining adequate sample sizes for maturity estimates difficult. However, the size- and age-at-maturity estimates obtained in this study suggest that female bronze whalers reach maturity at ~2.6 m TL and at an age of 16 years. These estimates aligned with previous estimates of age-at-maturity (13–19 years for males and 19–20 years for females) for the South African population (Walter and Ebert 1991; Cliff and Dudley 1992), but were lower than the estimates from Agentina (20 years for males and 21.7 years for females) (Lucifora 2003). Size-at-maturity estimates for this region were higher than in South Africa (~1.75 m PCL for males and ~1.90 m PCL for females) and Argentina (2–2.2 m TL males and 2.15–2.23 m TL females) (Cliff and Dudley 1992; Lucifora et al. 2005). The late size- and age-at-maturity for bronze whaler populations would likely result in a lower ability to withstand and recover from exploitation, even at low levels of fishing mortality. Additionally, low fecundity of this species also reduces their potential to recover from decline. The mean fecundity estimates (26 pups per litter) in this study were higher than in previous studies (Cliff and Dudley 1992; Lucifora et al. 2005), although the estimates from this study were only based on four litters.

EVALUATE THE ECOLOGICAL ROLE AND IMPORTANCE OF BRONZE WHALERS IN THE SOUTHERN AUSTRALIA TEMPERATE ECOSYSTEM

Diet and foraging ecology of sharks has historically been restricted to species for which adequate number of stomach contents were available (Hammerschlag and Sulikowski 2011). The application of biochemical methods such as stable isotope analyse (SIA) has allowed for non-lethal sampling and for foraging ecology to be assessed over varying time-scales, by the use of multiple tissue types with contrasting integration rates (Hammerschlag and Sulikowski 2011). The combination of dietary methods of stomach content analysis (SCA) and SIA allows for the species level description of diet and the description of foraging ecology over contrasting temporal resolutions.

This study identified that the bronze whaler is a generalist predator that relies on a highly diverse prey field and forages across multiple gulf and shelf habitats. These findings were consistent with previous dietary assessments in Australia, South Africa, and Argentina (Smale 1991; Cliff and Dudley 1992; Lucifora et al. 2009; Rogers et al. 2012). The key prey species identified in this study by both SCA and SIA were locally abundant cephalopods such as *Sepia novaehollandiae* and *Sepioteuthis australis,* and small pelagic teleosts such as *Sardinops sagax.* The observed dominance of cephalopods and small pelagic teleosts in the diet of bronze whalers was consistent with findings for the populations off South Africa, Argentina, and a previous study in South Australia (Smale 1991; Cliff and Dudley 1992; Lucifora et al. 2009; Rogers et al. 2012). The importance of these key prey species indicates the diet of bronze whalers may be temporally specialised and have a preference for exploiting locally abundant aggregations of cephalopods and small pelagic teleosts. Additionally, these key prey items have a strong association with seagrass habitats, suggesting it is an important habitat for the species.

The preference of seagrass habitats was also supported by the results of Chesson's habitat electivity index in chapter 4, which identified the habitat type had the highest electivity by juvenile bronze whalers out of six types of habitats available and present in the waters of Gulf St. Vincent.

The estimates of trophic position (4.48) places bronze whalers as a tertiary consumer, which is lower than what would be expected for a large-bodied shark species such as, bull sharks (*C. lecuas*) or dusky sharks (*C. obscurus*) which both had maximum trophic position estimates of >5, but was similar to the only other trophic position estimates of bronze whalers from South Africa (~4.4) (Hussey et al. 2014). The dominance of prey species of low trophic level in bronze whaler's diet resulted in low $\delta^{15}N$ estimate and is likely the driver for the low trophic position. The low $\delta^{15}N$ values irrespective of body size also suggests that ontogenetic variation does not occur in bronze whalers from southern Australia. Ontogenetic variation has, however, been identified in many carcharhinid species and has previously been shown for bronze whalers in Argentina, where they increasingly feed on other elasmobranchs as they grow larger (Lucifora et al. 2009). Although small-bodied elasmobranchs, such as the Australian angelshark (*Squatina australis*) and Southern eagle rays (*Myliobatis tenuicaudatus*), were identified in the diet of large bronze whalers in southern Australia, their overall contribution to the diet was low.

Bronze whalers are an important predator species in the temperate southern Australian ecosystem, their niche within this food web differs from other sympatric and high trophic level sympatric species, such as white sharks (*Carcharodon carcharias*), dusky sharks (*C. obscurus*), and seven gill sharks (*Notorynchus cepedianus*) which predate on elasmobranch and marine mammals (Barnett et al. 2010; Rogers et al. 2012). Bronze whalers exert a top-down control on low order prey species and likely play an integral role in the maintenance in lower trophic ecology. The dietary information for bronze whalers determined during this research will be incorporated into ecosystem-based models for the gulf, shelf, and oceanic waters of southern Australia, and will hopefully aid in the conservation and sustainabile use of this important temperate marine predator, and provide support for ecosystem-based fisheries management.

INVESTIGATE THE SPATIO-TEMPORAL VARIATIONS IN POPULATION DISTRIBUTION AND MOVEMENTS WITHIN THE COASTAL WATERS OF SOUTHERN AUSTRALIA

The increased seasonal presence of bronze whalers within South Australian gulfs waters was first noted by the increase in catches and targeting of this species by both the commercial and recreational fishers (Jones 2008; Rogers et al. 2013a). This study used passive acoustic telemetry (chapter 4) and pop-up satellite archival tags (chapter 5) to investigate the spatio-temporal movement dynamics of bronze whalers in the coastal waters of southern Australia. Juvenile bronze whalers displayed an increased seasonal presence in the northern Gulf St. Vincent waters (chapter 4). The peak in seasonal occurrence in September–April, which is through the Austral spring–summer seasons, aligned with seasonal increases in water temperatures which was further supported by explanatory modelling. The fall in water temperatures (May–June) also correlated with the timing of adult sharks transitioning from inshore to offshore habitats (Chapter 5). However, we could not identify the movements of juvenile sharks when they were not present in the area covered by the acoustic receivers (April–September).

Bronze whalers exhibited philopatry in areas of northern Gulf St. Vincent, with 77% of tagged sharks detected over multiple years and 36% detected over three years. The return visits over multiple years by juvenile sharks indicates that this area is important in the early life history stages and provides evidence for the northern Gulf St. Vincent waters as a seasonal nursery ground. The knowledge of nursery grounds or seasonal aggregations and how juveniles use these areas can identify temporal periods of increased vulnerability to anthropogenic treats and when temporal protection could be most effective (Heupel et al. 2007).

Although philopatry to northern Gulf St. Vincent was high, residency within the area of receiver coverage was low. Juvenile bronze whalers showed a strong affinity to seagrass habitats, as identified by Chesson’s electivity index. This strong affiliation to seagrass habitats was closely supported by the prey species identified through SCA from sharks sampled within the upper gulf region during the same seasonal period (chapter 3). Gulf St. Vincent has extensive seagrass meadows covering ~2,440 km^2 (Bryars et al. 2008), the low productivity and abundances of teleosts in this habitat likely results in the requirement of juvenile bronze whalers to roam extensively to source prey.

Adult female bronze whalers exhibited seasonally aligned regional- (<200km) to migratory-scale movements (>200km), with the furthest minimum horizontal displacement of ~1600 km. Bronze whalers undertook broad-scale movements across multiple jurisdictions, which has potential implications for managing this important component of the population. Adults sharks were tagged in the Austral spring–summer when adult females appear to have a short temporal inshore residency. Sharks that were tracked for >60 days transitioned from inshore (<50 m) to offshore habitats (50–130 m) in May–June. The timing of movements between habitats aligned with the cooling of the inshore coastal and gulf waters, and the eastward intrusion of the warm Leeuwin Current into the shelf waters of the Great Australian Bight (McClatchie et al. 2006).

The timing or drivers of movements of bronze whalers in southern Australia was closely linked to seasonal fluctuations in water temperatures. The seasonal variations in water temperatures may act as a cue for a change in behaviour, and prompt reproductive events or foraging strategies. For both adult females and juveniles an increase in presence occurred in the inshore waters when water temperatures are warmest (October–May). As the inshore water temperatures begin to decrease adult female bronze whalers transitioned into the offshore habitats. The thermal preferences identified of the tagged sharks suggest that when temperatures <16°C it prompted a cue for shark movement. The timing of bronze whaler movement and seasonal occurrence off Argentina and South Africa has also been linked to seasonal fluctuations in water temperatures. In Argentina, the seasonal increase in presence of bronze whalers in Anegada Bay, Northern Patagonia in October–April has been linked to the seasonal rise in water temperatures (Lucifora et al. 2005). Similarly, off South Africa, the mass migration of bronze whalers exploiting the aggregations of sardines during the sardine run is primarily driven by the seasonal flow of nutrient rich cold water northward up the South African coastline during June–July (Cliff and Dudley 1992; Dudley and Cliff 2010).

FUTURE OPPORTUNITIES AND CONCERNS

Several key biological parameters such as maturity indices, reproduction frequency and litter size were not able to be estimated and should be considered for future life-history studies of bronze whalers. The periodicity of band deposition on the vertebral edge requires validation. The two attempts of verification of band deposition used in this study was relatively inconclusive due to the lack of available samples throughout the year. A tag mark-recapture study was also attempted when acoustically tagging sharks for chapter 4 using a bio-chemical vertebrae marker. Unfortunately, no recaptures occurred throughout the duration of the study, inhibiting my ability to validate the periodicity of growth band deposition. It was assumed that a band pair was deposited annually on the vertebrae, however recent studies have identified that frequency of band deposition may vary throughout the life stages (Huveneers et al. 2013; Cailliet 2015), potentially underestimating ages of adult sharks (Francis et al. 2007). Annual band deposition was a key assumption underlying the age and growth dynamics section of this study. Inaccurate age counts can have severe implications for model outputs and the flow on management decisions, therefore accurate age estimations are vitally important (Campana 2001; Harry 2017). The frequency of reproduction and the duration of parturition of this population was also not identified. The proposed reproduction cycle for bronze whalers is considered to be a biennial with a ~12-month gestation (Cliff and Dudley 1992). However, reproduction cycles can vary between populations and regions as identified for the sympatric gummy sharks (*Mustelus antarcticus*) (Walker 2007). Additional sampling focusing on large individuals would be required to more accurately estimate size- and age-at-maturity and the reproductive cycle of bronze whalers in Southern Australia.

Sex segregation is evident for bronze whalers off southern Australia, with large adult males rarely encountered in the inshore targeted fishery. Anecdotal evidence suggest that large schools of adult males reside around the offshore islands and along the West coast of South Australia. Further studies are required to understand the distribution of this component of the southern Australian population. The investigation of adult male and female movement could potentially identify periods of spatial overlap and indicate important areas for reproduction.

CONCLUSION

This study shed new light on the bronze whaler population in southern Australia and identified the species as an important marine predator in the coastal and neritic environments. The low biological productivity, slow life-history traits, and high mobility of bronze whalers combined with the nearshore seasonal occurrence result in this species being susceptible to several potential anthropogenic threats. These important biological and ecological data will be used to assess the population status and have been incorporated into ecosystem-based models used to inform environmental and fishery management decisions in the southern Australian gulf and shelf waters.

References

Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In 2nd International symposium on Information Theory (Eds B. N. Petrov, and F. Csaksi), 267-281. Budapest: Akademiai Kiado

Arnold G, Dewar H (2001) Electronic tags in marine fisheries research: a 30-year perspective Electronic tagging and tracking in marine fisheries. Springer, pp 7-64

Assis CA (1996) A generalised index for stomach contents analysis in fish. Scientia Marina 60: 385-389

Barnes CJ, Butcher PA, Macbeth WG, Mandelman JW, Smith SD, Peddemors VM (2016) Movements and mortality of two commercially exploited carcharhinid sharks following longline capture and release off eastern Australia. Endangered Species Research 30: 193-208

Barnett A, Abrantes K, Stevens JD, Yick JL, Frusher SD, Semmens JM (2010) Predator–prey relationships and foraging ecology of a marine apex predator with a wide temperate distribution. Marine Ecology Progress Series 416: 189-200

Bass NC, Mourier J, Knott N, Day J, Gutteridge T, Brown C (2017) Long-term migration patterns and bisexual philopatry in a benthic shark species. Marine and Freshwater Research 68: 1414-1421

Baum JK, Blanchard W (2010) Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data. Fisheries Research 102: 229-239

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of shark populations in the North Atlantic. Science 299: 389-392

Beamish RJ, Fournier DA (1981) A method for comparing the precision of a set of age determinations. Canadian Journal of Fisheries and Aquatic Science 38: 982-983

Benavides MT, Feldheim KA, Duffy CA, Wintner S, Braccini JM, Boomer J, Huveneers C, Rogers P, Mangel JC, Alfaro-Shigueto J (2011) Phylogeography of the copper shark (*Carcharhinus* *brachyurus*) in the southern hemisphere: implications for the conservation of a coastal apex predator. Marine and Freshwater Research 62: 861-869

Bishop SDH, Francis MP, Duffy C, Montgomery JC (2006) Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus oxyrinchus*) in New Zealand waters. Marine and Freshwater Research 57: 143-154

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed G, Harrison A-L (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475: 86-90

Bonfil R (1994) Overview of world elasmobranch fisheries. FAO, Rome, Italy

Bonfil R, Meyer M, Scholl MC, Johnson R, O'Brien S, Oosthuizen H, Swanson S, Kotze D, Paterson M (2005) Transoceanic migration, spatial dynamics, and population linkages of white sharks. Science 310: 100-103

Braccini M (2017) Temporal patterns in the size of the main commercial shark species of Western Australia. Marine and Freshwater Research 68: 1112-1117

Branstetter S (1987) Age and growth validation of newborn sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Copeia 2: 291-300

Bruce B, Short D (1990) Observations on the distribution of larval fish in relation to a frontal zone at the mouth of Spencer Gulf, South Australia. Bureau of Natural Resources Proceedings 15: 124-137

Bruce BD, Stevens JD, Malcolm H (2006) Movements and swimming behaviour of white sharks (*Carcharodon carcharias*) in Australian waters. Marine Biology 150: 161–172

Brunnschweiler J, Queiroz N, Sims D (2010) Oceans apart? Short-term movements and behaviour of adult bull sharks *Carcharhinus leucas* in Atlantic and Pacific Oceans determined from pop-off satellite archival tagging. Journal of Fish Biology 77: 1343-1358

Bryars S, Wear R, Collings G (2008) Seagrasses of Gulf St Vincent and Investigator Strait. Natural History of Gulf St Vincent'(Eds SA Shepherd, S Bryars, I Kirkegaard, P Harbison and JT Jennings) pp: 132-147

Burgess GH, Beerkircher LR, Cailliet GM, Carlson JK, Cortés E, Goldman KJ, Grubbs RD, Musick JA, Musyl MK, Simpfendorfer CA (2006) Is the collapse of shark populations in the Northwest Atantic Ocean and Gulf of Mexico real? Fisheries 30: 19-26

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, USA

Cailliet G (2015) Perspectives on elasmobranch life-history studies: a focus on age validation and relevance to fishery management. Journal of Fish Biology 87: 1271-1292

Cailliet GM (1990) Elasmobranch Age Determination and Verification: An updated Review. In: Pratt HL, Jr., Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systemactics, and the status of fisheries NOAA Technical Report. US Department of Commerce NMFS, USA, pp 157-165

Cailliet GM, Goldman KJ (2004) Age determination and validationin chondrichthyan fishes. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Florida, USA, pp 399-448

Camhi M, Valenti S, Fordham S, Fowler SL, Gibson C (2009) The Conservation Status of Pelagic Sharks and Rays: Report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop. IUCN Species Survival Commission Shark Specialist Group., Newbury, UK

Campana SE (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59: 197-242

Carlson JK, Baremore IE (2005) Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southeast and Gulf of Mexico coasts: a comparison of methods. Fisheries Bulletin 103: 280-291

Carlson JK, Cortés E, Johnson AG (1999) Age and Growth of the Blacknose Shark, *Carcharhinus acronotus*, in the Eastern Gulf of Mexico. Copeia 3: 684-691

Cartamil D, Wegner N, Kacev D, Ben-Aderet N, Kohin S, Graham J (2010) Movement patterns and nursery habitat of juvenile thresher sharks *Alopias vulpinus* in the Southern California Bight. Marine Ecology Progress Series 404: 249-258

Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors (Δ15N and Δ13C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46: 443-453

Cerna FL, R. (2009) Age and growth of the shortfin mako (*Isurus oxyrinchus*) in the south-eastern Pacific off Chile. Marine and Freshwater Research: 394–403

Chang WYB (1982) A statistical method for evalutating the reproducibililty of age determination. Canadian Journal of Fisheries and Aquatic Science 39: 1208-1210

Chapman DD, Feldheim KA, Papastamatiou YP, Hueter RE (2015) There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. Annual Review of Marine Science 7: 547-570

Chapman DD, Pikitch EK, Babcock EA, Shivji MS (2005) Marine Reserve Design and Evaluation Using Automated Acoustic Telemetry: A Case-study Involving Coral Reef-Associated Sharks in the Mesoamerican Caribbean. Marine Technology Society Journal 39: 42-55

Chiaramonte GE (1998) Shark fisheries in Argentina. Marine and Freshwater Research 49: 601-609

Chin A, Heupel MR, Simpfendorfer CA, Tobin AJ (2016) Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators. Marine Ecology Progress Series 544: 197-211

Chin A, Tobin A, Simpfendorfer C, Heupel M (2012) Reef sharks and inshore habitats: patterns of occurrence and implications for vulnerability. Marine Ecology Progress Series 460: 115-125

Clarke C, Lea J, Ormond R (2011) Reef-use and residency patterns of a baited population of silky sharks, *Carcharhinus falciformis*, in the Red Sea. Marine and Freshwater Research 62: 668-675

Clarke SC, Harley SJ, Hoyle SD, Rice JS (2013) Population trends in Pacific Oceanic sharks and the utility of regulations on shark finning. Conservation Biology 27: 197-209

Clarke SC, Magnussen JE, Abercombie DL, McAllister MK, Shivji MS (2006) Identification of Shark Species Composition and Proportion in the Hong Kong Shark Fin Market Based on Molecular Genetics and Trade Records. Conservation Biology 20: 201-211

Cliff G, Dudley S (1992) Sharks caught in the protective gill nets off Natal, South Africa. 6. The copper shark *Carcharhinus brachyurus* (Günther). South African Journal of Marine Science 12: 663-674

Compagno LJV (2001) Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO, Rome, Italy

Conrath CG, J. Musick, J. (2002) Age and growth of the smooth dogfish (*Mustelus canis*) in the northwest Atlantic Ocean. Fish bullertin: 674 - 682

Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences 54: 726-738

Cortés E (2000) Life history patterns and correlations in sharks. Reviews in Fisheries Science 8: 299-344

Cortés E, Brooks E, Apostolaki P, Brown C (2006) Stock assessment of dusky shark in the US Atlantic and Gulf of Mexico. Panama City Laboratory Contribution 6

Daly R, Smale MJ, Cowley PD, Froneman PW (2014) Residency patterns and migration dynamics of adult bull sharks (*Carcharhinus leucas*) on the east coast of southern Africa. PloS One 9: e109357

Davidson LN, Krawchuk MA, Dulvy NK (2016) Why have global shark and ray landings declined: improved management or overfishing? Fish and Fisheries 17: 438-458

Domeier ML, Nasby-Lucas N (2008) Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. Marine Ecology Progress Series 370: 221-237

Domeier ML, Nasby-Lucas N (2012) Sex-specific migration patterns and sexual segregation of adult white sharks, *Carcharodon carcharias*, in the Northeastern Pacific. Global Perspectives on the Biology and Life History of the White Shark: 133-146

Drew M, Rogers P, Huveneers C (2016) Slow life-history traits of a neritic predator, the bronze whaler (*Carcharhinus brachyurus*). Marine and Freshwater Research

Drew M, White W, Harry A, Huveneers C (2015) Age, growth and maturity of the pelagic thresher *Alopias pelagicus* and the scalloped hammerhead *Sphyrna lewini*. Journal of Fish Biology 86: 333-354

Driggers WB, Carlson JK, Cullum B, Dean JM, Oakley D, Ulrich G (2004) Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the western North Atlantic Ocean with comments on regional variation in growth rates. Environmental Biology of Fishes 71: 171-178

Dudley SF, Cliff G (2010) Influence of the annual sardine run on catches of large sharks in the protective gillnets off KwaZulu-Natal, South Africa, and the occurrence of sardine in shark diet. African Journal of Marine Science 32: 383-397

Dudley SFJ, Cliff G, Zungu MP, Smale MJ (2005) Sharks caught in the protective nets off KwaZulu-Natal, South Africa. 10. The dusky shark *Carcharhinus obscurus* (Lesueur 1818). African Journal of Marine Science 27: 107-127

Duffy CA, Francis MP, Manning MJ, Bonfil R (2012) Regional population connectivity, oceanic habitat, and return migration revealed by satellite tagging of white sharks, *Carcharodon carcharias*, at New Zealand aggregation sites. Global perspectives on the biology and life history of the white shark: 301-318

Duffy LM, Olson RJ, Lennert-Cody CE, Galván-Magaña F, Bocanegra-Castillo N, Kuhnert PM (2015) Foraging ecology of silky sharks, *Carcharhinus falciformis*, captured by the tuna purse-seine fishery in the eastern Pacific Ocean. Marine Biology 162: 571-593

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LN, Fordham SV, Francis MP (2014) Extinction risk and conservation of the world's sharks and rays. Elife 3: e00590

Earl J, Fowler AJ, Dittmann S (2011) Temporal variation in feeding behaviour and trophic ecology of the temperate hemiramphid, *Hyporhamphus melanochir*. Environmental Biology of Fishes 90: 71-83

Ebert DA (2002) Ontogenetic changes in the diet of the sevengill shark (*Notorynchus cepedianus*). Marine and Freshwater Research 53: 517-523

Eckert SA, Dolar LL, Kooyman GL, Perrin W, Rahman RA (2002) Movements of whale sharks (*Rhincodon typus*) in South-east Asian waters as determined by satellite telemetry. Journal of Zoology 257: 111-115

Edyvane K (1999) Coastal and marine wetlands in Gulf St. Vincent, South Australia: understanding their loss and degradation. Wetlands Ecology and Management 7: 83-104

Ellis JK, Musick JA (2007) Ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in lower Chesapeake Bay and Virginia (USA) coastal waters. Environmental Biology of Fishes 80: 51-67

Escalle L, Speed C, Meekan M, White W, Babcock R, Pillans R, Huveneers C (2015) Restricted movements and mangrove dependency of the nervous shark *Carcharhinus cautus* in nearshore coastal waters. Journal of Fish Biology 87: 323-341

Espinoza M, Munroe SE, Clarke TM, Fisk AT, Wehrtmann IS (2015) Feeding ecology of common demersal elasmobranch species in the Pacific coast of Costa Rica inferred from stable isotope and stomach content analyses. Journal of Experimental Marine Biology and Ecology 470: 12-25

Estes JA, Tinker MT, Williams TM, Doak DF (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282: 473-476

Estrada JA, Rice AN, Natanson LJ, Skomal GB (2006) Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. Ecology 87: 829-834

Evans GT, Hoenig JM (1998) Testing and viewing symmetry in contingency tables, with application to readers of fish ages. Biometrics: 620-629

Feldheim KA, Gruber SH, Ashley MV (2004) Reconstruction of parental microsatellite genotypes reveals female polyandry and philopatry in the lemon shark, *Negaprion brevirostris*. Evolution 58: 2332-2342

Ferretti F, Myers RA, Serena F, Lotze HK (2008) Loss of Large Predatory Sharks from the Mediterranean Sea. Conservation Biology 22: 952–964

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. Ecology letters 13: 1055-1071

Ferry L, Cailliet G (1996) Sample size and data analysis: are we characterizing and comparing diet properly. Gutshop 96: 71-80

Field I, Meekan M, Speed C, White W, Bradshaw C (2011) Quantifying movement patterns for shark conservation at remote coral atolls in the Indian Ocean. Coral Reefs 30: 61-71

Field IC, Meekan MG, Buckworth RC, Bradshaw CJ (2009) Protein mining the world’s oceans: Australasia as an example of illegal expansion-and-displacement fishing. Fish and Fisheries 10: 323-328

Fitzpatrick R, Thums M, Bell I, Meekan MG, Stevens JD, Barnett A (2012) A comparison of the seasonal movements of tiger sharks and green turtles provides insight into their predator-prey relationship. PLoS One 7: e51927

Fowler A, Huveneers C, Lloyd M (2017) Insights into movement behaviour of snapper (*Chrysophrys auratus*, Sparidae) from a large acoustic array. Marine and Freshwater Research

Fowler A, McGarvey R, Steer M, Feenstra J (2016) Fishery statistics for the South Australian marine scalefish fishery: 1983/84-2015/16: Report to PIRSA fisheries and aquaculture. SARDI Research Report Series-South Australian Research and Development Institute

Fowler A, Short D (1998) Validation of age determination from otoliths of the King George whiting *Sillaginodes punctata* (Perciformes). Marine Biology 130: 577-587

Francis MP (1998) New Zealand shark fisheries: development, size and mangement. Marine Freshwater Research 49: 579-591

Francis MP, Campana SE, Jones CM (2007) Age under-estimation in New Zealand porbeagle sharks (*Lamna nasus*): is there an upper limit to ages that can be determined from shark vertebrae? Marine and Freshwater Research 58: 10-23

Gallagher A, Jackson T, Hammerschlag N (2011) Occurrence of tiger shark (*Galeocerdo cuvier*) scavenging on avian prey and its possible connection to large-scale bird die-offs in the Florida Keys. Florida Scientist: 264-269

Garrick JAF (1982) Shark in the genus *Carcharhinus*. NOAA technical report 445: 194

Geraghty PT, Macbeth WG, Harry AV, Bell JE, Yerman MN, Williamson JE (2013) Age and growth parameters for three heavily exploited shark species off temperate eastern Australia. ICES Journal of Marine Science: Journal du Conseil doi 10.1093/icesjms/fst164

Giannoulaki M, Machias A, Tsimenides N (1999) Ambient luminance and vertical migration of the sardine *Sardina pilchardus*. Marine Ecology Progress Series 178: 29-38

Goldman KJ (2005) Age and growth of elasmobranch fishes. In: Musick JA, Bonfil R (eds) Technical manual for the management of elasmobranchs FAO Fisheries Technical Paper No 474. FAO, Rome, Italy

Goldsworthy SD, Page B, Rogers PJ, Bulman C, Wiebkin A, McLeay LJ, Einoder L, Baylis AM, Braley M, Caines R (2013) Trophodynamics of the eastern Great Australian Bight ecosystem: Ecological change associated with the growth of Australia's largest fishery. Ecological modelling 255: 38-57

Gregory RS, Levings CD (1998) Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society 127: 275-285

Gutteridge A, Bennett M, Huveneers C, Tibbetts I (2011) Assessing the overlap between the diet of a coastal shark and the surrounding prey communities in a sub-tropical embayment. Journal of Fish Biology 78: 1405-1422

Hagan SM, Able KW (2008) Diel variation in the pelagic fish assemblage in a temperate estuary. Estuaries and Coasts 31: 33-42

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE (2008) A global map of human impact on marine ecosystems. Science 319: 948-952

Hammerschlag N, Gallagher A, Lazarre D (2011) A review of shark satellite tagging studies. Journal of Experimental Marine Biology and Ecology 398: 1-8

Hammerschlag N, Skubel R, Calich H, Nelson E, Shiffman D, Wester J, Macdonald C, Cain S, Jennings L, Enchelmaier A (2017) Nocturnal and crepuscular behavior in elasmobranchs: a review of movement, habitat use, foraging, and reproduction in the dark. Bulletin of Marine Science 93: 355-374

Hammerschlag N, Sulikowski J (2011) Killing for conservation: the need for alternatives to lethal sampling of apex predatory sharks. Endangered Species Research 14: 135-140

Harry AV (2017) Evidence for systemic age underestimation in shark and ray ageing studies. Fish and Fisheries

Harry AV, Macbeth WG, Gutteridge AN, Simpfendorfer CA (2011) The life histories of endangered hammerhead sharks (Carcharhiniformes, Sphyrnidae) from the east coast of Australia. Journal of Fish Biology 78

Heard M, Rogers PJ, Bruce BD, Humphries NE, Huveneers C (2017) Plasticity in the diel vertical movement of two pelagic predators (*Prionace glauca* and *Alopias vulpinus*) in the southeastern Indian Ocean. Fisheries Oceanography

Heithaus MR (2004) Fish communities of subtropical seagrass meadows and associated habitats in Shark Bay, Western Australia. Bulletin of Marine Science 75: 79-99

Heithaus MR, Burkholder RE, Hueter RE, Heithaus LI, Pratt HLJ, Carrier JC (2007) Spatial and temporal variation in shark communitites of the lower Florida Keys and evidence for historical population declines. Canadian Journal of Fisheries and Aquatic Sciences 64: 1302–1313

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Marine Ecology Progress Series 337: 287–297

Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Marine and Freshwater Research 57: 1-13

Heupel MR, Simpfendorfer CA, Fitzpatrick R (2010) Large–scale movement and reef fidelity of grey reef sharks. PloS One 5: e9650

Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive monitoring techniques. Environmental Biology of Fishes 71: 135–142

Hoenig J, Morgan M, Brown C (1995) Analysing differences between two age determination methods by tests of symmetry. Canadian Journal of Fisheries and Aquatic Sciences 52: 364-368

Hoenig JM, Gruber SH (1990) Life-history patterns in the elasmobranchs: implications for fisheries management. In: Pratt HL, Jr., Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of fisheries NOAA Technical Report 90. US Department of Commerce, NMFS, USA, pp 1-16

Hoffmayer E, Franks J, Driggers W, Grace M (2010) Movements and environmental preferences of dusky sharks, *Carcharhinus obscurus*, in the Northern Gulf of Mexico. SEDAR21-DW-37. Southeast Data, Assessment, and Review: North Charleston, SC. Available at: www. sefsc. noaa. gov/sedar/Sedar_Documents. jsp

Holmlund CM, Hammer M (1999) Ecosystem services generated by fish populations. Ecological Economics 29: 253-268

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson J, Kleypas J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301: 929-933

Humphries NE, Queiroz N, Dyer JR, Pade NG, Musyl MK, Schaefer KM, Fuller DW, Brunnschweiler JM, Doyle TK, Houghton JD (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature 465: 1066-1069

Hussey N, MacNeil M, Olin J, McMeans B, Kinney M, Chapman D, Fisk A (2012) Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. Journal of Fish Biology 80: 1449-1484

Hussey NE, Dudley SF, McCarthy ID, Cliff G, Fisk AT (2011) Stable isotope profiles of large marine predators: viable indicators of trophic position, diet, and movement in sharks? Canadian Journal of Fisheries and Aquatic Sciences 68: 2029-2045

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF (2015a) Aquatic animal telemetry: a panoramic window into the underwater world. Science 348: 1255642

Hussey NE, MacNeil MA, Fisk AT (2010) The requirement for accurate diet-tissue discrimination factors for interpreting stable isotopes in sharks. Hydrobiologia 654: 1-5

Hussey NE, MacNeil MA, McMeans BC, Olin JA, Dudley SF, Cliff G, Wintner SP, Fennessy ST, Fisk AT (2014) Rescaling the trophic structure of marine food webs. Ecology Letters 17: 239-250

Hussey NE, MacNeil MA, Siple MC, Popp BN, Dudley SF, Fisk AT (2015b) Expanded trophic complexity among large sharks. Food Webs 4: 1-7

Huveneers C, Rogers PJ, Drew M (2014) Monitoring shark species of conservation concern within the Adelaide metropolitan and Gulf St Vincent regions : final report to the Adelaide and Mount Lofty Ranges Natural Resources Management Board, SARDI Research Report Series 754

Huveneers C, Simpfendorfer CA, Kim S, Semmens JM, Hobday AJ, Pederson H, Stieglitz T, Vallee R, Webber D, Heupel MR (2016) The influence of environmental parameters on the performance and detection range of acoustic receivers. Methods in Ecology and Evolution

Huveneers C, Stead J, Bennett MB, Lee KA, Harcourt RG (2013) Age and growth determination of three sympatric wobbegong sharks: How reliable is growth band periodicity in Orectolobidae? Fisheries Research 147: 413-425

Huveneers C, Walker TI, Otway NM, Harcourt R (2007) Reproductive synchrony of three sympatric species of wobbegong shark (genus *Orectolobus*) in New South Wales, Australia. Marine and Freshwater Research 58: 765–777

Hynes H (1950) The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. The Journal of Animal Ecology: 36-58

Hyslop E (1980) Stomach contents analysis—a review of methods and their application. Journal of Fish Biology 17: 411-429

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80: 595-602

Jones GK (2008) Review of the Fishery Status for Whaler Sharks (Carcharhinus spp.) in South Australian and adjacent waters. SARDI Aquatic Sciences Publication 154

Junge C, Donnellan SC, Huveneers C, Bradshaw CJA, Simon A, Drew M, Rogers P, Johnson G, Cliff G, Braccini M, McAuley R, Duffy C, Peddemors V, Butcher P, Cutmore SC, Gillanders BM (In Prep) Comparative population genomics confirms little population structure in two commercially important carcharhinid sharks

Kämpf J, Payne N, Malthouse P (2010) Marine connectivity in a large inverse estuary. Journal of Coastal Research 26: 1047-1056

Katsanevakis S, Maravelias CD (2008) Modelling fish growth: multi-model inference as a better alternative to a priori using von Bertalanffy equation. Fish and Fisheries 9: 178-187

Kim SL, Casper DR, Galván-Magaña F, Ochoa-Díaz R, Hernández-Aguilar SB, Koch PL (2012) Carbon and nitrogen discrimination factors for elasmobranch soft tissues based on a long-term controlled feeding study. Environmental Biology of Fishes 95: 37-52

Klimley PA (1987) The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. Environmental Biology of Fishes 18: 27-40

Kneebone J, Natanson LJ, Andrews AH, Howell WH (2008) Using bomb radiocarbon analyses to validate age and growth estimates for the tiger shark, *Galeocerdo cuvier*, in the western North Atlantic. Marine Biology 154: 423–434

Knip D, Heupel M, Simpfendorfer C (2012) Habitat use and spatial segregation of adult spottail sharks *Carcharhinus sorrah* in tropical nearshore waters. Journal of Fish Biology 80: 767-784

Kroese M, Sauer W (1998) Elasmobranch exploitation in Africa. Marine and Freshwater Research 49: 573-577

Kusher DI, Smith SE, Cailliet GM (1992) Validated age and growth of the leopard shark, *Triakis semifasciata* with comments on reproduction. Environmental Biology of Fishes 35: 187-203

Lack M, Sant G (2006) World shark catch, production & trade 1990-2003. TRAFFIC, Sydney, Australia

Last PR, Stevens JD (2009) Sharks and Rays of Australia. CSIRO Australia, Australia

Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR, Matich P, Rosenblatt AE, Vaudo JJ, Yeager LA (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Reviews 87: 545-562

Logan JM, Lutcavage ME (2010) Stable isotope dynamics in elasmobranch fishes. Hydrobiologia 644: 231-244

Lombardi-Carlson LA, Cortés E, Parsons GR, Manire CA (2003) Latitudinal variation in life-history traits of bonnethead shark, *Sphyrna tiburo*, (Carcharhiniformes: Sphyrnae) from the eastern Gulf of Mexico. Marine and Freshwater Research 54: 875-883

Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, Galeocerdo cuvier, in Hawaiian waters. Environmental Biology of Fishes 47: 203-211

Lu C, Ickeringill R (2002) Cephalopod beak identification and biomass estimation techniques: tools for dietary studies of southern Australian finfishes. Museum Victoria

Lucifora LO, García VB, Menni RC, Escalante AH, Hozbor NM (2009) Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. Ecological Research 24: 109-118

Lucifora LO, Menni RC, Escalante AH (2005) Reproduction and seasonal occurrence of the copper shark, *Carcharhinus brachyurus*, from north Patagonia, Argentina. ICES Journal of Marine Science 62: 107-115

Lucifora LO (2003) Ecología y conservación de los grandes tiburones costeros de Bahía Anegada, provincia de Buenos Aires, Argentina. Thesis, Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales Instituto Nacional be Investigacion y Desarrollo Pesquero Mar del Plata.

Macbeth WG, Macbeth WG (2009) Observer-based study of targeted commercial fishing for large shark species in waters off northern New South Wales. Cronulla Fisheries Research Centre of Excellence. Industry and Investment NSW

MacNeil M, Skomal GB, Fisk AT (2005) Stable isotopes from multiple tissues reveal diet switching in sharks. Marine Ecology Progress Series 302: 199-206

Matich P, Heithaus MR, Layman CA (2011) Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. Journal of Animal Ecology 80: 294-305

Maxwell SM, Hazen EL, Bograd SJ, Halpern BS, Breed GA, Nickel B, Teutschel NM, Crowder LB, Benson S, Dutton PH (2013) Cumulative human impacts on marine predators. Nature communications 4

McAuley R, Braccini M, Newman S, O’Malley J (2015) Temperate Demersal Gillnet and Demersal Longline Fisheries Status Report, in WJ Fletcher and K Santoro (eds) Status Reports of the Fisheries and Aquatic Resources of Western Australia 2014/15 Western Australian Department of Fisheries, Perth: 261–272

McAuley R, Lenanton R, Chidlow J, Allison R, Heist E (2005) Biology and stock assessment of the thickskin (sandbar) shark, *Carcharhinus plumbeus*, in Western Australia and further refinement of the dusky shark, *Carcharhinus obscurus*, stock assessment. Fisheries Research Division, Western Australian Fisheries and Marine Research Laboratories, North Beach, available at www fish wa gov au/docs/frr/frr151/frr151 pdf

McAuley RB, Simpfendorfer CA, Hall NG (2007) A method for evaluating the impacts of fishing mortality and stochastic influences on the demography of two long-lived shark stocks. ICES Journal of Marine Science 64: 1710-1722

McCauley DJ, Young HS, Dunbar RB, Estes JA, Semmens BX, Micheli F (2012) Assessing the effects of large mobile predators on ecosystem connectivity. Ecological Applications 22: 1711-1717

McClatchie S, Middleton JF, Ward TM (2006) Water mass analysis and alongshore variation in upwelling intensity in the eastern Great Australian Bight. Journal of Geophysical Research: Oceans 111

McElroy WD, Wetherbee BM, Mostello CS, Lowe CG, Crow GL, Wass RC (2006) Food habits and ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in Hawaii. Environmental Biology of Fishes 76: 81-92

Meekan M, Choat J (1997) Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical reefs. Marine Biology 128: 373-383

Meyer CG, Clark TB, Papastamatiou YP, Whitney NM, Holland KN (2009) Long-term movement patterns of tiger sharks *Galeocerdo cuvier* in Hawaii. Marine Ecology Progress Series 381: 223-235

Meyer CG, Papastamatiou YP, Holland KN (2010) A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. Marine Biology 157: 1857-1868

Mourier J, Maynard J, Parravicini V, Ballesta L, Clua E, Domeier ML, Planes S (2016) Extreme inverted trophic pyramid of reef sharks supported by spawning groupers. Current Biology 26: 2011-2016

Mourier J, Planes S (2013) Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. Molecular Ecology 22: 201-214

Mucientes GR, Queiroz N, Sousa LL, Tarroso P, Sims DW (2009) Sexual segregation of pelagic sharks and the potential threat from fisheries. Biology Letters: rsbl. 2008.0761

Munroe S, Simpfendorfer C, Heupel M (2014a) Defining shark ecological specialisation: concepts, context, and examples. Reviews in Fish Biology and Fisheries 24: 317-331

Munroe SE, Heupel MR, Fisk AT, Simpfendorfer CA (2014b) Geographic and temporal variation in the trophic ecology of a small-bodied shark: evidence of resilience to environmental change. Canadian Journal of Fisheries and Aquatic Sciences 72: 343-351

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315: 1846-1850

Natanson L, Gervelis B, Winton M, Hamady L, Gulak SB, Carlson J (2014) Validated age and growth estimates for *Carcharhinus obscurus* in the northwestern Atlantic Ocean, with pre- and post management growth comparisons. Environ Biol Fish 97: 881-896

Natanson LJ, Casey JG, Kohler NE (1995) Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. Fishery Bulletin 93: 116-126

Officer R, A., Gason AS, Walker TI, Clement JG (1996) Sources of variation in counts of growth increments in vertebrae from gummy shark, *Mustelus antarcticus*, and school shark, *Galeorhinus galeus*: implications for age determination. Canadian Journal of Aquatic Science 53: 1765-1777

Papastamatiou YP, Lower CG, Caselle JE, Friedlander AM (2009) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90: 996-1008

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PloS one 5: e9672

Parsons GR (1993) Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo*. Environmental Biology of Fishes 38: 25-35

Passerotti M, Andrews A, Carlson J, Wintner S, Goldman K, Natanson L (2014) Maximum age and missing time in the vertebrae of sand tiger shark (*Carcharias taurus*): validated lifespan from bomb radiocarbon dating in the western North Atlantic and southwestern Indian Oceans. Marine and Freshwater Research 65: 674-687

Pauly D (1987) Application of information on age and growth of fish to fishery management. In: Summerfelt RC, Hall GE (eds) The age and growth of fish. The Iowa State University Press, Ames, Iowa, USA, pp 495-506

Payne NL, Gillanders BM, Webber DM, Semmens JM (2010) Interpreting diel activity patterns from acoustic telemetry: the need for controls. Marine Ecology Progress Series 419: 295-301

Petrusevics P (1993) SST fronts in inverse estuaries, South Australia-indicators of reduced gulf-shlef exchange. Marine and Freshwater Research 44: 305-323

Petrusevics P, Bye J, Fahlbusch V, Hammat J, Tippins D, van Wijk E (2009) High salinity winter outflow from a mega inverse-estuary—the Great Australian Bight. Continental Shelf Research 29: 371-380

Petrusevics P, Bye J, Luick J, Teixeira CE (2011) Summer sea surface temperature fronts and elevated chlorophyll-a in the entrance to Spencer Gulf, South Australia. Continental Shelf Research 31: 849-856

Phillips DL (2012) Converting isotope values to diet composition: the use of mixing models. Journal of Mammalogy 93: 342-352

Piercy AC, J. Sulikowski, J. Burgess, G. (2007) Age and growth of the scalloped hammerhead shark, *Sphyrna lewini*, in the north-west Atlantic Ocean and Gulf of Mexico. Marine and Freshwater Research: 34 - 40

Pikitch E, Santora C, Babcock E, Bakun A, Bonfil R, Conover D, Dayton P, et al., Doukakis P, Fluharty D, Heneman B (2004) Ecosystem-based fishery management. Science 305: 346-347

Pillay T (1952) A critique of the methods of study of food of fishes. Journal of the Zoological Society of India 4: 185-200

Pinkas L (1971) Food habits study. Fish Bulletin 152: 10

Pinnegar J, Polunin N (1999) Differential fractionation of δ13C and δ15N among fish tissues: implications for the study of trophic interactions. Functional Ecology 13: 225-231

Pinnegar J, Polunin N, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien M-L, Hereu B, Milazzo M, Zabala M, d'Anna G (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation 27: 179-200

Pistevos JC, Nagelkerken I, Rossi T, Olmos M, Connell SD (2015) Ocean acidification and global warming impair shark hunting behaviour and growth. Scientific reports 5: 16293

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703-718

Post DM, Conners ME, Goldberg DS (2000) Prey preference by a top predator and the stability of linked food chains. Ecology 81: 8-14

Pringle RM, Fox-Dobbs K (2008) Coupling of canopy and understory food webs by ground-dwelling predators. Ecology Letters 11: 1328-1337

Punt AE, Pribac F, Walker TI, Taylor BL, Prince JD (2000) Stock assessment of school shark, *Galeorhinus galeus*, based on a spatially explicit population dynamics model. Marine and Freshwater Research 51: 205-220

Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing Collapse of Coral-Reef Shark Populations. Current Biology 16: 2314–2319

Roff G, Doropoulos C, Rogers A, Bozec Y-M, Krueck NC, Aurellado E, Priest M, Birrell C, Mumby PJ (2016) The ecological role of sharks on coral reefs. Trends in Ecology & Evolution 31: 395-407

Rogers P, Huveneers C, Goldsworthy S, Cheung W, Jones G, Mitchell J, Seuront L (2013a) Population metrics and movement of two sympatric carcharhinids: a comparison of the vulnerability of pelagic sharks of the southern Australian gulfs and shelves. Marine and Freshwater Research 64: 20-30

Rogers PJ, Huveneers C, Goldsworthy SD, Mitchell JG, Seuront L (2013b) Broad-scale movements and pelagic habitat of the dusky shark *Carcharhinus obscurus* off Southern Australia determined using pop-up satellite archival tags. Fisheries Oceanography 22: 102-112 doi 10.1111/fog.12009

Rogers PJ, Huveneers C, Page B, Goldsworthy SD, Coyne M, Lowther AD, Mitchell JG, Seuront L (2015) Living on the continental shelf edge: habitat use of juvenile shortfin makos *Isurus oxyrinchus* in the Great Australian Bight, southern Australia. Fisheries Oceanography 24: 205-218

Rogers PJ, Huveneers C, Page B, Hamer DJ, Goldsworthy SD, Mitchell JG, Seuront L (2012) A quantitative comparison of the diets of sympatric pelagic sharks in gulf and shelf ecosystems off southern Australia. ICES Journal of Marine Science: Journal du Conseil 69: 1382-1393

Romine JG, Musick JA, Burgess GH (2009) Demographic analyses of the dusky shark, *Carcharhinus obscurus*, in the Northwest Atlantic incorporating hooking mortality estimates and revised reproductive parameters. Environmental Biology of Fishes 84: 277–289

Rooney N, McCann K, Gellner G, Moore JC (2006) Structural asymmetry and the stability of diverse food webs. Nature 442: 265

Rooney N, McCann KS (2012) Integrating food web diversity, structure and stability. Trends in Ecology & Evolution 27: 40-46

Rooney N, McCann KS, Moore JC (2008) A landscape theory for food web architecture. Ecology Letters 11: 867-881

Ruppert JL, Travers MJ, Smith LL, Fortin M-J, Meekan MG (2013) Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. PloS One 8: e74648

Santana FM, Lessa R (2004) Age determination and growth of the night shark (*Carcharhinus signatus*) off the northeastern Brazilian coast. Fisheries Bulletin 102: 156-167

Schindler DE, Scheuerell MD (2002) Habitat coupling in lake ecosystems. Oikos 98: 177-189

Seddon S, Connolly R, Edyvane KS (2000) Large-scale seagrass dieback in northern Spencer Gulf, South Australia. Aquatic Botany 66: 297-310

Seminoff JA, Bjorndal KA, Bolten AB (2007) Stable carbon and nitrogen isotope discrimination and turnover in pond sliders *Trachemys scripta*: insights for trophic study of freshwater turtles. Copeia 2007: 534-542

Shepherd S, Bryars S, Kirkegaard I, Jennings J, Harbison P (2008) Natural history of Gulf of St Vincent. Royal Society of South Australia, 496 pages

Shiffman D, Gallagher A, Boyle M, Hammerschlag-Peyer C, Hammerschlag N (2012) Stable isotope analysis as a tool for elasmobranch conservation research: a primer for non-specialists. Marine and Freshwater Research 63: 635-643

Sibert J (2001) Electronic tagging and tracking in marine fisheries Electronic Tagging and Tracking in Marine Fisheries. Springer, pp 1-6

Simpfendorfer CA (1992) Reproductive strategy of the Australian sharpnose shark, *Rhizoprionodon taylori* (Elasmobranchii: Carcharhinidae), from Cleveland Bay, northern Queensland. Australian. Marine and Freshwater Research 43: 67-76

Simpfendorfer CA (1999) Demographic analysis of the dusky shark fishery in Southwestern Australia. American Fisheries Society Symposium 23: 149-160

Simpfendorfer CA, Goodreid A, McAuley RB (2001a) Diet of three commercially important shark species from Western Australian waters. Marine and Freshwater Research 52: 975-985

Simpfendorfer CA, Goodreid AB, McAuley RB (2001b) Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. Environmental Biology of Fishes 61: 37-46

Simpfendorfer CA, McAuley R, Chidlow J, Unsworth P (2002) Validated age and growth of the dusky shark, *Carcharhinus obscurus*, from Western Australian waters. Marine and Freshwater Research 53: 567-573

Simpfendorfer CA, Milward NE (1993) Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environmental Biology of Fishes 37: 337-345

Sims DW (2010) Tracking and analysis techniques for understanding free-ranging shark movements and behavior. Sharks and their relatives II: biodiversity, adaptive physiology, and conservation CRC Press, Boca Raton, Florida: 351-392

Sims DW, Southall EJ, Humphries NE, Hays GC, Bradshaw CJA, Pitchford JW, James A, Ahmed MZ, Brierley AS, Hindell MA, Morritt D, Musyl MK, Righton D, Shepard EL, Wearmouth VJ, Wilson RP, Witt MJ, Metcalfe JD (2008) Scaling laws of marine predator search behaviour. Nature Letters 451: 1098–1102

Skomal GB, Zeeman SI, Chisholm JH, Summers EL, Walsh HJ, McMahon KW, Thorrold SR (2009) Transequatorial migrations by basking sharks in the western Atlantic Ocean. Current biology 19: 1019-1022

Smale M (1991) Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the Eastern Cape coast of South Africa. South African Journal of Marine Science 11: 31-42

Smart J, Chin A, Tobin A, Simpfendorfer C, White W (2015) Age and growth of the common blacktip shark *Carcharhinus limbatus* from Indonesia, incorporating an improved approach to comparing regional population growth rates. African Journal of Marine Science 37: 177-188

Smith SE, Au DW, Show C (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. Marine and Freshwater Research 49: 663-678

Speed C, Meekan M, Field I, McMahon C, Abrantes K, Bradshaw C (2012) Trophic ecology of reef sharks determined using stable isotopes and telemetry. Coral Reefs 31: 357-367

Speed C, Meekan M, Field I, McMahon C, Harcourt R, Stevens J, Babcock R, Pillans R, Bradshaw C (2016) Reef shark movements relative to a coastal marine protected area. Regional Studies in Marine Science 3: 58-66

Speed CW, Field IC, Meekan MG, Bradshaw CJ (2010) Complexities of coastal shark movements and their implications for management. Marine Ecology Progress Series 408: 275-293

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Sciences 57: 476-494

Sumpton W, Taylor S, Gribble N, McPherson G, Ham T (2011) Gear selectivity of large-mesh nets and drumlines used to catch sharks in the Queensland Shark Control Program. African Journal of Marine Science 33: 37-43

Takada M, Asada M, Miyashita T (2002) Cross-habitat foraging by sika deer influences plant community structure in a forest-grassland landscape. Oecologia 133: 389-394

Tanner J (2005) Three decades of habitat change in Gulf St. Vincent, South Australia

Teter SM, Wetherbee BM, Fox DA, Lam CH, Kiefer DA, Shivji M (2015) Migratory patterns and habitat use of the sand tiger shark (*Carcharias taurus*) in the western North Atlantic. Marine and Freshwater Research 66: 158-169

Thorson JT, Simpfendorfer CA (2009) Gear selectivity and sample size effects on growth curve selection in shark age and growth studies. Fisheries Research 98: 75–84

Tieszen LL, Boutton TW, Tesdahl K, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for δ13C analysis of diet. Oecologia 57: 32-37

Vander Zanden MJ, Casselman JM, Rasmussen JB (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401: 464

Vaz RAN, Lennon GW, Bowers DG (1990) Physical behaviour of a large, negative or inverse estuary. Continental Shelf Research 10: 277-304

Vianna GM, Meekan MG, Meeuwig JJ, Speed CW (2013) Environmental influences on patterns of vertical movement and site fidelity of grey reef sharks (*Carcharhinus amblyrhynchos*) at aggregation sites. PLoS One 8: e60331

Walker TI (1994) Fishery model of gummy shark, *Mustelus antarcticus,* for Bass Strait. In: Bishop I (ed) New opportunities: best practice Resource Technology '94 Conference Proceedings, Melbourne. University of Melbourne, Melbourne, Australia, pp pp. 422-438

Walker TI (1998) Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. Marine and Freshwater Research 49: 553-572

Walker TI (2007) Spatial and temporal variation in the reproductive biology of gummy shark (*Mustelus antarcticus*) harvested off southern Australia. Marine and Freshwater Research 58: 1–31

Walter J, Ebert D (1991) Preliminary estimates of age of the bronze whaler *Carcharhinus brachyurus* (Chondrichthyes: Carcharhinidae) from southern Africa, with a review of some life history parameters. South African Journal of Marine Science 10: 37-44

Ward TM, McLeay LJ, Dimmlich WF, Rogers PJ, McClatchie S, Matthews R, KÄMpf J, VAN R (2006) Pelagic ecology of a northern boundary current system: effects of upwelling on the production and distribution of sardine (*Sardinops sagax*), anchovy (*Engraulis australis*) and southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight. Fisheries Oceanography 15: 191-207

Watanabe H, Kubodera T, Moku M, Kawaguchi K (2006) Diel vertical migration of squid in the warm core ring and cold water masses in the transition region of the western North Pacific. Marine Ecology Progress Series 315: 187-197

Weigmann S (2016) Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. Journal of Fish Biology 88: 837-1037

Weng KC, Boustany AM, Pyle P, Anderson SD, Brown A, Block BA (2007) Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. Marine Biology 152: 877-894

Weng KC, Castilho PC, Morrissette JM, Landeira-Fernandez AM, Holts DB, Schallert RJ, Goldman KJ, Block BA (2005) Satellite Tagging and Cardiac Physiology Reveal Nich Expansion in Salmon Sharks. Science 310: 104-106

Weng KC, Foley DG, Ganong JE, Perle C, Shillinger GL, Block BA (2008) Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. Marine Ecology Progress Series 372: 253-264

Werry JM, Planes S, Berumen ML, Lee KA, Braun CD, Clua E (2014) Reef-fidelity and migration of tiger sharks, *Galeocerdo cuvier*, across the Coral Sea. PLoS One 9: e83249

Wetherbee BM, Gruber SH, Rosa RS (2007) Movement patterns of juvenile lemon sharks *Negaprion brevirostris* within Atol das Rocas, Brazil: a nursery characterized by tidal extremes. Marine Ecology Progress Series 343: 283–293

Wintner SP, Dudley SFJ, Kistnasamy N, Everett B (2002) Age and growth estimates for the Zambezi shark, *Carcharhinus leucas*, from the east coast of South Africa. Marine and Freshwater Research 53: 557-566

Worm B, Davis B, Kettemer L, Ward-Paige CA, Chapman D, Heithaus MR, Kessel ST, Gruber SH (2013) Global catches, exploitation rates, and rebuilding options for sharks. Marine Policy 40: 194-204

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2015) Ecological drivers of shark distributions along a tropical coastline. PloS One 10: e0121346

Zanden M, Rasmussen JB (2001) Variation in δ15N and δ13C trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography 46: 2061-2066

Zuur A, Ieno EN, Meesters E (2009) A Beginner's Guide to R. Springer Science & Business Media